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Some aspects of the rate of increase of a coccinellid

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ABSTRACT. 1. Fecundity, growth and development were determined at a range of feeding levels and temperatures and compared with the component models for the predator rate of increase.

2. Fecundity and growth rate show a linear dependence on rate of consumption, while development rate conforms to an alternative non-linear model. The non-linearity of development rate is due to a dependence of weight gain during an instar on rate of consumption.

3. The primary influence of temperature is on the rate of consumption, limiting fecundity and growth rate at temperatures below the optimum for the stage, while higher temperatures have a deleterious effect. Temperature has a more direct influence on development rates, allowing comparable growth despite the variation in rates of consumption.

Introduction

Two distinct aspects of arthropod predation are the prey death rate and the predator rate of increase (Lawton *et al.*, 1975; Hassell, 1978). The prey death rate concerns the number of prey eaten in relation to the abundance and distribution of prey and predators; while the predator rate of increase describes the reproduction, development and survival of the predator population. In a review of the latter, Beddington *et al.* (1976) provide simple models for the three main components: growth and development of the immature stages; their survival rate; and adult fecundity.

The models are expressed as functions of the rate of prey consumption (I), which is determined by the prey death rate. The growth rate (G) of each juvenile stage and the fecundity (F) of the adults are modelled as linear functions:

$$G = \alpha(I - a) \qquad (1)$$

$$F = \beta(I - b) \qquad (2)$$

where a and b are threshold rates of consumption for growth and egg production respectively and α and β are constants. The development rate of the juvenile stages, represented by the reciprocal of the instar duration ($1/d$), is similarly modelled as a linear function from the assumption of a constant weight gain (Wg) during each stage:

$$1/d = \frac{G}{\mathrm{Wg}} = \frac{\alpha}{\mathrm{Wg}}(I - a) \qquad (3)$$

In the present paper, results obtained from larval growth and development and adult fecundity of the coccinellid, *Adalia bipunctata* (L.), reared at various feeding levels and temperatures, are considered in relation to these models of the predator rate of increase.

Methods

The prey used were mixed instar pea aphids (*Acyrthosiphon pisum* Harris), reared on broad bean (*Vicia faba* L.) in a glasshouse at a mean temperature of 18°C with a 16 h photoperiod. Adult *Adalia bipunctata* collected from hibernation sites were fed on excess prey to bring

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them into reproductive condition for use as experimental animals and to provide a supply of coccinellid eggs.

Experimental mated adult females were kept individually in 7.5 x 2.5 cm glass tubes, lined by a 1.5 cm layer of plaster of paris at the base, which was kept moist to maintain a high humidity. Coccinellid larvae were reared individually in gelatin capsules (size 00). Five feeding levels were used, and for the larvae the daily ration corresponded to between 1x to 5x the average teneral weight of the instar, while for the adults it corresponded to between 1x and 2x the average adult female weight. Five temperatures, from 15 to 25°C, were used for larvae fed at the 4x daily ration and adults fed at 1.75x daily ration.

Consumption was determined collectively for each larval regime and individually for the adult coccinellids, from the fresh weight of aphids supplied and the dry weight of aphid remains, using the following relation for dry and fresh weight of the pea aphid culture:

$$\text{mg dry wt} = 0.1766 \text{ mg fresh wt} - 0.0156$$

$$(n = 25, r^2 = 0.996, P < 0.001)$$

Larval growth was measured as the fresh weight gain (including exuvia weight) between instars, and adult fecundity as the fresh weight of eggs produced per day over a period of 5 days, following an initial 3 day acclimatization period at the appropriate feeding level or temperature.

Results

The influence of rates of consumption

The larval growth rates at 20°C, expressed as the ratio of weight gain to instar duration, are linearly related to the rates of consumption as shown in Fig. 1. This agrees well with the linear model of Beddington *et al.* (1976); however, it is not intuitively clear as to why such a relation exists. From the energy balance equation for larval growth (e.g. Petrusewicz & Macfadyen, 1970):

$$\begin{aligned} G &= A - R \\ &= kI - R \qquad (4) \end{aligned}$$

where G is growth rate, A is rate of assimilation, R is respiratory rate, I is rate of consumption and k is digestive efficiency. .

