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PREY SELECTION BY LARVAE OF *PYRRHOSOMA NYMPHULA* (SULZER) (ZYGOPTERA: COENAGRIONIDAE)

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When offered *Aedes aegypti* larvae of two different sizes, *P. nymphula* larvae showed no frequency-independent or frequency-dependent prey preference. The two-prey version of D. ROGERS' (1972, *J. Anim. Ecol.* 41: 369-383) random predator equation predicted accurately the proportion of each prey type taken by the dragonflies; an optimal diet model did not. These results are contrasted with those obtained in similar experiments on *Enallagma cyathigerum* (S.H. CHOWDHURY et al., 1989, *Odonatologica* 18: 1-13).

INTRODUCTION

CHOWDHURY et al. (1989) showed that, when presented with a choice between two prey types which differed in size, final (F-0) and penultimate (F-1) instar larvae of *Enallagma cyathigerum* (Charp.) (Zygoptera: Coenagrionidae), exhibited patterns of prey preference which could be predicted by the classic optimal diet model (CHARNOV, 1976). Here we report similar, though not identical, experiments conducted on *P. nymphula,* a coenagrionid similar to *E. cyathigerum* in size. These experiments are of particular interest because the results for *P. nymphula* differ strikingly from those for *E. cyathigerum.* For *P. nymphula* we find the model which most accurately describes predation behaviour to be the two-prey version of ROGERS' (1972) random predator equation (LAWTON et al., 1974; COCK, 1978; HUBBARD et al., 1982). The optimal diet model provided a very poor fit to the animals' behaviour. Statistical analysis, using the methods of GREENWOOD & ELTON (1979) designed to detect both frequency-dependent and frequency-independent components of prey preference, failed to detect any evidence of prey selection.

Studies of prey selection by dragonfly larvae in the laboratory have shown that frequency-independent preferences are common (e.g. LAWTON et al., 1974; AKRE & JOHNSON, 1979; BLOIS, 1982; BERGELSON, 1985; COTHRAN & THORP, 1985; COLTON, 1987; CHOWDHURY et al., 1989; SHERRATT & HARVEY, 1989), and that frequency-dependent preferences are rare (LAWTON et al., 1974; AKRE & JOHNSON, 1979).

Our experiments were intended to duplicate the conditions used by CHOWDHURY et al. (1989) in Experiments 1 and 3 of their study of *E. cyathigerum.* We did, however, make a few changes which made the experimental design more appropriate to the ecology of *P. nymphula.* We chose a lower temperature (10° C rather than 18-20° C) corresponding to the temperatures *P. nymphula* larvae experience at the time of collection in the field (see CORBET & HARVEY, 1989, fig. 1). Because of the low feeding rate of *P. nymphula* larvae at this temperature, we ran experiments for 2 days, rather than 30 minutes, thus ensuring consumption of sufficient prey items. We also examined the effect of absolute prey density on prey selection behaviour.

Before describing our experiments, we briefly review models of prey selection behaviour.

MODELS OF PREY SELECTION

We use two types of model of prey selection. The first is a statistical technique, proposed by GREENWOOD & ELTON (1979). Prey selection behaviour may be divided into two components. The frequency-independent component of selection arises when a predator shows a preference for one prey type regardless of its abundance relative to another prey type. The frequency-dependent component of preference arises when predators take disproportionately more of the common (or rare) prey type. Two parameters in the model describe these components of selection and can be estimated from experimental data. These parameters are estimated from the following equation:

$$e_1/e_2 = (VA_1/A_2)^b \qquad (1)$$

where e_1, e_2 = number of prey types 1 and 2 eaten; — A_1, A_2 = number of prey types 1 and 2 available; — b = a measure of frequency-dependent selection; — V = a measure of frequency-independent selection.

If there is no frequency-dependent selection, then $b = 1$. Any significant departure of b from 1 indicates significant frequency-dependence. If $b < 1$, disproportionately more of the rare form are taken (anti-apostatic selection); if $b > 1$, selection is for the common form (pro-apostatic selection). Similarly, when $V = 1$ there is no frequency-independent selection. If $V > 1$, there is preference for prey type 1; if $V < 1$, there is a preference for prey type 2. In this study, we estimate b and V by non-linear least-squares regression (NLLS) (but see GREENWOOD & ELTON (1979) for a different method which, under some circumstances, is preferred) on the following form of equation (1):

$$p = (VA)^b/\{1 + (VA)^b\}$$

where $p = e_1/(e_1 + e_2)$, that is, the proportion of prey type 1 taken and $A = a_1/a_2$.

