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FEEDING RATES OF ZYGOPTERA LARVAE WITHIN AN INSTAR

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Feeding rates of *Ischnura elegans* and *Lestes sponsa* were constant within an instar when larvae were maintained at high prey densities. Feeding rates increased during an instar when larvae were maintained at low prey densities. This finding differs from published speculations. *Ischnura* larvae showed an increased feeding rate in response to increasing periods of food deprivation.

INTRODUCTION

There have been many studies of the feeding rates of odonate larvae under different prey density and temperature conditions in field and laboratory (e.g. LAWTON, 1971; THOMPSON, 1975, 1978b). Only LAWTON et al. (1980) have looked at the feeding rate throughout the instar. They reported the effects of prey density on survival and development rate and compared long term with short term functional responses. However they did not analyse the feeding rates of the larvae they used within the instar.

The aim of this paper is to re-analyse some of these data on *Ischnura elegans* (Vander L.) and provide new data from *Lestes sponsa* (Hans.). The only other work that we know of that considers feeding rates within instars for zygopteran larvae is that of JOHNSON (1973) who supposed that damselfly feeding rate was highest toward the beginning of each instar. This supposition arose not from a direct study of feeding rates, but indirectly from patterns of mortality in a prey species.

METHODS

Ischnura larvae were collected from the Pocklington Canal near York, U.K.; *Lestes* larvae came from a pond at Malpas, Cheshire, U.K. Larvae were returned to the laboratory, maintained at 16° C in separate containers with a plentiful food supply. They were assigned to instars by inspection of graphs of head width against body length (THOMPSON, 1975, for *Ischnura*) and head width against wing bud length (PICKUP et al., 1984, for *Lestes*). The animals entered the experiment on moulting into instars 10 and 11 (*Ischnura*) and 7, 8 and 9 (*Lestes*). The prey used were class C *Daphnia magna* Straus (THOMPSON, 1975) that were able to pass through a 1.00 mm mesh Endecott's Test Sieve, but not one of 0.85 mm mesh size. The mean length of such *Daphnia* is 1.695 ± 0.022 mm (1 S.E.); mean dry weight, 0.044 mg. Cladocerans of this size are typical natural prey items of late instar zygopteran larvae (THOMPSON, 1978a, 1978b).

Once the larvae under study entered the appropriate instar they were maintained in 75 ml of dechlorinated tap water in 100 ml beakers with a known density of *Daphnia*. The experiments were performed at 16° C, in dim light; the larvae were provided with a "fishing site" in the form of a cocktail stick. Each day the numbers of dead and live *Daphnia* were counted and removed, and the appropriate number of fresh *Daphnia* added. Control beakers with *Daphnia* but no damselfly larvae, showed that deaths from natural causes were negligible. Wasteful killing (JOHNSON et al., 1975) does occur with *Ischnura* and *Lestes* but is not pronounced.

Each animal was maintained at the same prey density until it moulted in to the next instar. Densities of 8,15 and 30 *Daphnia* 75 ml^{-1} and 10, 20 and 40 *Daphnia* 75 ml^{-1} was used for *Ischnura* instars 10 and 11 respectively while density of 20 and 40 *Daphnia* 75 ml were used for the three *Lestes* instars.

RESULTS

The beakers containing the larvae were monitored daily, so that there is a potential for error in noting the beginning and end of each instar of up to twenty--four hours. For this reason we have ignored data for day 1 of each instar. From examination of graphs of feeding rate throughout the instar (e.g. Fig. 1) it seems clear that there is a decline in feeding rate for one or two days at the end of the instar 'presumably when an animal is preparing to moult. Consequently, data from the last two days of each instar have also been ignored for the purpose of analysis. Figure 1 shows the number of *Daphnia* eaten by individuals of *Ischnura elegans* for one instar/prey density combination, namely instar 11 at 40 *Daphnia* 75 ml^{-1}. These data are typical for *Ischnura* and *Lestes*. Space does not permit us to display more graphs. We tested the data for trends on feeding rate during the instar by fitting a linear regression of numbers eaten against time and testing the slope for deviations away from a slope of zero.

