The Growth and Voracity of Larvae of *Leis conformis* (Boisd.) (Coleoptera : Coccinellidae) Fed on the Rose Aphid *Macrosiphum rosae* (L.) (Homoptera : Aphididae) in the Laboratory

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Abstract

The ladybird *Leis conformis* is one of the commonest predators of the rose aphid, and of other aphids in South Australia. When fed a surfeit of *M. rosae* the mean weights of larvae during development could be described by the equation: $y = 0 \cdot 45 \exp[(0 \cdot 0313t - 0 \cdot 2751)x]$ where t is temperature in degrees Celsius such that $15 < t < 29 \cdot 2$, and x is time in days, such that $y < 40 \cdot 6$ mg. The mean weights could also be described by: $y = \exp (0 \cdot 0347x - 0 \cdot 8551)$, with x in day-degrees above 10°C. The voracity of larvae could be described in third-instar aphid equivalents (TIES) by: $y = \exp (0 \cdot 0347x + 0 \cdot 6219)$ where y is cumulative number of TIES eaten, and x is less than $131 \cdot 4$ day-degrees. The TIE units used to convert predator wet weight to aphid units eaten were based on the numbers of aphids of each instar that had to be eaten for a predator larva to gain one milligram of wet weight. It is suggested that the voracities of different ladybirds feeding on different aphids can be compared when voracity is expressed as the cumulative number of aphids eaten per stadium. The quantification of voracity in the field, and the possible use of *L. conformis* for pest control, are briefly discussed.

Introduction

The 18-spotted ladybird, *Leis conformis* (Boisduval), is one of the largest and commonest coccinellids that feed on aphids in Australia. It is found over all the temperate areas, at least, and feeds extensively on introduced aphid species on rose, citrus, apple, peach and other plant species. Thus Froggatt (1902) records it as an efficient predator of *Eriosoma lanigerum* (Hausmann) and Ward (1934) records that in Victoria its numbers 'frequently reduce markedly' the numbers of *Myzus persicae* Sulzer in peach orchards in October–November. So, too, Wilson (1960) suggests that the comparative rarity of *Toxoptera aurantii* (Boyer de Fonscolombe) on citrus in Eastern Australia 'was attributed to the predator *Leis conformis*'. On the other hand it feeds on, but apparently makes little significant impact on, the numbers of *Aphis craccivora* Koch on peas (Grylls 1972), and it was not recorded by Gutierrez *et al.* (1971) as a predator of *Aphis craccivora* on subterranean clover.

The natural history of *L. conformis* was outlined by Froggatt (1902) but, although it is a common species and although it has been introduced (usually unsuccessfully) into several countries (Wilson 1963), little is known of the quantitative aspects of its biology. Moursi and Kamal (1946) studied some aspects of its biology in the laboratory in Egypt before it was released in the field, and other references (e.g. Watson and Thompson 1933; Muma 1955) come from Florida. However, R. I. Sailer (personal communication) is satisfied that the species in Florida now is *Leis dimidata 15-spilota*.

In South Australia, *L. conformis* is one of the main predators of *Myzus persicae* on peaches, of *Aphis gossypii* Glover on hibiscus and of *Toxoptera citricidus*

(Kirkaldy) on citrus. It is also one of the predators responsible for the relatively low numbers of *Macrosiphum rosae* (L.) on roses at most times of the year (Maelzer 1977).

This study of the growth and voracity of *Leis conformis* was undertaken to help quantify the relation between the predator and field populations of the aphid, *M. rosae*.

Life Stages of *Leis conformis*

The adults of *L. conformis* are '... of a uniform bright orange-yellow, thickly spotted with black, forming four black marks on the thorax and four transverse rows across the wing covers, the first and third containing five, the second six, and the last two spots...' (Froggatt 1902). The sexes are easily distinguished by the colour of the eusternum, which is white-yellow in the male and black in the female. In the male the area between the forelegs is also usually white, but the eusternum is a more reliable criterion. Mean weights and sizes of newly moulted adults of both sexes derived from well fed larvae are given in Table 1.

The eggs are yellow and laid in clusters, usually on the leaves of the plant on which the prey is feeding; their mean size and mean weight are also given in Table 1. There are four larval instars that are easily distinguished morphologically; they are also easily distinguished morphometrically if they are well fed (Table 1).