The second type of model we use are behavioural models, designed to predict an animal's behaviour. The first of these is based on the theory of optimal foraging (see STEPHENS & KREBS, 1986). Optimal diet theory seeks to answer the following question: if a predator is given a choice between two prey types, which differ in profitability, how should it feed on the two types if it is to maximise its rate of energy intake? Here, profitability of prey type 1 is defined as the energy content of the prey type (E_1) divided by the handling time Th_1:

$$E_1/Th_1$$

CHARNOV (1976) proposed a now widely-used model for such situations. The predictions of the model are as follows: (1) Predators will rank the prey items on the basis of the profitability. (2) The predator will always eat the more profitable of the two prey types (i.e. the one with the highest value of E/Th). (3) The predator will take the more profitable prey type alone when:

$$\frac{a_1N_1E_1}{1 + a_1N_1Th_1} > \frac{a_1N_1E_1 + a_2N_2E_2}{1 + a_1N_1Th_1 + a_2N_2Th_2} \qquad (2)$$

where: a_1, a_2 = rate of search for prey types 1 and 2; — Th_1, Th_2 = handling time for prey types 1 and 2; — E_1, E_2 = energetic content of prey types 1 and 2; — N_1, N_2 = initial densities of prey type 1 and 2.

In words, predators should take only the more profitable prey type when the rate of energy intake by doing so (given by the left-hand side of inequality (2) is greater than when both prey types are taken (the right-hand side of enequality (2)). Otherwise, it should take both prey types whenever it encounters them.

Inequality (2) is satisfied by values of N_i as follows:

$$N_1 > \frac{E_2}{a_1\,(E_1Th_2 - E_2Th_1)}$$

Therefore, there is a critical density $\hat{N}_1$ above which the predator should take only the more profitable of two prey types. $\hat{N}_1$ can be calculated as follows:

$$\hat{N}_1 = \frac{E_2}{a_1\,(E_1Th_2 - E_2Th_1)}$$

Note that $\hat{N}_1$ is independent of N_2, the density of the less profitable prey.

In order to predict the pattern of prey selection produced by an animal foraging in a manner consistent with CHARNOV's optimal diet model, allowance must be made for the fact that, unless prey are replaced, the animal will reduce the density of the prey populations (see HUBBARD et al., 1982). At the start of an experiment the density of the more profitable prey may be above $\hat{N}_1$, but as the animal exploits this prey type it reduces the density to below $\hat{N}_1$; the animal should then change its behaviour and take both prey types. Exploitation before $\hat{N}_1$ is reached can be described by ROGERS' (1972) random predator equation, because only prey type 1 is taken:

$$Na_1 = N_1 (1\text{-}\exp(-a_1 (T\text{-}Th_1Na_1))) \tag{3}$$

where: Na_1 = the number of type 1 eaten; — and T = time.

For the remaining period of the experiment extended versions of the random predator equation can be used to predict numbers of prey taken:

$$\left.\begin{aligned} Na_1 &= N_1 (1\text{-}\exp(-a_1 (T\text{-}Th_1Na_1\text{-}Th_2Na_2))) \\ Na_2 &= N_2 (1\text{-}\exp(-a_2 (T\text{-}Th_2Na_2\text{-}Th_1Na_1))) \end{aligned}\right\} \tag{4}$$

where: Na_2 = number of prey type 2 eaten.

The second behavioural model we use is one that assumes that the behaviour of a predator when feeding on two prey types simultaneously can be predicted from the behaviour of the predator when feeding on each of the prey types alone (LAWTON et al., 1974; COCK, 1978). The components of this model have already been presented: parameters derived from fitting functional response experiment data to ROGERS' (1972) random predator equation (3) are substituted into the extended random predator equations (4). Equations (4) can then be used to predict the number of each prey type eaten by a predator in a given time, when presented with known densities of two prey types. Any systematic departures of experimental data from predictions of equations (4) indicate a change in predatory behaviour in response to the presence of alternative prey.

