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Laboratory study of cannibalism and interspecific predation in ladybirds

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Abstract. 1. In the absence of aphids, adult females of *Adalia bipunctata* (L.) showed a greater reluctance to eat eggs than males.

2. Eggs and young larvae were more vulnerable to cannibalism than older larvae and starved larvae were more vulnerable than well-fed larvae.

3. Both egg and larval cannibalism is inversely related to the abundance of aphids.

4. Eggs are a better food, in terms of larval growth and survival, than aphids.

5. In the absence of aphids interspecific predation occurred, but not equally, between the coccinellids *A.bipunctata*, *A.decempunctata* (L.), *Coccinella septempunctata* L. and *C.undecempunctata* L.

6. Larvae and adults of *A.bipunctata* and *C.septempunctata* were reluctant to eat conspecific eggs painted with a water extract of the other species' eggs and larvae of *C.septempunctata* were more likely to die after eating a few eggs of *A.bipunctata* than vice versa.

7. These results indicate that cannibalism occurs mainly when aphid prey is scarce and is adaptive in that it improves the chances of survival, and coccinellids, to varying degrees, are defended against interspecific predation.

Key words. *Adalia bipunctata*, *Adalia decempunctata*, *Coccinella septempunctata*, *Coccinella undecempunctata*, cannibalism, defence, food quality, survival, aphid abundance, interspecific predation.

Introduction

Cannibalism or intraspecific predation is found in a wide variety of animals from Protozoa to mammals (Fox, 1975). Although most of the references to cannibalism are based on casual observations, there is general agreement that it occurs when prey are scarce, is of survival value and can have a self-regulatory role (Park *et al.*, 1965; Pienkowsky, 1965; Nummelin, 1989).

Ladybirds pass through egg, larval, pupal and adult stages and the larval and adult stages as well as eating aphids are known to eat eggs, larvae and pupae of their own species. Hawkes (1920) considered egg and larval cannibalism as a means of 'preserving the race during the period of aphid famine'. Banks (1956) thought that egg cannibalism by pre-dispersal larvae was of survival value. Dixon (1959) and Brown (1972) considered such egg cannibalism to be confined to the eating of non-viable eggs, and Kaddou (1960) found that delay in egg-hatch increased the probability of cannibalism by young larvae. Older larvae are acknowledged to be voracious, wide ranging and to eat eggs (Dimetry, 1974), young larvae (Takahashi, 1987) and prepupae (Kaddou, 1960). In the field, Mills (1982) recorded density-dependent egg cannibalism of 6–30% in *Adalia bipunctata* and Osawa (1989) that non-sibling egg cannibalism was more intense towards the end of the oviposition period in *Harmonia axyridis* Pallas. However, with the notable exception of the studies by Mills (1982) and Osawa (1989) there is little rigorous information on cannibalism in coccinellids.

Ladybirds have been recorded from a wide range of habitats feeding on many different species of aphids (Mills, 1981). Two or more species of ladybird have frequently been recorded in the same habitat (Hodek, 1973) attacking the same aphid colonies (Tamaki & Long, 1978; Frazer *et al.*, 1981; Agawala & Ghosh, 1988; Evans, 1991) and therefore likely to interact with one another.

The first objective of this study was to determine the

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vulnerability of the various developmental stages of ladybirds to cannibalism and in particular the effect of the abundance of aphids, their usual prey, on this vulnerability. The advantage of cannibalism in terms of survival and growth of the cannibal was also determined. The second objective was to determine whether the various stages of different species of ladybirds will readily attack and eat each other.

Materials and Methods

The two-spot ladybird beetle, *Adalia bipunctata* (L.) was used throughout this study except in the observations on interspecific predation where four species of ladybirds were used: *A.bipunctata*, *A.decempunctata* (L.), *Coccinella septempunctata* L. and *C.undecempunctata* L. Adults were obtained from the field and stock cultures were raised in the laboratory at 20°C and a 16 h photoperiod and fed pea aphids, *Acyrthosiphon pisum* (Harris). Ladybirds were starved for 24 h prior to an experiment in order to induce the same level of hunger. As far as possible, similar-aged ladybirds were used in each experiment, which was achieved by maintaining a large culture of larvae and adults. Experiments were carried out in clean, dry 5 or 9 cm diameter Petri dishes at 20°C and a 16 h photoperiod. All the weights are in mg. Fresh to dry weight conversion ratios were obtained by drying at 40°C for 8–10 days until of constant weight.

