

The influence of temperature and food supply on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae)

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Abstract. The development of *Adalia bipunctata* larvae feeding on the grain aphid *Sitobion avenae* was investigated at 15, 20 and 25°C and two different levels of food supply. Increased temperatures accelerated development and reduced mortality rates. A reduced food supply slowed down development and increased mortality at all life stages. The total food intake of larvae ranged from 24–65 mg, which is equivalent to up to 190 aphids. Larvae compensated for low food supply by reducing development rates, high prey exploitation efficiencies, reaching up to 100%, and by high prey-biomass conversion efficiencies, reaching over 40%. The findings are discussed under the aspect of suitability of *A. bipunctata* as a biological control agent for greenhouse-specific aphid pest species.

INTRODUCTION

Ladybirds have been used as biological control agents since the early 20th century (Hodek, 1970). The coccinophagous species such as *Rodolia cardinalis* (Mulsant) have been used very successfully. However, the control of aphids with ladybirds remains very difficult, because of the fast development of the aphids and their high rate of reproduction, as well as problems with the space and manpower required for mass rearing of coccinellids.

There are various factors that influence the success of a coccinellid aphid predator. Early work with *Adalia bipunctata* L. showed that the ability of larvae to survive depends on their success in finding suitable prey early enough (Banks, 1957). Other investigations led to the understanding that plant structure, plant volatiles and aphid prey quality play an important role in the foraging behaviour and predatory success (Carter et al., 1984; Grevstad & Klepetka, 1992; Ferran & Dixon, 1993; Kalushkov, 1999; Ninkovic et al., 2001). Kalushkov (1994, 1998) systematically investigated the effect of different aphid species on the development of *A. bipunctata* larvae. He suggested a link between the palatability of the aphid species and the secondary plant metabolites they accumulated by feeding on their host plants.

The grain aphid *Sitobion avenae* was known to be a prey species for *A. bipunctata*, as this prey can supply the predator with all essential nutrients. This makes this aphid a promising candidate for effective breeding of *A. bipunctata* in cultures. From work with *Coccinella septempunctata* L. it is known that prey availability in non-crop habitats can have an important influence on predator impact in the crop (Bianchi & van der Werf, in press). Previous experiments in greenhouses of the Federal Biological Research Centre for Agriculture and Forestry

(unpublished data) suggested using an open culture of such a highly palatable and host-specialised aphid species. This could maintain a permanent food source for aphidophagous coccinellids in the greenhouse and would help to establish a ladybird population with the aim to control other aphid species such as *Myzus persicae* (Sulzer), *Aphis gossypii* Glover or *Macrosiphum solani* (Kittel).

The aims of the research presented in this paper were to:

- 1) Identify the impact of temperature and quantity of food supply on the duration of development, mortality rate and final body weight of *A. bipunctata* larvae and pupae.
- 2) Investigate if there are mechanisms, by which a strong reduction in food supply could be compensated by the ladybirds.
- 3) Assess the potential of *A. bipunctata* for the biological control of aphids, e.g. their tolerance of physical stress, and to develop suggestions for optimising their practical use in greenhouses.

MATERIAL AND METHODS

Eggs of *A. bipunctata* were kept under controlled laboratory conditions at a constant temperature of 15°C, 20°C and 25°C and a photoperiod of 16L : 8D. Every morning, larvae hatch was recorded. On the day following the observation of hatch larvae were removed from the egg batch and then kept separately in 55 mm plastic Petri dishes lined with a filter paper and a piece of moist cotton wool. There were six different treatments (Table 1). Larvae were fed three times a week with a defined fresh weight (Table 2) of *Sitobion avenae*, which had been established on a 1×4 cm piece of wheat leaf after weighing. The amount of food given per feeding interval corresponded to the sum of daily food amounts as given in Table 2. At 20 and 25°C ladybird larvae were fed with aphid instars I and II only for the first two

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TABLE 1. Treatment combinations used to investigate the development of *Adalia bipunctata* larvae (with completed development). "Reduced" food supply was 25% of what larvae fed when aphids were offered in excess.

