

Nutritive cost of intraguild predation on eggs of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera: Coccinellidae)

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Abstract. *Coccinella septempunctata* was approximately 20% more reluctant to eat the eggs of *Adalia bipunctata* than the reverse. In addition, fourth instar larvae of *C. septempunctata* failed to complete their development on a diet of *A. bipunctata* eggs and only 30% of those of *A. bipunctata* completed their development on a diet of *C. septempunctata* eggs, and the survivors took nearly 2 times as long as those fed aphids. This is an indication that the costs of intraguild predation might outweigh the benefits.

INTRODUCTION

Associated with large aggregations of prey are usually large numbers of insect predators belonging to several taxa (Rosenheim et al., 1993). For example, two or more species of anthocorid bugs, hoverflies, ladybirds, mirid bugs and parasitoids may all attack a population of sycamore aphids, *Drepanosiphum platanoidis* (Schrank), at the same time (Dixon & Russel, 1972; Dixon, 1998). In summer, when immature individuals of the sycamore aphid become scarce the nymphs of *Anthocoris confusus* Reuter and *A. nemorum* (L.) resort to feeding on sycamore aphid mummies containing parasitoids. The proportion of anthocorid nymphs that reach maturity each year is dependent on the abundance of parasitized aphids (Dixon & Russel, 1972): when the main food resource becomes scarce the various members of this aphidophagous guild may resort to eating one another (Lucas et al., 1998; Obrycki et al., 1998a,b). Similarly, the frequency of intraguild predation in the field between the ladybirds *Adalia bipunctata* (L.), *Coleomegilla maculata* (De Geer) and *Hippodamia convergens* (Guerin) increases when the aphid population on maize crashes (Schellhorn & Andow, 2000). In addition, many ladybirds like *A. bipunctata* choose to oviposit near large aggregations of aphids and as a consequence their eggs suffer a higher mortality from predation by other insect predators attracted by the aphids than species like *C. maculata*, which oviposits far from large aggregations of aphids (Schellhorn & Andow, 1999). Intraguild predation is seen as adaptive as it supplies a source of food as well as removing potential competitors (Polis et al., 1989). As it is often asymmetrical (but see Rosenheim et al., 1995), with the sedentary stages of the various natural enemies more at risk of being eaten than the active stages, one would expect the more vulnerable species and stages to evolve means of avoiding being eaten. For example, parasitoids tend to cease ovipositing and leave areas where ladybirds are present and represent a threat to the survival of their offspring (Taylor et al., 1998). However, with a few notable exceptions little attention has been given to how species might defend themselves against intraguild predators (Canard & Duelli, 1984; Eisner et al., 1996).

All stages of ladybirds contain species specific alkaloids,

some of which are thought to be toxic to other ladybirds (Pasteels et al., 1973; Agarwala & Dixon, 1992). However, the consequences of this toxicity for intraguild predation has been largely ignored.

All stages of *A. bipunctata* and *Coccinella septempunctata* L. have been recorded coexisting in aphid colonies feeding, for example, on apple (Smee, 1922; Radwan & Lövei, 1982; Hemptinne, 1989), peach (Remaudière & Leclant, 1971), beans (Banks, 1955, 1956), broom (Smith, 1966), hops (Trouvé et al., 1996), maize (Radwan & Lövei, 1983b), nettles (Hemptinne & Naisse, 1988), spindle (Barczak et al., 1996) and wheat (Hemptinne, 1989). *A. bipunctata* is regarded as a polyphagous species (Nedvèd, 1999). Two surveys of the habitat preferences of predaceous ladybirds in Central Europe indicate that although both *A. bipunctata* and *C. septempunctata* have particular habitat preferences, shrubs and trees, and field plants, respectively, nevertheless, their habitat preferences do overlap and the indices of similarity cited range from 0.2–0.5 (Honěk, 1985; Nedvèd, 1999). Therefore, although intraguild predation between *A. bipunctata* and *C. septempunctata* has not been studied in the field it is likely to occur.

