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Are Aphidophagous Ladybirds (Coccinellidae) Prudent Predators?

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ABSTRACT

Aphidophagous ladybirds tend to lay eggs close to their prey and their voracious larvae forage in a way that results in them remaining in or close to aphid colonies. Although ladybird beetles have frequently been used to control aphids, they are rarely effective in reducing aphid abundance. Aphids have very high rates of increase and are very sensitive to changes in the quality of their host plants. On average, aphid colonies rarely last for more than a month. That is, they are a very unstable food resource for predators. In addition, the developmental time of ladybirds is about a month. As a consequence ladybirds face two risks. If they lay their eggs too late in the development of an aphid colony, the larvae will not mature before prey becomes scarce. If they lay too many eggs their larvae will severely restrict the rate of increase of the aphids and cause an earlier collapse of the colony. In order to survive the larvae will then have to resort to cannibalism. Theory indicates that the best strategy for optimizing fitness is for ladybirds to lay a few eggs at the beginning of the development of aphids colonies. Both experimental and field data indicate that is what ladybirds do, i.e., they behave as if they are 'prudent predators'. This accounts for why aphidophagous ladybirds have been very ineffective biological control agents.

INTRODUCTION

Biological control aims to reduce the abundance of a pest below its economic threshold. Because aphidophagous ladybirds mainly feed on aphids, they have always been regarded as potential biological control agents (Hodek, 1973). Ladybirds lay their eggs close to aphid colonies and their voracious larvae forage in a way that results in them remaining close to their prey (Ferran & Dixon, 1993). The voracity of both adults and larvae of many species has been assessed and used to support claims of their effectiveness or ineffectiveness in controlling populations of aphids (Markkula *et al.*, 1972; Frazer & Gilbert, 1976; Lapchin *et al.*, 1987; Kauffmann & Schwalbe, 1991; Crawley, 1992). The oviposition behaviour of females, however, is rarely seen as essential for evaluating the impact of ladybird beetles.

In temperate countries, the use of natural enemies to control aphids in field crops is still at an experimental stage. Efforts are mainly directed to manipulations of the biological environment to conserve and enhance populations of beneficial insects. Fields, their margins or adjacent areas are managed in an attempt to keep and increase the populations of indigenous predators and parasitoids in the vicinity (Van Emden, 1990; Fry, 1991; Sotherton, 1991). For example, hibernation shelters are created in the middle of large fields or around their edges. Sometimes, headlands are not sprayed with pesticides or strips of flowers are planted in order to provide alternative or essential food for the natural enemies. Generalist predators and hoverflies tend to be more abundant in these habitats (Nentwig, 1988; Thomas *et al.*, 1991). However, their presence does not guarantee that aphid abundance will be reduced. The key factor in this is how the females of the natural enemies distribute their eggs. This determines the density of larvae and consequently their effect on the abundance of pests.

Ladybirds start to lay eggs when the density of aphids reaches a particular threshold (Hodek, 1973; Honek, 1980) and aphid honeydew often acts as an arrestant and increases the probability of the prey being discovered (Carter & Dixon, 1984; Evans & Dixon, 1986). However, adult ladybirds do not oviposit in aphid colonies continuously through their development. This is possibly because the probability of egg cannibalism increases with the density of predators and females refrain from egg laying when the risk of cannibalism becomes too great, however abundant the prey. This possibly accounts for why ladybirds are generally ineffective biological control agents. In this paper we discuss the evidence for the above hypothesis in the light of the life history of *Adalia bipunctata* (L.).