Treatment	Larvae (start) [n]	Larvae (pupated) [n]	Temperature [°C]	Food supply
15r	118	42	15°C	reduced
15e	65	33	15°C	excess
20r	98	37	20°C	reduced
20e	61	32	20°C	excess
25r	92	40	25°C	reduced
25e	57	37	25°C	excess

days, with aphid instars I–IV only for the following two days and with instars and adult aphids thereafter. At 15°C ladybird larvae were fed with aphid instars I and II only for the first four days, with aphid instars I–IV only for the following four days and with instars and adult aphids thereafter.

The aphids not eaten until the next feeding event were removed and their fresh weight recorded in order to determine the larval food intake. Preliminary trials showed that the reduction in fresh weight due to desiccation was marginal, as it was compensated for by reproduction and growth of aphids established on a wheat leaf. It was impossible and unpractical to feed all larvae at exactly the same intervals, as they hatched on different days of the week. Consequently, daily food intake was calculated as the average food intake over a given period of time (two or three day feeding interval).

The food conversion rate (%) of the ladybirds was defined as follows:

$$\frac{\text{maximum fresh weight of ladybird larvae (mg)}}{\text{fresh weight of aphids consumed (mg)}} \times 100$$

The food exploitation efficiency (%), when food was scarce, was defined as follows:

$$\frac{\text{fresh weight of aphids consumed (mg)}}{\text{fresh weight of aphids offered (mg)}} \times 100$$

The larval development stage was assessed every day. The temperature threshold for egg and pupal development were extrapolated. It was assumed that a certain total energy input (measured in day degrees above the temperature threshold) is necessary for a physiological process. The threshold was determined by a process of multiple iteration. That temperature was defined as the threshold for the physiological process, at which the required day degrees (product of actually observed duration of the process times respective temperature above threshold) were closest together (measured as the smallest possible standard deviation of the mean of values of the three temperatures).

Only those larvae, which completed their development and pupated, were included in the analysis for food consumption and conversion rates and development times. Continuous data was tested for normal distribution. If normal distribution was given, data were analysed with an analysis of variance (ANOVA) and a Tukey post hoc procedure, if not, they were analysed with a non-parametric equivalent, the Kruskal-Wallis test and a post hoc procedure according to Zar (1999). Binomial data were analysed with a g-test and a post hoc procedure according to Wilcoxon & Wilcox (1964) as cited in (1999). Some data on growth development and food intake were analysed with a regression model.

TABLE 2. Fresh weight of grain aphids (*Sitobion avenae*) fed to *Adalia bipunctata* larvae in the six different treatments. Abbreviation of treatments as in Table 1.

Day after hatch	Treatments					
	15e	20e	25e	15r	20r	25r
	Aphids fed – fresh weight [mg]					
2	2.0	2.5	2.5	2.0	2.0	2.0
3	2.0	2.5	2.5	2.0	2.0	2.0
4	2.0	5.0	7.5	2.0	0.4	0.9
5	2.0	5.0	7.5	2.0	1.0	0.9
6	3.0	8.0	16.0	1.5	1.0	3.0
7	3.0	8.0	16.0	1.5	1.0	4.0
8	5.0	8.0	25.0	0.4	2.0	4.0
9	5.0	16.0	25.0	0.4	2.0	5.0
10	7.5	20.0	25.0	0.4	3.5	5.0
11	7.5	20.0		0.7	3.5	5.0
12	10	20.0		0.7	3.3	5.0
13	10	20.0		1.5	3.3	
14	10	20.0		1.5	3.3	
15	12.5	20.0		1.6	3.3	
16	12.5	20.0		1.6	3.3	
17	20			2.3	3.3	
>17	20			2.8	3.3	

RESULTS

Development of *A. bipunctata*

A total of 221 of the initial 491 larvae completed their development and pupated. The data for these are presented below.