Table 1. Mean sizes of different stages of *Leis conformis*

Stage	N	Weight (mg)	Egg	Length (mm) Hind tibia	SD
Newly emerged adults					
Males	13	27·6			2·25
Females	21	35·4			3·53
Eggs	31	0·61	1·53		0·04
Larvae					
1st instar	41	0·25[A]		0·561	0·022
2nd instar	51			0·741	0·028
3rd instar	27			1·026	0·036
4th instar	20			1·510	0·087

[A] At hatching.

The Influence of Temperature on the Increase in Weight of Larvae

Methods

After the eggs hatch, the larvae—like those of other coccinellids (Banks 1956; Hodek 1973)—spend a few hours on the egg-mass, during which time they eat other eggs that have not hatched or larvae that are 'weak'. At 20°C the larvae moved off the egg-mass in 36–40 h.

The development of larvae in relation to temperature was assessed for larvae which had just dispersed off their egg-masses. Each larva was put into a plastic vial 5 by 2·5 cm, with a surfeit of aphids of all instars, and was weighed every day or two until pupation. Fresh aphids were supplied daily. Ten larvae were reared at each temperature.

Results

The obvious linear trends in the mean logarithmic weights (Fig. 1) suggested that the regression of larval weight on time at any one temperature could be expressed as

$$\ln y = \ln a + bx + \varepsilon, \tag{1}$$

where *y* is the mean weight of larvae on days >1; *a* the mean weight of larvae on

day 1; x the time in days; and ε a random variable drawn from $N(0, \sigma_y. x)$ (Snedecor and Cochran 1973). Since $(\ln y - \ln a)$ may be expected to be proportional to x, and since the variance of ε is constant, the common ratio $(\ln y - \ln a)/x$ is best estimated as $\Sigma xy / \Sigma x^2$ (Snedecor and Cochran 1973).

The value of b thus obtained for each temperature was then fitted by the linear equation:

$$b = -0.2751 + 0.313t \quad (r = 0.996), \tag{2}$$
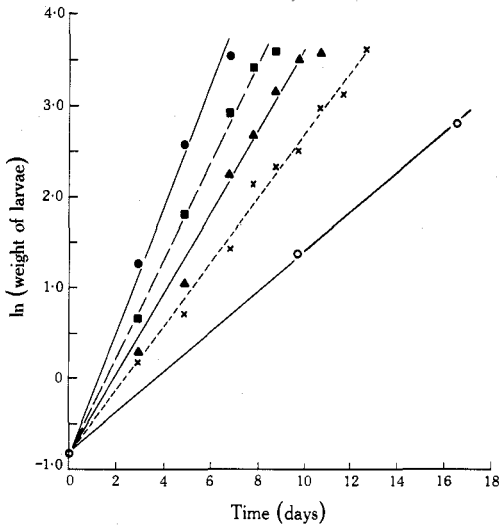
where t is temperature in degrees Celsius.

Fig. 1. Weight of larvae (to ln) during development at different temperatures.
● $29.2 \pm 0.3°C$; $y = 0.6314x - 0.7076$; $r = 0.997$;
■ $25.0 \pm 0.2°C$; $y = 0.5154x - 0.7842$; $r = 0.997$;
▲ $22.5 \pm 0.3°C$; $y = 0.4485x - 0.9447$; $r = 0.997$;
× $20.0 \pm 0.2°C$; $y = 0.3417x - 0.8204$; $r = 0.996$;
○ $15.0 \pm 0.2°C$; $y = 0.215x - 0.8000$; $r = 0.999$.

Data for larvae at 15°C are included in Fig. 1, but not in equation (2) because no larvae completed their development at 15°C.

The value of b in equation (2) may now be substituted in equation (1) to give:

$$\ln y - \ln a = x(0.0313t - 0.2751) + \varepsilon,$$

with the constraint $15°C < t < 29.2°C$. Or, putting in the original weight of the larvae and converting to arithmetic, deterministic form:

$$y = 0.45 \exp[(0.0313t - 0.2751)x], \tag{3}$$

with the constraint $y \leqslant 40.68$ mg, which was the mean weight of prepupae. Finally, the number of days (y) from the time the larvae walked off the egg-masses until pupation could be regressed on temperature (x) by: $y = 0.00693x - 0.08309$, and the number of days to adult emergence by: $y = 0.00482x - 0.05769$. Both these equations imply a threshold of development of 12°C. It is likely that some development can occur between 12°C and 15°C but that temperatures higher than 15°C are needed for its completion.

