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THE UNIVERSITY OF ALBERTA

SPACING BEHAVIOUR AND LIFE HISTORIES OF NYMPHAL ZYGOPTERA

by

ROBERT L. BAKER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Abstract

The objective of this study was to determine whether nymphs of some zygopteran species exhibit a form of spacing behaviour that could result in variation in nymphal development rate.

Diet altered development rate of Coenagrion resolutum and Enallagma boreale nymphs to the extent that some members of a cohort could emerge 1 year before other individuals of the same cohort. In the laboratory, solitary Coenagrion resolutum nymphs remained primarily at one feeding area, even if other feeding areas of equal food value were nearby. Solitary nymphs tended to remain at feeding areas that would result in maximum growth rate when areas of different food value were offered. When several nymphs were present, some were excluded from feeding areas; but use of a feeding area was never totally exclusive. Large nymphs excluded small nymphs, but nymphs with previous experience with feeding areas had no advantage in remaining at feeding areas when naive animals were added.

Nymphs exhibited an array of behaviours, some being interpreted as aggressive. Exclusion of some individuals from feeding areas was a result of aggressive interactions, but the result of interactions (win or lose) was not site-dependent. Dominant animals spent more time at the

feeding areas than subordinate animals.

In the laboratory, solitary nymphs of Lestes disjunctus disjunctus did not remain at areas of food concentration, and there was no evidence that some individuals were excluded from areas of food concentration when several nymphs were present. These results contrast with results of similar experiments using C. resolutum, but correlate with field life history studies on populations of both species. The C. resolutum populations had a variable life cycle; some individuals were univoltine while others were semivoltine. The entire L. d. disjunctus population developed synchronously and was univoltine.

Because diet markedly affected development rate, and because some nymphs were excluded from areas of food concentration, the results reported here support the hypothesis that spacing behaviour of some species may result in altered life histories. However, because the first animal at feeding areas had no advantage over intruding animals, and the outcome of aggressive interactions was not site dependent, spacing behaviour is considered to be based on the dominance and limited movement of some individuals instead of on a territorial system, as suggested by other authors.

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Table of Contents

List of Tables

Chapter 1.

Chapter 2.

Chapter 3.

Chapter 4.

Chapter 5.

Appendix 1.

List of Figures

Chapter 1.

Cahpter 2.

Chapter 4.

Chapter 5.

Appendix 2.

Appendix 3.

Introduction

A fundamental aspect of population biology is that increases in population densities are not limitless; all populations are regulated. Theories concerning mechanisms of population regulation can be separated into two categories. One set of theories proposes that factors external to the population, e.g. predation, weather, food supply, control population growth. The other set of theories, supported by the "self-regulation school" (Krebs 1978a), suggests that population regulation is the result of processes within the population itself. Among the theories supported by the self-regulation school, the behaviour hypothesis (Krebs 1978b) suggests that "mutual interactions involving spacing behaviour produce changes in birth, death, and dispersal rates and thereby prevent unlimited increase."

Theoretically, the idea that spacing behaviour can control population growth can be applied to most animal species with the possible exception of some planktonic species. However most studies have pertained to vertebrates, particularly birds (Brown, 1969). An often quoted exception to this pertains to spacing behaviour of adult odonates, where behavioural interaction between males is thought to control the number of individuals at mating and oviposition sites (Moore 1964). There has been very little analysis of spacing behaviour for other invertebrates. My study was designed to determine if a form of spacing behaviour occurs in nymphal odonates that could act as a mechanism in population regulation.

Life history studies of Odonata are common. Such studies normally entail the qualitative collection of animals (adults and nymphs) at regular intervals over a year's time, with subsequent length-frequency analysis to determine voltinism, periods of emergence, egg duration, and approximate rate of growth.

When life histories of a single species from different habitats are compared, significant differences are often found. This is particularly noticeable in respect to rate of development of nymphs and subsequently the number of generations per year (Appendix 1). Another frequently reported phenomenon is the separation of a single population into two factions. Within a single habitat a certain percentage of the population may be univoltine while the remainder of the population is semivoltine or bivoltine (Appendix 1).

Temperature and photoperiod have been suggested as reasons for differences in odonate life cycles between habitats (Corbet 1980); however few authors have attempted to explain different factions within a population. Pritchard (1976) suggests three basic causes for variation of life histories within a population of aquatic insects: "(a) inherited differences; (b) occupation of different sets of environmental conditions in space; or (c) subjection to different environmental conditions due to temporal separation (for example, in insects with a long period of adult emergence and no diapause, the larvae from adults emerging early in the period will experience different conditions from those that appear later in the season)."

Referring to a single population of zygopterans, Macan (1964, 1977) suggested that life cycle differences arise through variability in diet caused by differences in microhabitat. When nymphs of <u>Pyrrhosoma</u> <u>nymphula</u> were abundant, Macan found some nymphs taking 2 years to develop while others took 3 years. When nymphs were less abundant the entire population took 2 years to develop. He also found voltinism depending on the type of substrate, i.e. nymphs living in <u>Littorella</u> took 2 years to develop while those on <u>Carex</u> took 3 years. From these observations, Macan concluded that the number of hunting sites is limited and fast-growing nymphs are those able to remain in optimum hunting areas, while small, slow-growing nymphs are "relegated" to sub-optimum areas of little food. Macan notes this phenomenon may be a "self-regulating mechanism," which could control the number of nymphs reaching maturity.

Spacing behaviour may also be important in affecting predator-prey interactions in fresh water littoral communities. Several researchers have speculated on how nymphal odonates affect prey populations. Benke (1976) suggested that dense populations of anisopterans can destroy prey populations if the prey lack physical refuges. Lawton et al. (1974) and Akre and Johnson (1979) believe odonate nymphs exhibit "switching" behaviour, resulting in protection of less dense prey populations. Crowley (1979) suggested that zygopteran nymphs in areas of low prey density disperse to areas of higher prey density. Macan's suggestion is obviously important when considering effects of predation by nymphal odonates on prey populations. Spacing behaviour, by decreasing density of predators in an area, may reduce predation rates.

Because of the possible importance of Macan's ideas in interpreting data on life histories and predator-prey dynamics, and in an effort to stimulate work on spacing behaviour of invertebrates, I designed my research to test the major components of Macan's hypothesis.

I have divided my work into five chapters. The first section describes life histories of Coenagrion resolutum and Lestes disjunctus disjunctus populations from a pond in the boreal forest of Alberta. The major points in this section are to determine whether zygopteran populations in Alberta show variation in life history similar to that described by Macan and to test whether differences in life history are associated with different vegetation zones and with different diets.

Macan's suggestion would be supported if nymphal growth rates were dependent on the part of the pond nymphs were in and if differences in diet were associated with these different areas of the pond.

During the life history, I reared C. resolutum nymphs from the study pond and from other ponds in the same vicinity to ensure proper identification. This work resulted in a paper, "The nymphs of Coenagrion interrogatum and C. resolutum (Coenagrionidae: Odonata) from the boreal forest of Alberta, Canada". I have included the paper as Appendix 2.

The second chapter reports results from experiments with C. resolutum nymphs designed to test two hypotheses derived from Macan's argument: (1) solitary nymphs find and remain at productive hunting sites, and (2) when several nymphs are present some are excluded from productive hunting sites. Subsequent experiments tested effects of alternate feeding sites, nymphal size, and prior occupancy on use of space at productive hunting sites.

Chapter 3 reports results from an experiment designed to determine whether nymphs of L. d. disjunctus remain near areas of food concentration, and when several nymphs are present whether some nymphs are excluded. I compared the use of feeding areas by nymphs of L. d. disjunctus with use of feeding areas by nymphs of C. resolutum and related these results to the life histories reported in Chapter 1.

In the experiments reported in Chapter 2, single nymphs of C. resolutum did remain at areas of food concentration. Experiments presented in Chapter 4 were designed to determine if diet could alter growth rates to the extent suggested by Macan, and to determine if nymphs, when presented with several feeding areas representing a gradient in food quantity, remained at those areas that would result in maximum growth rates.

Experiments reported in Chapter 2 also indicated some nymphs are excluded from areas of food concentration. However, because I did not continually observe the nymphs in those experiments, I had no information on the behavioural aspects of the exclusion. Chapter 5 presents a description of C. resolutum's nymphal behaviour and the results of an attempt to classify functionally the behaviours. Using this classification of behaviours, I determined whether the outcome of behavioural interactions was site dependent. This analysis helped me to determine whether exclusion of some nymphs was a result of territoriality.

Literature Cited

Akre, B. G. and D. M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. J. Anim. Ecol. 48: 703-720.

Benke, A. C. 1976. Dragonfly production and prey turnover. Ecology, 57: 915-927.

Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bull. 81: 293-329.

Corbet, P. S. 1980. Biology of Odonata. Annu. Rev. Entomol. 25: 189-217.

Crowley, P. H. 1979. Behaviour of zygopteran nymphs in a simulated weed bed. Odonatologica, 8: 91-101.

Krebs, C. J. 1978a. Ecology: the experimental analysis of distribution and abundance (2nd ed.). Harper and Row, New York.

Krebs, C. J. 1978b. A review of the Chitty Hypothesis of population regulation. Can. J. Zool. 56: 2463-2480.

Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. In Ecological stability. Edited by M. B. Usher and M. H. Williamson. Chapman and Hall, London. pp. 141-158.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Moore, N. W. 1964. Intra- and interspecific competition among dragonflies (Odonata): an account of observations and field experiments on population control in Dorset, 1954-60. J. Anim. Ecol. 33: 49-71.

Pritchard, G. 1976. Growth and development of larvae and adults of <u>Tipula</u> <u>sacra</u> Alexander (Insecta: Diptera) in a series of abandoned beaver ponds. Can. J. Zool. 54: 266-284.

Chapter 1. Life cycles and food of Coenagrion resolutum (Coenagrionidae: Odonata) and Lestes disjunctus disjunctus (Lestidae: Odonata) populations from the boreal forest of Alberta, Canada [1]

Abstract

In a boreal forest pond of Alberta, Canada, some nymphs of Coenagrion resolutum were univoltine while others were semivoltine; all Lestes disjunctus disjunctus nymphs were univoltine. Life cycles and diet (mainly Cladocera and Chironomidae) of both species were similar in the different vegetation zones.

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[1] Co-authored by Hugh F. Clifford.

Introduction

Except for the studies of Pritchard (1964) and Pritchard and Pelchat (1977), little work has been done on the biology of Odonata in Alberta. Even distribution of Albertan odonates is poorly known; Cannings (1980) notes the most recent literature on distribution is that of Walker (1953, 1958) and Walker and Corbet (1975), and these records are limited for large areas of the province.

One purpose of this paper is to present life history data of two zygopteran species from Alberta so that results can be compared with results from other geographic areas. A second purpose was to test a hypothesis concerning variation of life cycles within a population. Macan (1977) suggested that life history variation within a population of odonates may be due to nymphs in some areas of a pond obtaining less food and thus growing slower than nymphs in other areas. We tested this by studying the life cycles of two zygopteran species in different areas of a pond and relating the results to data on nymphal diets in the different areas.

Study Area

The study pond lies in the boreal forest of Alberta, approximately 2 km north of the Bigoray River (53°31'N, 115°26'W); see Clifford (1978) for a description of the area. The pond was a "borrow pit," probably dug when Highway 753 was built, and is approximately 7 m from the road. The pit is rectangular in shape, approximately 85 m long by 12 m wide. The E, W, and S banks are steep, while the N bank slopes very gently. The gentle slope results in the length of the pond changing drastically with water level. In spring, the pond is about 85 m long; but during low water, it is less than 50 m long. The bottom is of mud and very soft.

There were four major types of vegetation; Carex sp. in the shallow parts of the pond, Potamogeton sp. and Myriophyllum sp. in slightly deeper water, and Sparganium sp. in the centre of the pond. In May of both 1978 and 1979 the water level was highest, and Carex beds were in at least 50 cm of water. As the 1978 season progressed, the water level dropped, but even by freeze-up (late October or early November) the Carex was still in at least 10 cm of water. In 1978, Potamogeton (Myriophyllum was rare in 1978) was in 30-50 cm of water during July and August. The summer of 1979 was unseasonably dry and by August 10 the Carex was completely out of water. In summer of 1979, part of the Potamogeton zone was also dry and Myriophyllum was very abundant in areas still under water. Sparganium was far more abundant in 1979 than 1978.

After ice-break-up in late April 1978, water temperature (measured with a thermograph) rose slowly during May and June (Fig. 1). The shallow pond was susceptible to changes in air temperature and water temperatures dropped during periods of cool, cloudy weather. Average daily water temperatures remained fairly constant from late June to mid-August, at which time the water started cooling. Water temperatures continued to drop until freeze-up in late October or early November. The higher water temperature in both spring and fall 1979 reflected the hot, dry weather during spring and summer of that year.

Dissolved oxygen values ranged from 5.0 to 14.4 mg/l (62 to 149% saturation). Although the DO content fluctuated widely between sampling dates, there was a tendency for higher values in late summer and early autumn. The pH ranged from 6.9 to 7.6, with no discernable seasonal pattern.

Methods

We sampled the pond approximately every 2 weeks during the ice-free periods of 1978 and 1979. Samples were taken with a dip net having a mesh size of 210 u. One sample was taken from the <u>Carex</u> bed and one from the <u>Potamogeton</u>-<u>Myriophyllum</u> bed on each trip, if the plants were present. In 1978 the mud bottom (devoid of vegetation) was also sampled but no nymphs were collected in this area. During 1979 we also took samples from the

Sparganium zone, but few zygopterans were found in this zone until late autumn, at which time the Carex bed and much of the Potamogeton-Myriophyllum zone was dry.

Samples were preserved in the field with Kahle's fluid. On most sampling dates, live Zygoptera nymphs were collected for gut contents analysis. Immediately after these were collected, the nymphs were isolated in 40 ml plastic vials half-filled with dechlorinated water. Vials were returned to the laboratory where the nymphs were kept alive for 3 or 4 days, during which time nymphs defecated. Fecal pellets of each individual were mounted on microscope slides in polyvinyl lactophenol with lignin pink dye added.

Life Cycles

Coenagrion resolutum

Coenagrion resolutum is widely distributed in ponds and weedy, slow moving streams of Canada, and is especially common in the north; it may be the most northerly occurring species of Zygoptera in North America (Walker 1953).

Instars (F indicates final nymphal instar, F-1 indicates penultimate nymphal instar, etc.) were determined by constructing a histogram of head widths for specimens collected in 1978 (Fig. 2). The resulting plot of average instar head width (log scale) against instar number is a straight line and follows Dyar's (1890) rule on insect growth. Only the final seven instars were used in the analysis, because younger instars were impossible to determine by the head width-frequency method. Also, small C. resolutum nymphs were difficult to distinguish from small nymphs of Enallagma boreale, which were also present in the pond. A nymph in the F-6 instar would have a total body length of about 8 mm and would have probably gone through about 5 or 6 instars.

Chi square tests of homogeneity (Daniel 1978) were used to determine whether frequency of nymphs in the different instars was related to the type of vegetation the nymphs inhabitated. We had to combine frequencies of instars F with F-1, F-2 with F-3, and F-4 with F-5 and F-6 to obtain a large enough sample size. Significance levels of these tests are given in Figure 3. Histograms without significance levels were not tested because only one vegetation zone was sampled or because expected cell frequency of two or more cells was less than five.

In early May 1978, nymphs were large, most being in instars F-3 to F (Fig. 3). By mid-May, many nymphs had entered the final instar and by June there were few F-5 or F-6 instar nymphs in the population. In 1978 adults were observed between 1 June and 14 July. This suggests emergence started in late May and corresponds with the decrease in numbers of final instar nymphs during June.

However, some nymphs present in June did not emerge during summer 1978; they were still present, in instars F-6 to F-2, in early July when emergence was probably completed. These nymphs grew during July, most being in instars F-4 to F-1 in late July. Late July was one of the few sampling dates in which distribution of instars between vegetation zones was not similar, there being a greater proportion of smaller individuals in the Potamogeton than in the Carex (extensive collecting indicated that zygopteran eggs were common in Potamogeton, but were absent from Carex and Sparganium.) In early August, some of the nymphs that started hatching in late June had achieved the F-6 and even the F-5 instar. At this time there was also a very large number of nymphs in instars younger than F-6. During August, September, and October, nymphs continued to grow and by late October many individuals were in the final instar. Some nymphs of the new generation grew to the same size as nymphs hatching the previous summer, and at this time it was impossible to distinguish between the two cohorts. During autumn there was no significant difference in instar distribution between Potamogeton and Carex, with the exception of early October, when most of the Potamogeton had died away and the number of nymphs collected from it was very small.

As was found in May, 1978, there was a wide spread of instars in early May 1979. However, only a few final instar nymphs were collected in early May 1979, and this would not appear to agree with the histogram of late October 1978. No nymphs emerged between these dates; perhaps many of the final instar nymphs died during the winter. It is also possible, however, that the low number of final instar nymphs in early May is an artifact due to small sample size. The late May 1979 histogram was similar to that of May 1978. As in 1978, the number of final instar nymphs decreased during June and this coincided with the flight period, 8 June - 25 July. As also found in 1978, there were some individuals hatching the year before that did not emerge in 1979. Some nymphs of the new generation started hatching in late June, and early July 1979, grew rapidly during autumn, and eventually achieved a comparable instar number to the non-emerging nymphs of the 1978 population. In autumn 1979 there was no significant difference in instar distribution between the Myriophyllum and Sparganium beds.

The results clearly show that some individuals were semivoltine, while others were univoltine. The large number of nymphs in instars F-3 to F in late autumn 1978 was a combination of two cohorts, some about 4 months in age and others about 16 months in age. There was no evidence that life histories were different in different vegetation zones.

Lestes disjunctus disjunctus

Lestes d. disjunctus populations are widely distributed in Canada, occurring from Newfoundland to British Columbia and extending north into the North West Territories and the Yukon. Walker (1953) reports L. d. disjunctus populations to be found in "permanent ponds with marshy or boggy margins and rich aquatic vegetation; marshy bays and slow weedy streams."

The life cycle of L. d. disjunctus was the same in both years. Small nymphs (total length 5 mm) were first collected in late May, and this suggests eggs started hatching sometime in May. Nymphs grew rapidly during late May and June; and several individuals were in the final instar by the third week of June, at which time there was a wide range of instars present. However, in July the population consisted mainly of mature nymphs. Adults were first collected during the first two weeks of July, suggesting emergence began in late June or early July. By late July almost all nymphs were in the final instar, and no nymphs were found after mid-August. The flight period lasted until late August. Due to small sample sizes it was impossible to test statistically whether frequency of instars was different in the Carex and Potamogeton beds. Figure 4 would indicate no obvious differences. In summary, the L. d. disjunctus population has a univoltine life cycle with a long egg stage in winter.

Food

Several authors have studied prey selection of odonate nymphs in relation to food availability (Chutter 1961, Pritchard 1964, Thompson 1978). The general conclusion is that nymphs eat prey in about the same proportion as prey occur in the field. However, some potential prey are not eaten as frequently as predicted by their occurrence in the field. This is usually explained by microhabitat differences between the odonates and the prey or by some characteristic of the prey (hard elytra, large size, slow movement, etc.) that makes it difficult for the odonate to find or kill the prey. In our study we were not concerned with comparing gut contents to prey availability, but only in comparing the diets of nymphs living in different vegetation zones.

Prey items were classified into 11 taxonomic groups, which were recognized by such characteristics as claws, mandibles, setae, etc. (Table 1). Prey were quantified by determining the minimal number of prey present in each taxon. For example, if a total of three Ephemeroptera mandibles was found, we scored the presence of two ephemeropteran nymphs. If, however, only caudal filaments of Ephemeroptera were found, only one ephemeropteran was recorded. Any number of oligochaete setae in a fecal pellet was scored as one oligochaete, any number of unrecognizable insect parts in a fecal pellet was scored as one unidentified insect.

To ensure an adequate sample size for statistical analysis, we combined the results of instars F with instars F-1 and F-2 and the results of instars F-3 with instars F-4, F-5, and F-6 (Table 1). Data of all sampling dates for each month were combined for the month in question. Chironomids and Cladocera were the most important food items in the diet of both large and small C. resolutum nymphs. On most sampling dates, chironomids and cladocerans constituted more than 50% of the prey items in the gut contents; on several days the total was much greater than 50%. Ostracods were also numerous in the fecal pellets and were occasionally more numerous than cladocerans. Rotifers and copepods were of less importance but were recorded throughout the seasons. Chaoborus larvae and small zygopteran nymphs were present in the pellets only in late summer and autumn. This probably reflects the seasonal abundance of these prey items in the pond, e.g. zygopterans were present in the fecal pellets only when large numbers of small zygopterans were present in the pond. Zygopteran nymphs were fairly common prey items in August; this is in contrast to other studies (Pearlstone 1971, Thompson 1978) which report coenagrionid nymphs not feeding extensively on other odonates.

As with C. resolutum nymphs, we combined the results of nymphal instars F, F-1, and F-2 of L. d. disjunctus.

We also combined the results of nymphs with head widths ranging from 1.6 to 2.4 mm. The percentage composition of gut contents of L. d. disjunctus nymphs was similar to results for C. resolutum; however, L. d. disjunctus nymphs had more prey items in their guts than C. resolutum nymphs (Table 2).

Mann-Whitney tests were used to compare nymphal diets in different vegetation zones. Data of instars F to F-2 were analysed separately from data of instars F-3 to F-6. Prey items were classified as "large" (unidentified insects, chironomids, culicids, Chaoborus, odonates, ephemeropterans, and oligochaetes) or "small" (cladocerans, ostracods, copepods, rotifers). Due to small sample sizes and because on some dates only one vegetation zone was sampled, there were only six dates available to compare diets of C. resolutum nymphs from Carex and Potamogeton. On four of these dates, we compared both the F - F-2 and F-3 - F-6 instar groups; on the remaining two dates we compared only the F-3 - F-6 instar groups, giving a total of 20 tests. It is important to note that when 20 tests are analysed on random data, approximately 1 would be expected to be "significant" at the 0.05 level. Only one comparison was possible of L. d. disjunctus. Results indicate there were only two instances of significant differences in diet of C. resolutum nymphs inhabiting either the Carex or Potamogeton beds (Table 3). And there was no significant difference in diets of L. d. disjunctus nymphs from Carex or Potamogeton.

Discussion

Coenagrion resolutum

The life cycle of the C. resolutum population of our study is different from that reported by Sawchyn and Gillot (1975) for a C. resolutum population near Saskatoon, Saskatchewan. The Saskatchewan population had a univoltine life cycle and the entire population overwintered in the final three instars. In contrast, nymphs of our study overwintered in a wide range of instars (F to some younger than F-6) and some nymphs were clearly semivoltine whereas others were univoltine.

Variation of C. resolutum's life cycle within our population (i.e. univoltine or semivoltine) may be due to several factors. Parr (1970) suggested the different life cycles of Coenagrion puella in a pond in northern England were under direct genetic control. The same point was made by Schaller (1962, in Parr 1970), who found the voltinism of Aeshna cyanea was influenced by genetic factors. We have no field data to suggest the slow and fast developing cohorts were determined by differences in genotype.