The mean duration of development from the egg to the emergence of the imago was affected by both temperature and the amount of food offered (Table 3). The development was slowest at 15°C and reduced food supply (44 days) and fastest at 25°C and food in excess (16 days). A reduction of food supply at the same temperature extended the total development time by up to four days, but this was not significant (Kruskal-Wallis test: $N = 185$, $df = 5$, $Chi^2 = 177.3$, $P > 0.05$, Table 3). An increase of temperature by 5°C at the same level of food given ("excess" or "reduced") significantly decreased the development time by up to 16 days (Kruskal-Wallis test: $N = 185$, $Chi^2 = 177.3$, $df = 5$, $P < 0.001$, Table 3).

Temperature influenced the duration of the separate development stages, with significant differences caused in the duration of first larval instar and pupae stages between all temperatures regardless of the level of food (previously) given (Kruskal-Wallis-test, details in Table 3). For other larval instars temperature only had a significant effect when comparing the same level of food given. For example, 2nd instar larvae fed in excess developed significantly faster at 25°C than at 20°C (Kruskal-Wallis test: $N = 221$, $df = 5$, $Chi^2 = 125.1$, $P < 0.001$, Table 3).

The amount of food given had a significant influence on larval development at the same temperature in two cases: the 3rd larval instar at 20 and 25°C (Kruskal-Wallis test: $N = 221$, $df = 5$, $Chi^2 = 123.5$, $P < 0.001$, Table 3). The variation of development time at 15°C was

TABLE 3. Development time (mean \pm SE) of life stages of *Adalia bipunctata*. Different letters in the same column indicate significant differences in the development time ($P < 0.001$). Abbreviations of treatments as in Table 1.

Treatment	Larvae [n]	Imago [n]	Development of stage [d]						
			Egg	L1	L2	L3	L4	Pupae	Total
15r	42	32	7.1 \pm 0.0a	6.4 \pm 0.2a	4.4 \pm 0.3a	4.9 \pm 0.3a	7.8 \pm 0.3a	13.8 \pm 0.1a	44.4 \pm 0.3a
15e	33	31	6.4 \pm 0.1a	5.9 \pm 0.3a	3.8 \pm 0.3ab	3.7 \pm 0.3ab	7.5 \pm 0.4a	13.7 \pm 0.2a	41.0 \pm 0.3ab
20r	37	31	4.3 \pm 0.1b	3.5 \pm 0.2b	3.5 \pm 0.2ab	2.7 \pm 0.1b	5.9 \pm 0.2a	9.2 \pm 0.1b	29.2 \pm 0.2bc
20e	32	29	4.1 \pm 0.1b	4.0 \pm 0.1b	2.9 \pm 0.1b	2.0 \pm 0.1c	3.6 \pm 0.2b	8.5 \pm 0.1b	24.9 \pm 0.2cd
25r	40	29	3.0 \pm 0.0c	2.8 \pm 0.3c	2.1 \pm 0.0c	2.8 \pm 0.1b	2.5 \pm 0.1bc	5.3 \pm 0.1c	18.4 \pm 0.3de
25e	37	33	3.0 \pm 0.0c	2.0 \pm 0.0c	1.9 \pm 0.1c	1.8 \pm 0.1c	1.9 \pm 0.1c	5.1 \pm 0.1c	15.6 \pm 0.1e
<i>P</i>			< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

so great that no significant differences between larvae fed in excess and at reduced food supply could be found.

The temperature threshold for egg development was extrapolated as 7.2°C (53 day degrees above threshold necessary until hatch), that for pupal development (based on pupae from larvae fed in excess) as 8.9°C (87 day degrees).

Feeding and growing of *A. bipunctata* larvae

The mean total food intake ranged between 24 mg and 60 mg per larva (Table 4) The maximum value amounted to 150 to 190 aphids and was achieved in larvae kept at 15°, where it was significantly higher than in all other treatments (ANOVA: $N = 221$, $df = 5$, $F = 185.3$, $P < 0.001$, Table 4).