The Voracity of Larvae

The voracity was measured for 34 larvae fed on various instars of *M. rosae* at $20.0 \pm 0.2°C$. Each larva was kept in a separate vial and fed a controlled surfeit of aphids each day. It was weighed daily and the numbers of aphids it ate each day were

recorded. Larvae were fed different numbers of different stages of aphids in two experiments during their development.

Before discussing the experiments it is useful to discuss the trend in mean log weight of all the larvae during their development. The trend is shown in Fig. 2 with the mean weights expressed to the base 10 for convenience. It is obviously not linear and is better expressed as a series of smooth curves, which have been drawn by eye.
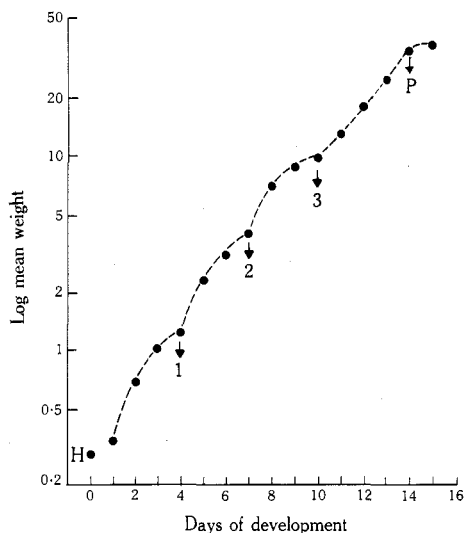

Fig. 2. Mean log weight of larvae of *Leis conformis* during development at $20 \cdot 0 \pm 0 \cdot 2°C$. Arrows, approximate weights and times at hatching (H), at the end of the first three stadia (1, 2, 3) and at the change to the prepupa (P).

The marked decreases in slope of the curves at days 4, 7, 10 and 14 coincide with modes of moulting to the next instar and with the change of larvae to prepupae. It is thus apparent that the voracity of larvae decreases before a moult, as has often been recorded before for insect predators [for example, see Hodek (1973)]. Hence the probability of capture of an aphid by a predator larva should vary with the stage of development of the predator within the stadium.

Experiment 1

The aim of this experiment was to determine whether there was any preference by *L. conformis* larvae for different aphid instars, as is shown by larvae of *Adalia decempunctata* (L.) for different instars of the aphid *Microlophium evansi* (Theobald) (Dixon 1959). Larvae were taken off egg-masses about a day after they hatched and before they left the egg-masses naturally (36–40 h at 20°C).

Four treatments consisting of different combinations of aphid instars were each fed to four larvae on each of days 2–9 of larval development (Table 2). The aphids were fed to the predators on young excised rosebuds inside small plastic vials, and the treatments were randomized each day amongst the 16 larvae.

The experiment was not designed to be analysed by treatments but rather by pooling the results of all the treatments for each day. The treatments were included so that preference could be tested over a range of probabilities of occurrence of different aphid instars.

The last line of Table 2 (totals) indicates that on each of the days 2–6, the 16 larvae were given a total of 240 aphids in the ratios 7 : 2 : 2 : 1 (first : second : third : fourth instars); and on each of the days 7–9 a total of 560 aphids were given in the ratios 2 : 1 : 1 (second : third : fourth). These ratios are converted to percentages of total

prey presented in columns 2 and 8 of Table 3. The proportion of any aphid instar eaten on one day was similarly estimated by totalling the numbers of that instar eaten that day by each of the 16 larvae and dividing by the total number of prey presented. The proportions are expressed as percentages in Table 3.

Table 2. Numbers of aphids of different instars fed to larvae of *Leis conformis* in experiment 1

Treatment number	No. of aphids given on days 2–6				No. of aphids given on days 7–9		
	Instar 1	Instar 2	Instar 3	Instar 4	Instar 2	Instar 3	Instar 4
1	10	5			15	5	15
2	10		5		15	15	5
3	10			5	20	10	5
4	5	5	5		20	5	10
Total	35	10	10	5	70	35	35

For no preference to be manifest, the percentages of prey eaten should be similar to the percentages presented. The data indicate an obvious preference for certain aphid instars. Chesson (1977) has shown that this preference is due to different probabilities of capture, as also manifest by *Adalia decempunctata* feeding on *Microlophium evansi* (Dixon 1959) and *Adalia bipunctata* (L.) feeding on *Eucallipterus tiliae* (L.) (Wratten 1973). The data also indicate clearly the changing preference of *L. conformis* for different aphid instars from day to day, with low proportions of prey—in particular, of others than first-instar—being eaten on days on which most of the larvae moulted. Only on day 8 was there no obvious preference.