Variation in life cycles may be related to the length of the flight period. Nymphs that hatch from eggs laid early in the flight period will have more time to develop than eggs laid late in the season. In our study the flight period lasted at least 6 weeks, and possibly some eggs were laid as much as 6 weeks earlier than others; this could account for some animals developing in one year while others (those hatching from eggs laid late in the season) are not mature by the next emergence period and overwinter a second time. However, the flight period recorded by Sawchyn and Gillot (1975) was even longer than ours (approximately 8 weeks) and their population was entirely univoltine.

Macan (1964, 1977) suggested variation in life cycles was due to different diets in different microhabitats. He found Pyrrhosoma nymphula nymphs living in Littorella developed to maturity in 2 years while nymphs living in Carex developed in 3 years; however he did not analyse gut contents of nymphs from the different vegetation zones. Pearlstone (1971) found Enallagma boreale nymphs living in "water lillies or horsetails" ate approximately twice as much food as nymphs found in "sedges", but he did not analyse the life cycles from the different areas separately.

In our study, the life cycle was not different in the different vegetation zones and there was no obvious difference in diet of nymphs in the different zones. Thus, there is no evidence that variation in growth rates is related to microhabitat use. However, this result does not rule out the possibility that the univoltine-semivoltine dichotomy was caused by differences in diet related to differences in location of nymphs. Baker (1980) showed that nymphs of C. resolutum in the laboratory remained near profitable hunting sites, and when several nymphs were present some were excluded. In the field, profitable hunting sites may be independent of vegetation types but dependent on factors such as proximity to the water surface or to the sediments, orientation of the substrate (horizontal, vertical, etc.), degree of light penetration, etc. Clearly, field evidence that different types of voltinism within a population is caused by diet related to microhabitat use will be difficult to obtain. Future studies of this problem may have to entail an extremely detailed analysis of growth and diet in relation to microhabitat use.

Lestes disjunctus disjunctus

The life cycle of the L. d. disjunctus population reported in this study is similar to the life cycle of L. d. disjunctus in Saskatchewan reported by Sawchyn and Gillot (1974). We first collected very small L. d. disjunctus nymphs in late May, and this compares well with Sawchyn and Gillot's findings that eggs hatched in early May and nymphs in instar F-4 were first collected in early June. In both studies, final instar nymphs were collected in late July and very few if any nymphs remained by the second week in August. The only difference in life histories between the Saskatchewan and Alberta populations appeared to be the spread of instars at any one time. Sawchyn and Gillot never found more than three instars in the population at any one time, while we found a large range of instars in late June; however there was little variation in instars by early July.

The life cycle of the L. d. disjunctus population from the boreal forest of Alberta was also similar to the life cycle of a L. disjunctus australis population of North Carolina reported by Ingram (1976). However, in the Alberta population small nymphs were present earlier in the spring than in the North Carolina population, and in the North Carolina population several nymphs in the final instar were still in the pond in mid-August.

All three reported life cycles of L. disjunctus were similar in that all individuals were univoltine, and this is, in part, apparently due to eggs overwintering in a diapause state and hatching synchronously in the spring (Sawchyn and Gillot 1974). However, Baker (1981) has shown nymphs of L. d. disjunctus, in contrast to C. resolutum, do not appear to remain at areas of food concentration, nor do they exclude other animals from such areas. Therefore, possibly the synchronous development of L. d. disjunctus nymphs is due in part to a lack of spacing behaviour in relation to feeding areas.

Acknowledgements

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Table 1. Percentage composition of prey, number of nymphs studied, and number of prey per individual of nymphs of <u>C</u>. <u>resolutum</u>. Large = instars F - F-2; Mid = F-3 - F-6.

	unident. insects	Chironomidae	Cladocera	Ostracoda	Copepoda	Rotifera	Culicinae	*Chaoborus*	Zygoptera	Ephemeroptera	Oligochaeta	prey/individual	no. of nymphs
<u>Carex</u>													
Jn 78													
Large		40	40		20							1.65	3
Mid		23	62	8	4	4						3.69	7
Jl 78													
Large	2	45	32	11	8					2		1.78	21
Mid	3	50	39	6	3							1.53	22
Au 78													
Large		41	12	23				2	14	8		1.55	31
Mid	15	46	31		3	3		3				0.68	38
Se 78													
Large	7	53	7	18				2		5	7	2.31	17
Mid	14	62			24							1.48	14
Oc 78													
Large		78	9	9	2							3.05	13
Mid		78	22									2.25	12
My 79													
Large		45	4	39	4	8						2.45	20
Mid		71		18	9		2					2.81	16
Jn 79													
Large	5	21	27	37	5	5						3.13	6
Mid		30	30	25							15	1.37	8
<u>Potamogeton</u>													
Jl 78													
Large			88	12								2.66	3
Mid		15	70	15								1.81	11

Table 1. (Continued)

	unident. insects	Chironomidae	Cladocera	Ostracoda	Copepoda	Rotifera	Culicinae	*Chaoborus*	Zygoptera	Ephemeroptera	Oligochaeta	prey/individual	no. of nymphs
Au 78													
Large	5	38	16	11				1	17	16		2.19	26
Mid		53	25	2		7		5		7		1.23	32
Se 78													
Large		61	17	22								2.54	9
Mid	2	50	33	10	2	2						2.19	19
Oc 78													
Large				100								0.33	3
Jn 79													
Large		50	25	25								2.65	3
Mid		28	37	32	4							1.20	18
Au 79													
Large	2	21		50		2		2	18	5		1.99	28
Mid		58	29		13							0.45	15
Myriophyllum													
Se 79													
Large		11		78						11		2.25	4
Mid		30	40	20						10		0.90	11
Oc 79													
Large	4	15	23	50	4					4		5.20	5
Mid		40	60									1.66	3
Sparganium													
Se 79													
Large	13	50		25				13				1.60	5
Mid												0.00	5

Table 2. Percentage composition of prey, number of nymphs studied, and number of prey per individual of nymphs of *L. d. disjunctus*. Large = instars F - F-2; Mid = head width 1.6 - 2.4 mm.

Carex	unident. insects	Chironomidae	Cladocera	Ostracoda	Copepoda	Rotifera	*Chaoborus*	Zygoptera	Ephemeroptera	Oligochaeta	prey/individual	no. of nymphs
22/6/78 Large	3	18	51	14	1	12			1		6.26	15
5/7/78 Large		37	29	20	6		3	3	3		3.18	11
8/6/79 Mid		5	33	5		38					4.00	10
26/6/79 Large	2	5	78	13		2	1				11.55	9
Potamogeton												
14/7/78 Large		17	42	25	8		8				3.00	4
26/6/79 Large	2	12	41	39	1	1	4			1	8.14	21

Table 3. Results of Mann-Whitney tests (U statistics) and sample sizes for diet of C. resolutum and L. d. disjunctus nymphs in Carex, C and Potamogeton, P. See text for details. * P=0.05; ** P=0.01.

	Large prey	Small prey	Number of specimens C	Number of specimens P
C. resolutum				
2/8/78				
F to F-2	52.0	63.0	13	9
F-3 to F-6	37.5	19.0	12	7
15/8/78				
F to F-2	23.0	34.0	10	9
F-3 to F-6	45.5**	120.0	16	15
24/8/78				
F to F-2	10.0*	24.0	7	8
F-3 to F-6	45.0	32.0	10	10
11/9/78				
F to F-2	11.0	14.0	8	5
F-3 to F-6	36.0	22.5	8	11
27/9/78				
F-3 to F-6	23.0	19.0	6	8
8/6/79				
F-3 to F-6	23.0	14.5	5	13
L. d. disjunctus				
26/6/79				
F to F-2	66.0	86.5	9	21

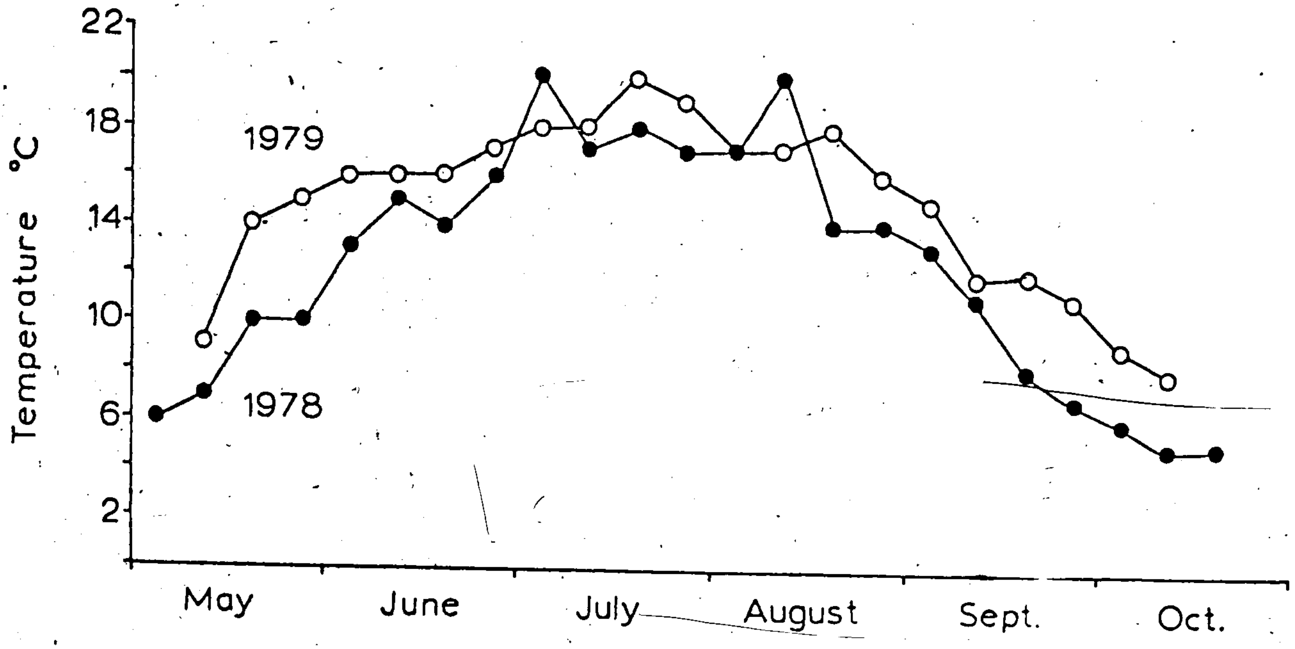

Figure 1. Mean weekly water temperature.

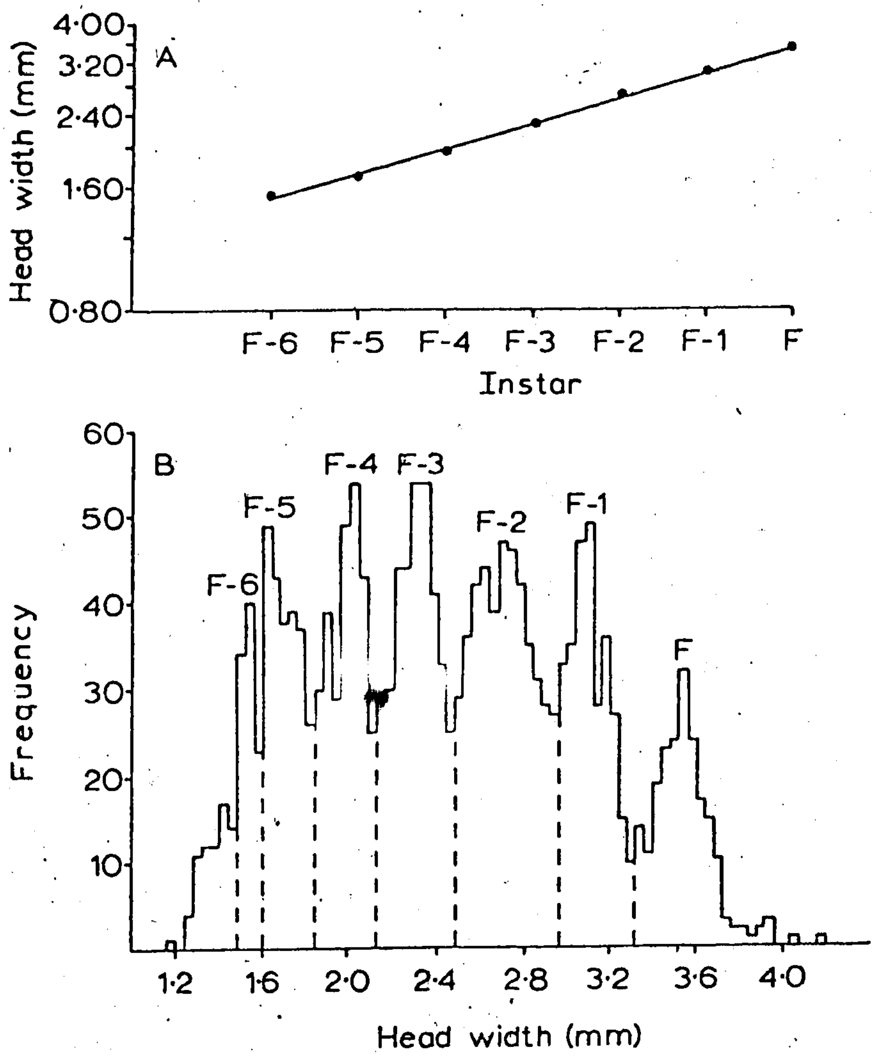

Figure 2. A, plot of average head width of C. resolutum nymphs against instar number. B, frequency of head widths of C. resolutum nymphs with probable instars indicated.

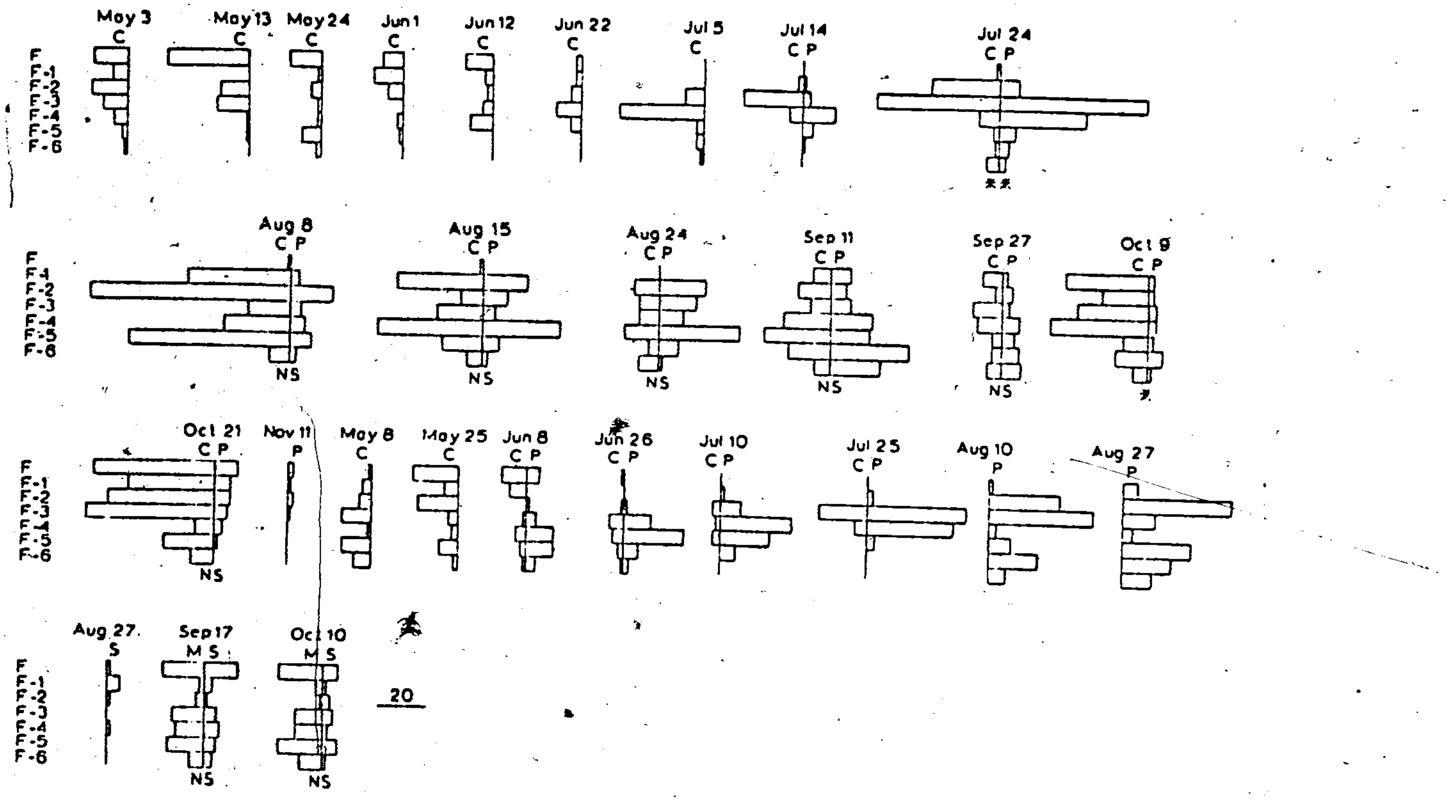

Figure 3. Instar-frequency distribution of C. resolutum nymphs in instars F to F-6. C=Carex, P=Potamogeton, M=Myriophyllum, S=Sparganium. Significance levels indicate the results of Chi square tests of homogeneity of instars in the vegetation zones indicated; $*=P < 0.05$, $**=P < 0.01$, NS=$P > 0.05$. Scale represents 20 specimens.

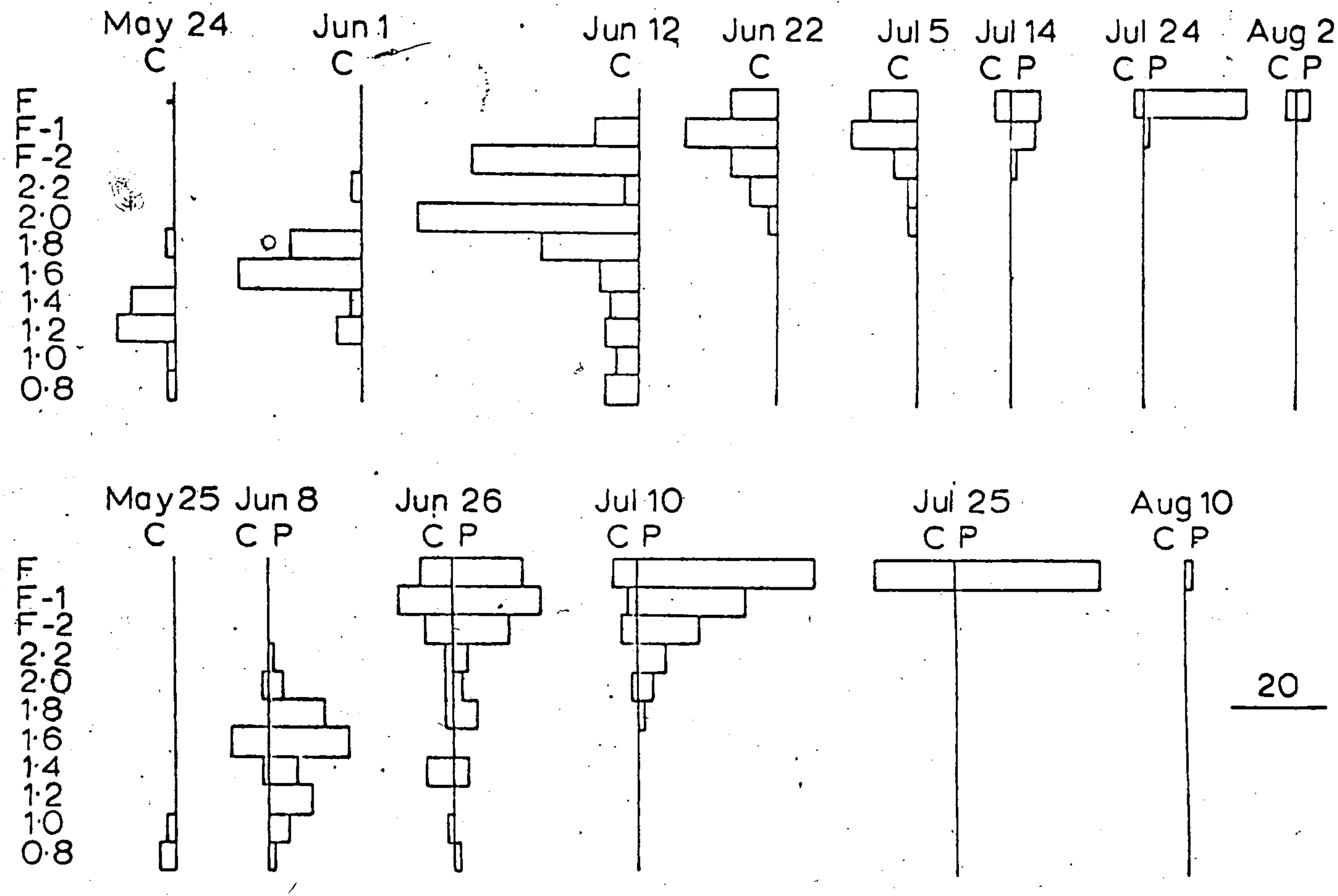

Figure 4. Instar-frequency distribution of *L. d. disjunctus* nymphs in instars F to F-2, and size frequency distribution for smaller nymphs. Symbols as in Figure 3.

Literature Cited

Baker, R. L. 1980. Use of space in relation to feeding areas by zygopteran nymphs in captivity. Can. J. Zool. 58: 1060-1065.

Baker, R. L. 1981. Use of space in relation to areas of food concentration by nymphs of Lestes disjunctus (Lestidae: Odonata) in captivity. Can. J. Zool. 59: 134-135.

Cannings, R. A. 1980. Some Odonata from the Crowsnest Pass Region, Alberta, Canada. Notul. Odonatol. 1: 88-89.

Chutter, F. M. 1961. Certain aspects of the morphology and ecology of the nymphs of several species of Pseudagrion Selys (Odonata). Arch. Hydrobiol. 57: 430-463.

Clifford, H. F. 1978. Descriptive phenology and seasonality of a Canadian brown-water stream. Hydrobiologia, 58: 213-231.

Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston.

Dyar, H. G. 1890. The number of molts in lepidopterous larvae. Psyche, 5: 420-422.

Ingram, B. R. 1976. Life histories of three species of Lestidae in North Carolina, United States (Zygoptera). Odonatologica, 5: 231-244.

Lawton, J. H. 1970. Feeding and food energy assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera) J. Anim. Ecol. 39: 385-423.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Macan, T. T. 1977. The influence of predation on the composition of freshwater animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Parr, M. J. 1970. The life histories of Ischnura elegans (van der Linden) and Coenagrion puella (L.) (Odonata) in south Lancashire. Proc. R. ent. Soc. Lond (A), 45: 172-181.