When fed in excess the calculated daily food intake of the larvae increased logarithmically with larval age (regression model: 15°C: $n = 33$, $df = 25$, $F = 220.0$, $R^2 = 0.898$, $P < 0.001$; 20°C: $n = 32$, $df = 13$, $F = 105.3$, $R^2 = 0.890$, $P < 0.001$; 25°C: $n = 37$, $df = 7$, $F = 81.8$, $R^2 = 0.921$, $P < 0.001$; Fig. 1). Towards the end of the development, shortly before pupation, the maximum calculated daily food intake was 20 mg, 13 mg and 10 mg at 25°C, 20°C and 15°C, respectively.

When given a reduced food supply, the larvae had a very high efficiency of exploiting the scarce food source. Exploitation efficiency was defined as the proportion of offered food eaten before the next feeding event. In all three treatments some individuals ate nearly 100% of all the aphids supplied during their whole development.

TABLE 4. Total food intake (fresh weight) and food conversion rate (mean \pm SE) of *Adalia bipunctata* larvae. Different letters in the same column indicate significant differences in the development time ($P < 0.001$). Abbreviations of treatments as in Table 1.

Treatment	[n]	Total food intake [mg]	[n]	Food conversion rate [%]
15r	42	25.4 \pm 0.5cd	31	40.3 \pm 0.9a
15e	33	64.7 \pm 1.7a	33	22.0 \pm 0.8e
20r	37	28.1 \pm 0.9c	32	34.2 \pm 1.5bc
20e	32	56.9 \pm 1.1b	31	28.1 \pm 0.7d
25r	40	24.1 \pm 0.6d	34	37.5 \pm 1.2ab
25e	37	51.5 \pm 1.6b	35	29.4 \pm 1.6cd
<i>P</i>		< 0.001		< 0.001

However, there was also evidence that the larvae had difficulty in exploiting the complete food supply at 15°C. With an overall exploitation rate of 75% at 15°C and it was significantly lower than at 20°C or 25°C (ANOVA: $N = 119$, $df = 2$, $F = 8.5$, $P < 0.001$, Fig. 2). At all temperatures the exploitation rate grew with larval age. At 15 and 20°C this growth was logarithmical (Regression analysis: 15°C: $n = 42$, $df = 11$, $F = 112.9$, $R^2 = 0.911$, $P < 0.001$; 20°C: $n = 37$, $df = 4$, $F = 22.2$, $R^2 = 0.848$, $P < 0.01$, Fig. 2). The development at 25°C was too fast to provide enough data for such an analysis.

Larvae which were fed reduced food amounts showed higher conversion efficiency (mg body mass increase per mg aphid eaten) than those fed in excess (ANOVA: $N = 196$, $df = 5$, $F = 38.4$, $P < 0.001$, Table 4). The reduced food supply treatments had values as high as 40%, i.e. built 0.4 mg biomass per mg aphid food eaten. The larvae fed in excess had food conversions efficiencies of 20–29%.

Eating a high number of aphids with a high efficiency led to a very fast increase in weight (gain) within a relatively short period of time (Fig. 3). Starting with 0.2 mg fresh weight at the end of the first larval stage individual larvae reached up to 19 mg at the end of the larval stage. The pupal weights of the larvae fed in excess, with values of 13–16 mg, were higher than those of respective variables with reduced food supply (9–10 mg). During the larval development the mean growth rates were 0.6, 1.0 and 1.9 mg/day for 15, 20 and 25°C respectively.

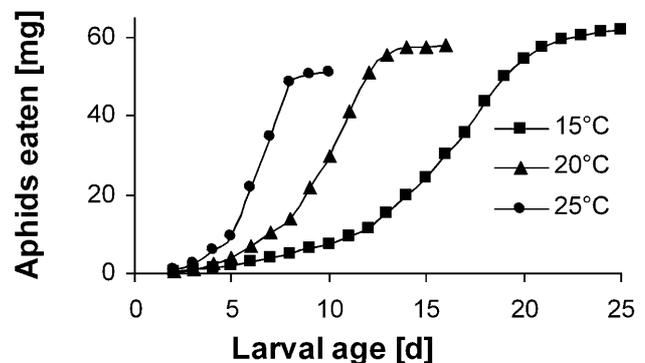


Fig 1. Accumulated food uptake by *Adalia bipunctata* larvae when fed in excess (fresh weight of *Sitobion avenae*). Lines end when pupation sets in.