Table 3. The percentages of different instars of *M. rosae* presented as prey, and the percentages of the instars eaten, by *L. conformis* larvae

Aphid instar No.	Percentage of total presented	Percentage eaten on day No.:				
		2	3	4[A]	5	6
First	58·3	28·3	29·2	29·8	44·6	47·5
Second	16·7	2·5	7·1	0·8	7·9	12·9
Third	16·7	2·5	4·6	0·8	8·8	2·9
Fourth	8·3	0	0·4	0·4	1·3	0·8

Aphid instar No.	Percentage of total presented	Percentage eaten on day No.:		
		7[A]	8	9
Second	50·0	15·7	45·0	32·5
Third	25·0	1·8	21·4	12·5
Fourth	25·0	0·7	20·0	5·4

[A] Days on which most of the larvae of *L. conformis* moulted to the next instar.

More extensive data on preference and on the probability of capture of *M. rosae* by *L. conformis* are given by Chesson (1977) who used Dixon's (1959) method of successful encounters as a measure of the probability of capture. It is of interest that the ratios of (percentage of instar eaten)/(percentage of total prey) for each instar calculable from Table 3 are often of the same relative magnitude to each other as the

probabilities estimated by Chesson (1977). Data of the sort given in Table 3 may, therefore, give good estimates of the relative probabilities of capture of aphids of different instars, especially because such data are obtained over much longer periods than are those used to estimate probabilities of capture by successful encounters, and thus probably span a number of periods of hunger and non-hunger.

Experiment 2

The aim of this experiment was to determine the numbers of aphids of different instars that had to be eaten by a predator for its wet weight to increase by a standard amount. Larvae were again taken off the egg-mass 1 day after hatching, but in this experiment each larva was fed a surfeit of aphids of only one instar from one moult to the next. First- and second-instar larvae were fed on first- or second-instar aphids; third- or fourth-instar larvae were fed on all aphid stages except the first instar. There were six larvae at each treatment.

Table 4. **Weight gains of *L. conformis* larvae fed on aphids**
Dixon's (1959) estimates of third-instar equivalents of aphid instars were calculated from dry weights
of *Microlophium evansi*

Aphid instar No.	Wt gain from eating one aphid (mg)	No. aphids for 1 mg gain wet wt (y_1)	Mean wt (mg) of these aphids		Third-instar equivalents based on:			Dixon's estimates
			Wet (y_2)	Dry (y_3)	y_1	y_2	y_3	
First	0.0443 ± 0.0038	22.57	0.205	0.047	0.19	0.30	0.32	0.16
Second	0.1379 ± 0.0125	7.25	0.428	0.094	0.60	0.63	0.64	0.54
Third	0.2283 ± 0.0217	4.38	0.678	0.147	1.00	1.00	1.00	1.00
Fourth	0.4457 ± 0.0283	2.24	1.161	0.316	1.96	1.71	2.15	1.97
Adult	0.6216 ± 0.0705	1.61	2.034	0.523	2.72	3.00	3.55	2.24

Table 4 gives the mean wet weight gained by a predator after eating one aphid of each instar, and hence the number of aphids that had to be eaten for a gain in wet weight of 1 mg. The table also gives the mean wet and dry weights of different instars of *M. rosae* used to feed the *L. conformis* larvae, and (in columns 7–9) the third-instar equivalents (TIES) based on the number of aphids that had to be eaten for a standard gain in weight (y_1), the wet weight of aphids (y_2) and the dry weight of aphids (y_3). Finally, Table 4 shows Dixon's (1959) estimates of TIES for *Adalia decempunctata* based on the dry weights of the aphid *Microlophium evansi*.