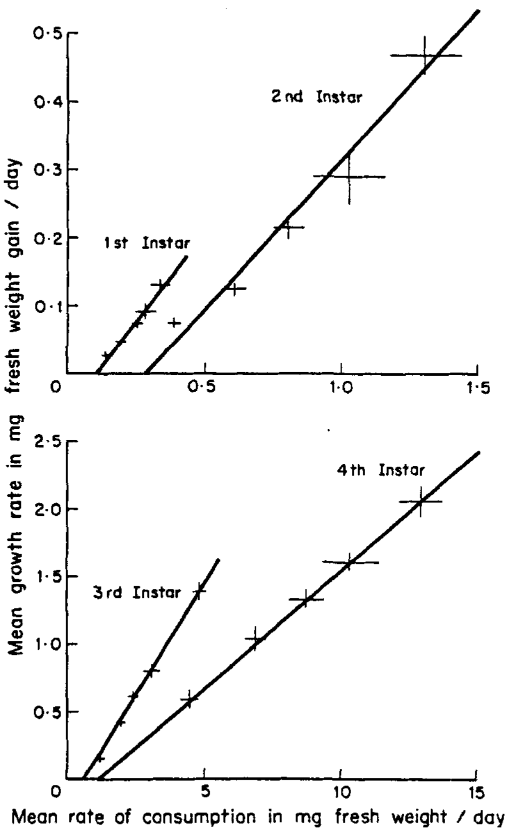

FIG. 1 The linear dependence of mean (±SE, n = 6–10) growth rates on rates of consumption for the four larval instars.

This provides a linear relationship between growth rate and rate of consumption, but assumes respiratory rate and digestive efficiency to be constant. While the latter may be appropriate for many insects (e.g. Lawton *et al.*, 1980), respiratory rate is likely to increase with rate of consumption. If the increase is linear, then equation (4) becomes:

$$G = k'I - B \qquad (5)$$

where B is the basal metabolic rate and k' is a measure of the gross conversion efficiency of consumed food to larval growth. However, if the increase in respiratory rate is non-linear, then growth rate would conform to a non-linear model, such as suggested by Beddington *et al.* (1976):

$$G = \gamma(\ln I - C) \qquad (6)$$

where C is the threshold rate of consumption for growth and γ is a constant.

TABLE 1. Regression analysis of the dependence of larval growth rate on rate of consumption. Intercept (*a*), slope (*b*), coefficient of determination (R^2) and a variance ratio (*F*) of the residual variances from linear and quadratic regression tests for non-linearity.

Instar	*a*	*b*	R^2	*F*	
1	−0.055	0.533	0.76	2.10	N.S.
2	−0.126	0.442	0.90	0.21	N.S.
3	−0.214	0.335	0.95	0.87	N.S.
4	−0.205	0.175	0.91	0.02	N.S.

The coccinellid growth rates show no indication of non-linearity (Table 1) and can therefore be interpreted in terms of equation (5). The slopes of the relationship, representing the gross conversion efficiency, decrease as the coccinellid progresses through the larval instars. While this is partly due to increased metabolic costs, as can be seen from the ordinate intercepts representing basal respiratory rates, the decrease is largely due to a decline in digestive efficiency. This results as a consequence of the larvae consuming a greater part of the total body of the prey as they increase in size in each successive instar.

The linear model for predator development rate (equation (3)) proposed by Beddington *et al.* (1976), assumes that the weight gain in each instar is constant. In Table 2, the weight gain during an instar is shown to be a function of the rate of consumption and the teneral weight. The multiple regression coefficient for teneral weight is significant for all but the first instar, which hatches at a fairly constant weight. However, teneral weight accounts for less than 5% of the variance, while rate of consumption explains 47–75%.