Table I shows the results of this analysis. For the most part there were no significant trends in feeding rate throughout the instar. None was observed with the limited *Lestes* data available and the slopes of the regression lines were as likely to be positive as negative. The data for *Ischnura* are more detailed and suggest a possible trend. At high prey densities, for both instars 10 and 11, there are no statistically significant deviations from a horizontal line and both positive

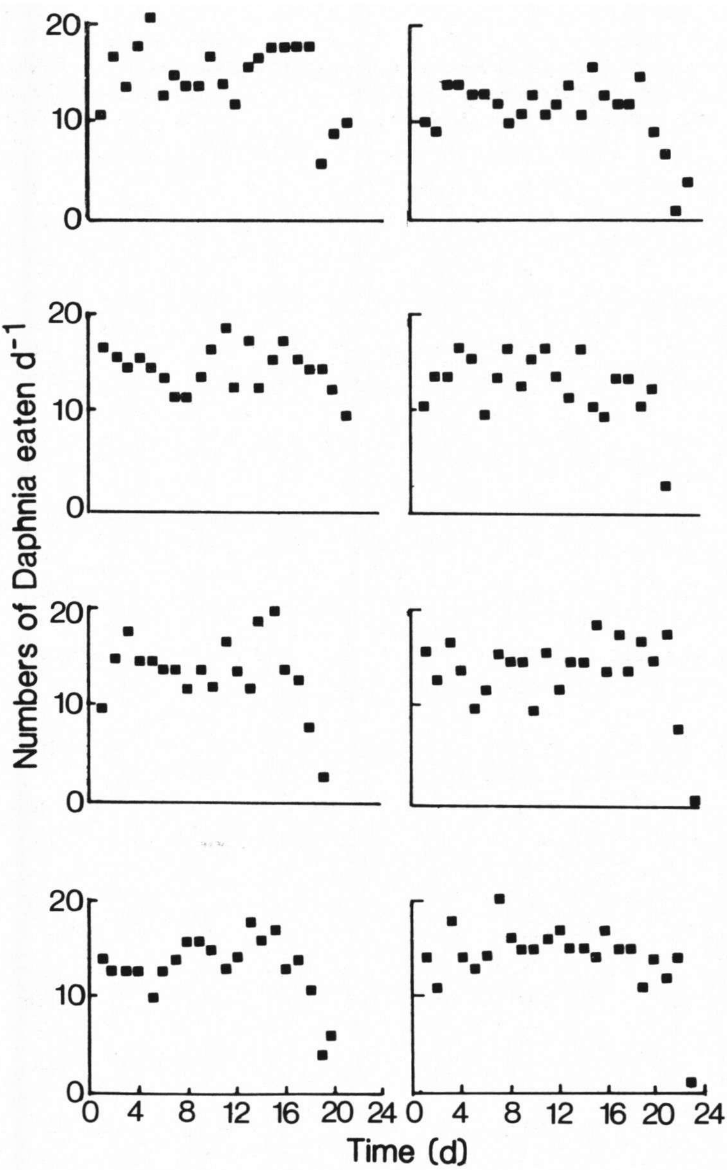

Fig. 1. The relationship between numbers of *Daphnia* consumed per day and time within an instar for eight individuals of instar 11 *Ischnura elegans* maintained at a prey density of 40 class C *Daphnia magna* 75 ml^{-1}.