Dixon (1959) used the dry weights of other instars of *Microlophium evansi* to determine the number of other instars that were equivalent to a third-instar aphid. However, the TIES based on dry weights of *M. rosae* are somewhat different from those necessary for a *L. conformis* larvae to gain 1 mg in wet weight. It is of interest, therefore, to ascertain which set of TIES is the more useful. A suitable test is to calculate expected mean weights of larvae based on the numbers of aphids they ate in the first experiment on voracity, and determine which TIES give weights that are closer to the observed mean weights of larvae. Since, by chance, the dry weight of a first instar of *M. rosae* (0.047 mg) is very close to the value of 0.044 mg for the gain in weight of a predator after eating one first-instar aphid, the dry weights were considered to produce gains in weight equivalent to their face values. The results are given in Table 5, from which it seems clear that TIES based on dry weights of

aphids are the less useful for predicting the wet weight of the predator larvae. The corollary is that they are also the less useful for predicting the numbers of other instars eaten by *L. conformis* larvae.

Discussion

The Comparative Voracity of Aphidophagous Coccinellids

Comparisons of the voracity of aphidophagous coccinellids are difficult because the number of aphids eaten is usually a function of the number available (the so-called functional response of the predator–prey relationship), and also because the species of aphids can influence a coccinellid's rate of development and survival [see Hodek (1973) for summary].

Table 5.   Observed mean weights of *L. conformis* larvae during the first 10 days of their development at 20°C, and their expected mean weights based on two types of aphid TIE

TIE, third-instar equivalent: type 1, based on numbers of aphids required to be eaten for an increase of 1 mg in the wet weight of a predator larva; type 2 based on the estimated dry weights of the aphids eaten. Data for experiment 1 only

Days from hatching	Observed mean wt (mg)	Expected mean wt (mg)	
		TIE type 1	TIE type 2
1	0·35	—	—
2	0·70	0·67	0·64
3	1·07	1·18	1·08
4	1·33	1·42	1·32
5	2·39	2·37	2·04
6	3·33	3·08	2·67
7	4·48	4·30	3·60
8	8·01	6·51	5·16
9	9·38	7·58	6·08
10	9·98	9·65	7·01

For aphid species that do not significantly influence the rates of survival or development of predators, it would be of interest to determine which properties of prey—other than prey density—and which properties of predators influenced the voracities of the latter.   Initially one requires a method of quantifying voracity. Since voracity varies within a stadium, the number of aphids eaten per unit time is unlikely to be a good criterion. Alternatively, voracity may be expressed as a function of physiological time (e.g. Gilbert and Gutierrez 1973), or as the number of aphids eaten per stadium.   The latter criterion is also independent of time and may be quantified simply.   Thus, for some species of predator and prey, mean log (number of prey eaten per stadium) is a linear function of the stadium [e.g. *Geocoris punctipes* (Say) feeding on eggs of *Pseudoplusia includens* (Walker) (Crocker *et al.* 1975)].   For many species of coccinellids, however, a better linear fit is given by the regression of log (cumulative number of aphids eaten) on the number of the stadium.   Thus the mean weights, at the end of the stadia, of the 34 *L. conformis* larvae in the two experiments were: 1·22, 3·39, 11·17 and 40·3 mg, which convert to 3·8, 13·3, 47·4 and 175 TIEs after subtracting the initial weight of the larvae (0·35 mg).   These

cumulative TIES (y) can be related to the number of the stadium (x) by the equation:
$\ln y = 1 \cdot 2706x + 0 \cdot 0465$.