Cannibalism of eggs and larvae. (i) *Eggs and larvae by adults*. The readiness with which similar-sized females and males of *A.bipunctata* eat aphids, and eggs and larvae of their own species was determined by keeping individual beetles in a Petri dish (5 cm) with either twenty fourth instar aphids, or forty 2-day-old eggs or forty 1-day-old first instar larvae for 24 h. This was repeated nineteen times for each sex, using a different beetle each time, except when aphids were offered, when it was repeated twenty times.

(ii) *Eggs by larvae*. 2-day-old larvae of all the four instars were kept individually with eggs for 24 h. This was replicated twenty times for each instar. The numbers of eggs offered to larvae of each instar was: first instar fifteen eggs, second instar twenty, third instar thirty and fourth instar forty. The number of eggs eaten after 24 h was noted.

(iii) *Within a larval age class*. The effect of hunger on the tendency of larvae of the same instar to eat one another was determined by raising two sets of larvae on aphids, one set of which was provided daily with sufficient aphids (20 ± 0.5 mg) to satiate them, referred to as well-fed larvae, and the other set was reared on about 30% less (14 ± 0.5 mg), referred to as starved larvae. Well-fed larvae of each stage, each marked on its head with a spot of coloured paint, were individually caged with either a well-fed or starved larva of the same age and any cannibalism was recorded at the end of 24 h. This was repeated twenty times for each stage and treatment, using different larvae each time.

Factors affecting cannibalism. (i) *Aphid abundance*. One of a range of numbers of fourth instar aphids (aphid density) was offered to a fourth instar larva of *A.bipunctata* that had previously been starved for 24 h. In addition each fourth instar larva was provided with a clutch of ten eggs (2 days old) or a well-fed third instar larva. Twenty different fourth instar larvae were provided with eggs and twenty with larvae at each aphid density. The number of clutches of eggs or larvae eaten at each aphid density (for eggs: 4, 12, 20, 28, 36 or 44; for larvae: 4, 8, 12, 16, 20 or 24) was recorded after 24 h. Mean proportion of the clutches of eggs and larvae eaten at each aphid density were subjected to linear regression analysis.

(ii) *Ladybird age structure*. A (2–3-day-old) larva that had been starved for 24 h was kept with a similarly treated larva of the same instar or with a number of well-fed larvae of a previous instar, equivalent, in terms of weight, to the number of eggs that the larva can eat in 24 h. Any cannibalism was noted after 24 h. This was repeated ten times for each interaction.

Advantages of cannibalism. (i) *Cost of feeding on eggs*. To determine whether there are any costs associated with eating eggs, twenty 1-day-old fourth instar larvae were fed daily thirty-seven eggs (4.14 mg) and twenty larvae were fed 12 mg of aphids for 4 days. A preliminary series of experiments had indicated that these quantities of the two foods would support similar growth rates. The comparisons were made on a dry weight basis by converting fresh weights to dry weights.

(ii) *Duration of survival when fed aphids and eggs of their own species*. This was determined by providing individuals of each larval instar of *A.bipunctata* ($n = 20$) a fixed quantity by weight of aphids and eggs. All the larvae used in the experiment were of the same age and the length of time for which they survived after feeding was noted.

Interspecific predation. In this experiment 8–10-day-old adults, taken at random from the culture, and 2–3-day-old fourth instar larvae of *A.bipunctata*, *A.decempunctata*, *C.septempunctata* and *C.undecempunctata* were used. Larvae and adults were each offered equal quantities (by weight) of their own or of another species eggs. This was repeated twenty to thirty times. Larvae and adults were each also offered one 2-day-old third instar larva of their own or of another species. This was repeated fifteen to twenty times. The number of larvae and weight of eggs eaten in 24 h was noted and the mean proportion of eggs eaten calculated.