THE LIFE HISTORY OF *A. BIPUNCTATA*

In Belgium, nettle patches, apple trees and wheat fields are the most important habitats of *A. bipuncata* in spring and early summer (Hemptinne, 1989). The ladybirds colonize and lay eggs on nettles in the first decade of June when the aphids start to increase in abundance. Their larvae are recorded a week later (Figure 1) and they pupate towards the end of June when the aphid population is collapsing rapidly. The second generation of ladybirds leave nettle beds before the second week of July. The phenology of *A. bipunctata* on apple trees is similar although eggs are laid and larvae appear slightly earlier (Figure 1). Adult ladybirds colonize wheat fields in the first week of July and providing aphids are abundant enough they lay eggs (Figure 1). In these different habitats most of the eggs are characteristically laid well before the aphid colonies reach their peak

(Figures 2 and 3). That is, there is only a very short period in time when ladybirds lay eggs in an aphid colony ('reproductive window'). The highly significant decrease in the number of eggs laid during the second half of the life of an aphid colony is not due to the sudden disappearance or the death of all the ladybirds. The windows of egg laying on nettles, wheat and apple occur sequentially and overlap each other slightly. The sequence is generated by the first generation adults moving from one habitat to another.

On nettles, apple trees or in wheat fields aphids persist for 4 to 9 weeks. Therefore individual aphid colonies probably have shorter life spans. As *A. bipunctata* takes a month to grow from egg to adult (Obrycki & Tauber, 1981), females must lay their eggs early in the development of an aphid colony. If they lay their eggs too late in the development of an aphid colony, the larvae will not mature before this prey becomes scarce. In addition if many eggs are laid, the larvae reduce the rate of increase of the aphids and cause an earlier collapse of the colony. If this happens the larvae resort to cannibalism to survive. Even in the early stages of development of an aphid colony, cannibalism is important for the survival of eggs and ladybird larvae. In the field, 19 to 33% of the eggs are

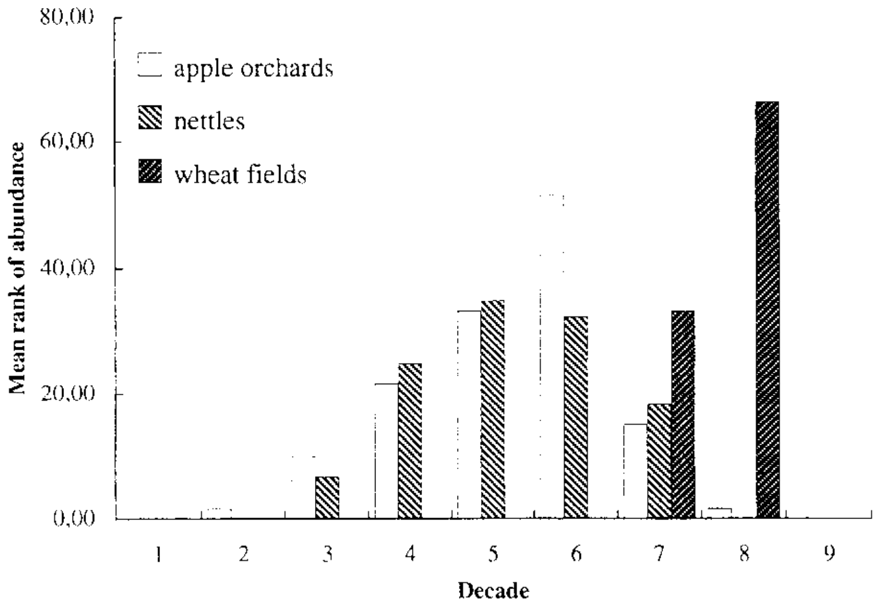

FIGURE 1. Distribution in time of third and fourth instar larvae of *Adalia bipunctata* (L.) in five stations of three habitats from 1980 to 1985 (from Hemptinne, 1989).
Data collected in each type of habitat during five years are pooled together. The variation in larval abundance is expressed by the mean rank of larval density per decade. Decade 1 corresponds to the second decade of May, decades 3 to 5 to June, decades 6 to 8 to July and decade 9 to the first 10 days of August.