Plots of data of this kind for numerous ladybird–aphid combinations yield groups with similar slopes (Figs 3, 4) and pose the questions: Why are the slopes in each group similar, and why are they different from those in the other group? Why do the slopes for *Leis conformis* differ when the predator eats *Macrosiphum rosae* (Fig. 3) and *Aphis durantae* Theobald (Fig. 4)? Can the slopes and intercepts of the lines be explained by the relative sizes of the aphids or of the ladybirds?
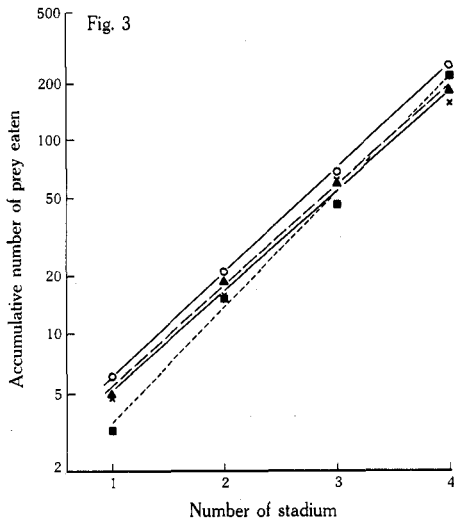
Fig. 3. Regression of the cumulative number of aphids (to ln) eaten on the number of the stadium. ○——○ *Harmonia axyridis* feeding on *Myzus persicae* (Hukusima and Ohwaki 1972). ▲— —▲ *Leis conformis* feeding on TIES of *Macrosiphum rosae* (this study). ×——× *Adalia decempunctata* feeding on *Microlophium evansi* (Dixon 1959). ■– – –■ *Hippodamia quinquesignata* Kirby feeding on *Macrosiphum pisi* (Kaltenbach) (Kaddou 1960) (mean of 80 and 86°F).
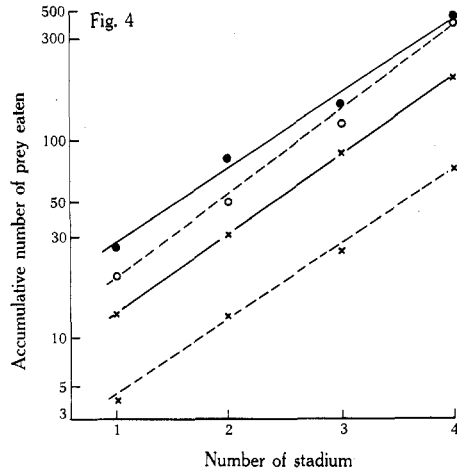
Fig. 4. Regression of the cumulative number of aphids (to ln) eaten on the number of the stadium. ●——● *Coccinella undecimpunctata aegypticae* Reiche feeding on *Aphis durantae* (Ibrahim 1955). ○– – –○ *Leis conformis* feeding on *Aphis durantae* (Moursi and Kamal 1946). ×– – –× *Propylaea japonica* Thunberg feeding on *Nasonovia lactucae* (L.) (Hukusima and Komada 1971). ×——× *Adalia bipunctata* (L.) feeding on *Myzus persicae* (Ellingsen 1969).

Similarly, Hukusima and Kamei (1970) fed a number of different aphid species to the coccinellid *Harmonia axyridis* Pallas. These data (Fig. 5) also suggest obvious questions about the similarity of differences in slope and intercept in terms of the properties of the aphids. Such questions can be answered only if authors included in their papers the following data on the properties of aphids and predators: mean wet weights and dry weights of aphids fed to predators; mean weights of predators at egg-hatch and at the end of the stadium; time for development to end of each stadium of the predator; the cumulative number of aphids eaten by the predator to the end of each stadium.*

* Dr Mary Carver informs me that: *Nasonovia lactucae* (L.) is better known as *Hyperomyzus lactucae* (L.); *Macrosiphum pisi* (Kaltenbach) is a synonym of *Acyrthosiphon pisum* (Harris); *Aphis durantae* Theobald is a synonym of *Aphis punicae* Passerini; *Hyalopterus arundinis* (F.) is a synonym of *Hyalopterus pruni* (Geoffroy); *Amphorophora oleraceae* (Van der Goot) is now known as *Hyperomyzus cardullinus* (Theobald).

In particular, the regressions of Figs 3–5 imply that the numbers of aphids eaten in any stadium may be expressed as:

$$y_n = y_1(\exp[b(n-2)])(\exp(b)-1) \quad \text{for } 4 \geqslant n \geqslant 2,$$

where n is the number of the stadium, y_n the number of aphids eaten in stadium n, and b the slope of regression (in Figs 3–5). y_1, the number of aphids eaten in the first stadium, and b may perhaps be explained by the properties of aphids and predators.
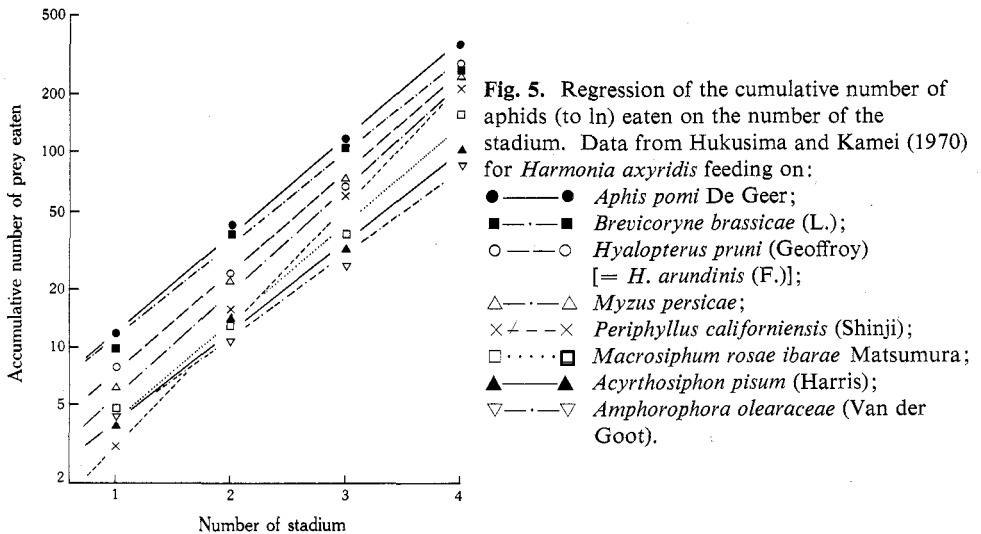