Are eggs of ladybirds defended against predation? To answer this question the interaction between *A.bipunctata* and *C.septempunctata* was studied further. Eggs of *A.bipunctata* and *C.septempunctata*, 1 mg of each, were crushed in 0.15 ml distilled water, centrifuged for 2 min and 0.05 ml supernatant painted on a batch of ten eggs of the other species with the help of a micropipette. These eggs were then left to dry for 2 h. Each batch of ten eggs was offered to a starving fourth instar larva or adult of *A.bipunctata* and *C.septempunctata* ($n = 20$ each), taken at random from the cultures, and the number eaten noted after 24 h. Eggs of *A.bipunctata* and *C.septempunctata* painted with a water extract of their own eggs were used as the control.

Consequence for A.bipunctata and C.septempunctata of eating the other's eggs. 2-day-old fourth instar larvae of *A.bipunctata* and *C.septempunctata* were each individually offered 4 mg of the other species eggs in a 5 cm Petri dish. After 24 h the quantity of eggs eaten was noted and the larvae were then fed an excess of aphids until they either pupated or died.

Results

Cannibalism of eggs and larvae

(i) *Eggs and larvae by adults.* Similar-sized hungry males and females might be expected to show the same level of consumption of food. However, males ate significantly more eggs, but fewer aphids than females (Table 1).

It is likely that the food requirement of females is far greater than that of males, because of formers' greater need of energy for reproduction, which is indicated by their greater consumption of aphids. Nevertheless, females appeared to be more reluctant than males to eat eggs, but not reluctant to eat first instar larvae (Table 1).

(ii) *Eggs by larvae.* As larvae increase in size, they consume more aphids and not unexpectedly they ate more eggs per unit time (Fig. 1). Fourth instar larvae consumed 10 times more eggs (35.15 ± 0.94) than first instar larvae (3.55 ± 0.28), when no alternative food was available.

(iii) *Within a larval age class.* In each instar, starved larvae were more vulnerable than well-fed larvae although not always significantly so. Fourth instar larvae showed a greater tendency to eat both starved and well-fed larvae of their own age than did the earlier instars (Fig. 2).

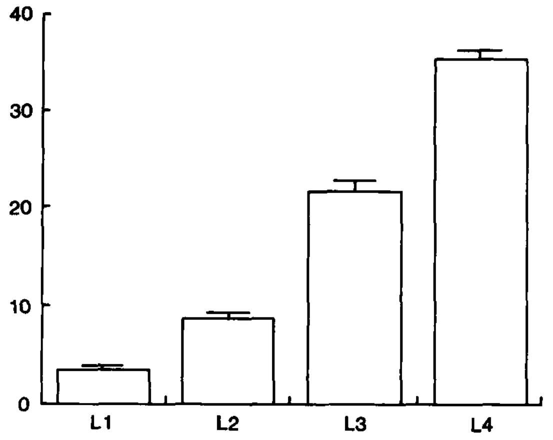

Fig. 1. Mean number of eggs eaten in 24 h by individuals of each of the four larval instars of *A.bipunctata* (bar indicates standard error, $n = 20$).

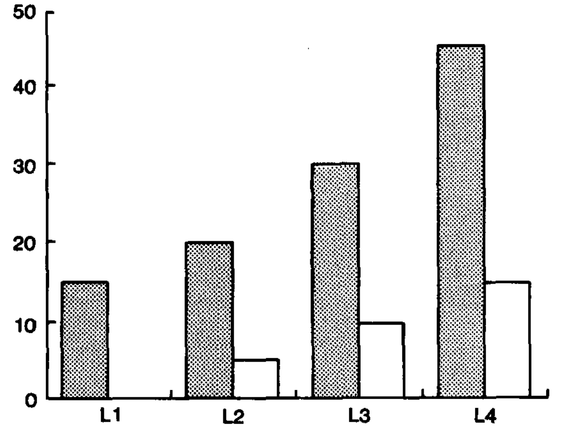

Fig. 2. The percentage of well-fed (open columns) and starved (hatched columns) larvae eaten in 24 h by well-fed larvae in the four larval instars.

