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Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms

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Abstract. Coccinellids and syrphids that feed on aphids and coccids face the same problem: an unstable food supply. Their eggs and larvae face cannibalism and/or starvation if the aphid colony they attack declines in abundance before they mature. Optimal foraging theory predicts that such predators should lay a few eggs early in the development of an aphid colony. Studies on two species of coccinellid and one species of syrphid revealed that they do respond to the quality as well as the abundance of their prey. By refraining from laying eggs in aphid colonies already exploited by predators and those that are shortly to decline in abundance when the aphids disperse, these predators are able to forage in a way that is consistent with the predictions of optimal foraging theory.

INTRODUCTION

Many species of predatory coccinellids and syrphids exploit temporary food resources, aphid colonies, which are patchily distributed and have a short life span (Dixon, 1985). The larvae of aphidophaga risk starvation if the aphid colony on which they are feeding becomes extinct before they complete their development. This could result when too many eggs are laid in a colony or too late in the development of the colony, i.e., when the aphids are preparing to disperse. Optimal foraging theory predicts that to maximize fitness these predators should lay a few eggs early in the development of an aphid colony (Kindlmann & Dixon, 1993).

The reproductive response of *Adalia bipunctata* (L.) to variations in aphid abundance is fairly well known. When aphids are scarce the young larvae are at a great risk of being eaten by older larvae of their own species. Egg cannibalism by larvae and adults is also inversely related to the abundance of aphids (Mills, 1982; Agarwala & Dixon, 1992). Laboratory experiments on *A. bipunctata* indicate that this species reduces the incidence of cannibalism by refraining from ovipositing in the presence of conspecific larvae (Hemptinne et al., 1992). It is suggested that this is the mechanism by which ladybirds avoid cannibalism (Hemptinne et al., 1990) and synchronize their development with that of an aphid colony (Dixon, 1959). The larvae of many species of Syrphidae are also aphidophagous and face the same risk as *A. bipunctata,* although cannibalism does not appear to be as important as in ladybirds. Females of four species of syrphids avoid laying eggs close to old aphid colonies (Kan, 1988a,b), which they recognize by the presence of winged aphids (Kan & Sasakawa, 1986). Egg production in aphidophaga is usually related solely to the availability of prey. However, the above studies indicate that fecundity is also influenced by the quality of the prey. Therefore, when assessing the efficiency of an aphidophagous predator as much attention must be paid to interactions between predators as between prey and predators.

Each species of aphidophagous predator is probably adapted to a particular habitat (Hodek, 1973; Honěk, 1979, 1983; Majerus & Kearns, 1989). However, all these predators exploit prey that varies rapidly in abundance both temporarily and spatially. The aim of this paper is to determine whether other aphidophaga also synchronize their development with that of their prey and avoid laying eggs in colonies that are already being exploited.

REPRODUCTIVE RESPONSE OF SYRPHIDS AND COCCINELLIDS

The syrphid, *Epistrophe nitidicollis* (Meigen)

In 1992 the syrphid *E. nitidicollis* laid eggs in *Aphis fabae* colonies that developed on bean plants in a field experiment consisting of five plots of 30 plants, near Gembloux. Analysis of these results (Hemptinne et al., 1993) revealed firstly, that *E. nitidicollis* laid its eggs well before the aphid populations peaked indicating a significant tendency to select young colonies for oviposition, secondly, that females avoided colonies already attacked by larvae (Fig. 1).

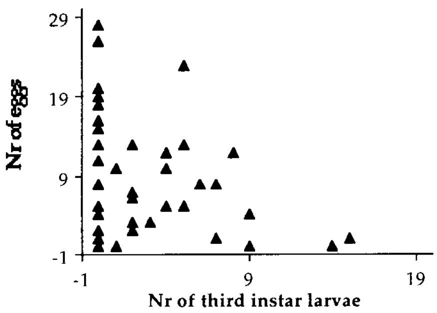

Fig. 1. Number of eggs of a hoverfly found on bean plants in relation to the number of third instar larvae of the same species.

The aphidophagous coccinellid, *Coccinella septempunctata* L.

The reproductive response of *C. septempunctata* was analyzed in the laboratory by subjecting gravid females to various stimuli over a period of 4 hours and measuring the number of eggs laid (Table 1). In a first test females were either exposed to a leaf cut from a vigorously growing bean plant (age: approximately 3 weeks) or a leaf from a senescent plant previously colonized by aphids (age: aproximately 2 months). In both cases an excess of aphids of different instars of *Acyrthosiphon pisum* (Harris) was provided. The level of activity and of egg laying by the females kept with old and young leaves did not differ significantly.

TABLE 1. Total numbers of eggs laid by females *C. septempunctata* kept in a Petri dish and subjected to various treatments for 4 h.