TABLE 2. Regression analysis of the dependence of weight gain on rate of consumption (*I*) and teneral weight (Wi). Intercept (*a*), slope (*b*), coefficient of determination (R^2) and *F*-test (*F*) for the regression.

Instar	*a*	b_I	b_{Wi}	R^2	*F*
1	0.006	1.015		0.47	28.97***
	0.006	1.016	−0.005	0.47	14.05***
2	−0.013	0.879		0.66	74.29***
	−0.338	0.817	0.916	0.69	41.88***
3	0.290	0.645		0.73	88.05***
	0.264	0.629	0.058	0.73	42.73***
4	1.964	0.509		0.75	82.26***
	2.138	0.393	0.252	0.76	43.04***

The derivation of the predator development rate model in equation (3) is:

$$1/d = G/Wg \tag{7}$$

Considering weight gain (Wg) to be simply a linear function of the rate of consumption, and growth rate (*G*) as in equation (5), then:

$$1/d = \frac{k'I - B}{K(I - i)} \tag{8}$$

where *i* is the threshold rate of consumption for survival of the instar and *K* is a conversion efficiency equivalent to $k'd$. Equation (8) describes a negatively accelerating curve rather than a straight line for the relationship between development rate and rate of consumption.

The rate of development of the coccinellid larval instars is given in Fig. 2. The data were

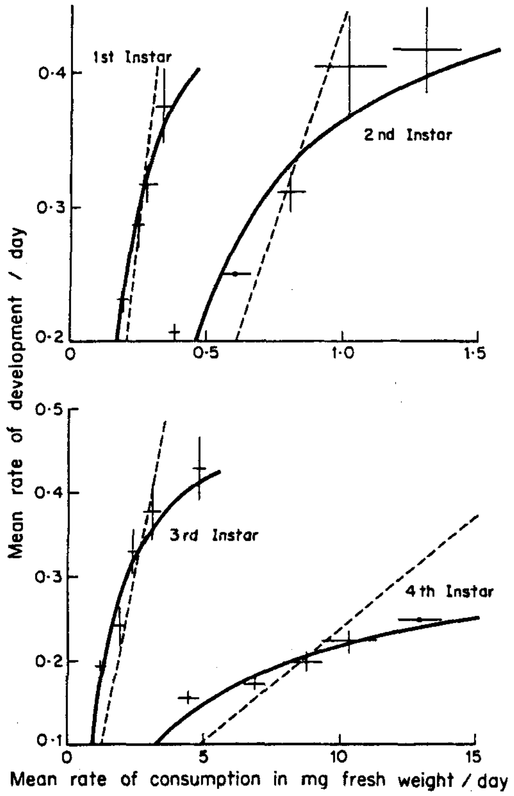

FIG. 2. The relation between mean (±SE, n = 6–10) development rate and rate of consumption for the four larval instars, indicating the fit of the linear (– – –) and non-linear (——) models. (Points without errors for the mean rate of development are where all individuals completed the instar on the same day.)

TABLE 3. A comparison of the residual sum of squares (RSS) for the fit of the development rate data to the linear and non-linear models. The coefficient of determination (R^2) for the non-linear model and a variance ratio test (F) for the reduction in RSS indicate a better fit of the non-linear model.

Instar	Linear model RSS	Non-linear model RSS	Non-linear model R^2	F
1	0.163	0.083	0.45	14.9***
2	0.666	0.179	0.57	49.1***
3	0.737	0.163	0.60	54.7***
4	0.067	0.013	0.71	56.2***

fitted to both the linear model of equation (3) and the non-linear model of equation (8). The estimates from linear regression of growth rate in relation to the rate of consumption (Table 1) were used for both models. A mean value for weight gain was used for the linear model, and the regression estimates for the dependence of weight gain on rate of consumption (Table 2) for the non-linear model. In Table 3 the residual sums of squares are given for the fit of both models to the data.