Pearlstone, P. S. M. 1971. Observations on a natural population of damselfly larvae. M.Sc. thesis, University of British Columbia, Vancouver.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in northern Alberta. Can. J. Zool. 42: 785-800.

Pritchard, G. and B. Pelchat. 1977. Larval growth and development of Argia vivida (Odonata: Coenagrionidae) in warm sulphur pools at Banff, Alberta. Can. Entomol. 109: 1563-1570.

Sawchyn, W. W. and C. Gillot. 1974. The life histories of three species of Lestes (Odonata: Zygoptera) in Saskatchewan. Can. Entomol. 106: 1283-1293.

Sawchyn, W. W. and C. Gillot. 1975. The biology of two related species of coenagrionid dragonflies (Odonata: Zygoptera) in western Canada. Can. Entomol. 107: 119-128.

Thompson, D. J. 1978. The natural prey of larvae of the damselfly, Ischnura elegans (Odonata: Zygoptera). Freshwater Biol. 8: 377-384.

Walker, E. M. 1953. The Odonata of Canada and Alaska, Vol. 1. University of Toronto Press, Toronto.

Walker, E. M. 1958. The Odonata of Canada and Alaska, Vol. 2. University of Toronto Press, Toronto.

Walker, E. M. and P. S. Corbet. 1975. The Odonata of Canada and Alaska, Vol. 3. University of Toronto Press, Toronto.

Chapter 2: Use of space in relation to feeding areas by nymphs of Coenagrion resolutum (Coenagrionidae: Odonata) in captivity

Abstract

Spacing behaviour by nymphs of Coenagrion resolutum was studied in the laboratory. Solitary nymphs found and remained at feeding sites; when several nymphs were present some were excluded from feeding sites. Nymphal size had no effect on positioning of solitary nymphs at feeding sites, but when nymphs occurred together, large nymphs excluded smaller nymphs. Prior occupancy at a feeding site by a nymph did not enhance its chances of remaining there when an intruder was added. When presented with a number of feeding sites, solitary nymphs stayed at only one site as frequently as did nymphs presented with only one site. Results are discussed in relation to possible effects of spacing behaviour on zygopteran life history and predator-prey dynamics.

Introduction

Nymphs of Odonata are common predators in the littoral areas of lakes and ponds and in the benthos of streams; they feed mainly on aquatic invertebrates, particularly insect larvae and small crustaceans. Population densities of nymphal odonates are sometimes very high (Benke 1976), and this, coupled with their impressive appetites (Lawton 1971), has prompted several authors to suggest possible mechanisms for predator-prey coexistence.

Benke (1976) suggested that dense populations of anisopterans can destroy prey populations that lack refuges. Lawton et al. (1974) and Akre and Johnson (1979) suggested that zygopteran nymphs may concentrate their predation on the more common prey, resulting in protection of prey populations from extinction. Crowley (1979) suggested that zygopteran nymphs in areas of low prey density disperse to areas of higher prey density.

Based on evidence from field populations, Macan (1973, 1977) suggested that territoriality of nymphs may be important in maintaining predator-prey systems. When nymphs of Pyrrhosoma nymphula were abundant, Macan (1964) found that some took 2 years to complete nymphal development, others 3 years; when nymphs were less abundant, the entire population completed nymphal development in 2 years. Macan concluded that the number of hunting sites is limited and that fast-growing nymphs are those that remain in optimum hunting areas, while slow-growing nymphs are "relegated" to sub-optimal areas of little food.

The purpose of my paper is to report results from experiments designed to test two major hypotheses that follow from Macan's observations: (1) solitary nymphs find and remain at productive hunting sites, and (2) when several nymphs are present, some are excluded from productive hunting sites. Results from my initial studies prompted me to experiment with the effects of alternate feeding sites, nymphal size, and prior occupancy on the use of space at productive hunting sites.

Materials and Methods

Nymphs of Coenagrion resolutum (Hagen) were used in all experiments. Cannings and Stuart (1977) report the nymphs "inhabit a wide variety of still waters from marshy ponds and grassy ditches to sphagnum bogs and weedy streams."

All nymphs used were collected with a dip net on 8 May 1979 from aquatic vegetation (primarily Carex) of a small pond in the boreal forest zone of Alberta, near the Bigoray River (53°31'N, 115°26'W). For a general site description of the area see Clifford (1969).

In the laboratory, nymphs in instars F-4 to F-1 (final instar nymphs were designated as F, penultimate as F-1, etc.) were placed individually in 40 ml plastic vials supplied with a small stick for a perch. Approximately 400 nymphs were housed in this fashion. Animals were kept at room temperature (20°C) and at a photoperiod of 16L:8D. Each nymph was fed one small enchytraeid (Oligochaeta) worm each day.

Plastic tanks (29 by 18 by 13 cm), each containing a "lattice" of 2.0 mm dowels, were used in all experiments. In experiments 1, 2, and 3 the lattice was a rectangle (10 by 15 cm) supported at the four corners by vertical dowels 10 cm high (Fig. 1). The base of one upright dowel rested in a plastic vial (2.0 cm high by 2.5 cm in diameter) that contained food. This dowel will be referred to as the "food stick." Tanks were covered on three sides with white paper and arranged so nymphs could not see into neighbouring tanks. Tanks were filled to the brim with water. The lattice was divided into eighteen 5 cm units for classifying location of nymphs. Position of nymphs not on lattices was recorded according to which corner of the tank they were nearest.

Nymphs in tanks that contained more than one individual were marked by clipping the tips of the caudal lamellae the day before the experiment.

Experiments

Experiment 1. Effects of food level and nymph density on position of nymphs

The first experiment was designed to test the hypotheses that (1) solitary nymphs find and remain at productive hunting sites, and (2) when several nymphs are present, some are excluded from productive hunting sites.

Methods

Three food levels (no worms, two worms/day, abundant worms, i.e. more than all the nymphs in the tank could eat in a day) and three densities of nymphs (one nymph/tank, two nymphs/tank, four nymphs/tank) gave a total of nine experimental conditions. Each experimental condition was replicated in eight tanks.

At 1000 hrs, 12 May 1979, nymphs in instars F-4 or F-3 were gently poured into the centres of the tanks. The position of each nymph was recorded five times a day, for 10 days, at approximately 2-h intervals, starting at 0900 hrs; observations began at 1200 hrs on May 12.

Results

Single nymphs in groups with food were usually first seen on the food stick within the first 2 days of the experiment, although one was not seen at the food stick during the first 8 days. After finding food sticks, nymphs remained there for extended periods, often more than 5 days. Six of the fifteen nymphs that found the food stick early in the experiment remained on the food stick until the end of the experiment, nine of the fifteen left food sticks after remaining there for several days. Four of these nymphs moved only a short distance from the food stick and returned after three or four observations, but five nymphs left the food stick and did not return to it for periods of 8 to 19 observations.

While on food sticks, nymphs showed little preference for either the top or bottom of the stick, even though the bottom was closer to the food. Therefore I analysed the data with respect to frequencies of observations of nymphs on and off the stick (Table 1). If a nymph died during an experiment the results from that tank were not analysed.

When only one nymph was in a tank, nymphs in the no-food group were on the food stick in 11% of the observations, while those in the two-worm and abundant-food groups were on the food stick in 60% and 51% of the observations respectively. A Kruskal-Wallis test showed a significant ($P < 0.05$) difference among the groups. This difference was due to the low frequency in the no-food group, since a Mann-Whitney test showed no difference between the two-worm and abundant-food levels ($P > 0.05$). Thus, the hypothesis that solitary nymphs find and remain near food is supported.

I used Kruskal-Wallis tests to determine effects of nymphal density on frequencies of observations of nymphs on food sticks. Both the two-worm and abundant-food levels showed differences $(P < 0.05)$ among the one-, two-, and four-nymph groups. The number of times individual nymphs were on the food stick, relative to the number of nymphs present, was reduced with increasing density. This indicates that nymphs were not behaving independently of each other and suggests that some were excluded. No significant difference $(P > 0.05)$ among groups was found in the no-food level.

The effect of nymphal density on frequency of observations of nymphs on the food stick suggests that behavioural interactions may limit the use of feeding areas. However, this indicates only that there are interactions; it provides no evidence that some nymphs are observed on the food stick more than others. To determine whether some nymphs are excluded from the food stick the results from each tank must be analysed separately. The question of interest here is whether the number of observations of individuals on the food stick is equally divided among those present. Unfortunately it is difficult to statistically analyse the results from each tank separately because each observation cannot be used as an independent sample. That is, the position of a nymph at one time will influence its position at a later time. Therefore, rather than use an inappropriate test, I have simply presented the frequency of individual nymphs on the food stick in Table 2.

Of the 16 tanks with two nymphs and food present, many tanks showed large differences between the two nymphs with respect to number of observations on food sticks. That is, one nymph remained at the stick while the other was rarely recorded there. In the tanks with small differences between the two nymphs, individuals were rarely at the stick at the same time. Instead, one would be at the stick for part of the time and then be replaced by the other. This replacement was often sudden, i.e. one nymph would be on the stick for 10 to 20 observations in a row and then another nymph would appear on the food stick and the first nymph would be displaced. In tanks with four nymphs, most of the tanks showed large differences among the four with respect to number of observations on the food stick. In many tanks, one or two of the individuals were rarely, if ever, seen on the stick.

Experiment 2. Effect of prior occupancy on position of nymphs

Results from Experiment 1 indicated that some nymphs were excluded from the food stick. To test whether the nymphs' previous experience in the tanks had an effect on exclusion, I designed an "Intruder" experiment.

Methods

Nymphs (intruders) were added to tanks that contained a nymph, and the positions of both animals were recorded. Original nymphs were added at 2100 hrs 25 May to 24 tanks.

All tanks had abundant food. Tanks were separated into three groups (A, B, C) of eight. At 0900 hrs 29 May, a single marked intruder was added to each A tank. Single intruders were added to each B tank at 0900 hrs 31 May and to each C tank at 0900 hrs 2 June. Thus, original occupants were alone for three different durations (A, 84 h; B, 132 h; C, 180 h) before intruders were added. Observations (as in Experiment 1) began at 0900 hrs 26 May and continued until 1700 hrs 5 June.

Results

For each of groups, A, B, C, Table 3 shows the proportion of observations on the food stick out of the first 19 observations after introduction of intruders. Because the C group was observed only 19 times after introduction of intruders, only the first 19 observations from the A and B groups were used in the analysis to avoid effects caused by differences in the length of time nymphs were together. A Kruskal-Wallis test indicated there was no significant difference ($P > 0.05$) in frequency of original nymphs on food sticks. Similarly there was no significant difference in frequency of intruder nymphs on food sticks. There was no difference (Mann-Whitney, $P > 0.05$) between frequency of original and intruder nymphs on the food stick when the groups were combined. These results suggest that prior occupancy confers no advantage to original nymphs with respect to occurrence on the food stick. This differs from many studies on territorial animals in which previous residency enhances the resident's chances of remaining in the area.

Experiment 3. Effect of nymphal size on position of nymphs

The third experiment was designed to test whether body size had an effect on single nymphs remaining at hunting sites and to test whether size was related to exclusion from hunting sites.

Methods

To compare the positioning of solitary nymphs of different sizes, I added single "medium-sized" nymphs (instar F-4 or F-3, total length 10 to 13 mm) to each of eight tanks and single "large" nymphs (instar F-1, total length 19 to 20 mm) to eight other tanks at 2100 hrs 25 May. All tanks had abundant food. Observations (as in Experiment 1) began at 0900 hrs 26 May and ended 1700 hrs 5 June.

To compare the positioning of different sized nymphs in the same tank, a pair of nymphs (one medium-sized and one large) was added to eight other tanks. Observations were made for the same period as for the solitary nymphs of different sizes.

Results

The frequency of observations of single large nymphs on the food stick was not different (Mann-Whitney, $P > 0.05$) from the frequency of single medium-sized nymphs on the food stick (Table 4). When large and medium-sized nymphs were together, the large individuals were on the food stick in 52% of the observations, the medium-sized nymphs in only 8% of the observations. A Mann-Whitney test indicated these results were significantly different ($P < 0.05$). The frequency of observations of solitary large nymphs on the food stick was not significantly different from that of large nymphs when medium-sized nymphs were present (Mann-Whitney $P > 0.05$). However, the frequency of observations of solitary medium-sized nymphs on the food stick was greater than that of medium-sized nymphs on the food stick when large nymphs were present (Mann-Whitney $P < 0.05$).

Thus solitary large and medium-sized nymphs remained at a food site with equal frequency; but when placed together, large nymphs excluded the smaller nymphs from the preferred sites. In one tank, the large nymph killed and ate the smaller one. Clearly, whatever the nature of the interaction, body size is important.

Experiment 4. Effect of alternate feeding sites on position of nymphs

Experiment 1 indicated that nymphs position themselves at productive hunting sites when only one site is available. The fourth experiment was designed to test whether nymphs position themselves at only one site when a number of equally profitable sites are available.

Methods

For this experiment the lattice structure was modified. Food vials were added to the base of all four supports, and an extra vertical support was added to the middle of each of the long sides of the rectangle. The extra vertical supports were added so that nymphs would have easier access to the lattice from the tank bottom.

Thirty-two tanks were arranged in four groups (A, B, C, D) of eight tanks each. Individuals in the A group received one worm each day in only one of the four dishes (the same dish each day). Individuals in the B group received one worm in each dish each day. Individuals in the C group received two worms in one food dish (the same dish each day) each day and those in the D group received two worms in each food dish each day. A single nymph in instar F-3 or F-2 was added to each tank at 0800 hrs 14 June. Observations (as in Experiment 1) began at 1000 hrs 14 June and ended 0900 hrs 24 June.

Results

Results are shown in Table 5. A "best stick," the upright stick that most often had a nymph on it, was determined for each nymph. In groups A and C (only one dish with food) the best stick was always the one with food in the dish. Within each food level (one or two worms) there was no difference between groups in frequency of observations at the best stick (Mann-Whitney $P > 0.05$). That is, in tanks with four feeding areas, nymphs stayed at one of the sticks as frequently as did nymphs in tanks with only one feeding area. This may be important in extrapolating my results to field situations. In the littoral area of a lake or pond profitable hunting areas may be more abundant than in the tanks with a single food dis[illegible]er, these results suggest that in areas with a hu[illegible] hunting sites, nymphs stay chiefly at one site.

Discussion

Wilson (1975) defined territory as "an area occupied more or less exclusively by animals or groups of animals by means of repulsion through overt aggression or advertisement." With respect to the "more or less" exclusive use of an area, my results support Macan's suggestion that zygopteran nymphs are territorial. Solitary nymphs remained in areas of food concentration, even if food concentration was low and other areas of food concentration were nearby. When several nymphs were present some individuals remained at profitable feeding areas while others were excluded. With respect to the means of repulsion section of Wilson's definition, my data suggest only that nymphs interact and that body size in important in the interaction. The hypothesis that nymphs are territorial cannot be completely tested until, as suggested by Murie and Harris (1978), information is collected on both the use of space, and the location and outcome of interactions.

Whatever the nature of zygopteran spacing behaviour, the fact that nymphs do exhibit spacing behaviour may have profound effects on the life history and population dynamics of zygopterans. Chironomid larvae and cladocerans are usually reported as the most common prey of Zygoptera (Lawton 1970, Pearlstone 1973, Thompson 1978). As suggested by Macan (1964, 1977), these prey items are not randomly distributed but clumped. The distribution of many cladoceran species in littoral areas of lakes and ponds depends in part on water depth, species of vegetation, and substrate type (Smyly 1957, Quade 1969, Goulden 1971). Whiteside (1974) has shown some chydorids exhibit clumped distributions even over "apparently uniform habitat." Species of chironomid larvae also show preferences for particular microhabitats. Similar to littoral cladocerans, distribution of chironomid larvae can depend on species of vegetation, substrate type, etc. (Boerger 1978). Given a contagious distribution of prey, my results suggest that some nymphs will remain in areas of prey concentration while others are excluded. If nymphs in productive feeding areas grow faster than those in poor feeding areas, the exclusion will result in retarded growth of some nymphs. In fact, growth may be so retarded that the slow-growing nymphs cannot emerge in the same season as the fast-growing nymphs. Thus, spacing behaviour may help determine the number of adults that emerge in a season.

Results of my study are important in interpreting the results of Akre and Johnson (1979) and Crowley (1979). Akre and Johnson (1979) found that nymphs of Anomalagrion hastatum concentrated their predation on the most common prey species when Daphnia and Simocephalus were offered together. They hypothesized that this "switching" behaviour was due to a change in search mode. That is, when mobile prey are most abundant the nymphs wait and ambush the prey whereas when the prey are sessile the nymphs walk around, thereby increasing the encounter rate. Crowley (1979) did find that nymphs of Ischnura verticalis spent more time walking when no prey or sessile prey was offered compared to when mobile prey was offered, but he noted that the difference in time spent walking was small. He also noted that the Daphnia and Simocephalus he used in his experiments tended to occupy different areas of his tanks. Crowley suggested that the increase in time spent walking by hungry nymphs represented a "dispersal" of nymphs to a new ambush site rather than a change in search mode. Thus the switching behaviour reported by Akre and Johnson (1979) may be explained by the nymphs feeding in different areas. My results confirm, in part, Crowley's hypothesis. Single nymphs of C. resolutum did move from areas of no food to areas of food concentration and then remained at that area. It is important to note that the experiments of Akre and Johnson (1979) were done with a single nymph in each tank. If ~~several~~ nymphs were used, the results from my experiments suggest some nymphs would have remained in the area of high prey concentration while others would be excluded to areas of lower prey concentration. Thus, some nymphs, i.e. the excluded ones, may have fed more heavily on the less abundant prey than on the more abundant prey.

My results are also relevant to Benke's (1976) suggestion that "interference among odonate larvae" is unlikely to alter the effect of nymphal odonates on prey populations. Benke bases this idea on his suggestion that interference is "most likely to be manifested by interodonate predation" and on the fact that such predation is rare. My results show that nymphs do "interfere" with each other but without predation. By limiting the number of predators in an area of prey concentration, spacing behaviour may reduce predation pressure on prey populations.

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Table 1. Proportion of observations of nymphs on food sticks out of the total number of observations. N represents number of observations.

	Nymph density 1	2	4
no food			
N	400	800	1000
Proportion	0.11	0.06	0.08
2 worms			
N	400	800	1600
Proportion	0.60	0.35	0.23
abundant food			
N	400	800	1400
Proportion	0.51	0.39	0.20

Table 2. Frequency of observations of individual nymphs on food sticks out of the total number (50) observations. Nymphs are ranked according to frequency on food stick. 2w = 2 worms; ab = abundant food.

Tank #	2 nymphs				4 nymphs							
	2w		ab		2w				ab			
	1	2	1	2	1	2	3	4	[illegible]	2	3	4
1	32	0	27	2	16	14	9	5	20	19	10	0
2	25	5	35	13	33	32	1	0				
3	17	12	11	10	23	8	4	0	36	13	1	1
4	20	3	29	21	27	6	5	0	27	19	12	8
5	30	23	24	22	20	6	5	1	26	15	14	7
6	24	11	34	8	32	10	9	0	30	12	5	2
[illegible]	27	9	34	10	32	12	4	0	33	12	8	0
8	22	19	32	3	22	21	1	0	25	17	[illegible]	4

Table 3. Proportion of observations of nymphs on food sticks out of the first 19 observations after the addition of intruders. N represents number of observations. See text for explanation of groups.

	Group A	Group B	Group C
original			
N	152	133	152
Proportion	0.47	0.38	0.18
intruder			
N	152	133	152
Proportion	0.13	0.47	0.30

Table 4. Proportion of observations of medium- and large-sized nymphs on food sticks. N represents number of observations.

	large alone	medium alone	large with medium	medium with large
N	440	385	385	385
Proportion	0.56	0.50	0.52	0.08

Table 5. Proportion of observations of nymphs on "best sticks". N represents number of observations. See text for explanation of groups.

	A	B	C	D
N	357	357	357	357
Proportion	0.33	0.32	0.24	0.25

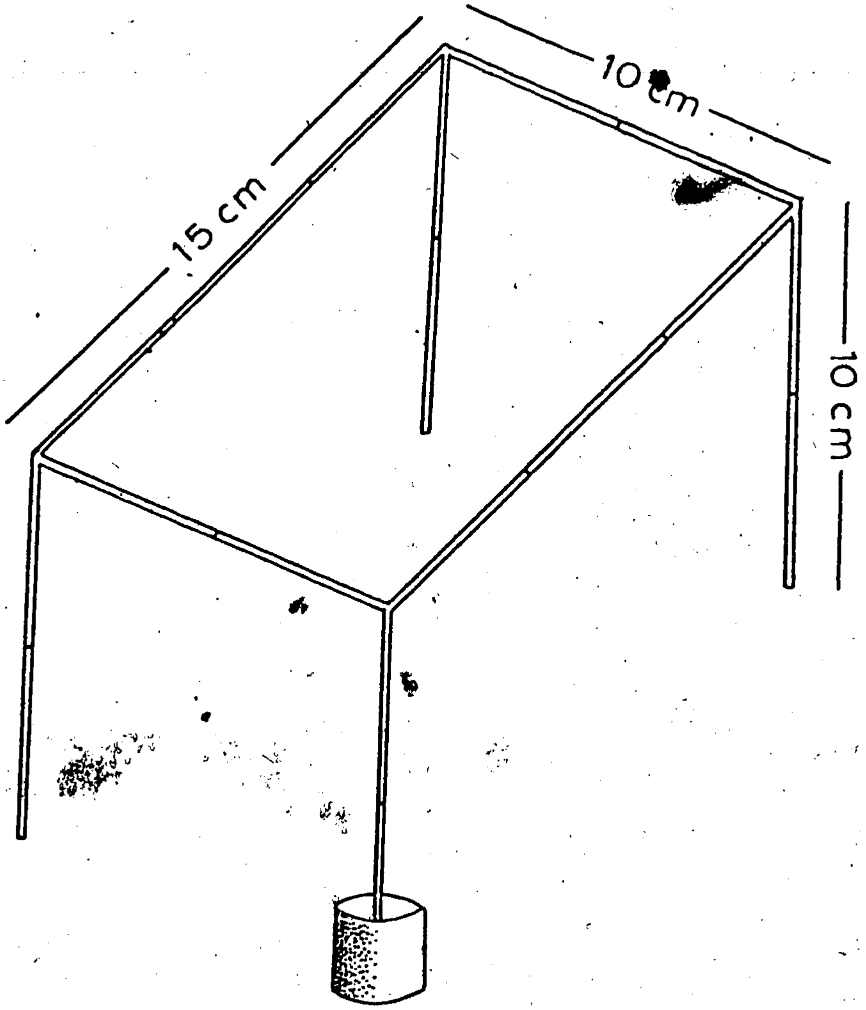

Figure 1. Diagram of the lattice. Lattices were fastened to the tank bottoms with silicon.