Fig. 5. Regression of the cumulative number of aphids (to ln) eaten on the number of the stadium. Data from Hukusima and Kamei (1970) for *Harmonia axyridis* feeding on:
●———● *Aphis pomi* De Geer;
■—·—■ *Brevicoryne brassicae* (L.);
○———○ *Hyalopterus pruni* (Geoffroy) [= *H. arundinis* (F.)];
△—·—△ *Myzus persicae*;
×⊥– –× *Periphyllus californiensis* (Shinji);
□·····□ *Macrosiphum rosae ibarae* Matsumura;
▲———▲ *Acyrthosiphon pisum* (Harris);
▽—·—▽ *Amphorophora olearaceae* (Van der Goot).

Numbers of Prey Eaten in the Field

Until recent computer simulation (Frazer and Gilbert 1976; Gilbert *et al.* 1976), two main methods have been used to estimate the numbers of aphids or other prey species eaten by coccinellids in the field. Wratten (1973) used an algebraic expression —for *Adalia bipunctata* (L.) feeding on *Eucallipterus tiliae* L.—which includes: (1) the area covered by the predators in unit time; (2) the density of prey per unit of leaf area; (3) the number of prey captured in 100 encounters; (4) the proportion of the available time the predators spend in feeding; (5) the age structure of the prey population; (6) the age structure and numbers of the predators. It would seem, however, that Wratten has not tested his model, and although he allowed for the influence of temperature on the movement of predators he did not study its influence on the probability of capture, on the length of time spent in searching and in feeding, and on other processes of predation in the field. As Gilbert *et al.* (1976) say, Wratten overlooked the overwhelming importance of temperature on the whole predation process.

Other workers have used Bombosch's (1963) model, or modifications of it, in which the variables 1–4 measured by Wratten (1973) are integrated into a single estimate of predator voracity. In particular, Tamaki *et al.*'s (1974) modification estimates the efficacy of a number of predator species feeding on aphids. However, predator efficacy, so measured, is a function not only of the interaction of predators and the density of the prey but also of the influence, on the prey population, of other

'...biotic and abiotic factors that are not yet incorporated into (the) model...', such as rain, temperature, and inter- and intraspecific competition (Tamaki *et al.* 1974). So the measurement of predator efficacy cannot lead us to a better understanding of the interaction between predators and prey. It may sometimes, however, be useful for the purpose for which it was devised, i.e. predicting the numbers of a pest in field populations.

Finally, Frazer and Gilbert (1976) have recently attempted to apply component analysis to predation of the pea aphid *Acyrthosiphon pisum* (Harris) by the ladybird *Coccinella trifasciata* Mulsant in the field. Their study, although restricted to adult ladybirds, illustrates the complexity of predation in the field and the need for suitable field experimentation. In addition, they suggest that temperature has a double effect on adult ladybirds and conclude that it has an overriding effect in both laboratory and field.

Similarly, the interaction of *Leis conformis* and *Macrosiphum rosae* in South Australia is likely to be dominated by temperature which, in Adelaide, ranges from a mean of 14·1°C in July to 27·8°C in January. Furthermore, predation by *Leis conformis* is mainly by larvae, so that the predation rate is also influenced by the changing age structure of the predator population.