The non-linear model produces a significant reduction in the residual sums of squares and accounts for 45–71% of the variance in development rate. The explained variance remains relatively low due to the crude measurement of instar duration to the nearest day.

The fecundity of adult females expressed as mg fresh weight of eggs produced per day (mean egg weight is 0.13 mg), is a linear function of the rate of consumption (Table 4). The dependence of fecundity on adult female weight, determined at an excess level of food, is negligible and does not reduce the residual variance, over the range (11.0–19.1 mg) of adult weight used.

This supports the linear model proposed by Beddington *et al.* (1976) in equation (2) but is better interpreted in terms of the larval growth model of equation (5). The slope of the regression, representing the gross conversion efficiency is greater than that of fourth instar larvae (Table 1) while the intercept, representing the basal respiratory rate, is considerably higher. The higher metabolic costs are associated with the production of eggs.

TABLE 4. Regression analysis, with elevation (a), slope (b), coefficient of determination (R^2) and variance ratio test (F), for the dependence of adult fecundity on: 1, the rate of consumption (I), and 2, the rate of consumption and adult weight (W).

	a	b_I	b_W	R^2	F
1	−1.230	0.205		0.89	210.4***
2	−1.245	0.205	0.001	0.89	101.0***

The influence of temperature

Although given a constant food ration, the rate of consumption varied with temperature. The larval growth rates and development rates are well correlated with the changes in rate of consumption at the different temperatures (Table 5). The primary effect of temperature is therefore through its influence on the rate of consumption. However, adult fecundity declines at higher temperatures despite an increase in rate of consumption.

The influence of temperature on growth, development and fecundity rather than consumption is assessed by a comparison of the mean rates at the experimental temperatures with those predicted from the regressions determined at 20°C for the appropriate rates of consumption. Cochran's t-test approximation for means with differing variance (Snedecor & Cochran, 1967) indicates significant departures from the predicted rates at 20°C (Table 5).

For temperatures below 20°C, growth rate and fecundity differ little from that expected from the rates of consumption. However, above 20°C fecundity of the adults and growth rates for the first two larval instars are reduced, while growth rates for the last two instars are enhanced. The maximum fecundity and growth rate is attained at 20°C, 20°C, 22.5°C, 22.5°C and 25°C for adult, first, second, third and fourth instars respectively.

The differing temperature optima may reflect the increasing temperatures experienced by the coccinellids as they progress through the life-cycle in the field. While these temperatures are higher than ambient air temperatures, the coccinellids are likely to experience higher temperatures due to absorption of sunlight (e.g. Digby, 1955). Growth and egg production may then be limited by the rate

TABLE 5. Mean rates of consumption (C), growth (G), development ($1/d$) and fecundity (F) in relation to temperature, with correlations (r) between mean rate of consumption and mean rate of growth/development and t-tests for significant departures (+ or −) from the rates expected at 20°C for the rate of consumption. (− or + $0.05 > P > 0.01$; −− or ++ $0.01 > P > 0.001$; −−− or +++ $P < 0.001$.)

Temp. (°C)	Stage 1			Stage 2			Stage 3			Stage 4			Adult	
	C	G	1/*d*	C	G	1/*d*	C	G	1/*d*	C	G	1/*d*	C	F
15	0.196	0.037	$\overset{---}{0.113}$	0.706	0.155	$\overset{---}{0.167}$	1.764	0.406	$\overset{---}{0.154}$	5.587	0.738	$\overset{---}{0.095}$	11.550	0.975
17.5	0.275	0.063	$\overset{---}{0.204}$	0.921	0.280	$\overset{---}{0.250}$	2.529	$\overset{+}{0.736}$	$\overset{-}{0.287}$	9.805	1.498	$\overset{--}{0.196}$	14.804	$\overset{-}{1.224}$
20	0.337	0.131	0.346	1.028	0.291	0.405	3.061	0.808	0.379	10.326	1.611	0.225	13.909	1.468
22.5	0.366	$\overset{-}{0.093}$	0.333	1.227	$\overset{--}{0.336}$	$\overset{--}{0.333}$	3.412	$\overset{+}{1.091}$	$\overset{+++}{0.500}$	11.362	$\overset{++}{2.088}$	$\overset{++}{0.250}$	17.402	$\overset{---}{1.248}$
25	0.315	$\overset{--}{0.071}$	$\overset{--}{0.273}$	0.904	$\overset{--}{0.214}$	0.336	2.625	$\overset{++}{0.793}$	0.345	13.191	$\overset{+}{2.481}$	$\overset{++}{0.310}$	17.384	$\overset{---}{0.975}$
r		0.81	0.95		0.94	0.70		0.97	0.98		0.98	0.99		0.03