Literature Cited

Akre, B. G. and D. M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. J. Anim. Ecol. 48: 703-720.

Benke, A. C. 1976. Dragonfly production and prey turnover. Ecology, 57: 915-927.

Boerger, H. 1978. Life history and microhabitat distribution of midges (Diptera: Chironomidae) inhabiting a brown-water stream of central Alberta, Canada. Ph.D. thesis, University of Alberta, Edmonton.

Cannings, R. A. and K. M. Stuart. 1977. The dragonflies of British Columbia. British Columbia Provincial Museum Handbook, no. 35.

Clifford, H. F. 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. 82: 578-597.

Crowley, P. H. 1979. Behaviour of zygopteran nymphs in a simulated weed bed. Odonatologica, 8: 91-101.

Goulden, C. E. 1971. Environmental control of the abundance and distribution of the chydorid Cladocera. Limnol. Oceanogr. 16: 820-831.

Lawton, J. H. 1970. Feeding and food assimilation in larvae of the damselfly <u>Pyrrhosoma nymphula</u> (Sulzer)

(Odonata: Zygoptera). J. Anim. Ecol. 39: 669-689.

Lawton, J. H. 1971. Maximum and actual feeding rates in larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). Freshwater Biol. 1: 99-111.

Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. In Ecological stability. Edited by M. B. Usher and M. H. Williamson. Chapman and Hall, London, pp. 141-158.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Macan, T. T. 1973. Ponds and Lakes. George Allen and Unwin Ltd., London.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Murie, J. O. and M. A. Harris. 1978. Territoriality and dominance in male Columbian ground squirrels (Spermophilus columbianus). Can. J. Zool. 56: 2402-2412.

Pearlstone, P. S. M. 1973. The food of damselfly larvae in Marion Lake, British Columbia. Syesis, 6: 33-39.

Quade, H. W. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. Ecology, 50: 170-179.

Smyly, W. J. D. 1957. Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere. Hydrobiologia, 11: 59-72.

Thompson, D. J. 1978. The natural prey of larvae of the damselfly, *Ischnura elegans* (Odonata: Zygoptera). Freshwater Biol. 8: 377-384.

Whiteside, M. C. 1974. Chydorid (Cladocera) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. Ecology, 55: 538-550.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Harvard University Press, Cambridge.

Chapter 3. Use of space in relation to areas of food concentration by nymphs of <u>Lestes disjunctus disjunctus</u> (Lestidae: Odonata) in captivity

Abstract

Laboratory experiments provided no evidence that solitary nymphs of <u>Lestes disjunctus disjunctus</u> remain near areas of food concentration; also, there was no evidence that the presence of other nymphs affected the use of feeding areas. These results are in contrast to previous results for nymphs of <u>Coenagrion resolutum</u> and support the hypothesis that life histories are affected by spacing behaviour of nymphs.

Introduction

Macan (1973, 1977) suggested that differences in growth rate of nymphs of *Pyrrhosoma nymphula* (Sulzer) (Coenagrionidae) from a single population were due to some nymphs excluding others from areas of food concentration. Baker (1980) showed that under laboratory conditions single nymphs of *Coenagrion resolutum* (Hagen) (Coenagrionidae) find and remain at areas of food concentration and that when several nymphs are present some are excluded. In the population from which the experimental animals for that study were taken, some animals completed development in 1 year, others in 2. Another zygopteran, *Lestes disjunctus disjunctus* (Selys) (Lestidae), collected in the same pond from which the *C. resolutum* nymphs were collected, showed very little variation in life history. The synchronous development of nymphs of *L. d. disjunctus* is no doubt partly due to eggs overwintering in a diapause state and to hatching being synchronized (Sawchyn and Gillot 1974). However, I felt the synchronous development of *L. d. disjunctus* nymphs may also reflect a lack, or at least a different form, of spacing behaviour as seen in *C. resolutum*. The purpose of this paper is to report the results from experiments designed to test (1) whether nymphs of *L. d. disjunctus* remain at areas of food concentration and (2) whether when several nymphs are present some are excluded from areas of food concentration.

Materials and Methods

Nymphs of L. d. disjunctus were collected from the same pond that animals for the C. resolutum experiments were collected from (Baker 1980) on 28 May 1980. The pond is near the Bigoray River, Alberta ($53^{\circ}31'$N, 115° $26'$W); see Clifford (1969) for a general site description.

In the laboratory, 60 nymphs with head widths ranging from 2.5 to 3.0 mm (no nymph was in the final instar) were kept individually in 40 ml plastic vials supplied with a small stick for a perch. Animals were kept at room temperature (20 °C) and at a photoperiod of 16L:8D. Each nymph was fed one small enchytraeid (Oligochaeta) worm each day.

Plastic tanks (20 x 18 x 13 cm) each containing a "lattice" of 2 mm dowels were used for observations. The tanks and lattices were identical to those used in the experiment with C. resolutum. The lattice was a horizontal rectangle (10 x 15 cm) supported at the four corners by vertical dowels 10 cm high. The base of one upright dowel (referred to as the food stick) rested in a plastic vial (2.0 cm high x 2.5 cm diameter) that was used to hold food. Tanks were covered on three sides with white paper and arranged so nymphs could not see into neighbouring tanks. Tanks were filled to the top with dechlorinated water. The lattice was divided into eighteen 5-cm units for classifying location of nymphs.

Position of nymphs not on lattices was recorded according to which corner of the tank they were nearest. Nymphs in tanks that contained more than one individual were marked by clipping the tips of the caudal lamellae the day before the experiment.

There were three experimental conditions: (1) one nymph/tank with no food, (2) one nymph/tank with abundant food, (3) four nymphs/tank with abundant food. Each condition was replicated in 10 tanks.

At 0930 hrs, 31 May 1980, nymphs were gently poured from their vials into the centres of the tanks. The position of each nymph was recorded five times a day for 7 days at approximately 2 h intervals, starting at 0830 hrs; four observations were made on 31 May starting at 1100 hrs giving a total of 34 observations.

Results

A Mann-Whitney test indicated there was no significant difference ($P > 0.1$) between the single nymph/no food group and the single nymph/food group with respect to the number of observations on the food stick (Table 1). Thus, the hypothesis that solitary nymphs remain near areas of food concentration is not supported. I also used a Mann-Whitney test to determine the effects of density of nymphs on the number of observations of nymphs on the food stick. There was no significant difference

$(P > 0.1)$ between the single nymph/food group and the four nymphs/food group. Thus there is no evidence that presence of other animals affected any nymph's use of the feeding area.

There is a problem in comparing these results to the results from the C. resolutum experiments, because L. d. disjunctus nymphs in tanks with abundant food were observed on the lattice in only 18.5% of the observations compared to 94.5% for C. resolutum. If L. d. disjunctus nymphs preferred to be on the bottom of the tank rather than on the lattice (as suggested by the low frequency of observations on the lattice) then analysis of results based on frequency of observations of nymphs on the food stick may not adequately test hypotheses on the use of space. Therefore, I analysed the results with respect to frequency of observations of nymphs in the corner of the tank that contained the food dish. Nymphs could feed at the food dish by crawling into it from the tank bottom. A Mann-Whitney test indicated there was no significant difference $(P > 0.1)$ between the single nymph/no food group and the single nymph/food group with respect to the number of observations of nymphs in the corner of the tank containing the food vial. A Mann-Whitney test also indicated there was no significant difference $(P > 0.1)$ between the single nymph/food group and the four nymphs/food group with respect to the number of observations of nymphs in the corner containing the food vial. Thus, as in the original analysis, there is no evidence that *L. d. disjunctus* nymphs remain at areas of food concentration, or that use of the feeding area is affected by presence of other nymphs.

Discussion

On the basis of this study alone, it would be premature to suggest that some nymphs of *L. d. disjunctus* do not remain at areas of food concentration and exclude other nymphs from the area. The light and temperature regime, size of tanks, lattice structure, my presence, etc., may all have affected the behaviour of the nymphs. Also, all observations were made during the day and it is possible that the behaviour of nymphs was different at night than in the day. I doubt whether type of food was an important factor in the results because *L. d. disjunctus* nymphs eat worms readily, and, as in the experiments with *C. resolutum*, I often had to add worms to the food vials to maintain an abundance of worms.

Despite difficulties with interpretation of "negative" results, it is clear that under the same laboratory conditions nymphs of *L. d. disjunctus* and *C. resolutum* behave differently with respect to use of feeding areas. The results support the hypothesis that life histories of zygopteran nymphs are related to use of space at areas of food concentration. In the laboratory, some nymphs of *C. resolutum* excluded others from areas of food concentration (Baker 1980), and in the field some nymphs developed to maturity in 1 year, others took 2 years. Nymphs of *L. d. disjunctus* did not exclude others from areas of food concentration, and the field population showed no obvious separation into slow- and fast-developing animals. Detailed comparisons of the hunting methods of various odonate species may be useful in interpreting data on field life histories and population dynamics.

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Table 1. Percentage of observations of *L. d. disjunctus* nymphs on food sticks and corners with the food vial.

	One nymph no food	One nymph food	Four nymphs food
Stick	3.5	3.8	4.0
Corner	34.0	29.1	28.0

Literature Cited

Baker, R. L. 1980. Use of space in relation to feeding areas by zygopteran nymphs in captivity. Can. J. Zool. 58: 1060-1065.

Clifford, H. F. 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. 82: 578-597.

Macan, T. T. 1973. Ponds and Lakes. George Allen and Unwin Ltd., London.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Sawchyn, W. W. and C. Gillot. 1974. The life hi[illegible] of three species of *Lestes* (Odonata: Zygo[illegible]a) in Saskatchewan. Can. Entomol. 106: 1283-1293.

Chapter 4. Effects of food abundance on growth, survival, and use of space of nymphs of <u>Coenagrion</u> <u>resolutum</u> (Coenagrionidae: Odonata)

Abstract

In the laboratory, nymphs of <u>Coenagrion</u> <u>resolutum</u> that were fed large and frequent meals grew faster, emerged earlier and had higher survivorship than nymphs that were fed smaller, less frequent meals. When given a choice of feeding areas, nymphs tended to remain near areas of food concentration that would promote high growth rates; however, nymphs did not always remain at those areas of high food concentration that promoted maximum growth rate.

Introduction

Odonate nymphs within a single population frequently show different patterns of development; a population may be part univoltine and part semivoltine (Corbet 1957, Macan 1964, Ingram and Jenner 1976). Macan (1964, 1977) suggested that variation in life history may arise through different diets in different microhabitats. Nymphs remaining at good hunting sites grow rapidly, while nymphs relegated to areas of little food grow more slowly. Baker (1980) showed that solitary <u>Coenagrion resolutum</u> nymphs, under laboratory conditions, remain at areas of food concentration; and when several nymphs are present, some are excluded from feeding areas.

Although nymphal odonates are known to withstand long periods of starvation (Pritchard 1964, Hassan 1976), there are few studies on how diet affects nymphal growth (Fischer 1961, Hassan 1976, Lawton et al. 1980). The first purpose of my paper is to report results from an experiment designed to test effects of food quantity on growth and survival of nymphs of <u>C. resolutum</u>. Lawton et al. (1980) suggested that, because the inclusive fitness of univoltine animals is probably higher than that of semivoltine animals, zygopteran nymphs will select the best possible feeding areas to reduce development time. The second purpose of my paper is to report results from an experiment designed to test whether nymphs offered a range of food concentrations will spend more time at areas of food concentration that result in maximum growth.

Experiments

Experiment 1. Effects of food quantity on growth and survival

Methods

Coenagrion resolutum nymphs were collected from a pond in the boreal forest zone of Alberta, near the Bigoray River; see Clifford (1969) for a description of the general area. Fifty small nymphs (metathoracic femur lengths 1.2-1.[illegible] mm, total length approximately 7.0 mm) were collected from the pond on 15 August 1978. Nymphs were housed separately in 40 ml plastic vials containing dechlorinated water and a small stick for a perch. Animals were maintained at 20°C and at a photoperiod of 16L:8D.

Animals were starved until 22 August 1978, when feeding began. Nymphs were fed *Daphnia*, collected from a small pond near the University of Alberta campus, and enchytraeid (Oligochaeta) worms from a laboratory culture. Nymphs were randomly arranged into five groups of ten animals each; each group (labelled A-E) was maintained on a different diet. Diets, in numbers of *Daphnia*, were as follows: (A) 8/day, (B) 4/day, (C) 2/day, (D) 1/day,

(E) 1/2 days. On 22 September 1978, I increased the diets to (A) 12/day, (B) 6/day, (C) 3/day, (D) 3/2 days, (E) 3/4 days. In the D and E diets, the number of Daphnia fed was spread over the feeding period, i.e. animals in the E group received one Daphnia every day for three days and then none on the fourth. On 23 October, I changed diet to medium-size worms; schedule of feeding was (A) 4/day, (B) 2/day, (C) 1/day, (D) 1/2 days, (E) 1/4 days. For groups D and E the worm was removed if not eaten in 24 hrs.

Nymphs were checked daily to determine if any nymph had died or molted. Exuviae were stored in 95% ethanol. I measured the metathoracic femur length of each exuviae to determine rate of growth.

Results

Survival and metathoracic femur lengths are shown in Figure 1. Due to the nymphs' small size, I mistook some nymphs of Enallagma boreale for C. resolutum at the beginning of the experiment. Data from E. boreale nymphs were not included in the analysis; hence the number of nymphs per group were not equal on day 0.

Eight of the ten nymphs in group E died during the first 30 days of the experiment; the remaining two nymphs lived for more than a year but died before emerging. Number of nymphs alive in the D group declined less sharply than in the E group, but only one nymph emerged.

Survival was highest in group A and group C, where seven [illegible] nine and five [illegible]t of eight nymphs emerged respectively. Only two o[illegible]ght animals emerged in group B.

Growth curves were produced by plotting the natural logarithim of the metathoracic femur length at 15 day intervals; a 30 day interval was used in Figure 1 to simplify the graph. Because the curves were approximately linear and to allow for statistical analysis, I assum[illegible] growth was exponential and calculated an instantaneous growth rate (mm mm^{-1} day^{-1}) for each animal according to the exponential equation:

$$L_t = L_0 e^{bt}$$

where L_t and L_0 [illegible]etath[illegible]ic femur lengths at days t and 0 respecti[illegible] and b is the instantaneous growth rate.

I used Mann-Whitney tests to compare each group with each other group with respect to instantaneous growth rate. Only results from animals that lived at least 60 days were used in the analysis. Growth rates (mm mm^{-1} day^{-1}) of groups A (0.00492) and B (0.00521) were not significantly different ($P > 0.05$) but both were significantly larger than all other groups ($P < 0.05$). Growth rate of [illegible]oup C (0.00306) was not significantly different from that of group D (0.00269) ($P > 0.05$), but was significantly larger (P < 0.05) than the growth rate of group E (0.00166). Growth rates of groups D and E were not significantly different (P > 0.05).

Emergence periods generally reflected growth rates. Animals of the well-fed groups emerged earlier than those of the poorly fed groups. Although there was no significant difference in growth rates of animals in groups A and B, animals in group A emerged earlier than those in group B.

Experiment 2. Effects of food quantity on position of nymphs

Methods

Ten tanks (29 cm by 18 [illegible] 15 [illegible]), each with four feeding areas of different food concentration, were used to determine the effects of food concentration on positioning of nymphs. Each feeding area [illegible] a plastic vial, 2.0 cm by 2.5 cm in diameter, attached to the tank bottom with silicon. Vials were arranged at the corners of a square pattern (10 cm by 10 cm). A dowel, 2.0 mm in diameter and 10 cm long, was attached to the centre of the bottom of each vial with silicon. The four dowels led from the vials to a cork approximately 7 cm above the tank bottom. The upper ends of the dowels were sharpened to penetrate the cork. Food concentrations used matched those in the growth experiments; vials labelled B, C, D, E received 2 worms/day, 1 worm/day, 1 worm/2 days, 1 worm/4 days respectively. I did not include the 4 worms/day level, because there was no significant difference between the A and B groups in Experiment 1 with respect to growth rate. Food levels were checked every day between 0830-0900 hrs, at which time worms were removed or added to the appropriate vials. Tanks were covered with white paper on three sides and arranged so nymphs could not see into adjacent tanks.

On 28 May 1980, 10 nymphs of C. <u>resolutum</u> in instars F-1 and F-2 (final instars were designated F, penultimate instars F-1, etc.) were collected from the pond mentioned in the preceding section. Nymphs were housed individually in 40 ml plastic vials supplied with a small stick for a perch. Animals were fed 1 worm/day until 31 May when they were added to the tanks. Nymphs were lifted from their vials in a large bore pipette and placed on top of the cork; thus, each nymph started the experiment at a position equidistant from the four feeding areas. From 31 May until 16 June, the position of each nymph was recorded five times a day at 2 hr intervals. The position recorded was simply which of the four dowels the nymph was on. Position of nymphs not on the dowels (i.e. on the cork or tank bottom) was recorded but not used in the analysis. The 17 day duration of the experiment allowed four cycles of the feeding regime, e.g. the E vial in each tank received a worm five times. One nymph died during the experiment, and data of this animal were not used in the analysis.

Results

I correlated the number of observations of a nymph at each feeding site with the number of worms removed from that site to determine if use of a feeding area was related to diet. There was a positive correlation ($P < 0.01$) between number of worms eaten and number of observations, and this supports the suggestion that nymphs spend more time in areas where they receive more food. However, despite the significant correlation, Table 1 indicates that use of feeding areas was variable. Although there was a trend towards heavier use of the areas with more food, there was no indication that all nymphs spent most of their time at areas with the most food. Only four of the nine nymphs remained at vial B more than at other vials, and one of the remaining five nymphs stayed at vials B and C an equal amount of time. Of the remaining four nymphs, three utilized at least two other vials more than vial B. Individual nymphs also spent considerable time away from their areas of maximum use (Table 1). The number of observations at the most frequently used areas, relative to time spent at all feeding areas combined, ranged from 31% to only 56%. This use of secondary feeding areas was reflected by the number of worms eaten. A Kruskal-Wallis test indicated there was no significant difference ($P > 0.05$) among feeding areas with respect to number of worms eaten relative to the number offered (Table 2). Thus, the probability of a worm being eaten was not dependent on which vial the worm was in.

Discussion

Results support the suggestion that food availability may have pronounced effects on life history of coenagrionid nymphs. Growth of well-fed nymphs was faster than growth of nymphs in poorly fed groups. Also, emergence periods of well-fed groups were advanced compared to those of poorly fed groups. Thus, nymphs in an area of a pond or lake where they receive abundant food may develop more rapidly and emerge earlier than nymphs living in areas of less food. In the field population from which the experimental animals were taken, some nymphs completed development in 2 years, others completed development in 1 year. If food shortage is severe, the nymphs will simply die. Lawton et al. (1980) suggested starvation of _Ischnura elegans_ nymphs is rare in the field, but their conclusions were based on experiments involving only the final three nymphal instars. The sharp decrease in number of nymphs alive near the beginning of my experiment suggests poor diets may be most critical to young instars. The total emergence period was long, 140 days, and this supports Macan's suggestion that diet may alter growth rate to the extent that slow-growing nymphs may be forced to miss an emergence period and emerge the following year.

There are problems, however, in extrapolating these results to field situations. Some odonate nymphs are suspected of undergoing some form of diapause, initiation of which is determined by temperature, photoperiod, and stage of development (Corbet 1962, Lutz 1974a, b). Some odonates are also known to have different thermal coefficients for growth in different instars, i.e. a low temperature may allow growth in young instars but inhibit growth in the older instars (Lutz 1968). Also, odonate nymphs can use light and temperature as cues for emergence periods (Corbet 1962). Thus, a better test of the effects of diet on odonate life histories would be to run the experiments at field conditions of photoperiod and temperature.

Results from Experiment 2 suggest there was a tendency for nymphs to remain at feeding areas that would promote fairly rapid growth. If a diet of 2 worms/day results in a maximum growth rate, as suggested by results of Experiment 1, and if nymphs "forage optimally" by selecting the best possible "fishing sites" as predicted by Lawton et al. (1980), then one would expect the nymphs in Experiment 2 to remain primarily at vial B. But nymphs did not always stay primarily at vial B, and this suggests that either a diet of 2 worms/day does not result in maximum possible growth rates or nymphs do not forage in a way that achieves maximum growth rates.

Possibly the diet of 2 worms/day did not result in maximum growth rate. Although there was no significant difference in growth rates between animals maintained on diets of 4 worms/day and those maintained on 2 worms/day, animals fed 4 worms/day did emerge earlier than those fed 2 worms/day. It is also possible that the worms fed in Experiment 2 were of less food value than worms used in Experiment 1. This seems unlikely, however, because they were cultured in the same manner. If 2 worms/day in Experiment 2 were not sufficient for maximum growth rates, and nymphs do forage in a manner resulting in maximum growth, one would expect nymphs to move to other areas to supplement the diet available at vial B. Nymphs would be expected to forage optimally by selecting the fewest areas that in combination result in maximum growth. Nymphs remained primarily at vials B and C and this gives some support to the hypothesis of optimal foraging. However, according to the model of Charnov (1976), an optimal forager in a "patchy" environment should remain at a feeding area until the food left in that area drops to the average food level for all feeding areas. If nymphs did forage in this manner, it should be reflected in the number of worms removed from the vials; for example, a greater proportion of the worms offered should have been taken from vials B and C than from vials D and E. Because there was no significant difference among the feeding areas with respect to the percentage of worms eaten (approximately 50% of the worms offered were eaten from each vial) the suggestion is that the nymphs did not forage in an optimal manner. It is possible that the lack of optimal foraging behaviour by nymphs of *C. resolutum* was due to the laboratory conditions. Factors such as the light and temperature regime, type of dowels, size of tanks, etc., may have stressed the nymphs and caused them to move more than they would under natural conditions. Also, the feeding areas were fairly close together, animals had only to crawl along 20 cm of dowel to get from one vial to another; it is possible that nymphs cannot discriminate between patches on such a small scale. If the food vials had been farther apart nymphs may have spent more time at the vials with the most food.

In conclusion, although there is little evidence to suggest that nymphs forage in an optimal manner, growth rates are highly dependent on diet and nymphs remain near areas of food concentration that result in rapid growth.

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Table 1. Number of observations of nymphs at the feeding areas.

	Feeding Area			
Nymph #	B	C	D	E
1	18	10	10	2
2	13	39	14	4
3	18	18	15	7
4	17	23	4	15
5	10	13	26	15
6	31	20	11	10
7	13	27	19	8
8	25	12	13	5
9	25	10	15	11
$\bar{x}$	18.9	19.1	14.1	8.6

Table 2. Percentage of worms eaten relative to the number offered.