MATERIAL AND METHODS

Larvae of *Pyrrhosoma nymphula* were collected by handnet from a pond in Tentsmuir Forest, Fife (NO 484275; 56°27'N, 2°50'W) during October 1988. Only final instar larvae were used in experiments (head width greater than 3.6 mm). After collection each larva was held in a separate container in a controlled temperature room at 10° C and an artificial photoperiod of 12 h. All experiments were conducted under these conditions. F-0 larvae collected at this time of year are in diapause (CORBET & HARVEY, 1989), but continue to feed. Larvae were checked periodically for external signs of metamorphosis (CORBET & PROSSER, 1986): no larva began to metamorphose during the time of experiments, which were completed within two months of collection.

Experimental containers, (each accommodating 1 dragonfly larva and its prey) were white, opaque, circular plastic tubs (diameter of top and bottom 8.2 and 6.6 cm, height 5.5 cm) containing 150 ml of tapwater. Prey were larvae of the mosquito *Aedes aegypti* (L.) of two sizes: 1-day old ("small", comprising instars II (mainly) and I), and 5-days old ("large", comprising instar IV). To standardise, as far as possible, hunger levels at the start of each experiment, dragonfly larvae were fed ad libitum with a mixture of *Ae. aegypti* larvae for at least 24 h and then denied food for 24 h before the experiment began.

We conducted two experiments. The first, corresponding to Experiment 1 of CHOWDHURY et al. (1989) was designed to determine the functional response to prey density of F-0 *P. nymphula* larvae feeding on the two types of prey, and to provide estimates of a and Th for each prey type. The second, corresponding to Experiment 3 of CHOWDHURY et al. (1989), was designed to examine the effects of absolute and relative densities of large and small prey on predator-choice.

Experiment 1. — Prey larvae were provided, once only, at the beginning of each replicate, at each of 4 densities per predator: 4, 8, 16 and 32. At the end of each experiment the numbers of prey consumed were recorded. Each treatment was replicated 5 times. Rates of search and handling times were estimated from the data using ROGERS' (1972) random predator equation by non-linear least-squares regression.

Experiment 2. — Prey larvae were provided, once only, at the beginning of each replicate, at three densities (absolute densities: 8, 16 & 32), and different proportions (relative densities: 2.5:7.5 (small:large), 5:5 and 7.5:2.5), giving 9 treatments. Five replicates of each treatment were carried out in each of two blocks, giving a total of 10 replicates.

Model predictions. — Predictions from the two-prey random predator equations (4) were obtained by substituting estimates of rates of search and handling times for each prey type obtained in experiment 1 and solving the equations using function minimisation and non-linear least-squares techniques.

Calorific values of *Ae. aegypti* larvae reared in a manner identical to those used in the experiments presented here were used in estimating profitability (S. Jordan, unpublished). Calorific values, which are the average for one larva, were: small larvae — 0.429 J; large larvae — 10.2 J. These values, together with a and Th for each prey type, were substituted into the optimal diet model, using equations (3) and (4) as appropriate to describe exploitation of the prey populations by the predator, and the optimal number of each prey type predicted for each treatment.

RESULTS

EXPERIMENT 1. — Figure 1 shows the functional response curves to 2 sizes of prey, together with estimates of a and Th for each of the two prey types.

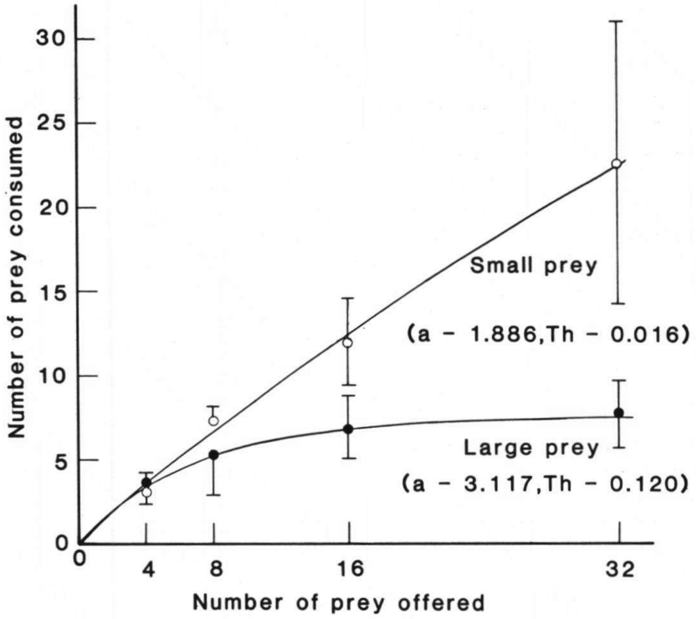

Fig. 1. Functional response curves for *P. nymphula* offered *Aedes aegypti* larvae as prey. Means are based on 8 replicates of each prey density. Bars represent standard error of the mean. For each result the estimates of rate of search (a) and handling time (Th) are shown. Units of a are tub volumes per two days and Th are two days. Line shows the best fit of ROGERS' (1972) model.