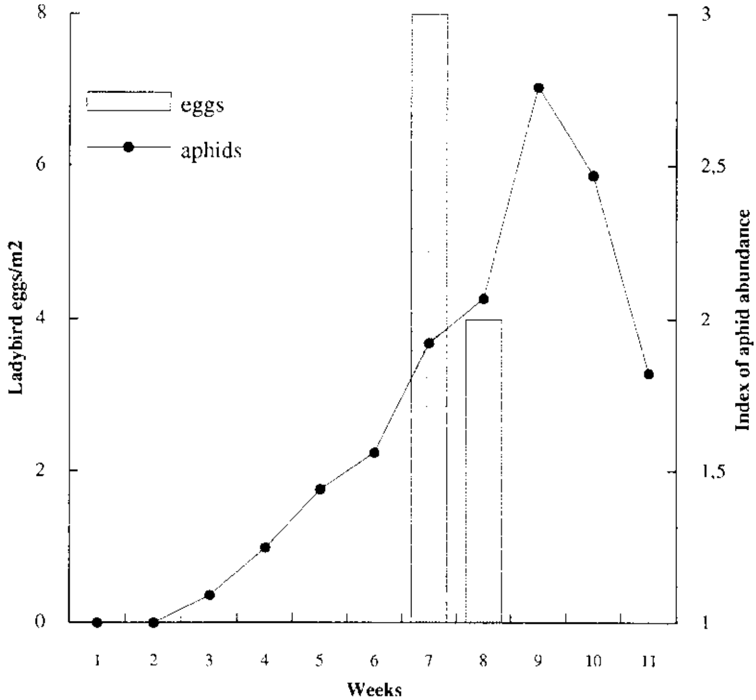

FIGURE 2. Development of the number of *Sitobion avenae* (F.) and variation of the average density of ladybird eggs in ten plots of 1 m^2 in a wheat field in 1985 (from Hemptinne, 1989). Weeks 2 to 5 correspond to June, 6 to 10 to July. Index of aphid abundance: 1 = no aphid, 2 = aphids only detected using a sweep net, 3 = aphids detected by eyes but only scattered individuals.

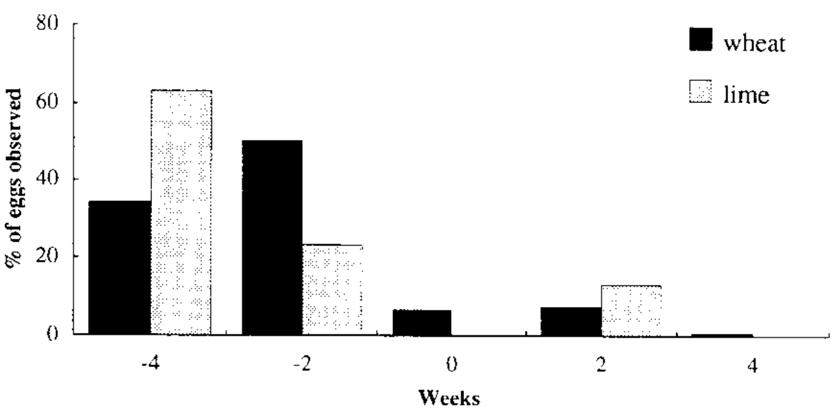

FIGURE 3. Distribution in time, relative to peak aphid abundance, of ladybird egg batches in wheat fields and on lime trees (from Hemptinne *et al.*, 1992). Peak of aphid abundance occurs in week 0. There are 105 batches from wheat fields (χ^2 = 95.54, $p < 0.001$) and 30 on lime trees (χ^2 = 39.22, $p < 0.001$).

eaten and there is a negative correlation between cannibalism and prey abundance (Mills, 1982).