In this paper the effect of feeding fourth instar larvae of *A. bipunctata* and *C. septempunctata* on their own and the other species eggs was studied under laboratory conditions. In order to (a) exclude physical defence as a factor eggs rather than larvae were used as prey so that differences in performance of the predator could be attributed to nutritive effects, and (b) facilitate the measurement of performance fourth instar larvae were used as predators as they have the greatest growth potential of all the instars.

MATERIALS AND METHODS

Ladybird culture

The ladybirds were reared as previously described in Hemptinne et al., (1998) except the adults of *A. bipunctata* and *C. septempunctata* were kept at 15° and 25°C, respectively, in order to encourage egg production. The egg clusters were removed from the paper on which they were usually laid by cutting round them with fine scissors. From the beginning of the

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third instar the larvae were isolated in 5-cm diameter Petri dishes lined with filter paper.

Nutritive value of hetero- and conspecific eggs for fourth instar larvae of *A. bipunctata* and *C. septempunctata*

A third instar larva of *A. bipunctata* was isolated in a 5-cm diameter Petri dish and fed daily an excess of pea aphids (*Acyrtosiphon pisum* Harris). As soon as it moulted to the fourth instar, it was weighed. It was then fed daily an excess of pea aphids until it pupated when it was weighed again. This was repeated 19 times (control). The experimental procedure involved either feeding daily 15 larvae kept in isolation with batches of freshly laid conspecific eggs or 10 larvae with batches of eggs of *C. septempunctata*. Their survival, time spent in the fourth instar and consumption of eggs were recorded and their relative growth rates calculated as follows:

$$\frac{\ln W_f - \ln W_i}{D}$$

where W_f is the weight of a pupa less than 24 h old, W_i the weight of the larva at the beginning of the fourth instar and D the duration of the instar in days.

The mortalities were compared by means of χ^2 tests, the duration of development and relative growth rates by means of Mann-Whitney's and Kruskal-Wallis tests and non parametric multiple comparisons (Zar, 1996).

The same experiment was repeated using fourth instar larvae of *C. septempunctata*. In this case 17 larvae were fed aphids, 17 conspecific eggs and 20 the eggs of *A. bipunctata*.

All these experiments were done at a temperature of $20^\circ\text{C} \pm 1^\circ\text{C}$, under artificial lighting of 2,000 lux. and a photoperiod of 16 h light and 8 h darkness.

RESULTS

Nutritive value of hetero- or conspecific eggs for fourth instar larvae of :

(a) *A. bipunctata*

Fourth instar larvae of *A. bipunctata* developed and survived as well on a diet of conspecific eggs as on a diet of pea aphids (Table 1). In contrast, a diet of *C. septempunctata* eggs resulted in 70% of the larvae dying, a mortality rate significantly greater than when fed either conspecific eggs or aphids ($\chi^2 = 16.57$; 2 d. f.; $P < 0.001$). Those that survived took significantly longer to complete the fourth instar (Kruskal-Wallis statistics = 22.861; 2 d.f.; $P < 0.001$), and had a tendency to grow more slowly than larvae fed aphids or conspecific eggs (Kruskal-Wallis statistics = 6.536; 2 d.f.; $P = 0.038$). One of the three larvae that survived

was lighter at the end than at the beginning of the fourth instar. Frequently, after ingesting yolk from seven-spot eggs, two-spot larvae were observed to vomit a black liquid.

(b) *C. septempunctata*

Larvae of *C. septempunctata* fed conspecific eggs grew significantly slower than those fed aphids (Mann-Whitney's $U = 2.000$; $P < 0.001$). Similarly, there was also a significant difference in the length of the fourth instar (Mann-Whitney's $U = 282.000$; $P < 0.001$; Table 1). However, as the larvae often ate all the eggs provided they were probably never satiated. It was not possible to give them more than 62 eggs per day on average because the supply of eggs was limited by the size of the culture of *C. septempunctata*. The observed differences in growth rate and development time could therefore result from a relative shortage of food.

A diet of eggs of *A. bipunctata* resulted in the death of all the larvae of *C. septempunctata*, after an average of 8.5 days. The mortality was significantly greater than that observed when larvae were fed pea aphids or conspecific eggs ($\chi^2 = 74.01$; 2 d.f.; $P < 0.001$; Table 1). That is, the eggs of *A. bipunctata* appeared to be more toxic to *C. septempunctata*, than the reverse.