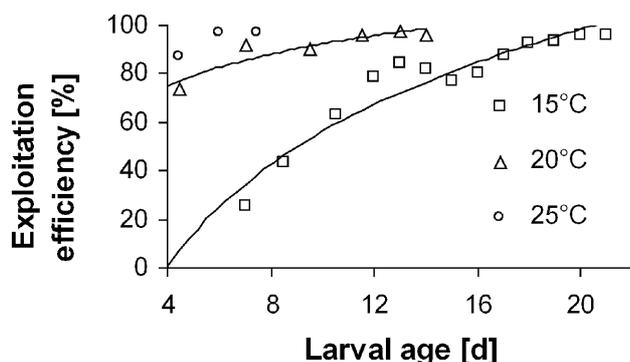


Fig. 2. Exploitation efficiency of *Adalia bipunctata* larvae at different temperatures and with reduced food supply in relation to larval age. Lines for 15°C and 20°C represent logarithmic best fit trend line.

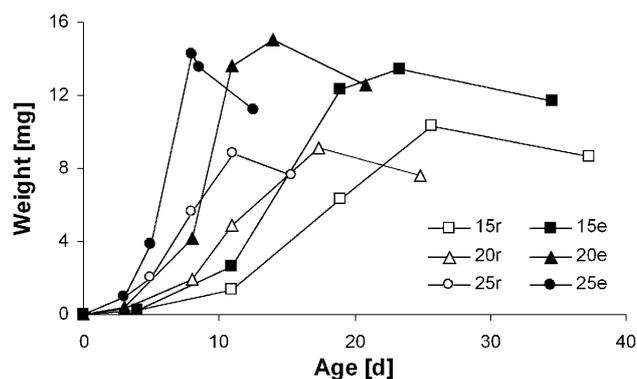


Fig. 3. Fresh body weight of *Adalia bipunctata*: egg (1st datapoint), larvae (2nd–4th datapoint), pupae (5th datapoint) and newly emerged adults (last datapoint) after feeding. Abbreviations of treatments as in Table 1.

Life-stage specific mortality rates of *A. bipunctata*

When compared within each larval instar, the treatment (temperature and food supply) did not have significant effects on mortality of specific larval stages except the second instar (G-test for second instar: $N = 191$, $df = 5$, $G = 11.7$, $P < 0.05$, Table 5). However, the mortality rate over the whole larval stage in the different treatments did differ significantly (G-Test: $N = 491$, $df = 5$, $G = 17.5$, $P < 0.01$, Table 5). It was highest, with a value of 62%, at 15°C with reduced food supply and was lowest, with a value of 33 %, at 25°C with food in excess. In all treatments mortality was highest during the first larval stage (28–46%) followed by the pupal stage (6–30%). The stages in between had much lower mortality rates.

There was a trend of high temperatures reducing the mortality rate in general. Comparing the effects of feeding regime without regard to the temperature showed that supplying insufficient food raised the mortality rates by 6 to 30%. For some stages such as the first larval stage or the pupal stage, where mortality was already high when aphids were fed in excess the mortality was increased even more (Table 5).

DISCUSSION AND CONCLUSIONS

Development of *A. bipunctata* larvae

The observations show that *S. avenae* could be a good food source for breeding *A. bipunctata*. For example, the larval development of *A. bipunctata* took 17 days when

fed with *M. persicae* at 20°C (Hämäläinen et al., 1975), which is four days longer than in the present study. Similarly at 14°C, development with *Eucallipterus tiliæ* L. as food source resulted in a development duration of 30 days (Wratten, 1973), whereas with *S. avenae* in our results it was only 21 days at 15°C.