The data presented in this paper are only the first step towards the study of the interaction of *Leis conformis* and *Macrosiphum rosae* in the field. They suggest that when prey density is not limiting, as in spring (Maelzer 1977), the voracity of *L. conformis* between two sampling times can be estimated as the change in weight of each predator; and the influence of temperature on voracity can then be allowed for from equation (3) as:

$$y_2 - y_1 = 0 \cdot 45[(\exp(0 \cdot 0313t - 0 \cdot 2751)x_2) - (\exp(0 \cdot 0313t - 0 \cdot 2751)x_1)],$$

where x_1 and x_2 are days, y_1 the mean weight of predators at time x_1, y_2 the mean weight of predators at time x_2 and t the mean temperature in degrees Celsius in the interval $x_2 - x_1$.

The change in mean weight $(y_2 - y_1)$ can then be converted to numbers of aphids eaten by dividing by any of the constants in column 2 of Table 4. For example, $(y_2 - y_1)/(0 \cdot 2283)$ will yield the numbers of aphids eaten in TIES.

Alternatively, the mean voracity of *L. conformis* larvae may be expressed as a function of day-degrees, as has been done for syrphid larvae feeding on *Masonaphis maxima* (Mason) (Gilbert and Gutierrez 1973). Such data can be fed directly into a computer simulation model, e.g. that of Gilbert and Gutierrez (1973), or they can be expressed algebraically for comparison with other predator–prey combinations. For *L. conformis*, such data can be obtained by transforming the data of Fig. 1 in two steps. Firstly, log weight of the predator can be regressed on day-degrees $>10°C$ [which is the threshold of development for its prey, *M. rosae* (Maelzer 1977)] as:

$$\ln y = 0 \cdot 0347x - 0 \cdot 8551; \quad (r = 0 \cdot 992). \tag{4}$$

Since the mean weight of prepupae was 40·6 mg, the number of day-degrees required for development of the larvae is estimated as 131·4. So equation (4) has the constraint $x \leqslant 131 \cdot 4$.

Secondly, the weight of larvae can be converted to numbers of aphids eaten. Thus, to convert weight to third-instar equivalents of *M. rosae*, each value of y can be multiplied by $(1/0 \cdot 2283)$, or 4·38. The result is to add ln 4·38 (1·4770) to the

value of the intercept in equation (4) to give:

$$\ln y = 0 \cdot 0347x + 0 \cdot 6219, \tag{5}$$

with y now being the cumulative number of aphids eaten. This equation also has the constraint $x \leqslant 131 \cdot 4$, so that the maximum number of TIES a larva can eat during its development is $177 \cdot 9$.

A similar regression of cumulative numbers of aphids eaten on day-degrees for syrphid larvae feeding on *Masonaphis maxima* (data from Gilbert and Gutierrez 1973) yields: $\ln y = 0 \cdot 0788x + 1 \cdot 2630$; $(r = 0 \cdot 9996)$.

When prey are abundant, so that the functional response of *L. conformis* to the density of *M. rosae* is not a source of variability, the numbers of *M. rosae* that are expected to be eaten by *L. conformis* larvae in any interval of day-degrees can be estimated from equation (5) as the difference in the value of y at the start and at the end of the interval. In particular, the numbers of aphids of each growth stage that are eaten in the field may perhaps be estimated from equation (4) and from: (1) the age-structure of the aphid population; (2) the relative probabilities of capture of different instars by *L. conformis* larvae of different weights.

It will be interesting to determine if the estimates discussed above allow for the effect of temperature on predation sufficiently to be useful in the field, or whether the estimates will need to be multiplied by an activity coefficient, as used by Frazer and Gilbert (1976) for adults of *Coccinella trifasciata*.

Use of Leis conformis *in Pest Control*

Finally, it is of interest to speculate on the manipulation of *L. conformis* for use in pest control. *L. conformis* has a relatively high threshold of development and activity (about 15°C in South Australia), and it usually does not become numerous until late spring, by which time much damage has already been done by aphids to a variety of plant species.

The adults seem not to hibernate in large, aggregated masses, as do those of many species in the northern hemisphere (Hodek 1973), but have been found hibernating in small groups under the bark of trees. The species is also known to breed slowly, but in fairly large numbers, throughout winter if suitable prey is available—as on the native tree *Casuarina stricta* Ait. when infested by the psyllid *Acanthocnema casuarinae* (Froggatt) (R. Cook, unpublished data). So it may be possible to encourage the earlier arrival in crops of large numbers of adults by planting trees that support natural, alternative prey in suitable proximity to crops. A study of the interaction of *L. conformis* with its natural prey may, therefore, be of considerable value to pest control in Australia.

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