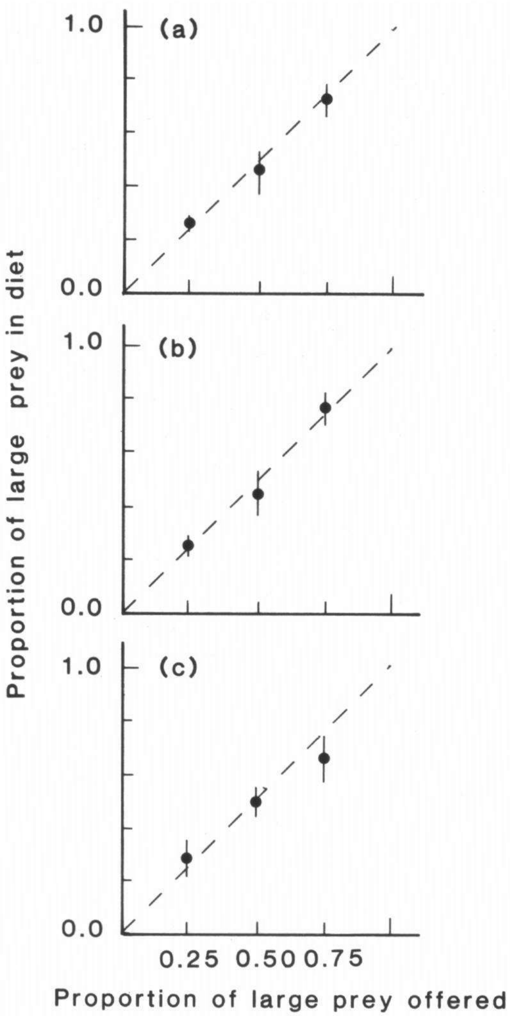

Fig. 2. Proportion of large prey consumed by *P. nymphula* larvae when presented with small and large prey larvae in differing proportions at densities of (a) 8, (b) 16, and (c) 32 prey. Bars represent standard error of the mean. Sample size is 10 for each treatment.

EXPERIMENT 2. — Figure 2 shows the relationship between proportion of large prey offered and eaten at each of the three absolute densities. Values of b and V, together with 95% confidence intervals are given in Table I. At all three absolute densities the confidence intervals of both b and V include 1; so there is no evidence of frequency-dependent or frequency-independent prey selection.

A comparison of the mean proportion of large prey in the diet for each treatment and the predictions of the random predator model and optimal diet model are shown in Figure 3. For 8 of the 9 treatments, the 95% confidence limits of the experimental data overlap the predictions of the random predator model, but do not overlap the predictions of the optimal diet model. The one exceptional treatment (6 small: 2 large prey; Fig. 3 (a) at 0.25) is unusual in that an optimally foraging predator exhibits behaviour very close to that of random predator, and so the confidence limits of the experimental data overlap predictions of both models.

DISCUSSION

Results presented here show clearly that, in contrast to *E. cyathigerum, P. nymphula* larvae forage in a manner that fits a random predator model rather than an optimal diet model. Why should this be so? Notwithstanding the