of consumption below the temperature optimum while temperatures above the optimum have a deleterious effect through increased respiratory costs.

At the lower temperatures, the rates of larval development are dramatically reduced, allowing a comparable weight gain in each instar at the low rates of consumption. For temperatures above 20°C the rate of development tends to be reduced for the smaller instars indicating a deleterious effect above the optimum, while it is enhanced for the larger larval instars with higher temperature optima.

The resultant larval development

The end result of the influence of temperature and feeding level on the growth and development of *Adalia bipunctata* is summarized in Fig. 3. A two-fold increase in the total food consumed by the larval stages at 20°C results in a similar increase in the rate of development from egg hatch to adult emergence and a three-fold increase in adult weight. Mean adult female weight is greater than that for males, although both are influenced to the same extent by changes in feeding level.

As temperature increases from 15°C, the total larval food consumption decreases to an asymptotic value. Hodek (1973), in reviewing the data for coccinellids, suggests that temperature has no effect on total food consumption by larvae, although the work of Gurney & Hussey (1970) shows a similar decline with rise in temperature. The development rate increases to an asymptote, while adult weights remain constant over the temperature range. The rate of development is reduced at the lower temperatures, allowing comparable growth despite the low rates of consumption.

Discussion

The linear relationship between growth rate, fecundity and rate of consumption is a general result common to both phytophagous and predatory arthropods (Beddington *et al.*, 1976). Many of these arthropods also show a linear dependence of development rate on rate of consumption (see examples in Beddington *et al.*, 1976). However, the present study indicates that, at least for coccinellid larvae, the weight gain during an instar is itself a function of the rate of consumption which generates a non-linear model for development rate.

Recently, Lawton *et al.* (1980) have shown that development rates for *Ischnura elegans* (van der Lind.) conform to a non-linear model, based on the non-linear growth rate model of equation (6) with a constant weight gain per instar. They cite examples of other non-linear development rates in arthropods, but, as in the case of the coccinellid larvae, such non-linearity is not always attributable to non-linearity of growth rates.