Table I

Analysis of feeding rate within an instar for 13 individuals of *Lestes sponsa* and 48 of *Ischnura elegans*. Prey were class C *Daphnia magna* (cf. text) except for *Lestes* instars 7 and 8, which fed on class D (mean length 1.439 mm ± 0.023 (1 S.E.); mean weight 0.0286 mg). A linear regression model was fitted to the data and the slope tested with a t-test against the null hypothesis of a slope of $b = 0$

Species	Instar	Prey density (*Daphnia*/75 ml)	Intercept	Slope	t-value	Probability
Lestes sponsa	7	40	20.5	-1.50	1.57	ns
	7	40	16.0	-0.08	0.69	ns
	7	20	14.0	0.30	0.54	ns
	7	20	18.5	-1.00	1.05	ns
	8	40	24.0	1.00	1.37	ns
	8	40	22.1	0.49	0.56	ns
	8	20	16.7	0.04	0.10	ns
	8	20	16.2	0.60	1.57	ns
	9	40	31.7	-0.57	0.47	ns
	9	40	29.9	-0.46	0.33	ns
	9	40	30.4	-0.82	1.47	ns
	9	20	16.1	0.19	0.86	ns
	9	20	19.5	0.04	0.78	ns
Ischnura elegans	10	30	9.2	0.16	0.66	ns
	10	30	5.9	0.17	1.20	ns
	10	30	7.8	0.29	1.89	ns
	10	30	7.8	0.22	1.39	ns
	10	30	7.3	0.11	0.62	ns
	10	30	8.0	0.02	0.16	ns
	10	30	10.8	-0.18	1.16	ns
	10	30	9.2	-0.05	0.34	ns
	10	15	7.1	-0.12	1.33	ns
	10	15	8.0	-0.18	1.07	ns
	10	15	7.8	0.01	0.13	ns
	10	15	6.1	0.13	1.05	ns
	10	15	7.1	0.10	0.59	ns
	10	15	6.5	0.01	0.12	ns
	10	15	6.9	0.09	0.63	ns
	10	15	7.1	0.05	0.49	ns
	10	8	4.7	0.03	0.48	ns
	10	8	2.8	0.16	3.47	<0.01
	10	8	3.4	0.19	3.31	<0.01
	10	8	1.6	0.32	6.06	<0.001
	10	8	3.6	0.22	2.90	<0.02
	10	8	4.4	0.14	2.01	ns
	10	8	4.2	0.13	1.58	ns
	10	8	3.1	0.15	2.20	<0.05
	11	40	15.3	0.09	0.74	ns
	11	40	14.8	0.03	0.30	ns
	11	40	14.8	0.01	0.09	ns
	11	40	13.1	0.11	1.03	ns
	11	40	12.7	-0.06	0.67	ns
	11	40	15.4	-0.15	1.43	ns
	11	40	12.8	0.18	2.07	ns
	11	40	15.6	-0.07	0.84	ns
	11	20	13.2	0.08	0.75	ns
	11	20	9.7	0.16	1.88	ns
	11	20	6.4	0.11	1.61	ns
	11	20	11.6	<0.01	<0.01	ns
	11	20	9.9	0.27	2.50	<0.05
	11	20	10.5	0.23	2.68	<0.02
	11	20	12.1	-0.06	0.54	ns
	11	20	15.2	-0.08	0.78	ns
	11	10	6.6	0.08	2.06	ns
	11	10	7.6	0.04	1.12	ns
	11	10	7.1	0.05	1.12	ns
	11	10	5.3	0.08	1.60	ns
	11	10	8.9	0.25	2.40	<0.05
	11	10	8.0	-0.01	1.12	ns
	11	10	4.9	0.15	3.98	<0.001
	11	10	6.7	0.13	1.92	ns

and negative slopes are found. However at the lowest prey densities, 62.5% and 25% of the lines depart significantly from a slope of zero for instars 10 and 11 respectively. All these deviations are for lines with a positive slope, indicating that feeding rate increases during the instar at low prey densities. In fact notwithstanding statistical significance, as prey density decreases, the proportion of larvae that gave positive regression slopes increases.

The results indicate that there were no trends in larval feeding rate during an instar when larvae were maintained at high prey densities, but that feeding rate increases during an instar at low prey densities. The implication of this finding is that the response of larvae to increasing hunger levels is to increase feeding rate. In order to test this, we looked at the feeding rates of instar 11 *Ischnura* larvae that had been starved for varying lengths of time, from 0 to 168 hours. From three to five larvae were tested for each starvation period. Each larva was placed in a beaker as before but at a density of 50 *Daphnia* 75 ml^{-1}. The numbers eaten in the first ninety minutes are shown in Figure 2. There is an increase in numbers eaten with food deprivation time until about forty-eight hours, after which the curve levels off to an asymptote.