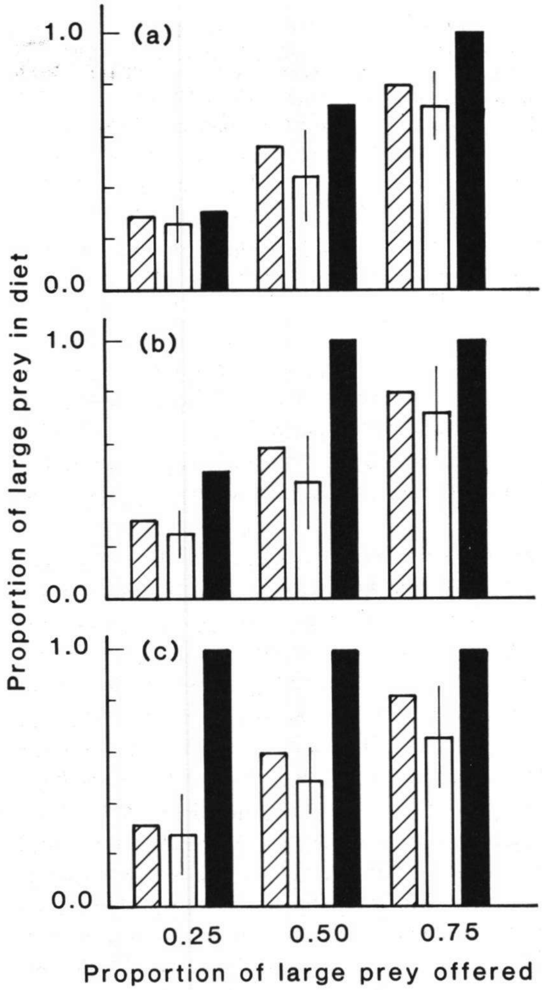

Fig. 3. Comparison of prey selection behaviour of *P. nymphula* larvae (open bars) with the predictions of ROGERS' two prey random predator equation (hatched bars) and CHARNOV's (1976) optimal diet model (solid bars). Small and large prey larvae were offered at total densities of (a) 8, (b) 16 and (c) 32.

difficulties in interpreting deviations from optimal foraging models, it would seem that the differences between these species are so marked that they call for a functional interpretation; however, an obvious explanation does not present itself. It would be unsurprising to find a difference between a semivoltine species such as *P. nymphula* and a very rapidly developing species, such as *Lestes sponsa* (Hans.), but both *P. nymphula* and *E.cyathigerum* are mainly semivoltine, at least in northern Britain (MACAN, 1964; HARVEY & CORBET, 1989). The difference in prey selection between *P. nymphula* and *E. cyathigerum* is only one aspect in which there is interspecific variability in larval foraging behaviour. Species differ, for example, in territorial behaviour, foraging mode (active foraging and sit-and-wait) and response to the presence of enemies. JOHNSON & CROWLEY (1980) suggest that minimizing risk of predation may be an important aspect of the foraging behaviour of some larval odonates, and that odonates can be divided into two groups: "sit-and-wait" species which minimise the risk of being eaten by other predators but show slow growth; and actively-searching species which are subject to greater predation pressure, but develop rapidly. Our feeling is that *P. nymphula* belongs to the first

Table I

Experiment 2. Prey selection by larvae of *P. nymphula* when offered a choice between small and large prey at three prey densities. b and V parameters of the GREENWOOD & ELTON (1979) model which describe, respectively, frequency-dependent and frequency-independent predation. — [LCL = lower 95% confidence limit, UCL = upper 95% confidence limit]

Prey density	LCL	b	UCL	LCL	V	UCL
8	0.420	0.802	1.183	0.595	0.886	1.320
16	0.572	1.024	1.475	0.677	0.961	1.364
32	0.262	0.708	1.154	0.504	0.863	1.478

group and *E. cyathigerum* to the second. However, this is hard to reconcile with the fact that the two species have similar life-histories. Clearly, more detailed studies of odonate larval foraging behaviour are necessary before a full understanding of the interesting differences between apparently similar species will be possible.

A lack of frequency-dependent preference is not perhaps surprising in the light of previous studies (see Introduction). To our knowledge, the only studies which have convincingly demonstrated frequency-dependent predation, although using different coenagrionid larvae (*Anomolagrion hastatum* (Say) and *Ischnura elegans* (Vander L.)) as predators, used similar prey, that is the cladoceran *Simocephalus vetulus* (O.F. Müller) as one prey type and *Daphnia* (*D. magna* Straus in the study of AKRE & JOHNSON (1979), and *D. obtusa* Kurz in the study of LAWTON et al. (1974)) as the alternative prey. *Daphnia* and *Simocephalus* differ markedly in their behaviour, *Simocephalus* spending most of their time on the substrate, interspersed with only short periods of swimming. The behavioural differences between the prey types mean that the dragonfly larvae must forage actively for *Simocephalus* but can adopt a sit-and-wait foraging mode when feeding on *Daphnia*. A change in search mode in response to changing relative densities of the two prey types may well generate frequency-dependent predation, as suggested by AKRE & JOHNSON (1979).

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