Factors affecting cannibalism

(i) *Aphid abundance.* Egg cannibalism was inversely related to the number of aphids present (Fig. 3A). The inverse relationship possibly resulted from a decline in the probability of encountering eggs as aphid density increased.

Larval cannibalism was also found to inversely related to aphid abundance (Fig. 3B). Strong negative correlation occurred between larval cannibalism and aphid abundance, up to 20 aphids/9 cm diameter Petri dish. When aphids were more abundant, third instar larvae were not attacked and eaten by fourth instar larvae. This implies that when food is abundant, cannibalism is a function of mobility, behaviour and abundance of the vulnerable stages. Eggs, which are immobile and abundant, are more likely to be encountered and eaten than larvae.

Table 1. The number of eggs and first instar larave of *A.bipunctata*, and aphids eaten in 24 h by similar-sized males and females of *A.bipunctata*.

	Males		Females				
	n	Mean ± SE	*n*	Mean ± SE	*t*	df	*P*
Eggs*	19	35.2 ± 0.7	19	23.2 ± 2.4	4.8	36	<0.001
Larvae*	19	32.8 ± 1.3	19	33.2 ± 1.4	0.2	36	N.S.
Aphids	20	6.1 ± 0.3	20	11.5 ± 0.3	13.4	38	<0.001

* *A.bipunctata*.

(ii) *Ladybird age structure.* The above indicates that the incidence of cannibalism depends on both the age structure of ladybird beetle populations and the abundance of aphids. When the incidence of cannibalism within and between larval instars was measured in the absence of aphids, first instar larvae ran a great risk of being eaten by larger larvae and not unexpectedly fourth instar larvae ran little risk of being eaten (Table 2). Cannibalism by individuals of the same age class was uncommon. First instar larvae showed the least and fourth instar larvae the greatest tendency to eat larvae. Thus, the early stages are potentially at great risk of death from cannibalism.

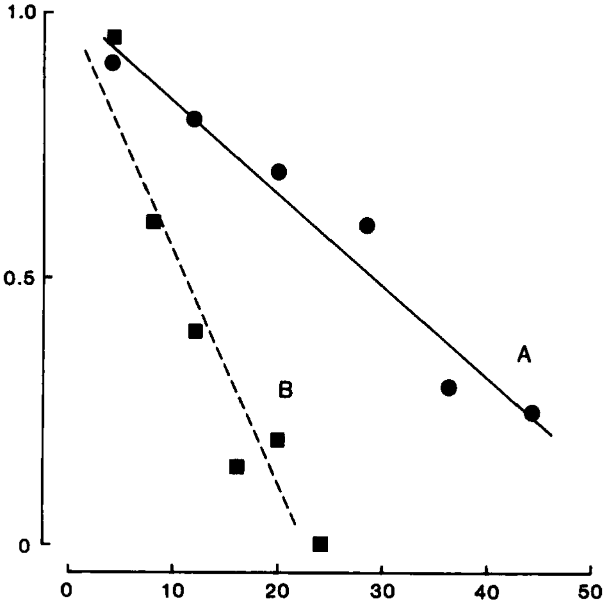

Fig. 3. The proportions of the clutches of eggs (A, ●) and larvae (B, ■) eaten in relation to aphid density in 24 h. (Eggs: $r^2 = 0.95$; $y = 1.007 - 0.0017x$; larvae: $r^2 = 0.91$; $y = 1.003 - 0.044x$; means of twenty observations).

Table 2. The proportion of first (L1), second (L2), third (L3) and fourth (L4) instar larvae of *A.bipunctata* offered eaten in 24 h by larvae of their own and other ages.