New born larvae need a higher density of prey for survival than older larvae and their feeding success is negatively correlated with aphid size (Dixon, 1959). Thus, females should only oviposit when the abundance of first and second instar aphids is sufficient for the survival of their first instar larvae. Interaction between ovipositing females and larvae possibly signals that an aphid colony is no longer suitable for egg laying. A model of the interaction between aphids and ladybirds, which takes the requirements of first instar larvae and the risk of cannibalism into account, indicates that the best strategy is for the ladybirds to lay a few eggs at the beginning of the development of aphid colonies (Kindlmann & Dixon, 1993). This is commonly observed in the fields (Hemptinne *et al.*, 1992, 1994).

Experimental results also confirm the predictions of the model (Hemptinne *et al.*, 1992). In the laboratory, females of *A. bipunctata*, kept on their own, show a marked reproductive numerical response to increase in aphid abundance. In the presence of conspecific larvae, however, the threshold density of prey for egg production increases five fold and the maximum egg production was always lower than in the absence of larvae (Figure 4). That is, the presence of the larvae dramatically affects the rate of egg laying. In addition, females almost refrain from ovipositing for the first 3 h when placed with larvae (Table 1). This effect progressively decreases with the passage of time and is not due to competition between the female and the larvae for food (Hemptinne *et al.*, 1992). Moreover, the overall activity of females is significantly greater in the presence of larvae (Figure 5). In the field the increased activity would result in the females leaving the area and ovipositing elsewhere.

TABLE I

Average number of eggs laid in 3, 6 and 9 h by females of *Adalia bipunctata* (L.) kept in isolation (= control) or with three fourth instar larvae of their own species (= two spot larvae) (from Hemptinne *et al.*, 1992). In each line, means followed by different letters differ significantly ($p < 0.01$)

Duration (h)	Treatment	
	Control x (SE)	Two spot larvae x (SE)
3	7.6 (1.5) a	1.5 (1.1) b
6	10.3 (1.6) a	1.9 (1.1) b
9	11.8 (1.5) a	3.7 (1.4) b

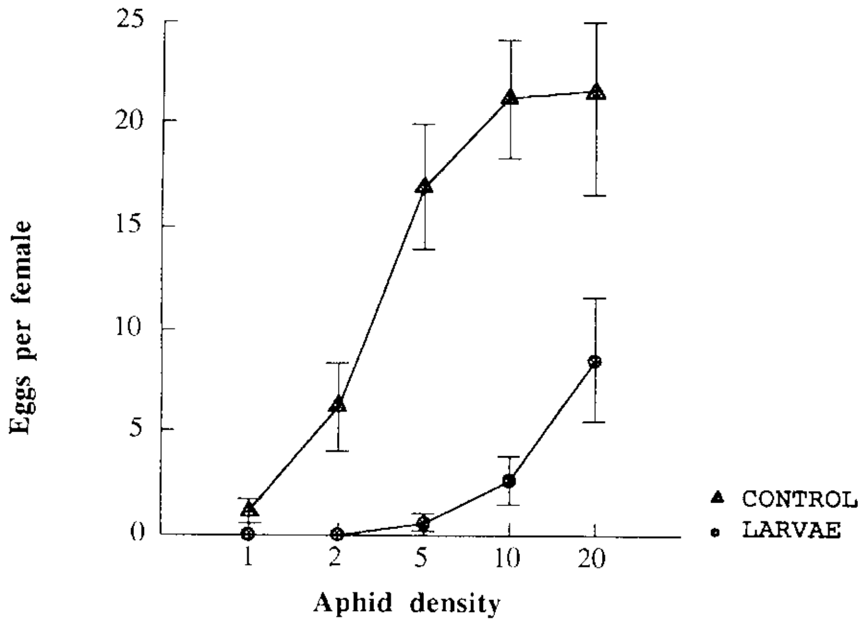

FIGURE 4. Daily egg production of *Adalia bipunctata* (L.) at different aphid densities in the absence (= control) or presence (= larvae) of three fourth instar larvae of their own species (from Hemptinne *et al.*, 1992).