Treatments	n	Eggs	X^2stat
1. YL + mixture of aphid instars	19	138	
OL + mixture of aphid instars	19	166	$p > 0.05$
2. YL + young aphids	40	284	
OL + old aphids	40	161	$p < 0.01$
3. Larva present	41	312	
Larva absent	41	365	$p > 0.05$
4. Eggs present	41	295	
Eggs absent	41	262	$p > 0.05$
5. Female added	31	0	
Female absent	31	182	$p < 0.01$

YL – young leaf; OL – old leaf (see text for explanation).

However, when the females were presented with either young or old leaves as above, but with aphids that matched the phenology of the leaves, i.e., immature aphids on young leaves and adult aphids on mature leaves, they showed a clear preference for laying eggs on young leaves with young aphids and were significantly less active. The presence of conspecific eggs or second instar larva did not inhibit egg laying. However, the presence of another female in the Petri dish resulted in the complete inhibition of egg laying and a strong reduction in activity.

The coccidophagous coccinellid, *Cryptolaemus montrouzieri* Mulsant

C. montrouzieri only lays eggs in the ovisacs of its prey, the mealybug *Eupulvinaria hydrangea*, and its larvae eat the mealybug's eggs and young larvae (Lemaitre, 1992; Merlin, 1993). Females were isolated and kept for 24 hours in the absence of ovisacs before being supplied with two fresh ovisacs and either 0, 1, 2, or 4 conspecific larvae. The eggs laid after 2 hours were counted. *C. montrouzieri* clearly refrains from laying eggs when conspecific larvae are present and the inhibition is proportional to the number of larvae (Table 2).

TABLE 2. Average numbers of eggs laid by females of *C. montrouzieri* in 2 h in a Petri dish in the presence of various numbers of conspecific larvae (after Lemaitre, 1992).

Numbers of larvae	n	Eggs laid (x ± SD)
0	15	8.9 ± 5.2
1	15	4.6 ± 5.6
2	15	2.0 ± 3.5
4	15	1.3 ± 2.8

DISCUSSION

In the case of *A. bipunctata* (Hemptinne et al., 1992) and several species of Syrphidae (Kan, 1988a,b) egg production is not only related to the the abundance of aphids but also to their quality as a source of food. *A. bipunctata* refrains from laying eggs where aphids are abundant if conspecific larvae are present, and syrphids, where winged aphids indicate that the colony will shortly disperse.

Similarly, the field and laboratory results reported here indicate that other species of aphidophaga and coccidophaga tend to forage in the same way. The syrphid *E. nitidicollis* usually oviposits in aphid colonies at an early stage in their development and rarely on plants where conspecific larvae are present. This is very similar to the strategy of *A. bipunctata* (Hemptine et al., 1992). In the laboratory *C. septempunctata* females stop laying eggs and become less active in the presence of other females. They are also reluctant to lay eggs on old bean leaves bearing old aphid colonies, but unlike *A. bipunctata*, do not react to the presence of conspecific larvae. Coccids probably also constitute an unstable food supply for *C. montrouzieri*, which lays its eggs inside the ovisac of its prey. The ladybird is also reluctant to oviposit when conspecific larvae are present (Lemaitre, 1992). Avoiding egg laying in such situations decreases the probability of intraspecific competition between larvae and/or cannibalism.

These examples indicate that several species of Coccinellidae and Syrphidae respond to both the abundance and quality of their prey. This common strategy is achieved by different tactics. The egg laying behaviour of *C. montrouzieri* is similar to the optimal progeny allocation of parasitoïds (Waage, 1986). A comparison between *A. bipunctata* and *C. septempunctata* reveals differences that may be associated with exploiting different habitats. *A. bipunctata* is more dependent on aphids living on trees and shrubs than the aphids on herbaceous plants preferred by *C. septempunctata*. Aphids living on herbaceous plants have generally a more clumped distribution and each colony lasts for a shorter period of time (Dixon et al., 1993). Although being less common than tree dwelling species aphids on herbaceous plants reach very high densities locally. Thus there is possibly a stronger selection pressure for *C. septempunctata* to oviposit in young aphid colonies than for *A. bipunctata*, which may account for the strong positive reaction of seven-spot females to young bean leaves bearing young aphids. Refraining from egg laying when other females are present is also likely to reduce the incidence of cannibalism (Mills, 1982; Agarwala & Dixon, 1992). In addition *C. septempunctata* lays relatively large eggs that ensure the relatively fast development of its larvae (Stewart et al., 1991), an adaptation to feeding on the short lived aphid colonies on herbaceous plants.

Thus, there is evidence that both coccinellids and syrphids have evolved behavioural mechanisms that have enabled them to forage in a way that is consistent with optimal foraging theory, avoiding aphid colonies and coccid colonies that are already exploited and/or will not last long enough to support the development of their larvae.

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