	Feeding Area			
	B	C	D	E
Nymph #				
1	44	35	44	60
2	21	71	56	20
3	68	76	78	40
4	35	47	22	60
5	56	59	67	100
6	59	35	33	40
7	44	82	78	60
8	74	47	56	40
9	50	53	33	40
$\bar{x}$	50.1	56.1	51.9	51.1

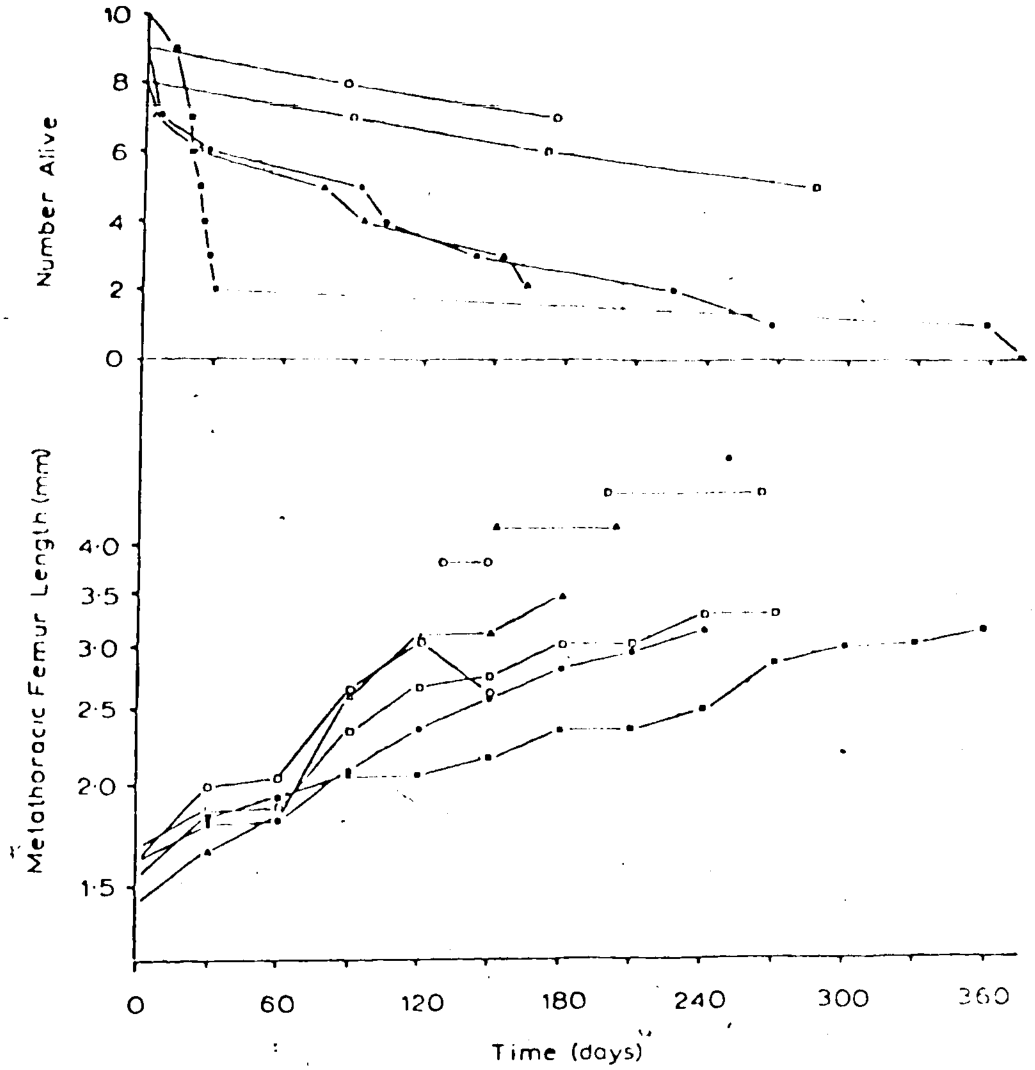

Figure 1. Metathoracic femur lengths and number alive of animals in groups A, open circles; B, triangles; C, open squares; D, solid circles; E, solid squares. Horizontal lines in the lower figure represent emergence periods.

Literature Cited

Baker, R. L. 1980. Use of space in relation to feeding areas by zygopteran nymphs in captivity. Can. J. Zool. 58: 1060-1065.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Biol. 9: 129-136.

Clifford, H. F. 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. 82: 578-597.

Corbet, P. S. 1957. The life-history of the Emperor Dragonfly <u>Anax</u> <u>imperator</u> Leach (Odonata: Aeshnidae). J. Anim. Ecol. 26: 1-69.

Corbet, P. S. 1962. A biology of dragonflies. Witherby, London.

Fischer, Z. 1961. Cannibalism among the larvae of the dragonfly <u>Lestes</u> <u>nympha</u> Selys. Ekologia Polska, Seria B, 7: 33-39.

Hassan, A. T. 1976. The effect of food on the larval development of <u>Palpopleura</u>-<u>lucia</u> <u>lucia</u> (Drury) (Anisoptera: Libellulidae). Odonatologica, 5: 27-33.

Ingram, B. R. and C. E. Jenner. 1976. Influence of photoperiod and temperature on development time and number of molts in nymphs of two species of Odonata. Can. J. Zool. 54: 2033-2045.

Lawton, J. H., B. A. Thompson, and D. J. Thompson. 1980. The effects of prey density on survival and growth of damselfly larvae. Ecol. Entomol. 5: 39-51.

Lutz, P. E. 1968. Effects of temperature and photoperiod on larval development in *Lestes eurinus* (Odonata: Lestidae). Ecology, 49: 637-644.

Lutz, P. E. 1974a. Effects of temperature and photoperiod on larval development in *Tetragoneuria cynosura* (Odonata: Libellulidae). Ecology, 55: 370-377.

Lutz, P. E. 1974b. Environmental factors controlling duration of larval instars in *Tetragoneuria cynosura* (Odonata). Ecology, 55: 630-637.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Macan, T. T. 1977. The influence of predation on the composition of freshwater animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in northern Alberta. Can. J. Zool. 42: 785-800.

Chapter 5. Behavioural interactions and use of feeding areas by nymphs of <u>Coenagrion</u> <u>resolutum</u> (Coenagrionidae: Odonata)

Abstract

Behaviour of <u>Coenagrion</u> <u>resolutum</u> nymphs was studied in the laboratory. Based on characteristics of the behaviour, analysis of the effects of inter-nymph distance on behaviour, and association analysis between behaviours, some of the observed behaviours were classified as grooming, feeding/aggression, retreat or defense.

In an experiment on use of space, some nymphs excluded others from feeding areas through aggressive interactions. Frequency of interactions won by those nymphs seen most often at the feeding site was not associated with location of interactions. However, use of the feeding area was positively associated with dominance status. Exclusion of some nymphs is interpreted as a combination of dominance and limited movement rather than a territorial system.

Introduction

Macan (1973, 1977) suggested nymphal Zygoptera may be territorial at areas of food concentration. I have shown that, under laboratory conditions, solitary nymphs of Coenagrion resolutum remain at areas of food concentration; and, when several nymphs are present, some are excluded from areas of food concentration (Baker 1980). However, because I had no information on location and outcome of behavioural interactions between nymphs, the experiments did not test hypotheses concerning the nature of the exclusion. In particular, I did not know whether use of the feeding areas was maintained by "overt defence or advertisement" (Wilson 1975).

An understanding of the nature of the exclusion may be crucial to understanding the impact of nymphal odonate predation on prey populations. Several papers, Akre and Johnson (1979), Benke (1976, 1978), Lawton et al. (1974), Macan (1977), deal with the impact of nymphal predation; and some authors, Johnson (1973), Johnson et al. (1975), Thompson (1975, 1978), have designed their studies as precursors to models for predicting the effects of nymphal predation on prey populations. That some nymphs are excluded from areas of prey concentration must be an important factor in future models, and to accurately predict the impact of nymphal predation, the nature of the exclusion must be understood. If nymphs are territorial, models may include components designed to deal with compression and expansion of territory size under various conditions of prey availability and nymphal density. However, if nymphs are not territorial, and the use of feeding areas is dependent on a dominance system, then the effects of prey availability and nymphal density may have a completely different effect on nymphal spacing than seen under a territorial system. For example, a dominance system may be related to individual distance, which may not be affected at all by changes in prey av~~ailability~~ or nymphal density.

This paper reports results from an experiment designed to test whether use of feeding areas was maintained by "overt defense or advertisement," i.e. territoriality; or whether use of feeding areas was based on a dominance hierarchy. In particular, I tested a hypothesis concerning a corollary of Wilson's definition (suggested by Willis, 1967), namely that dominance is site-specific.

Before testing the relationship between outcome and location of behavioural interactions, I established criteria for recognizing an interaction and for determining the outcome of interactions in terms of win and lose. To do this, I analysed a series of "trials" in which two nymphs were placed together and their behaviour recorded. Based on characteristics of the behaviours, the effects of inter-nymph distance on frequency of the behaviours, and on association analysis of the behaviours, I could define interaction and outcome of interactions.

Behaviour of nymphs

Methods

Nymphs were collected on 26 June 1979 with a dip net from a small pond in the boreal forest zone of Alberta, near the Bigoray River (See: Clifford 1969, for a description of the general area). Approximately 150 nymphs in instars F-4 to F-2 (final instars were designated F, penultimate instars F-1, etc.) were brought to the laboratory and housed individually in 40 ml plastic vials equipped with a small stick for a perch. Nymphs were maintained at 20°C and at a photoperiod of 16L:8D. Nymphs were fed one enchytraeid (Oligochaeta) worm each day.

I observed the behaviour of nymphs in a plastic tank (29 by 18 by 13 cm) filled with dechlorinated water. A single dowel (2 mm in diameter, 15 cm long) was supported horizontally 5 cm above the tank bottom on two insect pins. The dowel was marked at 1 cm intervals for use in determining inter-nymphal distance.

Each trial consisted of selecting two nymphs at random and placing one nymph on each side of the dowel midpoint. Nymphs were separated by a thin piece of opaque plastic (5 by 5 cm), with a slit the width of the dowel cut into it from one side to the centre. The plastic rested on the dowel midpoint at the inner end of the slit, thereby blocking each nymph's view of the other. Nymphs were removed from vials with a large bore pipette and gently forced out of the pipette onto the dowel. If a nymph did not cling to the dowel after being released from the pipette, it was returned to its vial and not used in a trial until the next day. After two nymphs had been placed on either side of the plastic, I waited 5 minutes, then slowly raised the plastic and began recording. All recording was done with a twenty-channel event recorder connected to a panel of switches that controlled the pens. Each recording period lasted 15 minutes or until one nymph swam away from the dowel. I recorded the occurrence of the behaviours described below, the direction nymphs faced, and distance between nymphs. There were five classes of distance: greater than 5 cm apart, 3-5 cm apart, 1-3 cm apart, less than 1 cm apart, and overlap. Overlap was recognized when any part of one nymph was beside the other nymph. Trials were run from 5 to 20 days after the nymphs were collected. A total of 65 trials was observed; each nymph was used in only one trial.

Descriptions of behaviours were based on observations of nymphs described above, observations made during experiments on nymphal growth, and observations in tanks similar to the trial tank that were set up for qualitative observation of behaviour.

Description of behaviours

Fourteen behaviours are described below; there is no inference of function (the "empirical" method of Lehner 1979).

Crawl Forward. All walking gaits where direction of movement is anterior, except for Run Forward. Crawl Forward was never more than 3-4 mm/s; it often lasted for a minute or more, but occasionally it occurred as short, 2-3 s bouts. Crawl Forward was recorded as either To or Away from the other nymph.

Crawl Sideways. A slow crawl in any direction other than along the anterior-posterior axis. Crawl Sideways was only seen when nymphs were on flat surfaces and was always away from other nymphs.

Run Forward. A rapid movement in the anterior direction that lasted less than 1 s. Distance travelled was usually 0.5-1.0 cm. Movement To or Away from the other nymph was recorded.

Run Backward Away. Identical to Run Forward except in the posterior direction. Run Backward was always away from the other nymph. I never saw a nymph crawl backward slowly.

Mouthpart Flex. A short, slow extension of the labium, often repeated several times in succession, or movement of labial palps without extension of the labium.

Scratch. All movements in which a leg was rubbed against the head, body, or another leg.

Labial Strike. A rapid, complete extension of the labium.

Head Movement. A turning or lifting of the head.

Slash. A rapid lateral bending of the abdomen, resulting in the caudal lamellae being displaced 90° or more.

Rigid Abdomen Wave. A repeated lateral bending of the abdomen at segments 1-3 with the remaining segments bent only slightly and raised slightly above the substrate, and with the caudal lamellae having an angle of approximately 40° between them (Fig. 1). The abdomen is displaced approximately 30° on each side of the midline before moving to the alternate side. Each circuit, left to right to left, takes approximately 1 s to complete. Rigid Abdomen Wave often lasted for 5 minutes or more. Occasionally a more rapid movement of the abdomen was observed for 1 or 2 s.

Abdomen Bend. The entire abdomen bends slowly to one side until the caudal lamellae approach the head or thorax (Fig. 2). The abdomen then straightens slowly and the bending is repeated either to the same side or opposite side. Caudal lamellae are held together, and they usually tremble. The abdomen often remains bent for a few seconds while the caudal lamellae tremble near the head. Movement of the abdomen from straight to beside the head and back to straight often takes up to 10 s, but less if the caudal lamellae only reach the thorax.

Rotate. A rapid, lateral movement of the body lasting less than a second. Rotate was seen only when nymphs were on the dowel.

Turn. A movement that resulted in the nymph facing a different direction without displacement. On the dowel, Turn resulted in nymphs facing the opposite direction. On flat surfaces, Turn resulted in nymphs facing a variety of directions. Direction of Turn, To or Away from the other nymph was recorded.

Swim. The animal swims by means of a repeated, lateral bending of the abdomen. Because recording stopped as soon as either nymph swam, records of Swim indicate only initiation of Swim.

Effect of inter-nymph distance on behaviour

To determine the effects of location on outcome of interactions, I needed criteria for recognizing an interaction. Preliminary observations suggested that inter-nymph distance was clearly important; nymphs that were far apart appeared to behave as if the other animal was not present. I analysed the effects of inter-nymph distance on frequency of behaviours to determine at what inter-nymph distance animals were likely to interact.

To produce the histograms in Figure 3, I divided the entire recording time (approximately 700 minutes) into 5,658 units of 7.43 s. The 7.43 value was the shortest period discernable between adjacent grid lines on the chart paper. I counted the number of time units in which each behaviour occurred (one-zero sampling; Lehner 1979) for each distance zone, and divided the total by percent of time nymphs spent in that zone.

Because Turn Away, Crawl Forward To, Crawl Forward Away, and Run Backward Away could occur only if the nymph was facing in the proper direction, their relative frequencies were based on time spent in the distance zones while facing the proper direction. I did not analyse Crawl Sideways, Head Movement, Run Forward To or Turn To because they seldom, if ever, occurred during trials.

Altmann (1974) has criticized the use of one-zero data because of confusion over interpretation of frequency of a behaviour and frequency of intervals that include that behaviour. However, occurrences of Swim, Labial Strike, Rotate, Slash, Run Backward Away, and Turn Away were of very short duration and rarely occurred twice in one unit. Therefore, the one-zero data give an accurate estimate of the actual frequency. Abdomen Bend, Rigid Abdomen Wave, Scratch, and Mouthpart Flex normally occurred over several time units and successive occurrences of each behaviour were usually separated by long time intervals. Given these conditions, Lehner (1979) suggests one-zero data can be used as an estimate of duration of behaviour. Crawl Forward occurred for both long and short periods; thus, the histogram for this behaviour may not accurately represent either frequency or duration.

I used chi-square goodness-of-fit tests to determine if inter-nymph distance had any effect on frequency of behaviours. I analysed data by counting the number of time units in each distance zone that a behaviour occurred in, and then comparing it to the expected number based on the total time spent in each zone. There is a problem with this analysis because behaviour of a nymph in any time unit will almost certainly be dependent on the behaviour in the preceding time unit; therefore, each time unit is not an independent observation.

Frequencies of occurrence of behaviours Crawl Forward Away, Mouthpart Flex and Run Backward Away were not related to inter-nymph distance ($P > 0.1$). All other behaviours showed significant differences ($P < 0.05$) between the observed and expected frequencies.

Rotate, Swim, Slash, Labial Strike and Turn Away were more frequent when nymphs were less than 1 cm apart than when they were further apart. Abdomen Bend was also most frequent when nymphs were near each other, although a peak in frequency occurred when nymphs were more than 5 cm apart.

Scratch and Rigid Abdomen Wave were more frequent at greater distances between nymphs. Although frequency of Crawl Forward To was significantly different from the expected frequency, it showed no pattern with respect to inter-nymph distance.

Association analysis

Based on data in the preceding section, I planned to define an interaction as any nymph moving away from another when the two animals were less than a set distance apart. However, movement away did not appear adequate to define an interaction. This is because one nymph could pass close to, or even crawl over, another nymph without any apparent change in the behaviour of either nymph. Thus, although nymphs were close and one "moved away," the nymphs did not appear to interact; there was no evidence that the crawling nymph was even aware of the other's presence. I needed some idea of the function of the various moving behaviours, i.e. was the nymph that crawled over the other nymph and then moved away retreating, or was it simply crawling in the same direction as it was before reaching the other nymph? To help interpret the function of these behaviours, I used chi-square tests to test whether they were associated with the behaviour of other nymphs and whether they were associated with other behaviours in the same nymph.

Swim, Crawl Forward Away, and Run Backward Away resulted in the nymph moving away from another nymph. Rotate and Turn Away by a nymph facilitated movement of that nymph away from another; by Crawl Forward after Rotate or Turn Away, a nymph could move away from the other nymph. Since Rotate, Turn Away, and Run Backward Away were rare, I combined these into a new category labelled Short Retreat. I also consider Crawl Sideways as moving away from another nymph, but it never occurred during trials and was not included in the analysis.

I also determined associations between the described behaviours and Abdomen Bend, a behaviour Corbet (1962) suggested may be a threat display to deter predation, and one I felt may be used to discourage approach of another nymph.

The association analysis was based on occurrence of the behaviours in each "encounter," (one-zero data). Slater (1978) suggests one-zero data are suitable for correlating behaviours. An encounter began when two nymphs moved from the 1-3 cm zone to the less than 1 cm apart zone and ended when they were separated by more than 1 cm. Thus, there was no set time period for each encounter. The encounter distance defined here was based on most occurrences of the moving away behaviours occurring when nymphs were less than 1 cm apart. I observed a total of 52 encounters.

In interpreting the association analysis, note that out of the 27 associations made, one or two would be expected to be significant at the 0.05 level due to chance alone. Between nymphs, Swim was positively associated with Labial Strike and Crawl Forward To, and negatively associated with the other animal's Short Retreat and Crawl Forward Away (Table 1). Short Retreat was also positively associated with the other animal's Labial Strike. Crawl Forward Away was negatively associated with the other animal performing Abdomen Bend and Swim.

Within an individual, Swim was negatively associated with Labial Strike as was Crawl Forward Away. Short Retreat was positively associated with Abdomen Bend at the 0.05 level.

All associations with Scratch and Rigid Abdomen Wave had expected cell frequencies less than five and were not tested.

Discussion

Scratch and Mouthpart Flex appear to be grooming behaviours. Scratch was more frequent when other animals were far away compared to when other animals were nearby. Mouthpart Flex, which was particularly common after nymphs had fed, probably functions in cleaning and arranging the setae on the labium. Rigid Abdomen Wave also was most common when nymphs were alone and may be related to oxygen uptake (Corbet 1962). Rowe (1980) suggested Rigid Abdomen Wave is an "intraspecific threat display" in nymphs of <u>Xanthocnemis</u> <u>zealandica</u> (McLachlan); however I found no evidence of this in nymphs of <u>C</u>. <u>resolutum</u>.

Labial Strike was a feeding behaviour or possibly an aggressive behaviour or both. It occurred most frequently in the trials when another nymph was near; Labial Strike directed at another nymph may be an attempt at predation. Head Movement commonly preceded Labial Strike in the growth experiment when I dropped worms near the nymphs; Head Movement resulted in the head being directed towards the worm.

Run Backward Away, Rotate, Run Forward Away, and Turn Away by one nymph usually followed Labial Strike by the other and resulted in movement away from the striking nymph; this suggests these behaviours are retreat behaviours. I could induce a nymph to exhibit these behaviours by closely approaching or touching it with fine forceps. I also consider Crawl Sideways a retreat, because it only occurred when another nymph was within 1 or 2 cm and movement was always away from the other nymph.

Swim, the most obvious retreat behaviour, was almost always preceded by Labial Strike by the other nymph. Swim often lasted for 15-20 s, which, in a field situation, would take the swimmer a considerable distance from the point of take-off. Swim was also seen when nymphs were alone; in these cases it could not be interpreted as a retreat.

Slash was apparently a defensive behaviour. It occurred after a nymph suffered a Labial Strike from another animal or when I picked up an animal with forceps.

Nymphs also used Slash if another nymph simply approached within 1 or 2 cm. Abdomen Bend occurred most often when nymphs were less than 1 cm apart and was associated within a nymph with the retreat behaviours, suggesting that Abdomen Bend may be a defensive behaviour. However, in my study, Abdomen Bend did not appear to deter approach of another nymph; in fact, the rapid quivering of the caudal lamellae seemed to attract the other nymph. Abdomen Bend may be a generalized defensive behaviour used whenever an animal is approached by another animal of similar or larger size. The movement may deter some predators, or, alternatively, act as a "deflection behaviour" similar to that used by some snakes (Wickler 1968). When a nymph struck at a nymph performing Abdomen Bend, the strike was usually directed towards the lamellae. On two occasions, the attacking nymph grasped and pulled out the lamellae of the nymph exhibiting Abdomen Bend; immediately after, the nymph that was struck swam away while the attacker started to eat the lamellae.

Based on these interpretations of the function of the behaviours, I operationally defined an interaction as the retreat of one animal from another. Any case of an animal exhibiting Swim, Turn Away, Crawl Sideways, Run Forward Away, or Run Backward Away was considered a retreat if it occurred when two animals were within 2 cm of each other. The retreating animal "lost" the interaction while the animal that did not move, or moved towards the other animal, "won" the interaction. I used the 2 cm limit instead of the 1 cm limit used in the association analysis because Crawl Sideways often occurred on flat surfaces when nymphs were within 1-2 cm of each other.

Behavioural interactions and use of feeding areas

Methods

I used eight tanks (29 by 18 by 13 cm) each with a single feeding area. I covered the tank bottoms with window screening because nymphs moved awkwardly on the smooth surface of the tank. I did not use the lattice structure of previous experiments (Baker 1980), because preliminary observations indicated it was difficult to observe interactions on the lattice without the observer having to move around to different sides of the tank; I was concerned that my movements would disturb the animals. The bottom of each tank was marked with a grid pattern of 32 areas (4.0 by 3.25 cm; 4 rows labelled A-D by 8 rows labelled 1-8). The feeding area was a hole (20 mm diameter) in the tank bottom, which led to a vial (20 mm deep, 25 mm diameter). The hole was centred on the line between areas C1 and C2. Two dowels (2 mm diameter and 4 cm long) were attached to the centre of the vial bottom with silicon; one dowel extended out of the vial to C1, the other to C2. The vial was always supplied with more worms than the nymphs could eat in one day. Tanks were three-quarters filled with dechlorinated water, covered with white paper on three sides, and arranged so nymphs could not see into neighbouring tanks.