The results suggest that a reduction in temperature has a stronger impact on development times of larvae than a reduction in food supply. At the same temperature a strong reduction in food supply prolonged the total duration of larval development by 8–15% (3–4 days). Even though significant differences for the duration of individual instars were generally not obtained, there was an overwhelmingly clear pattern that larvae feeding in excess developed on average faster than those with a reduced food supply (Table 3).

However, comparing the same feeding regimes (food in excess or reduced food supply), reducing the temperature by 5°C prolonged the development by 34–39% (9–15 days, Table 3). The observation of Wratten (1973) of doubling or even tripling duration times with reduced food supply could not be confirmed.

The extrapolation of thresholds for egg and pupal development should be regarded as a guideline only, as it is only based on three temperature regimes and other general assumptions such as non-linear response to temperature (Bonhomme, 2000) could not be taken into account. However, they give a good indication that *A. bipunctata*

TABLE 5. Mortality rates (% dying in each life stage) of *Adalia bipunctata* at different life stages (L = larval instar). Different letters in the same column indicate significant differences in the mortality rate. Treatment abbreviations as in Table 1.

Treatment	Larvae (hatch) [n]	Pupae [n]	Imago [n]	Mortality rate at life stage						
				L1	L2	L3	L4	Larvae	Pupae	Total
15r	118	42	32	46	9a	12	12	62a	29a	73a
15e	65	33	31	42	5ab	3	6	49ab	6b	52ab
20r	98	37	31	38	15a	4	16	57a	26b	68a
20e	61	32	29	28	14a	3	8	44ab	15ab	52ab
25r	92	40	29	43	8ab	6	9	55a	29a	68ab
25e	57	37	33	28	0b	0	5	32b	15ab	42b
<i>P</i>				0.089	< 0.05	0.077	0.499	< 0.01	< 0.05	< 0.001

could have a slow but steady development even at low greenhouse temperatures during colder seasons. The calculated temperature threshold for egg development of 7.2°C, with 53 day degrees (DD) required, is below that found by Frazer & McGregor (1992, 8.4°C, 48 DD). Apparently, *A. bipunctata* has a lower egg development threshold than other Coccinellidae (Frazer & McGregor, 1992; Xia et al., 1999). More research at lower temperatures would be necessary to confirm the observed trends and proposed thresholds.

The total food intake of *A. bipunctata* larvae at 20°C (57 mg) was comparable to values found for the same species when fed on *Aphis fabae* Scopoli (58 mg), but lower than that recorded for *M. persicae* (69 mg, Blackman, 1967). At 15°C the total food intake was probably higher than at 20 or 25°C, because of the much longer duration of the development and a higher cost for the metabolism. Hämäläinen et al. (1975) expressed the amount of *M. persicae* eaten in the number of aphids (863 at 20°C). Similar data is given for the consumption of *A. fabae* at 15°C (240 aphids, Olszak, 1987). However, the number of prey seems a rather imprecise measure, especially when comparing aphids of different size.

Depending on temperature and age, the larval exploitation efficiency at low prey densities ("reduced" food supply) rose to nearly 100%. This means that – at least on a small scale – larvae find nearly all aphids and the risk of starvation stays low even at low prey densities. The very high exploitation efficiencies observed in our own studies were much higher than those found by Blackman (1967) for fourth instar *A. bipunctata* larvae feeding on *M. persicae* (40%) or *A. fabae* (24%). Exploitation efficiencies at 20°C (74%) were more in line with results from first instar *A. bipunctata* feeding on *Drepanosiphum platanoides* (Schrank) at 21°C (85–93%, Dixon, 1970).

The larvae displayed several mechanisms to compensate for a lack of food. One of them was to slow down the development. Once there is food in excess again they are able to respond to a high food supply. The other was an increase in the conversion efficiency. The established food conversion rates into biomass (34–40% when fed with reduced food supply, Table 4) were between the values found for *A. bipunctata* fourth instar larvae fed on *M. persicae* (45%) or *A. fabae* (28%, Blackman, 1967). From the second larval stage onwards there could potentially be an exponential rise in food consumption.