Larval instar	*n*	Proportion of larvae eaten L1	L2	L3	L4
1	10	0.1			
2	10	0.28	0.15		
3	10	0.51	0.51	0.2	
4	10	0.60	0.55	0.31	0.3

Advantages of cannibalism

(i) *Cost of feeding on eggs.* When prey is scarce, predatory animals seek alternative food, which may well be members of its own species. To determine whether there is a cost associated with eating the eggs of their own species, different quantities of eggs and aphids were offered to fourth instar larvae (Table 3). For a similar growth rate fourth instar larvae required a greater biomass of aphids than coccinellid eggs. This clearly indicates that eggs are a better food than aphids when measured in terms of larval growth.

(ii) *Duration of survival when fed aphids and eggs of their own species.* When prey is scarce larvae need to be able to survive for long periods without food. Cannibalism could be a way of prolonging survival. Larvae of all instars that ate eggs survived significantly longer than those that ate a similar quantity of aphids (Table 4) and this cannot be attributed to different water contents of these two foods (cf. Table 3). Fourth instar larvae appear to derive the maximum benefit from cannibalism.

Interspecific predation

Quite often the same species of aphid is attacked by more than one species of ladybird. Therefore, it is likely that the ladybirds will interact but the extent to which this occurs both between species of the same genus and between species of different genera is unknown. The tendencies of ladybirds to cannibalize their own eggs and larvae and eat those of other species was determined (Tables 5 and 6). In the absence of aphids both predation between species and between genera occurred. However, it did not occur

Table 3. The total quantity of aphids and conspecific eggs supplied, average fresh and dry weight eaten and the growth rate (GR) achieved by fourth instar larvae of *A.bipunctata* measured over 4 days at 20°C.

Food	Quantity given (mg)	Mean weight eaten (mg) Fresh weight	Dry weight	GR of larva (mg/day)
Aphids	48.0	48.0	8.4	1.7 ± 0.3
Eggs	16.56	15.7 ± 0.5	2.5 ± 0.1	1.7 ± 0.3
df		38	38	38
t		69.4	77.6	0.1
P		<0.001	<0.001	N.S.

Table 4. The time for which larvae of *A.bipunctata* survived after feeding on equal weights of eggs and aphids.

Larval instar	Food quantity (mg)	Survival (days) Eggs *n*	Mean ± SE	Aphids *n*	Mean ± SE	df	*t*	*P*
I	1.4	20	6.2 ± 0.1	20	3.9 ± 0.2	38	9.1	<0.001
II	2.5	20	6.3 ± 0.2	20	4.8 ± 0.2	38	4.7	<0.001
III	4.0	20	5.9 ± 0.3	20	4.6 ± 0.2	38	3.1	<0.001
IV	4.7	20	12.0 ± 0.2	20	5.8 ± 0.2	38	24.0	<0.001

Table 5. Mean proportion of the eggs of four species of ladybird beetles eaten by fourth instar larvae and adults of the same species and of the other three species. (Values on the same line followed by the same letter not significantly different from one another at the 5% level, Mann-Whitney test; overall proportion χ^2).

Predatory species	*n*	Mean proportion (±SE) of eggs eaten			
		A.bipunctata	*A.decempunctata*	*C.septempunctata*	*C.undecempunctata*
(A) Larvae					
Adalia					
bipunctata	30	1.0 ± 0 (a)	0.99 ± 0.002 (b)	0.62 ± 0.065 (c)	0.46 ± 0.017 (d)
decempunctata	30	0.42 ± 0.047 (a)	0.86 ± 0.038 (b)	0.88 ± 0.03 (b)	0.93 ± 0.015 (b)
Coccinella					
septempunctata	30	0.23 ± 0.052 (a)	0.351 ± 0.064 (a)	0.91 ± 0.016 (b)	1.0 ± 0 (c)
undecempunctata	30	0.29 ± 0.032 (a)	0.83 ± 0.029 (b, d)	0.91 ± 0.018 (c, d)	0.86 ± 0.013 (b)
(B) Adults					
Adalia					
bipunctata	20	0.8 ± 0.06 (a)	0.68 ± 0.03 (b)	0.10 ± 0.01 (c)	0.29 ± 0.04 (d)
decempunctata	20	0.04 ± 0.01 (a)	0.83 ± 0.03 (b)	0.30 ± 0.04 (c)	0.54 ± 0.04 (d)
Coccinella					
septempunctata	20	0.29 ± 0.06 (a)	0.57 ± 0.05 (b)	0.97 ± 0.01 (c)	1.0 ± 0 (d)
undecempunctata	20	0.14 ± 0.02 (a)	0.35 ± 0.02 (b)	0.49 ± 0.03 (c)	1.0 ± 0.013 (d)
Overall mean proportion of interspecific predation		0.23 (a)	0.62 (b)	0.55 (c)	0.70 (d)