On 18 May 1980, I collected nymphs of _C_. _resolutum_ from the same pond mentioned in the preceding section. Thirty nymphs [illegible] instars F-2 to F (total length 15-22 mm) were returned to the laboratory and housed individually in 40 ml plastic vials. Final instar nymphs were checked to ensure emergence was not imminent; swollen appearance of the wing pads indicated impending emergence. Nymphs were fed ad lib from 18 to 21 May. At 0930 hrs, 22 May, I added four nymphs to each of six tanks and three nymphs to the remaining two tanks. Nymphs were added by pouring them out of their vials into the centre of the tanks. Nymphs were individually marked by clipping the tips of the caudal lamellae the day before the experiment began.

From 22 May until 27 May, I observed the nymphs for 4-5 h/day between 0830 and 1700 hrs. I normally watched continuously for 1 h, but occasionally I watched for a shorter or longer time. During these periods I recorded the location of any interaction between nymphs, the nymphs involved, and the outcome (winner and loser of the interaction). I did not include in the analysis the few interactions when both animals retreated.

Location of each animal was recorded seven times a day at intervals of approximately 1 h, giving a total of 42 observations for each nymph. At 1700 hrs, 27 May, I removed the animals from the tanks and placed them in individual vials. All nymphs were fed while in the vials. At 0930 hrs, 29 May, I returned the nymphs to their original tanks and observed for approximately 3 h/day for 2 days. This removal and return of nymphs allowed me to record interactions taking place in the tank at places other than the normal feeding site.

Results

The number of times each nymph was observed on the feeding area is shown in Table 2. The feeding area was defined as the vial, both dowels, and areas C1 and C2. Tank 5 had three nymphs at the start of the experiment but one nymph died; in tank 7, one of the four nymphs was killed and eaten by another nymph. Results from these animals were not used in the analysis. Results in Table 2 indicate there were large differences among the nymphs with respect to the number of observations of a nymph at the feeding area.

To determine whether outcome of interactions was related to location, I tested (Chi-square) for association between location of interactions and frequency of interactions won and lost. I analysed only the results of animals seen on the feeding area for at least 50% of the observations. I refer to these animals as "residents." Thus, for each interaction that involved a resident, I classified the interaction as "win" or "lose" and "on" or "off" the feeding area. Murie and Harris (1978) pointed out there are problems with this analysis because an interaction between residents would be scored twice, once for each animal. To avoid this problem, I flipped a coin to randomly select which animal's results would be analysed for each interaction involving two residents. Chi-square analysis indicated there was no significant association ($P > 0.9$, n=79) between location of interactions on and off the feeding areas and frequency of interactions won and lost. A possible problem with this analysis is that outcome of resident-resident interactions may not be affected by location but outcome of resident-nonresident interactions may depend on location. Therefore, inclusion of resident-resident interactions in the analysis may reduce the power of the test to detect the effects of location on outcome of resident-nonresident interactions. To avoid this problem, I reanalysed the data using only resident-nonresident interactions; again, there was no significant association ($P > 0.5$, n=41) between location and outcome of interactions.

To determine whether dominance status was associated with the use of the feeding area, I classified animals as "dominant" or "subordinate" and compared the number of observations of each group on the feeding area. I determined the dominance hierarchy within each tank according to the method of Brown (1975), i.e. dominance rank was based on the ratio of interactions won and lost between nymphs. In tanks with four animals, the two animals at the top of the hierarchy were classified as dominant. Subordinate animals were the two at the bottom of the hierarchy. In tanks with only three nymphs, results from the "middle" animal were not used. If the hierarchy was not linear, results from animals involved in the non-linear section of the hierarchy were not used. For example, if animals A, B, and C were in a triangle hierarchy, but all three were dominant over animal D, then D was classified as subordinate and the results from A, B, and C were not used. A Mann-Whitney test indicated that dominant animals (n=8) spent more time at the feeding area than subordinate animals (n=10) ($P < 0.025$).

I also determined whether sex or relative size was associated with time spent at the feeding area. I classified the two largest animals in each tank as Large (n=12) and the two smallest as Small (n=12) and compared these two groups with respect to the number of observations on the feeding area. In tanks with only three animals, results of the mid-size animal were not used. In one tank of four animals, two animals had equal head widths, which were between the largest and smallest animals; results from these middle animals were not used. A Mann-Whitney test showed no significant difference ($P > 0.05$) between the two groups. I also compared only the largest (n=8) and smallest (n=8) animals in each tank with respect to number of observations on the feeding area, and, again, there was no significant difference ($P > 0.05$). There was also no significant difference ($P > 0.05$) between male (n=17) and female nymphs (n=11) with respect to number of observations on the feeding area.

Discussion

Wilson (1975) defined territory as an "area occupied more or less exclusively through overt defense or advertisement." My results (this and previous studies) indicate that some nymphs do have "more or less" exclusive use of an area. The present study also indicates that nymphs are aggressive towards each other and the outcome of aggressive interactions is usually the retreat of one nymph. Nymphs rarely seen at the feeding areas did in fact enter the feeding areas, but they were forced out by the resident nymphs, which struck, slashed, or simply crawled towards the intruder. If "defense" is simply equated with aggression, then resident nymphs were territorial according to Wilson's definition. However, aggression does not necessarily imply defense. Wilson (1975) notes there are several types of aggression, including territorial aggression, dominance aggression, antipredator aggression, and others.

Some authors, Willis (1967), Wolf (1970), Agren (1976), and Murie and Harris (1978), have shown a change in dominance in relation to an animal's area of most frequent use. That is, animals were dominant within their areas of most frequent use but less so outside these areas. In such cases, aggression within the areas of most frequent use can be considered defense and the animals can be classified as territorial. I found no evidence of a dominance reversal of residents in areas away from the feeding area. Thus, if site-specific dominance is used as a criterion of territoriality, the resident nymphs should not be considered territorial. Rowe (1980) suggested nymphs of <u>Xanthocnemis</u> <u>zealandica</u> are territorial, although he does not define the term nor discuss the criteria used to recognize territoriality. He has shown that, in contrast to results for <u>C</u>. <u>resolutum</u> (Baker 1980), "occupant" nymphs were less likely to be displaced by "intruder" nymphs; but he provides no data on the effect of location on outcome of interactions. His "intruder" nymphs may be generally subordinate animals, which are displaced by more dominant animals no matter where they are.

Rather than explaining exclusive use of feeding areas in terms of territoriality, my data can be interpreted as the result of two separate phenomena. First, single nymphs tend to stay near areas of food concentration, and secondly, subordinate nymphs move away from dominant nymphs. When several nymphs are in a tank, all will attempt to stay at the feeding site, but the animal ultimately controlling the site will be the most dominant. These phenomena will result in a "more or less" exclusive use of an area, which is maintained by aggressive interactions. This hypothesis of dominance and limited movement is supported by the significant association of dominance status with time spent at the feeding area. This hypothesis is also supported by the results of an "intruder" experiment (Baker 1980). In that experiment, animals with previous experience in the tank had no advantage over naive intruder nymphs in maintaining the feeding area. This is in contrast to typical territorial systems where familiarity with the area usually increases an animal's chances of defending the area against intruders. However, this result does support the hypothesis of dominance and limited movement. By chance alone, the intruder nymph should have been dominant over the original nymph in 50% of the tanks; thus, summed over all tanks, there should be no difference between original and intruder nymphs with respect to time spent at the feeding area. A Mann-Whitney test showed no significant difference ($P > 0.05$) in time spent at the feeding area between original (n=23) and intruder nymphs (n=23).

Nymphal size was not associated with use of the feeding areas, and this is in contrast to a previous experiment (Baker 1980) in which large nymphs (total length 19 - 20 mm) excluded smaller nymphs (total length 10 - 13 mm) from areas of food concentration. Size may be important in determining which nymphs will be excluded from a feeding area only when the size difference is large. In the present study, the ratio of total length of the largest nymph over total length of the smallest nymph in each tank ranged from 1.03 to 1.46, while in the previous study the ratio ranged from 1.45 to 2.00.

In conclusion, my results indicate that use of space by nymphs can best be explained in terms of a general dominance system and a tendency for nymphs to remain near areas of food concentration.

Acknowledgements

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Table 1. Significance levels of the Chi-square values for the association analysis of behaviours. ns = not significant ($P > 0.05$), X = expected frequency < 5, + = positive association, - = negative association.

	Labial Strike	Short Retreat	Crawl Forward To	Crawl Forward Away	Abdomen Bend	Swim
Between Animals						
Swim	0.01 +	0.01 -	0.01 +	0.01 -	ns	X
Short Retreat	0.01 +	X	ns	ns	ns	0.01 -
Crawl Forward Away	ns	ns	X	X	0.05 -	0.01 -
Abdomen Bend	ns	ns	ns	0.05 -	X	ns
Within Animals						
Swim	0.01 -	ns	ns	ns	ns	
Short Retreat	ns		ns	ns	0.05 +	ns
Crawl Forward Away	0.01 -	ns	X		ns	ns
Abdomen Bend	ns	0.01 +	ns	ns		ns

Table 2. Frequency of observations of individual nymphs on feeding areas out of the total number (42) of observations. Nymphs are ranked according to frequency.

	Rank			
Tank #	1	2	3	4
1	20	16	13	--
2	31	29	8	1
3	31	29	23	9
4	33	17	15	8
5	35	3	--	--
6	36	13	9	4
7	35	9	4	--
8	39	33	23	8

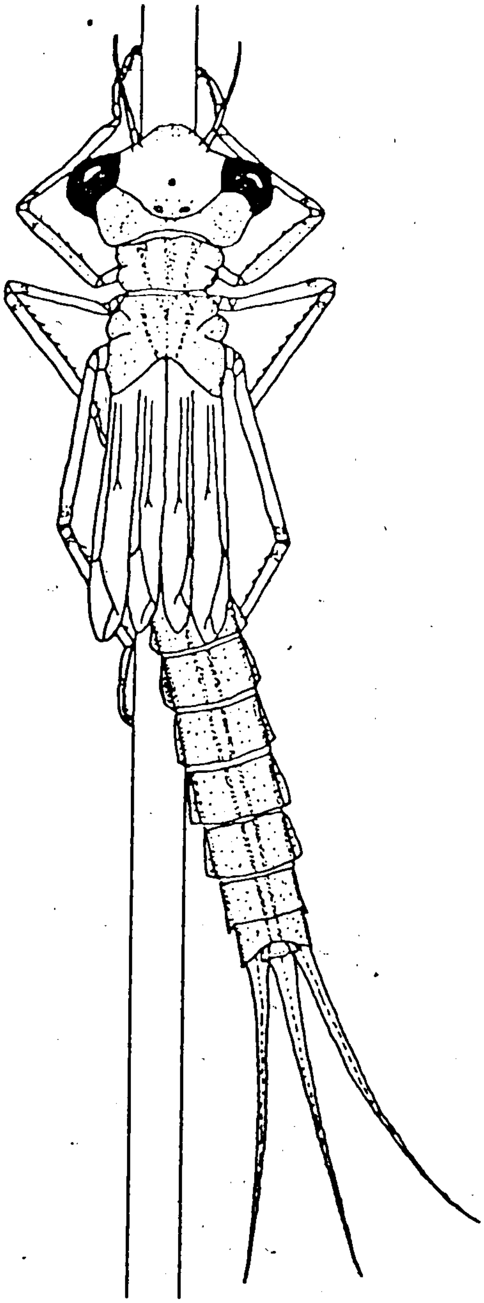

Figure 1. Rigid Abdomen Wave, showing maximum displacement of the abdomen.

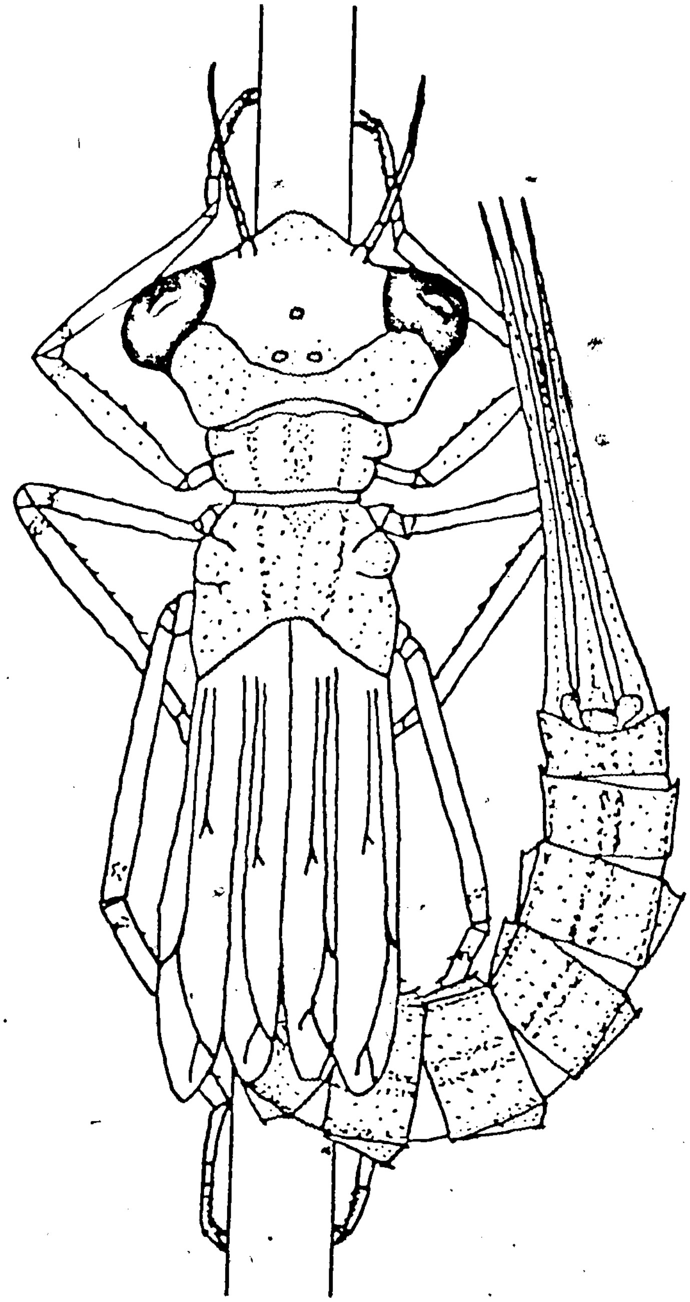

Figure 2. Abdomen Bend, showing maximum displacement of the abdomen.

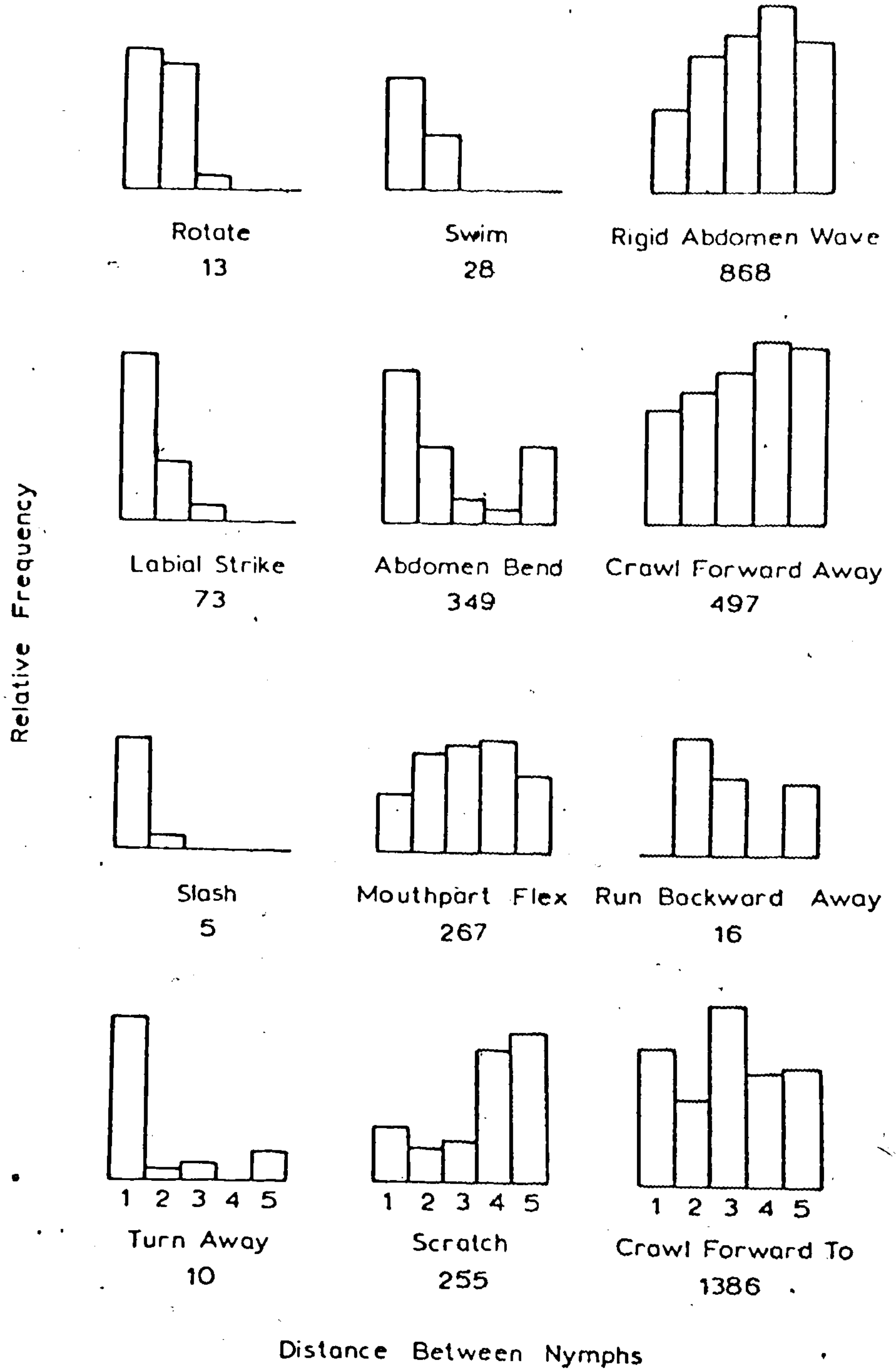

Figure 3. Relative frequencies (number of time units in which the behaviour occurred in each distance zone divided by percent of time spent in that zone) at the inter-nymph distances indicated. 1, overlap, 2.5% of total time; 2, overlap-1 cm, 29.8%; 3, 1-3 cm, 21.4%; 4, 3-5 cm, 13.5%; 5, greater than 5 cm, 32.8%. Number below behaviour label indicates total number of time units in which the behaviour occurred.

Literature Cited

Agren, G. 1976. Social and territorial behaviour in the mongolian gerbil (Meriones unguiculatus) under seminatural conditions. Biol. Behav. 1: 267-285.

Akre, B. G. and D. M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. J. Anim. Ecol. 48: 703-720.

Baker, R. L. 1980. Use of space in relation to feeding areas by zygopteran nymphs in captivity. Can. J. Zool. 58: 1060-1065.

Benke, A. C. 1976. Dragonfly production and prey turnover. Ecology, 57: 915-927.

Benke, A. C. 1978. Interactions among coexisting predators - a field experiment with dragonfly larvae. J. Anim. Ecol. 47: 335-350.

Brown, J. L. 1975. The evolution of behaviour. W. W. Norton, New York.

Clifford, H. F. 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. 82: 578-597.

Corbet, P. S. 1962. A biology of dragonflies. Witherby, London.

Johnson, D. M. 1973. Predation by damselfly naiads on cladoceran populations: fluctuating intensity. Ecology, 54: 251-268.

Johnson, D. M., B. G. Akre, and P. H. Crowley. 1975. Modelling arthropod predation: wasteful killing by damselfly naiads. Ecology, 56: 1081-1093.

Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. In Ecological stability. Edited by by M. B. Usher and M. H. Williamson. Chapman and Hall, London. pp. 141-158.

Lehner, P. N. 1979. Handbook of ethological methods. Garland STPM Press, New York.

Macan, T. T. 1973. Ponds and lakes. George Allen and Unwin Ltd., London.

Macan, T. T. 1977. The influence of predation on the composition of freshwater animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Murie, J. O. and M. A. Harris. 1978. Territoriality and dominance in male Columbian ground squirrels (Spermophilus columbianus). Can. J. Zool. 56: 2402-2412.

Rowe, R. J. 1980. Territorial behaviour of a larval dragonfly Xanthocnemis zealandica (McLachlan) (Zygoptera: Coenagrionidae). Odonatologica, 9: 285-292.

Slater, P. J. B. 1978. Data collection. In Quantitative ethology. Edited by P. W. Colgan. John Wiley and

Sons, Inc., New York.

Thompson, D. J. 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of Daphnia magna by Ischnura elegans. J. Anim. Ecol. 44: 907-916.

Thompson, D. J. 1978. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of the damselfly, Ischnura elegans. J. Anim. Ecol. 47: 757-767.

Wickler, W. 1968. Mimicry in plants and animals. McGraw-Hill, Toronto.

Willis, E. D. 1967. The behaviour of bicolored antbirds. Univ. Calif. Berkeley Publ. Zool. 79: 1-132.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Harvard University Press, Cambridge.

Wolf, L. L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. Condor, 72: 1-14.

Thesis Discussion

Spacing behaviour and life histories of odonate nymphs

Results of my study support Macan's (1964, 1977) suggestion that nymphal spacing behaviour affects life histories of some odonate species. This conclusion is based on the following argument. First, diet of nymphal odonates has a profound effect on rate of development. My work on development rate of C. resolutum (Chapter 4) and E. boreale (Appendix 3) suggests diet can alter growth rates to the extent that poorly fed animals miss an emergence period. Other authors (Fischer 1961, Hassan 1976, Lawton et al. 1980) have also shown that nymphs on better diets, in terms of both quantity and quality of food, grow faster than nymphs on poorer diets.

Secondly, solitary nymphs of C. resolutum find and remain at areas of food concentration (Chapter 2). Not only do nymphs remain at an area of food concentration when only one area is available, but they tend to remain at only one area when several areas of equal food value are offered. When a series of feeding areas are offered that represent a range in food value, nymphs also remain at those areas of food concentration that result in higher growth rates.

Finally, when several C. resolutum nymphs are presented with a limited number of feeding areas, use of the feeding area is not equally divided among the nymphs;

some individuals were rarely, if ever, observed at the feeding areas (Chapter 2). From these points I conclude that some nymphs will remain in areas of food concentration when food is patchily distributed. These nymphs will grow faster and emerge earlier than nymphs excluded from areas of food concentration. I have no evidence to support the assumption that food in the field is patchily distributed; however several authors (Smyly 1957, Quade 1969, Boerger 1978) have indicated that odonate prey are often clumped.