There were remarkable differences in larval mortality (32–62%) depending on temperature and food supply (Table 5). There were clear trends of increasing mortality with decreasing temperature and reduced food supply. The latter effect appeared to be stronger, highlighting the need of a permanently available food source to help the establishment and growth of a population. When using other aphid species such as *A. pomi* as the food source the mortality rate can be as high as 93%, but with other species, such as *A. fabae*, also slightly lower (27%) (Olszak, 1987).

The larval growth rates were between 0.6 and 1.9 mg/day in comparison to 0.4–0.9 mg/day when fed with

Aphis pomi DeGeer or *Rhopalosiphum insertum* (Walker) (Olszak, 1987). Maximum larval weight found for diets with aphid species such as *Microlophium carnosum* (Buckton), *M. persicae*, and *A. fabae* were between 12 and 16 mg at 20°C (Blackman, 1967), which compares to 15.1 mg mean larvae weight found when fed with *S. avenae* at 20°C.

Implications for the use of *A. bipunctata* as biological control agent

The active larval period between egg hatch and pupation is the time period when larvae are available for biological control. This period was between six and 17 days long. To avoid an interruption in the feeding activity while pupation is taking place, new larvae would have to be introduced at appropriate intervals.

Under the optimal conditions used here (20°C and 16 hours light), 12 generations were bred in the laboratory, exclusively on *S. avenae* without any obvious detrimental effect on the viability of *A. bipunctata*. High temperatures, artificial light sources and a satisfactory food supply in the greenhouse (introduced *S. avenae* colonies) could break the natural univoltine cycle and bring forth several generations, which would multiply the total food intake of the ladybirds.

It can be concluded that *S. avenae* could be used in two ways:

(1) Breeding of *A. bipunctata* larvae in the laboratory for later release of larvae or adults in the greenhouse.

The data suggest that first instar larvae should not be used as natural enemies:

(a) The mortality of first instar larvae is very high, even when food is supplied in excess (Table 5).

(b) Young larvae tend to cannibalise, especially if aphid prey is scarce (Merritt Hawkes, 1920; Hodek, 1970; Agarwala, 1991; Agarwala & Dixon, 1992; Yasuda & Ohnuma, 1999). In our own studies cannibalism was avoided by growing larvae separately as soon as they became active (day 2).

(c) Young larvae have a relatively high activity rate. However, their mobility is strongly limited, they are not very efficient and they mainly capture small aphids, which may prevent equal and appropriate coverage of the crop to be protected (Wratten, 1973). At low densities they are likely to die before they find suitable prey (Hodek, 1967). In the presented experiments low efficiency was demonstrated by low exploitation rates at low aphid densities.

(d) Young larvae have a very low daily food intake. The food intake starts growing exponentially from the end of the second larval stage (Fig. 1).

(2) Introduction of open cultures with *S. avenae* colonies into the greenhouse to maintain a permanent and secure food source for all stages of *A. bipunctata*, which may then spread into the greenhouse to keep levels of target pest species low.

(a) It was shown that *A. bipunctata* develops well when fed exclusively on *S. avenae* (i.e. before target pest species occur or once they have been successfully reduced to low levels).

(b) It was shown that *A. bipunctata* has relatively good survival rates at low prey densities (Table 5) and that it has compensation mechanisms through exploitation efficiency (Fig. 2) and conversion efficiency (Table 4).

One problem with adult ladybirds is that they tend to go to the roof of the greenhouse, which would favour release of larvae or the introduction of a population with a range of instars. Other research suggests that combination with other aphidophagous predators such as lacewings and gall midges should be carefully considered to gain optimum results (Hindayana et al., 2001).

Future work should investigate the impact of mixed diets (*S. avenae* and target pest aphid species in greenhouse), the influence of this diet during the larval stage on adult oviposition performance and the ability of *A. bipunctata* to control target pest species on a larger scale.

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