Table 6. Total number of third instar larvae of four species of ladybirds eaten by fourth instar larvae of their own and three other species of ladybirds. (Values on the same line followed by the same letter not significantly different from one another at 5%, χ^2 and Fisher Exact test).

Predatory species	*n*	Total number of larvae eaten				Homogeneity χ^2 d.f. = 3
		A.bipunctata	*A.decempunctata*	*C.septempunctata*	*C.undecempunctata*	
Adalia						
bipunctata	20	19 (a)	20 (a)	20 (a)	20 (a)	3.04 NS
decempunctata	20	19 (a)	20 (a)	14 (b)	20 (a)	15.5 $P < 0.01$
Coccinella						
septempunctata	20	6 (a)	12 (b, d)	18 (c)	13 (c, d)	15.3 $P < 0.01$
undecempunctata	15	0 (a)	9 (b)	10 (b)	13 (b)	25.2 $P < 0.01$

equally between species of the same or different genera. Larvae of species of *Adalia* and *C.undecempunctata* consistently ate eggs of the other species more readily than did the adults of these species (Table 5) whereas *C.septempunctata* larvae and adults ate similar proportions of the eggs of the other species. Notably, the eggs of *A.bipunctata* were relatively less frequently eaten by the larvae and adults of the three other species and to a lesser extent so were those of *C.septempunctata*, which the adults of the other species were also reluctant to eat (Table 5). This suggests that eggs of *A.bipunctata* and *C.septempunctata* are defended in some measure from predation. Larvae of species of *Adalia* showed a stronger tendency to eat larvae of other species than did the larvae of species of *Coccinella* ($\chi^2 = 60.8$, $P < 0.001$; Table 6). Thus the response of larvae and adults to the eggs and larvae of other species varies.

Are eggs of ladybirds defended against predation?

Starving fourth instar larvae and adults of *A.bipunctata* and *C.septempunctata* ate significantly fewer eggs of their own species when painted with a water extract of the other species' eggs. Thus the eggs of both these species are protected to some extent from predation and the protective chemical was water soluble (Table 7).

Table 7. The effect on egg cannibalism in *A.bipunctata* and *C.septempunctata* of painting conspecific eggs with water, a water extract of conspecific eggs and a water extract of the other species' eggs. (Ten eggs offered to each of twenty different larvae or adults in each test).

	Mean number of eggs eaten by:			
	Larvae		Adults	
Eggs	*A.bipunctata*	*C.septempunctata*	*A.bipunctata*	*C.septempunctata*
Painted with water			6.1 ± 1.6 (1.5)*	5.7 ± 1.4 (1.9)*
A water extract of:				
A.bipunctata eggs	7.9 ± 1.9	4.3 ± 1.5	6.6 ± 2.4 (6.4†)	1.5 ± 1.1 (10.7†)
C.septempunctata eggs	5.0 ± 1.4	8.6 ± 1.5	3.3 ± 1.2	8.13 ± 1.8
df	38	38	2,76	2,76
t	5.4	9.3	19.9	103.9
P	<0.001	<0.001	<0.001	<0.001

* t values of treatments of eggs painted with water and a water extract of own eggs n.s.

† t values of treatments of eggs painted with water and a water extract of other species eggs, $P < 0.001$.