Although my data support Macan's idea that spacing behaviour of nymphal odonates can affect life histories, they do not support his suggestion that the behaviour is territorial. I have rejected Macan's suggestion of territoriality for nymphs of C. resolutum because the outcome of behavioural interactions was not site dependent. This suggests there is no defense of the feeding area. Also, solitary nymphs at feeding areas had no advantage in remaining there when naive animals were added. Results are best explained in terms of a dominance system; dominant animals spend more time at feeding areas than subordinate animals. Large animals exclude smaller animals from feeding areas and this supports hypotheses concerning both territoriality and dominance.

A major purpose of my study was to determine if odonate nymphs exhibited the kind of spacing behaviour that could affect life histories. Although I have shown that such a behaviour does exist for C. resolutum, there is no evidence that variation in life histories is a result of spacing behaviour. There are two basic approaches available to test the effects of spacing behaviour on the life histories of animals in the field. The most direct, but probably the most difficult method, is a detailed study of growth and behaviour of individually marked nymphs in the field. One would have to show that growth rates of individual nymphs depend on what microhabitat they are in; for example, one may be able to show that nymphs grow faster on horizontal plant stems than on vertical stems. It would also be necessary to show that nymphs in these areas of rapid growth exclude intruding animals through some form of aggression or advertisement. Finally, and most importantly, one would have to remove animals from areas where nymphs grow rapidly and then test whether nymphs from areas of little food move into the more productive areas and grow faster than nymphs left in the areas of little food. Difficulties with this research lie in marking and observing individuals. External markings, such as paint, will be lost when the animal molts, and tags will interfere with the molting process. Also, most odonate nymphs live in dense vegetation, making the nymphs difficult to observe for extended periods. Such a study could be done, however, if nymphs of the species in question were large, markable, and lived in vegetation which had a simple growth form.

Another, less direct, but possibly more feasible line of research is a comparative study. If spacing behaviour of nymphs is important in affecting variation of life histories, those species showing strong spacing behaviour should have more varied life histories than species exhibiting weak or no spacing behaviour. This hypothesis could be tested by studying the spacing behaviour of a variety of odonate species and comparing the results with published life history data. I have done this, on a small scale, by comparing the life history and spacing behaviour of _C. resolutum_ and _L. d. disjunctus_ (Chapters 1, 2, 3). The most serious difficulty with this method lies in deriving a method of comparing life histories.

Invertebrate spacing behaviour

Spacing behaviour is a commonly reported phenomenon. Wilson (1975) notes that "nearly all vertebrates and a large number of the behaviourally most advanced invertebrates conduct their lives according to precise rules of land tenure, spacing, and dominance." Among invertebrates, spacing behaviour has been reported in several taxa; examples come from molluscs, insects, annelids, crustaceans, phoronids, and spiders (Brown and Orians 1970, Wilson 1975).

Price (1975) lists numerous examples of territoriality or probable territoriality in insects. Of his 35 examples, he suggests that the main function of the territory is related to reproduction in 20 of these. Examples are mating areas of field crickets (Alexander 1961), protection of females by male odonates (Moore 1964), leks of fruitflies (Spieth 1968), and protection of nests by termites, eusocial ants, wasps, and bees (Wilson 1971). Of the thirteen examples involving food, eight were cases of an adult defending larval feeding sites. Most of the examples pertained to dipterans and hymenopterans, in which the adult defended the feeding site by marking it with some chemical to prevent other females from ovipositing in the same area. The remaining five examples involved the protection of nests and food sources, e.g. eusocial ants, wasps and bees (Wilson 1971) and burying beetles (Pukowski 1933, in Wilson 1975).

Dominance hierarchies are also known to occur in insects. Gauthreaux (1978) lists studies on insects that indicated some form of dominance. Most cases involve the eusocial insects, particularly wasps and bees, where dominance is related to the queen protecting her eggs against workers that would eat them (Huber 1802, Hoffer 1882, both in Wilson 1971); or it is related to dominance status among females. Female wasps dominate others and the dominant animals receive more food and lay more eggs. However, the higher reproductive rate of these dominant animals is not simply a function of more food. Dominance rank affects ovarian development even in the absence of food differences (Wilson 1975).

A few workers have reported examples of dominance in solitary insects. Beebe (1947) describes the aggressive interactions between male hercules beetles (*Dynastes hercules*), where the dominance appears directly related to mating because females do not fight. Ewing (1972) described how the social system of the cockroach (*Nauphoeta cinerea*) changes from a territorial system to a dominance system with increasing population density, but the function of spacing is unclear. Ewing suggests dominant animals may mate unmolested by other animals, but protection of feeding areas may also be involved. Crane (1957) described how male heliconiid butterflies chase each other, but concluded the chase is simply part of the courtship pattern, If males are attempting to dominate each other, the purpose of the aggression appears related to mating rather than use of a feeding area.

The apparent function of *C. resolutum*'s spacing behaviour is in contrast to the functions reported in the studies described above. Because the nymphs are sexually immature, spacing behaviour is not directly related to reproduction; also, nymphs control food resources for themselves rather than for their offspring. Recently, Hildrew and Townsend (1980) reported similar results for the larvae of the caddisfly *Plectrocnemia conspersa*.

They found individual larvae remaining in areas of food concentration, but some individuals were excluded from these areas. Their results differ from mine in that the first individual to arrive at a feeding site of their study had an advantage in remaining there over intruding larvae; this suggests the behaviour may be territorial. As was found for *C. resolutum*, spacing between larvae of *P. conspersa* appears related to food rather than to reproductive purposes.

The function of spacing behaviour of *C. resolutum* nymphs and *P. conspersa* larvae is similar to that shown by some non-insect invertebrates. Stimson (1970) has shown that owl limpets (*Lottia gigantea*) remain in well-defined areas on rock faces and actively defend these areas against conspecifics and other grazing or settling animals. The function of the spacing behaviour appears directly related to food. A thick algal mat, on which the animals feed, grows in the limpet's area but not in areas outside; the algae die if the limpet is removed. This spacing behaviour is territorial because the areas are exclusive and the defense by the occupant is site specific. Individuals were more aggressive when on their areas than when away from their areas. Branch (1975) has shown similar results for the limpet *Patella longicosta*, and Connell (1963) indicates that the amphipod *Erichthonius braziliensis* grazes the plant material around its tube and defends this area against intruding conspecifics. Rollo and Wellington (1979) found large individuals of some terrestrial slug species stay close to shelters located near areas of food concentration, and these slugs exclude conspecifics and individuals of less aggressive species from these shelters.

Some comparisons can be made between results of the studies discussed above. For example, in those studies in which protection of a food source appeared to be the major function of the spacing behaviour, the animals were either slow moving, e.g. limpets and nymphal odonates, or they were sedentary or semi-sedentary, e.g. the tube-dwelling amphipod and the larval caddisfly. However, such comparisons are of doubtful value, because spacing behaviour has not been studied in enough invertebrate species from different habitats to draw valid conclusions. In the next section, I discuss the implications of this paucity of information to future research.

Use of invertebrates in studies of spacing behaviour

Brown and Orians (1970) concluded their review paper on spacing behaviour of mobile animals by suggesting enough data existed on spacing patterns to formulate theoretical predictions that could be rigorously tested. They foresaw studies designed to measure differences in fitness of individuals in populations with spaced distributions and studies designed to analyse spacing behaviour of species occupying various habitats. Research in the past 10 years has, in part, substantiated Brown and Orian's predictions. For example, Davies (1978) devotes most of his chapter on territorial behaviour to the question: "how does spacing out influence fitness?". Wilson (1975) also discusses the importance of spacing behaviour to fitness.

Invertebrates may prove to be good subjects for studies suggested by Brown and Orians, because similar studies with vertebrates often suffer from small sample sizes. Invertebrates may be more suitable for experimental testing of hypotheses simply because of the abundance of invertebrates. In field situations, large numbers of individuals of some species can be marked and observed in a small area. For example, several researchers have marked members of adult odonate populations for studies on territoriality (Moore 1964, Campanella and Wolf 1974, Parr 1980). The abundance and small size of invertebrates also facilitate laboratory experiments. More treatments and more replicates of treatments can be tested with invertebrates in restricted laboratory space than can be done with most vertebrates.

I agree with Brown and Orians that there is a need for more experimental testing of hypotheses on spacing behaviour. But even though many invertebrate species appear to be good experimental subjects, I believe it would be premature to concentrate on testing theoretical predictions about spacing behaviour of invertebrates. This apparent contradiction results from most of the theoretical and practical work, to date, being done on vertebrates. Brown and Orians (1970) point out that, due to the array of spacing behaviours among animals, it has taken a long time to assemble "a general picture of the variety of patterns which must be explained by any theory." There is no "general picture" of spacing behaviour for invertebrates, and any current predictions on invertebrate spacing will necessarily be based on experience with vertebrates. For example, Wilson (1975) presents a figure (13-5, p. 296) of the "general pattern of scaling in aggressive behaviour among animals", in which he shows how the form of aggressive behaviour (territoriality, dominance, despotism, etc.) depends on the sociality of the species and on population density. He concedes that most vertebrates studied fit the pattern; but "Invertebrates, including insects, have not been systematically studied with respect to plasticity of aggressive behaviour and possible existence of behavioural scaling. When they are, a good chance exists that new kinds of transitions will be found that deviate far from the standard vertebrate pattern." This lack of a general view of spacing and aggressive behaviour in invertebrates stems partly from there being few studies on invertebrate behaviour. Despite the greater diversity of invertebrates, the number of studies on spacing behaviour of vertebrates vastly outnumber the number of studies on invertebrates.

Another problem pertaining to the formation of a general theory of invertebrate spacing is in the use of terms. Some authors appear to have little familiarity with behavioural terms and use words such as territory without adequate definitions. For example, Rowe (1980) describes nymphs of Xanthocnemis zealandica as territorial; but does not refer to a definition of territoriality, nor does he describe the criteria used to recognize it. Other researchers, even if aware of the diversity of spacing behaviours, lump all forms of aggressive behaviours, no matter what the context, into such broad definitional categories that terms become meaningless. For example, Davies (1978) recognizes a territory "whenever individual animals or groups are spaced out more than would be expected from a random occupation of suitable habitats." Price (1975) lists female insects marking oviposition sites along with male butterflies protecting mating areas as examples of territoriality. Although some similarities exist between such behaviours, there are obvious differences, and I feel such differences should be recognized through the use of more precise terminology.

In conclusion, the study of invertebrate spacing behaviour is still in a formative state compared to the study of vertebrate spacing behaviour. Invertebrates admittedly can be used as subjects for studies designed to ask such questions as: what is the difference in fitness between dominant and subordinate individuals? However, there is at present a need for more studies that ask: does this species show spacing behaviour? what form does the behaviour take? and, in what context does it occur?

Literature Cited

Alexander, R. D. 1961. Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). Behaviour, 17: 130-223.

Baker, R. R. 1972. Territorial behaviour of the nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). J. Anim. Ecol. 41: 453-469.

Beebe, W. 1947. Notes on the hercules beetle, *Dynastes hercules* (Linn.), at Rancho Grande, Venezuela, with special reference to combat behavior. Zoologica, 32: 109-116.

Boerger, H. 1978. Life history and microhabitat distribution of midges (Diptera: Chironomidae) inhabiting a brown-water stream of central Alberta, Canada. Ph.D. thesis, University of Alberta, Edmonton.

Branch, G. M. 1975. Mechanisms reducing intraspecific competition in *Patella spp.*: migration, differentiation and territorial behaviour. J. Anim. Ecol. 44: 575-600.

Brown, J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1: 239-262.

Connell, J. H. 1963. Territorial behavior and dispersion in some marine invertebrates. Res. Popul. Ecol. 5: 87-101.

Crane, J. 1957. Imaginal behavior in butterflies of the family Heliconiidae: changing social patterns and irrelevant actions. Zoologica, 42 135-145.

Davies, N. B. 1978. Ecological questions about territorial behaviour. *In* Behavioural ecology. *Edited by* J. R. Krebs and N. B. Davies. Blackwell Scientific Publications, Oxford. pp. 317-350.

Ewing, L. S. 1972. Hierarchy and its relation to territory in the cockroach *Nauphoeta cinerea*. Behaviour 42: 152-174.

Fischer, Z. 1961. Cannibalism among the larvae of the dragonfly *Lestes nympha* Selys. Ekologia Polska Seria B, 7: 33-39.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. Perspectives in Ethology, 3: 17-54.

Hassan, A. T. 1976. The effect of food on the larval development of *Palpopleura lucia lucia* (Drury) (Anisoptera: Libellulidae). Odonatologica, 5: 27-33.

Hildrew, A. G. and C. R. Townsend. 1980. Aggregation, interference and foraging by larvae of *Plectrocnemia conspersa* (Trichoptera: Polycentropodidae). Anim. Behav. 28: 553-560.

Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology, 36: 566-586.

Lawton, J. H., B. A. Thompson, and D. J. Thompson. 1980. The effects of prey density on survival and growth of damselfly larvae. Ecol. Entomol. 5: 39-51.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Moore, N. W. 1964. Intra- and interspecific competition among dragonflies (Odonata): an account of observations and field experiments on population control in Dorset, 1954-60. J. Anim. Ecol. 33: 49-71.

Pechuman, L. L. 1967. Observations on the behaviour of the bee Anthidium manicatum (L.). J. N. Y. Entomol. Soc. 75: 68-73.

Price, P. W. 1975. Insect ecology. J. Wiley & Sons, Toronto.

Quade, H. W. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. Ecology, 50: 170-179.

Rollo, R. J. and W. G. Wellington. 1979. Intra- and inter-specific agonistic behaviour among terrestrial slugs (Pulmonata: Stylommatophora). Can. J. Zool. 57: 846-855.

Rowe, R. J. 1980. Territorial behaviour of a larval dragonfly Xanthocnemis zealandica (McLachlan) (Zygoptera: Coenagrionidae). Odonatologica, 9: 285-292.

Smyly, W. J. D. 1957. Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere. Hydrobiologia, 11: 59-72.

Spieth, H. T. 1968. Evolutionary implications of sexual behaviour in Drosophila. Evol. Biol. 2: 157-193.

Stimson, J. 1970. Territorial behaviour of the owl limpet, Lottia gigantea. Ecology, 51: 113-118.

Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Harvard University Press, Cambridge.

Appendix 1. Voltinism of odonates

Table 1 indicates the voltinism of 37 odonate species or sub-species determined in a total f 52 life history studies. The list is not meant to be exhaustive but it does represent the vast majority of published life history studies. A question mark in the voltinism column indicates the author of the study was not sure of the voltinism; for example, 1?-2 indicates some individuals were definitly semivoltine but others may have been univoltine.

The voltinism of nine species was determined in more than one study; six of these species, <u>Coenagrion resolutum</u>, <u>Enallagma cyathigerum</u>, <u>Ischnura elegans</u>, <u>Pyrrhosoma nymphula</u>, <u>Argia vivida</u>, and <u>Epitheca cynosura</u> showed differences in voltinism in the different areas. <u>Lestes disjunctus disjunctus</u> and <u>Lestes sponsa</u> were univoltine in all areas studied. Both studies of <u>Coenagrion puella</u> indicated the populations split into univoltine and semivoltine factions.

In seventeen of the fifty-two studies there was at least some evidence that a cohort of nymphs had split into two factions. Most of the examples are from the Coenagrionidae in which 14 of the 27 studies provided evidence of cohort splitting; examples came from all but one, <u>Pseudagrion</u>, of the seven genera studied. Aeshnids and cordulids showed examples of cohort splitting in two out of three and one out of four studies respectively. None of the eleven studies on lestids and none of the six studies on libellulids provided evidence of cohort splitting.

Table 1. Voltinism of odonate species. See text for details.

Species	Voltinism (y)	Authority
Zygoptera		
Calopterygidae		
<u>Calopteryx virgo</u>	2	Corbet 1957a
Lestidae		
<u>Lestes congener</u>	1	Sawchyn & Gillot 1974a
<u>Lestes unguiculatus</u>	1	Sawchyn & Gillot 1974b
<u>Lestes d. disjunctus</u>	1	Sawchyn & Gillot 1974b
<u>Lestes d. disjunctus</u>	1	Baker & Clifford 1981
<u>Lestes d. australis</u>	1	Ingram 1976
<u>Lestes dryas</u>	1	Sawchyn & Gillot 1974b
<u>Lestes vigilax</u>	1	Ingram 1976
<u>Lestes eurinus</u>	1	Lutz 1968
<u>Lestes sponsa</u>	1	Corbet 1956
<u>Lestes sponsa</u>	1	Macan 1964
<u>Archilestes grandis</u>	1	Ingram 1976
Coenagrionidae		
<u>Coenagrion resolutum</u>	1	Sawchyn & Gillot 1975
<u>Coenagrion resolutum</u>	1-2	Baker & Clifford 1981
<u>Coenagrion angulatum</u>	1	Sawchyn & Gillot 1975
<u>Coenagrion pulchellum</u>	1-2?	Johannson 1978
<u>Coenagrion puella</u>	1-2	Parr 1970
<u>Coenagrion puella</u>	1-2	Lawton 1972

Table 1. continued

Coenagrion mercuriale	1?-2	Corbet 1957b
Ceriagrion tenellum	1?-2	Corbet 1957b
Enallagma najas	1-2	Johannson 1978
Enallagma cyathigerum	1	Johannson 1978
Enallagma hageni	1	Ingram & Jenner 1976
Enallagma aspersum	½-1	Ingram & Jenner 1976
Enallagma ebrium	1	Kormondy & Gower 1965
Ischnura elegans	1	Johannson 1978
Ischnura elegans	1-2	Thompson 1978
Ischnura elegans	1-2	Parr 1970
Ischnura verticalis	1	Kormondy & Gower 1965
Pyrrhosoma nymphula	2	Lawton 1971
Pyrrhosoma nymphula	2-3	Macan 1964
Pyrrhosoma nymphula	2	Corbet 1957a
Pyrrhosoma nymphula	2	Corbet 1957a
Pyrrhosoma nymphula	1?-2	Corbet 1957a
Argia vivida	1-2?	Pritchard & Pelchat 1977
Argia vivida	1	Pritchard 1980
Argia vivida	2	Pritchard 1980
Pseudagrion salisburyense	1	Chutter 1961
Anisoptera		
Aeshnidae		
Aeshna juncea	2-3	Macan 1964
Anax imperator	1-2	Corbet 1957c
Oplonaeschna armata	3	Johnson 1978

Table 1. continued

Corduliidae		
Epitheca cynosura	1-2	Lutz & Jenner 1964
Epitheca cynosura	2	Kormondy & Gower 1965
Epitheca cynosura	1	Benke & Benke 1975
Epitheca semiaquea	1	Benke & Benke 1975
Libellulidae		
Libellula incesta	1	Benke & Benke 1975
Celithemis fasciata	1	Benke & Benke 1975
Celithemis ornata	1	Benke & Benke 1975
Ladona deplanata	1	Benke & Benke 1975
Sympetrum striolatum	1	Corbet 1956
Leucorrhinia dubia	3	Norling 1976

Literature Cited

Baker, R. L. and H. F. Clifford. 1981. Life cycles and food of Coenagrion resolutum (Coenagrionidae: Odonata) and Lestes disjunctus disjunctus (Lestidae: Odonata) populations from the boreal forest of Alberta, Canada. Aquatic Insects, in press.

Benke, A. C. and S. S. Benke. 1975. Comparative dynamics and life histories of co-existing dragonfly populations. Ecology, 56: 302-317.

Chutter, F. M. 1961. Certain aspects of the morphology and ecology of the nymphs of several species of Pseudagrion Selys (Odonata). Arch. Hydrobiol. 57: 430-463.

Corbet, P. S. 1956. The life-histories of Lestes sponsa (Hansemann) and Sympetrum striolatum (Charpenter) (Odonata). Tijdschr. Ent. 99: 217-229.

Corbet, P. S. 1957a. The life-histories of two spring species of dragonfly (Odonata: Zygoptera). Ent. Gaz. 8: 79-89.

Corbet, P. S. 1957b. The life-histories of two summer species of dragonfly (Odonata: Coenagriidae). Proc. zool. Soc. Lond. 128: 403-418.

Corbet, P. S. 1957c. The life-history of the emperor dragonfly Anax imperator Leach (Odonata: Aeshnidae). J. Anim. Ecol. 26: 1-69.

Ingram, B. R. 1976. Life histories of three species of Lestidae in North Carolina, United States (Zygoptera). Odonatologica, 5: 231-244.

Ingram, B. R. and C. E. Jenner. 1976. Life histories of Enallagma hageni (Walsh) and E. aspersum (Hagen) (Zygoptera: Coenagrionidae). Odonatologica, 5: 331-345.

Johannsson, O. E. 1978. Co-existence of larval Zygoptera (Odonata) common to the Norfolk Broads (U.K.). I. Temporal and spatial separation. Oecologia Berl.), 32: 303-321.

Johnson, C. 1968. Seasonal ecology of the dragonfly Oplonaeschna armata Hagen (Odonata: Aeshnidae). Am. Midl. Nat. 80: 449-457.

Kormondy, E. J. and J. L. Gower. 1965. Life history variations in an association of Odonata. Ecology, 46: 882-886.

Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. 40: 385-423.

Lawton, J. H. 1972. Sex ratios in odonate larvae, with particular reference to the Zygoptera. Odonatologica, 1: 209-219.

Lutz, P. E. 1968. Life-history studies on Lestes eurinus Say (Odonata). Ecology, 49: 576-579.

Lutz, P. E. and C. E. Jenner. 1964. Life-history and photoperiodic responses of nymphs of Tetragoneuria cynosura (Say). Biol. Bull. 127: 304-316.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-360.

Norling, U. 1976. Seasonal regulation in Leucorrhinia dubia (Vander Linden) (Anisoptera: Libellulidae). Odonatologica, 5: 245-263.

Parr, M. J. 1970. The life histories of Ischnura elegans (van der Linden) and Coenagrion puella (L.) (Odonata) in south Lancashire. Proc. R. ent. Soc. Lond. (A), 45: 172-181.

Pritchard, G. 1980. The life cycle of Argia vivida Hagen in the northern part of its range (Zygoptera: Coenagrionidae). Odonatologica, 9: 101-106.

Pritchard, G. and B. Pelchat. 1977. Larval growth and development of Argia vivida (Odonata: Coenagrionidae) in warm sulphur pools at Banff, Alberta. Can. Entomol. 109: 1563-1570.

Sawchyn, W. W. and C. Gillot. 1974a. The life history of Lestes congener (Odonata: Zygoptera) on the Canadian prairies. Can. Entomol. 106: 367-376.

Sawchyn, W. W. and C. Gillot. 1974b. The life histories of three species of Lestes (Odonata: Zygoptera) in Saskatchewan. Can. Entomol. 106: 1283-1293.

Sawchyn, W. W. and C. Gillot. 1975. The biology of two related species of coenagrionid dragonflies (Odonata:

Zygoptera) in western Canada. Can. Entomol. 107: 119-128.