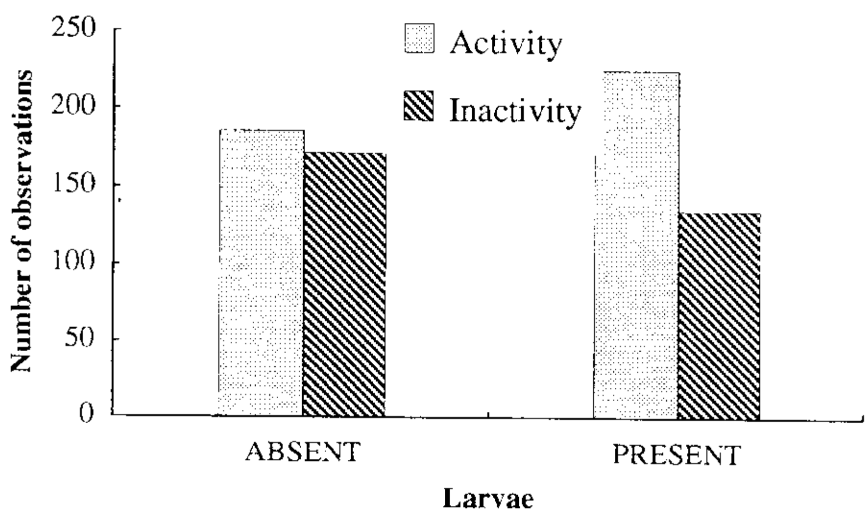

FIGURE 5. Level of activity of female *Adalia bipunctata* (L.) kept singly or with a fourth instar larva of its own species (from Hemptinne *et al.*, 1992). The activity of the ladybirds is observed every 5 min. over a period of 1 h 40 min. Females are referred to as active when moving, inactive when they are stationary.

CONCLUSION

Temporal changes in aphid abundance pose a considerable challenge to female ladybirds because aphid colonies rarely exist for much longer than it takes a ladybird larva to complete its development (Obrycki & Tauber, 1981; Dixon, 1985). Ladybirds should synchronize their reproduction with the early stages of their prey because the survival of newborn coccinellid larvae is very dependent on the abundance of young aphids (Dixon, 1959). In addition, oviposition late in the development of an aphid colony could result in the older larvae being short of food and failing to mature. Thus, the best strategy is for ladybird to lay eggs early in the growth of an aphid colony when these two constraints are met (Kindlmann & Dixon, 1993). Field observations of several species of aphids indicate that ladybirds tend to oviposit only over a very short period of time prior to each aphid population reaching peak abundance, whereas ladybirds can lay eggs for at least three months without interruption (Hodek, 1973). Thus, there is strong evidence that ladybirds prefer to oviposit in aphid colonies early in their development. This implies that the immediate food supply for female ladybirds is not the only factor controlling their egg production (Beddington *et al.*, 1976; Gutierrez & Baumgaertner, 1984) and that the females appear to assess the potential of an aphid colony for supporting their offspring before starting laying eggs. The presence of conspecific larvae affects the quality of a breeding site. It indicates a risk of egg cannibalism and that the new born larvae would probably face tough competition for food from older larvae. In addition it could also be a symptom that the aphid population is in a late stage of development.

Therefore, females of *A. bipunctata* appear to forage as if they were prudent predators (May & Watts, 1992) and there is also evidence that several species of aphidophagous hoverflies behave similarly (Kan, 1988a, 1988b; Hemptinne *et al.*, 1993). This accounts for why aphidophagous ladybirds have generally been ineffective biological control agents. If aphid specific predators generally show 'prudent' reproductive behaviour then the usefulness of manipulating habitats to encourage these predators to maintain aphid populations under their economic threshold is open to question. Before recommending that this kind of 'biological control' be used on a large scale we need to know whether it significantly increases the density of eggs of specific aphidophagous predators in crops.

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