Consequence of eating the eggs of another species

Fourth instar larvae of *C.septempunctata* were significantly more likely to die after eating a few eggs (3.1 ± 1.4 mg) of *A.bipunctata* than after eating a similar weight of their own eggs (ten larvae of each species; $\chi^2 = 4.97$, $P < 0.001$). In contrast, fourth instar larvae of *A.bipunctata* ($n = 20$) that had consumed a few eggs (2.24 ± 1.5 mg) of *C.septempunctata* survived as well as those fed ($n = 10$) the eggs of their own species ($\chi^2 = 0.28$, n.s.). Thus the eggs of *A.bipunctata* appear to be better defended against predation by *C.septempunctata* than vice versa.

Discussion

Cannibalism occurs mainly when aphid prey are scarce and coccinellids are starving. But not all individuals and life stages are equally vulnerable. Older larvae and adults pose a potential threat to eggs and younger larvae. The reluctance of adult females to eat eggs may be adaptive as it would reduce the chance of their eating their own eggs, whereas males are less likely to come across eggs they have sired.

As there are apparently no penalties associated with eating conspecific eggs one would expect cannibalism to occur even when aphids are very abundant, which is what was observed. The low level of cannibalism when aphids are abundant reflects the low relative frequency of encounters between adults and larvae and eggs. To further reduce this risk ladybirds should synchronize oviposition (Hemptinne *et al.*, 1990; Hemptinne & Dixon, 1991) and not oviposit in or close to an aphid colony as that is where the adults and larvae aggregate. However, the eggs should not be laid at too greater a distance because newly hatched larvae are inefficient at locating and capturing aphids (Dixon, 1959; Brown, 1972; Kawai, 1978). There is some evidence that ladybirds do lay their eggs slightly away from aphid colonies (Banks, 1954; Dixon, 1959; Osawa, 1989) and that eggs are more at risk from cannibalism if laid near an aphid colony (Osawa, 1989). On the positive side, cannibalism improves the chances of surviving to find prey, eliminates potential competitors and ensures future availability of food when aphids are scarce.

Ladybird beetles defend themselves with bitter-tasting alkaloids and volatile pyrazine and quinolenes (Rothschild, 1961; Pasteels *et al.*, 1973; Mueller *et al.*, 1984; Rothschild *et al.*, 1984). The alkaloids coccinelline and adaline occur in *C.septempunctata* and *A.bipunctata*, respectively (Pasteels *et al.*, 1973). Intravenous injections of an homogenate of ladybirds can kill guinea-pigs (*Cavia porcellus*) (Frazer & Rothschild, 1960), and nestling blue tits (*Parus caeruleus*) fed 5⅓ seven-spot ladybirds per day died within 2 days but were apparently unaffected by an equivalent amount of two-spot ladybird beetles (Marples *et al.*, 1989).

In this study, the eggs of *A.bipunctata* were much less frequently eaten by the larvae and adults of other species of ladybirds than by their own species. Similarly, the larvae and adults of *A.bipunctata* were reluctant to eat the eggs of *C.septempunctata*. Thus, the eggs of *A.bipunctata* and *C.septempunctata* have some protection against predation. Significantly higher levels of mortality occur in fourth instar larvae of *C.septempunctata* fed the eggs of *A.bipunctata* than of *A.bipunctata* fed *C.septempunctata* eggs, which implies that in this interaction *A.bipunctata* is better protected than *C.septempunctata* and the eating of eggs of the other species is not without risk. As these two species frequently attack the same aphid colonies and the smaller two-spot is at a greater risk of being eaten by the larger seven-spot, one would expect the smaller species to be better defended.

These results indicate that ladybirds are not only defended against vertebrates but against predation by other species of ladybirds. This is particularly marked in the case of the two-spot ladybird and is possibly attributable to the adaline content of this species. The seven-spot ladybird is a large and conspicuous sun-loving species, which not surprisingly is well defended chemically against predation by birds. The small two-spot ladybird is less conspicuous and possibly more at risk from predation by larger species of ladybirds and other predatory insects, which may account for why it is better defended against such predators.

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