Thompson, D. J. 1978. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, Ischnura elegans. J. Anim. Ecol. 47: 757-767.

Appendix 2. The nymphs of <u>Coenagrion</u> <u>interrogatum</u> and <u>C</u>. <u>resolutum</u> (Coenagrionidae: Odonata) from the boreal forest of Alberta, Canada [1]

Abstract

In this paper, we point out differences between published descriptions of <u>Coenagrion resolutum</u> nymphs and our reared specimens, and we describe for the first time the nymph of <u>Coenagrion</u> <u>interrogatum</u>. A species key to the nymphs of <u>Coenagrion</u> in Alberta is presented along with characters to separate <u>Coenagrion</u> nymphs from <u>Enallagma</u> nymphs.

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[1] Co-authored by Hugh F. Clifford.

Introduction

The three North American species of *Coenagrion* are found in Alberta, Canada. *Coenagrion angulatum* Walker and *C. resolutum* (Hagen) are widespread in the province; *C. interrogatum* is not as common, Walker (1953) records it from Nordegg and we have collected specimens near Cynthia, Alberta.

During preliminary studies of zygopteran life histories from ponds in the boreal forest of central Alberta, we found that, despite collecting large numbers of adult *C. resolutum*, it was difficult to identify any nymphs as *Coenagrion* using keys of Walker (1953), Gloyd and Wright (1959), Cannings and Stuart (1977), and Pennak (1978). To be certain of the identity of *C. resolutum* nymphs and in an attempt to discover the undescribed nymph of *C. interrogatum* (a few adults had been collected at the study ponds), we collected nymphs from ponds 14 km N of Cynthia, Alberta on 8 May and 25 May 1979 and reared them in the laboratory for positive identification. Nymphs were reared individually in 40 ml plastic vials filled with dechlorinated water held at a temperature of 20°C and a photoperiod of 16L:8D. Small sticks were placed in the vials for nymphs to emerge on; nymphs were fed enchytraeid worms from a laboratory culture.

The purposes of this paper are to (1) point out differences between published descriptions of C. resolutum nymphs and our reared nymphs and (2) describe for the first time the nymph of C. interrogatum

Taxonomic features of Coenagrion resolutum

Forty-seven C. resolutum nymphs were reared to adults, 24 females and 23 males. Forty-five of the final instar nymphs had six antennal segments, one nymph had seven segments, and one nymph was badly damaged making it impossible to determine the number of antennal segments. Our single specimen with seven-segmented antennae had lengths of 0.22, 0.47, 0.46, 0.21, 0.30, 0.19, 0.21 mm. Of the 45 nymphs with six antennal segments, the average lengths were 0.22, 0.46, 0.56, 0.34, 0.26, 0.37 mm. Thirty-four of our 45 nymphs had segment 2 more than twice as long as segment 1. The average ratio of segment 2 to 3 was 0.83, ranging from 0.65 to 1.00.

Of the 47 specimens, 14 nymphs had four setae and 23 had five setae on each side of the prementum. One nymph had three setae on one side of the prementum and four on the other, seven nymphs had both four and five setae and two nymphs had both five and six. Some specimens had one or two setae reduced in size. Twenty of our specimens had six setae on each palp, 19 had seven setae on each palp, and one had eight setae on each palp, Two nymphs had five setae on one palp and six on the other, three nymphs had both six and seven palpal setae, and two nymphs had both seven and eight palpal setae.

Twelve of our 24 female nymphs possessed ovipositors that did not reach to the distal end of the 10th abdominal segment.

Description of <u>Coenagrion</u> <u>interrogatum</u>, final instar nymph

Described from six reared exuviae, five males and one female. Total length, 18.7-20.7 mm; hind wing, 4.1-4.75 mm; metafemur, 2.6-2.8 mm; caudal lamellae, 5.4-6.4 mm. The specimens are deposited in the Canadian National Collection, Ottawa, Ontario.

General colouration pale brown with small, dark brown dots marking the position of setae on the head, thorax, and abdomen (Fig. 1). Dots less conspicuous on darker specimens. Black spots at coxopleural articulations and at the mesothoracic and metathoracic spiracles. Black spots at the lateral tergal articulation of the abdominal segments. Legs pale with slightly darker, indistinct annulations near the distal end of femur and near the proximal end of the tibia. Body without distinct pigment pattern.

Antenna with six segments; average length of segments: 0.23, 0.42, 0.48, 0.30, 0.24, 0.34 mm. Average ratio of antennal segments 1:2 is 0.55, range 0.54-0.57.

Average ratio of antennal segments 2:3 is 0.87, range 0.79-0.91.

Labium extending to anterior edge of mesosternum. Greatest width of prementum approximately 4/5 its length. Three marginal setae on distal third of mentum; single seta at articulation of labial palp. Three or four mental setae, one often very small; number of setae not always equal on each side. Five or six palpal setae, number not always equal on each side. Labial palps with five or six denticles on distal margin, the smallest near the movable hook tend to fuse together.

Width of lateral caudal lamella equal to or less than 1/5 its length. Width of median lamella equal to or slightly more than 1/5 its length (Fig. 2B). Greatest width slightly before the nodus, which is beyond the middle of the lamella. Nodal line transverse. 19-33 dorsal and 12-25 ventral antenodal setae on median lamella. Lamellar tracheae very lightly pigmented; main branches leave trunk at acute angles and tend to run longitudinally. No distinct markings on lamellae.

Cerci of male with a dorso-mesal concavity (Fig. 2D). Ovipositor of female not projecting beyond sternum of abdominal segment 10.

Discussion

The number and relative length of antennal segments and the number of premental setae described for C. resolutum and C. interrogatum by us indicate that these two species cannot be distinguished from Enallagma using existing keys. Also, we suspect that nymphs of C. angulatum (the only other North American Coenagrion species) in Alberta have six antennal segments and cannot be keyed. We conclude this because C. angulatum adults are widely distributed and common in Alberta, yet nymphs with seven antennal segments are found only rarely.

Five species of Enallagma (E. boreale Selys, E. cyathigerum (Charpentier), E. hageni (Walsh), E. ebrium (Hagen), and E. anna Williamson) are known to occur in Alberta. Also, Enallagma civile (Hagen) and E. carunculatum Morse occur in Saskatchewan and British Columbia (Walker 1953, Cannings and Stuart 1977), and these species also will probably be found in Alberta. According to our descriptions of C. interrogatum and C. resolutum and Walker's description of C. angulatum, Coenagrion can be readily separated from the Enallagma species of Alberta. Coenagrion nymphs have numerous small dark dots on the head, thorax, and abdomen, and the caudal lamellae are without patches of profusely branched and deeply pigmented tracheae. According to Walker's description of the Enallagma species and our observations of reared specimens of *E. boreale*, *E. cyathigerum*, *E. ebrium*, and *E. anna* from central and southern Alberta, *Enallagma* nymphs either lack the dots on the head and body or, if the dots are present, the caudal lamellae have patches of profusely branched and deeply pigmented tracheae.

Within the genus *Coenagrion*, nymphs can be separated using the following key.

Key to the nymphs of *Coenagrion* in Alberta

1\. Tracheae of caudal lamellae leaving trunk at approximately 45°, distal branches not tending to run longitudinally .... *C. angulatum*

Tracheae of caudal lamella leaving trunk at less than 45°, distal branches tending to run longitudinally 2

2\. Cerci of male nymph broadly rounded (in dorsal view) (Fig. 2C); width/length of lateral caudal lamella greater than 1/5 (Fig. 2A).... *C. resolutum*

Cerci of male nymph with a dorsomedial concavity (Fig. 2D); width/length of lateral caudal lamella less than or equal to 1/5 (Fig. 2B) .... *C. interrogatum*

The structure of the cerci of mature male nymphs is the best character for separating *C. resolutum* and *C. interrogatum*. Differences in the ratio of width to length of the lateral caudal lamellae can also be used to separate the reared nymphs of C. resolutum and C. interrogatum and may be useful for female nymphs; however, the differences may not hold when the range of measurements of C. interrogatum is better known.

Acknowledgements

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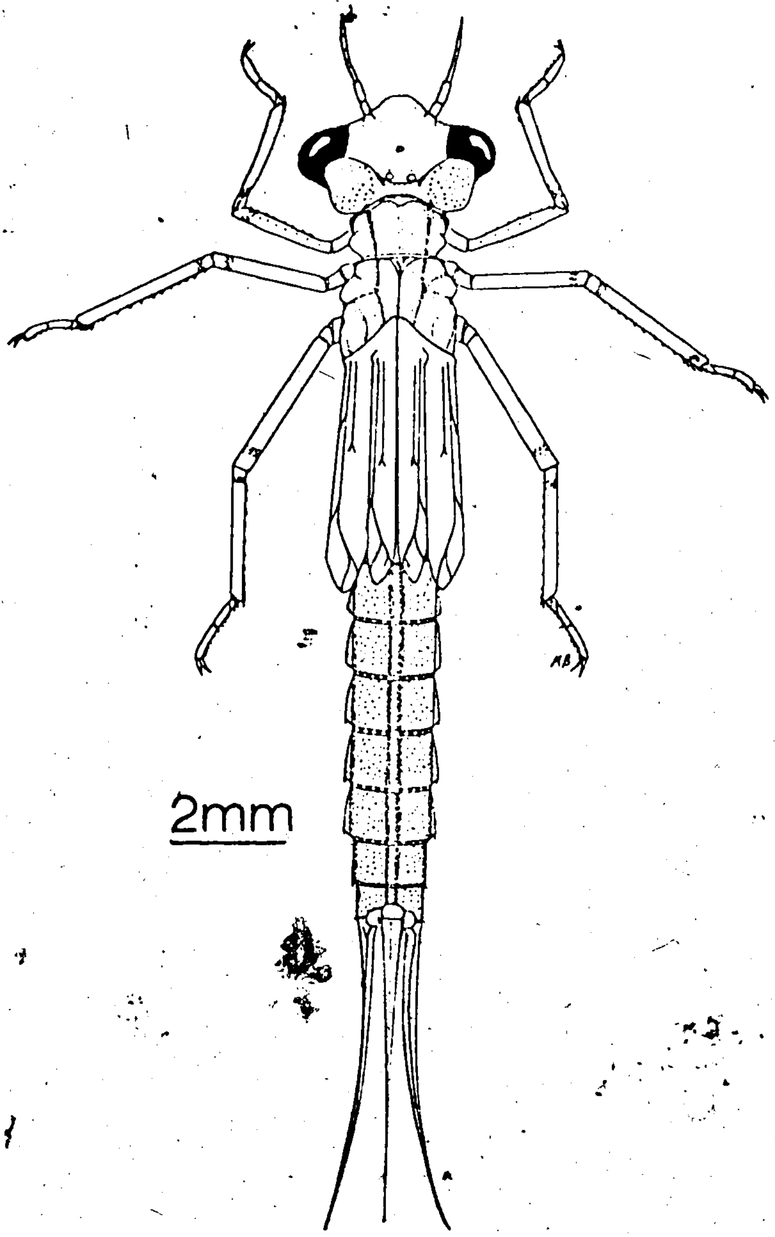

Figure 1. *Coenagrion interrogatum*, dorsal view of final instar nymph. Drawn from exuviae.

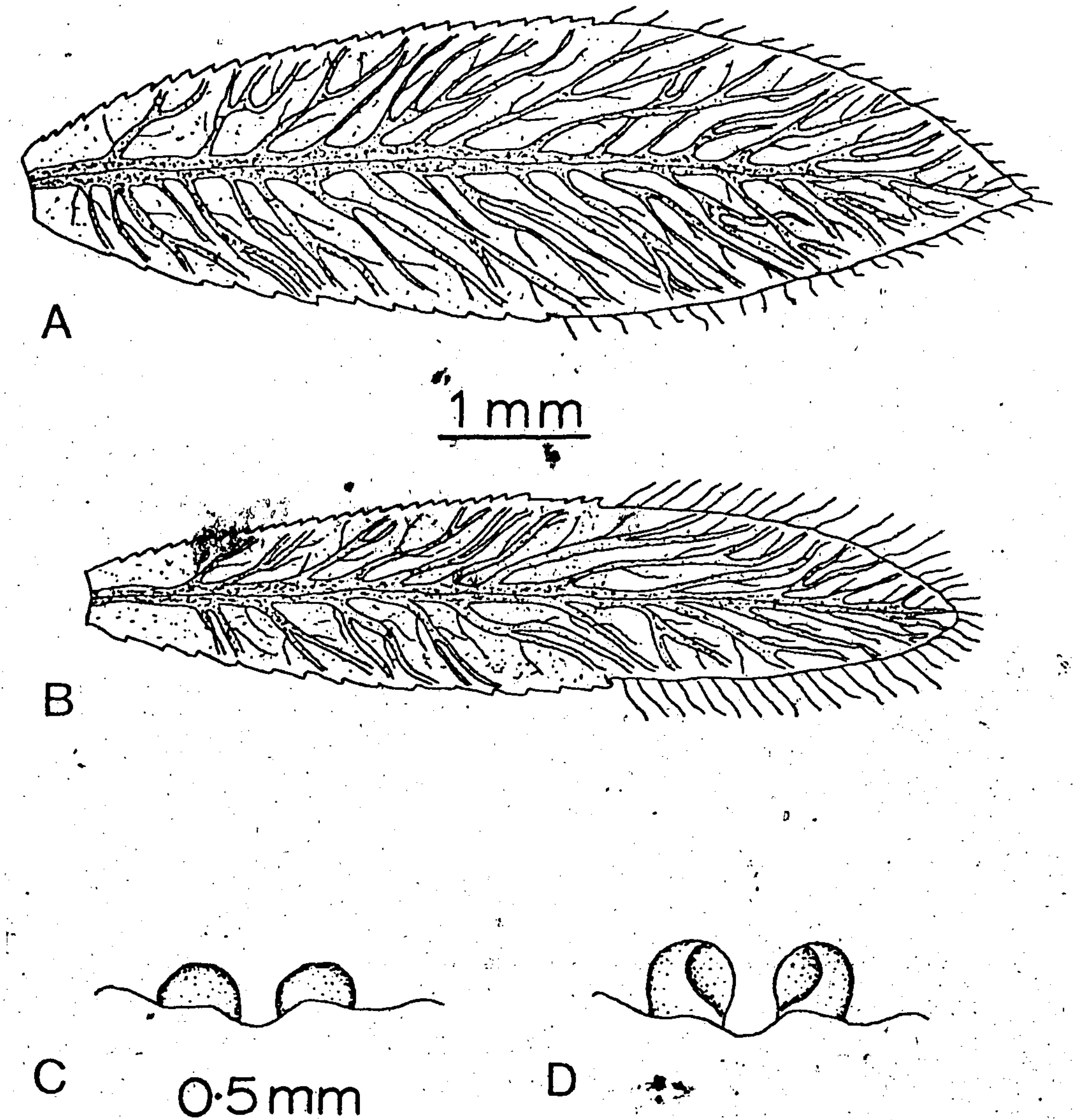

Figure 2. Median caudal lamella and cerci (dorsal view) of male *Coenagrion resolutum* (A and C) and *C. interrogatum* nymphs (B and D).

Literature Cited

Cannings, R. A. and K. M. Stuart. 1977. The dragonflies of British Columbia. British Columbia Provincial Handbook, no. 35.

Gloyd, L. K. and M. Wright. 1959. Odonata. In Freshwater Biology (2nd ed.). Edited by W. T. Edmondson. John Wiley and Sons, New York, pp. 917-940.

Pennak, R. W. 1978. Freshwater invertebrates of the United States. Ronald Press, New York.

Walker, E. M. 1953. The Odonata of Canada and Alaska, Vol. 1. University of Toronto Press, Toronto.

Appendix 3. Effects of food abundance on growth and survival of Enallagma boreale nymphs (Coenagrionidae: Odonata)

Introduction

In Chapter 4, I showed that differences in diet could affect the voltinism of C. resolutum nymphs. I controlled diet by feeding the animals different size meals. In this section, I present results from an experiment designed to test whether differences in diet, when maintained by controlling the frequency of feeding, can affect voltinism of Enallagma boreale nymphs.

Materials and Methods

Enallagma boreale nymphs were collected from a small pond within the city of Edmonton. Nymphs were fed Daphnia collected from a small pond near the University of Alberta campus, and enchytraeid (Oligochaeta) worms from a laboratory culture. Nymphs were housed separately in 40 ml plastic vials supplied with a small stick for a perch; the nymphs were maintained at 20°C and at a photoperiod of 16L:8D.

One hundred and twenty five nymphs (metathoracic femur length 1.1-1.8 mm, total length approximately 5.0 mm) were collected from the pond on 23 July 1978 and placed in the vials containing dechlorinated water.

Each nymph was randomly assigned to one of five groups (labelled A-E) of 25 animals each. Animals were starved until 25 July 1978 when feeding began. Quantity of food was controlled by "pulsing" the availability of food, i.e. the A group received an unlimited amount of food (Daphnia) every day, the B group received unlimited food every other day (food was removed after the 24 h feeding period), and the C, D, and E groups received unlimited food for 24 h every 4, 8, and 16 days respectively. On 23 October 1978, I switched the food from Daphnia to worms.

Nymphs were checked daily to determine if any had died or molted; exuviae were stored in 95% ethanol. I measured the metathoracic femur length of each exuviae to determine rate of growth.

Results and Discussion

Growth and survivorship are shown in Figure 1. Survivorship was poor in groups D and E, no nymphs in either group being alive after the 35th day. Nymphs in the C group lived longer than those in the D and E groups; however, the number alive declined steadily and only two emerged. Nymphs in the A and B groups had a much higher survivorship than those in the C group, with 18 emerging in each group. Most of the nymphs that died in groups A and B died when they were in the final instar; death may have been due to problems in emerging.

Growth curves in Figure 1 were produced by plotting average femur lengths of each group at 30-day intervals. Data for groups D and E were not plotted or analysed. Average femur lengths of groups A, B, and C were not significantly different at day 0 (analysis of variance, $P > 0.5$). However, analysis of variance indicated that average femur lengths were significantly different ($P < 0.05$) at every 30-day interval after day 0 until day 180. Duncan's multiple range tests indicated that average femur lengths of groups A and B were never significantly different and that average femur length of group C was significantly different ($P < 0.05$) from groups A and B at every 30-day interval after day 0.

In accordance with the growth of groups A and B, emergence periods of the two groups were similar. Although only two animals in group C emerged, the emergence period was clearly later than in the A and B groups. The first animal to emerge in group A developed to maturity in approximately half the time it took the first emerging animal of the C group to develop. Also, despite many more animals emerging in groups A and B, duration of the emergence period was longer in group C.

The total emergence period of this experiment was approximately 200 days and was much longer than field emergence periods. For example, Walker (1953) reports the flight season in southern Ontario lasts approximately six weeks and in south-western British Columbia, where the flight season is extremely long, the emergence period is approximately 90 days (Pearlstone 1971). This agrees with results of the growth experiment reported in Chapter 4 and supports Macan's idea that diet may alter life histories. Nymphs living in an area of a pond where they receive small meals (Chapter 4) or infrequent large meals may miss an emergence period and hence overwinter a second time.

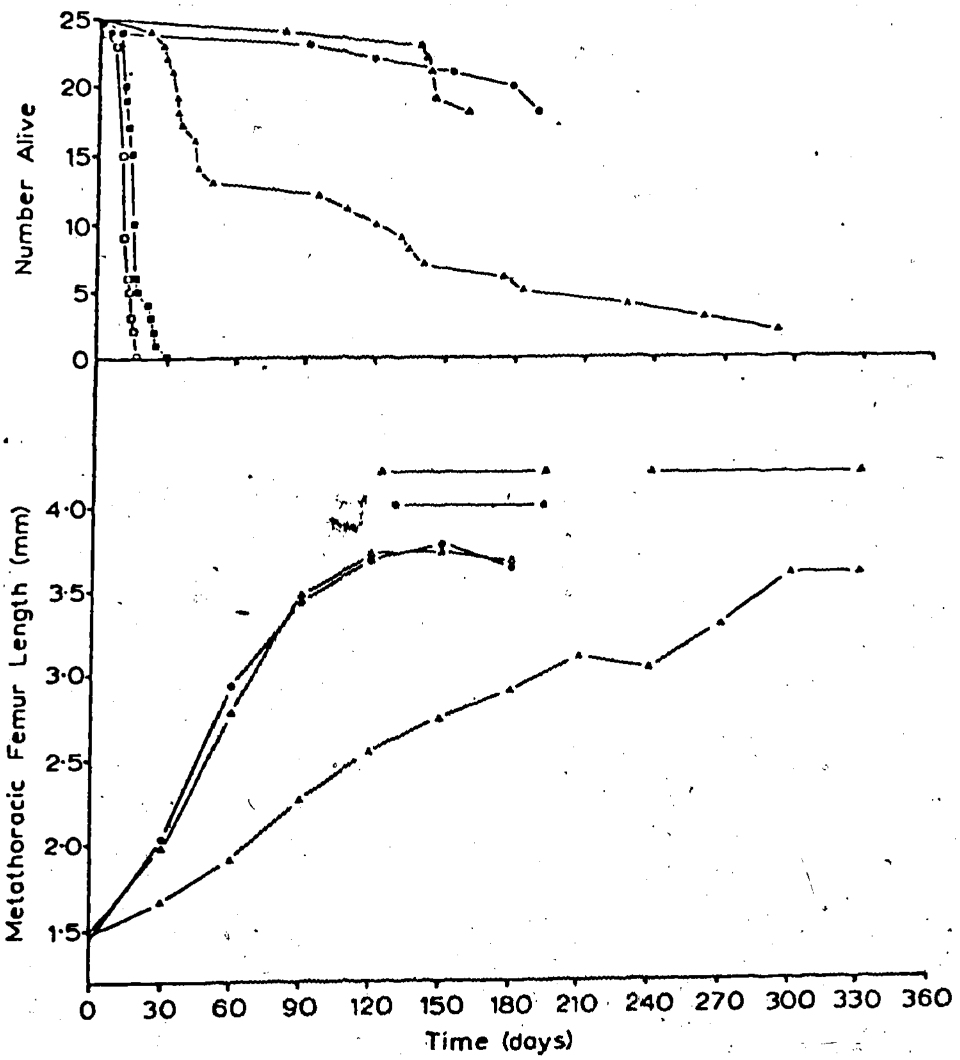

Figure 1. Metathoracic femur lengths and number alive of animals in groups A, open triangles; B, circles; C, solid triangles; D, solid squares; E, open squares. Horizontal lines in the lower figure represent emergence periods.

Literature Cited

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Gesamten Hydrobiol. 49: 325-3[illegible]0

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biol. Rev. Cambridge Philos. Soc. 52: 45-70.

Pearlstone, P. S. M. 1971. Observations on a natural population of damselfly larvae. M.Sc. thesis, University of British Columbia, Vancouver.

Walker, E. M. 1953. The Odonata of Canada and Alaska, Vol. 1. University of Toronto Press, Toronto.