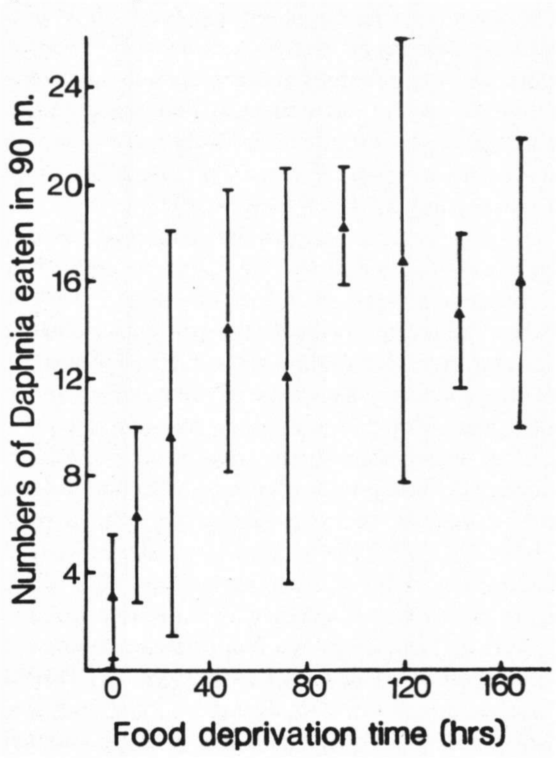

Fig. 2. The relationship between numbers of class C *Daphnia magna* consumed in 90 minutes and length of prior food deprivation. The density of *Daphnia* was 50 *Daphnia* 75 ml^{-1}. Means and 95% confidence intervals are displayed.

Ischnura larvae show increased feeding rates if hunger levels increase during an instar, but otherwise feed at a more or less constant rate.

DISCUSSION

JOHNSON (1973) pointed to two studies in which female spiders fed intensively following ecdysis, but then fed at a much lower rate later in the instar (HAYNES & SISOJEVIC, 1966; MIYASHITA, 1968). He suggested that this pattern was likely to be typical of arthropod predators in the prensence of abundant prey. He suggested that *Ischnura verticalis* (Say) adopted this feeding pattern; this was an ingenious explanation to account for intermittent mortality patterns in populations of *Simocephalus serrulatus* (Koch). The direct evidence from the present study suggests that zygopteran larvae feed at a constant rate throughout the instar (except for the last day or two) if prey densities are high, but can increase during the instar if prey densities are low. This is the opposite picture to that proposed by JOHNSON (1973).

It is interesting to note that the feeding rate was constant during the instar at those prey densities which led the larvae to pass through the instar at maximum development rates (cf. LAWTON et al., 1980). When development rates fell below the asymptotic level, this corresponded with prey densities at which larvae showed increased feeding rates during the instar. This suggests that increased feeding rates were a response to a reduced energy intake; larvae were not taking in sufficient energy to grow at the maximum rate.

That zygopteran larvae are able to respond to increased hunger levels by increased feeding rates is supported by the data shown in Figure 2. The likely mechanism for the increased feeding rate is that the reactive distance *(sensu* HOLLING, 1963, 1966) of the larvae increases; larvae were seen to let go of their fishing sites with the front pair of legs, thus increasing the maximum distance from the perch at which they were able to respond to prey.

Where it can be shown that odonate populations are not food limited in the field (FOLSOM & COLLINS, 1982; THOMPSON, 1982) feeding rates are likely to remain constant during an instar. This would be a great benefit to those who would model arthropod prey-predator interactions, since one parameter, the mean feeding rate, would suffice to describe predator feeding throughout an entire instar.

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