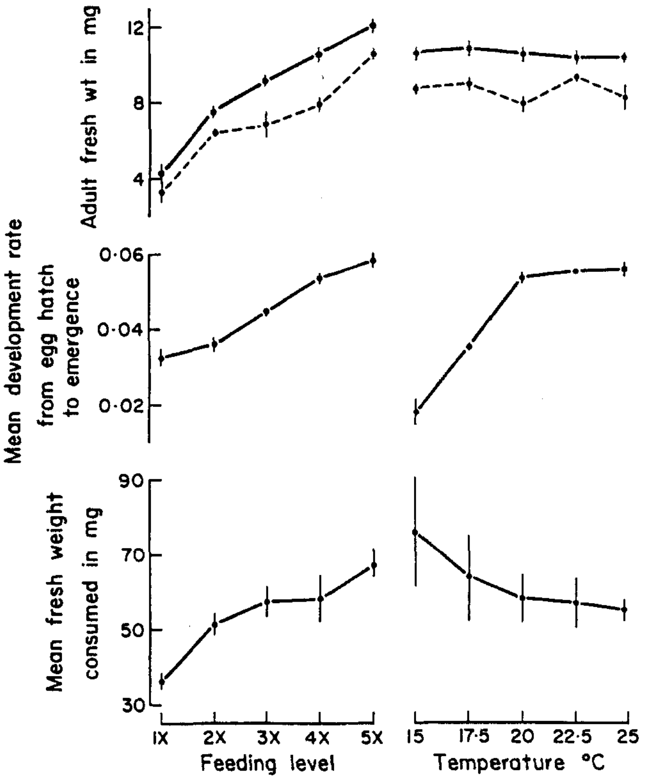

FIG. 3. The mean (±SE, $n = 6–10$) consumption and development rate of the juvenile stages and final adult weight (– – –, ♂; ——, ♀) in relation to the level of feeding (at 20°C) and temperature (at 4 X feeding level).

In the quantitative study of growth and development of *Podisus maculiventris* (Say) by Mukerji & Le Roux (1969), the development rates appear to be non-linear while growth rates are clearly linear. Similarly, for *Pseudaletia unipunctata* (Haw.), Mukerji & Guppy (1970) found linear growth rates with non-linear rates of development.

Growth and development in arthropods therefore appears to vary for different species. Since the dependence of growth rate on rate of consumption can be linear or non-linear, this leads to both linear and non-linear functions of development rate, under the assumption of a constant weight gain during an instar. Then if, as for the coccinellid, weight gain is also a function of the rate of consumption, the resulting models for development rate exhibit a greater degree of non-linearity.

Despite the obvious importance of fluctuations in field temperatures, little interest has been shown in the influence of temperature on predator–prey interactions. The primary influence of temperature is through its effect on the rate of consumption. At each temperature there is a maximum rate of passage of food through the gut, setting an asymptotic value for the prey death rate at higher prey densities. As pointed out by Anderson *et al.* (1978), the asymptote of the functional response can equally well be generated by the effects of handling time or satiation. The two are related in that:

$$N_{\max} = T/T_{\mathrm{h}}$$

where $N_{\max}$ is the maximum rate of consumption, T is the total time available for predation and T_{h} is the handling time.

From this relation, the handling time for each coccinellid stage can be determined from the reciprocal of the rates of consumption (Table 6), assuming these to be near the maximum at each temperature. The handling time decays exponentially with rise in temperature,

TABLE 6. The handling time of the coccinellid stages, in days per mg fresh weight consumed, in relation to temperature.

Temp. (°C)	Stage				
	1	2	3	4	Ad
15	5.10	1.42	0.57	0.18	0.09
17.5	3.64	1.09	0.40	0.10	0.07
20	2.97	0.97	0.33	0.10	0.07
22.5	2.73	0.81	0.29	0.09	0.06
25	3.17	1.11	0.38	0.08	0.06

as was found by Thompson (1978) for *Ischnura elegans.* However, at higher temperatures this trend can be reversed, as in instars 1–3.

The predator rate of increase is dependent on the rate of consumption, as influenced by prey density and temperature. While Beddington *et al.* (1976) have produced models based on prey density, the data presented here indicate that temperature is also important in determining the dynamics of the predator population. It may be that the temperatures experienced by coccinellids in the field are largely responsible for the fluctuations in their abundance from year to year.

In years when field temperatures fall below the optimum, oviposition would be reduced and the prolonged period of larval development would increase their exposure to mortality. This could result in a reduction of coccinellid abundance, even when prey availability is not limiting. In contrast, when field temperatures approach the optimum for each stage, and prey are sufficiently abundant, enhanced oviposition and development could produce unusually large populations of emergent adult coccinellids.

Thus temperature, through its influence on the rate of passage of food through the gut, sets the level of satiation and the asymptote of the prey death rate. It provides an upper limit to the predator rate of increase, the realization of which is determined by the functional response to prey density. There is therefore a need to estimate predator rates of consumption in the field in relation to both prey density and temperature. This would give a clearer picture of the impact of predation on prey populations and of the application of the component approach to arthropod predation to the field situation.

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