DISCUSSION

The study of Agarwala & Dixon (1992) on *A. bipunctata* and *C. septempunctata*, that of Agarwala et al. (1998) on *Menochilus sexmaculatus* (F.) and *C. transversalis* and that of Cottrell & Yeargan (1998) on *Harmonia axyridis* Pallas and *C. maculata* indicate that these species are more reluctant to eat each other's eggs than their own eggs. In the two first cases, interestingly, it is the eggs of the smaller species that are less likely to be eaten. This is also supported by our results. As all stages of ladybirds contain species specific alkaloids (Pasteels et al., 1973), which are known to be toxic to vertebrates (Frazer & Rothschild, 1960; Marples et al., 1989), it is not unreasonable to assume that these alkaloids also afford the ladybirds protection from invertebrate predators. *A. bipunctata* adults contain more alkaloid per unit weight than *C. septempunctata* (de Jong et al., 1991; Holloway et al., 1991).

The results presented here on the incidence of predation by *A. bipunctata* on *C. septempunctata* eggs (50%) and that of *C. septempunctata* on *A. bipunctata* eggs (30%) are very similar to the 62% and 23%, respectively, reported by Agarwala & Dixon (1992). Therefore, *A. bipunctata* eggs appear to be more strongly protected than those of *C. septempunctata*. In addition, our results show that only 30% of the *A. bipunctata* larvae

TABLE 1. Number dying, egg consumption, duration of development and relative growth rate of fourth instar larvae of *Adalia bipunctata* and *Coccinella septempunctata* fed either pea aphids, conspecific or heterospecific eggs.

	Nr of larvae tested	Nr of larvae dying	Average nr. of eggs per larva		Duration of 4th instar (1)	Relative growth rate (1)
			given	eaten		
<i>A. bipunctata</i>						
Aphids	19	2	-	-	4.1 a	0.143 a
Conspecific eggs	15	1	205.2	159.7	6.1 b	0.107 a,b
Eggs of <i>C. septempunctata</i>	10	7	159.3	74.3	7.0 b	0.068 b
<i>C. septempunctata</i>						
Aphids	17	0	-	-	4.1 a	0.266 a
Conspecific eggs	17	0	388.5	281.7	6.5 b	0.133 b
Eggs of <i>A. bipunctata</i>	20	20	≈350.0	119		

(1) Figures followed by the same letter in the same column and for each species do not differ significantly at $\alpha = 0.05$.

completed their development on a diet of *C. septempunctata* eggs and took nearly two times longer to do so, whereas none of the *C. septempunctata* larvae completed their development on a diet of *A. bipunctata* eggs. This indicates that the eggs of both species are clearly toxic to the other species. As all stages of ladybirds contain similar concentrations of the species specific alkaloids (Pasteels et al., 1973), it could be assumed that all stages of both species are toxic to the other species. Although the prey in this study were eggs it is likely that similar results would have been obtained with larvae as prey.

In the field it is very unlikely that ladybird larvae would feed solely on ladybird eggs. It is more likely they eat ladybird eggs and larvae along with aphids, i.e., a mixed diet. However, when an aphid population on which ladybirds are feeding crashes the proportion of conspecific and heterospecific larvae in the diet may be very high. The eating of eggs and larvae of other species of ladybird is likely to reduce the quality of the diet of the ladybird. Poor quality food generally prolongs larval development in ladybirds (Blackman, 1965, 1967; Radwan & Lövei, 1983a; Obrycki et al., 1998a,b), which as well as delaying maturity is also likely to increase the risk of the larvae being killed. Consequently, there are potential costs associated with intraguild predation.

In conclusion, well fed larvae should avoid eating the immature stages of other ladybirds because the costs in terms of prolonged development and decreased survival are potentially large. However, when starving the eating of the immature stages of other ladybirds, even though they are toxic, could be advantageous because it may prolong their survival, especially if combined with other more acceptable prey. That is, for intraguild predation to be advantageous the benefits should outweigh the costs.

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