THE LADYBIRD FANTASY - PROSPECTS AND LIMITS TO THEIR USE IN THE BIOCONTROL OF APHIDS

DIXON, A.F.G.[1], HEMPTINNE, J.-L.[2] AND KINDLMANN, P.[3]

[1] School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.
[2] UER de Zoologie générale et appliquée, Faculté des Sciences agronomiques, 2 passage des Déportés, B-5030 Gembloux, Belgium
[3] Faculty of Biological Sciences, University of South Bohemia and Institute of Entomology, Czech Academy of Sciences, Branisovská 31, CS37005 Ceské Budejovice, Czech Republic

Introduction

Predators are generally considered to be less effective biocontrol agents than parasites. This is supported by many observations: out of 93 cases of "substantial" or "complete" biological control reported by van den Bosch & Messenger (1), only 10 cases of "substantial" and two cases of "complete" control involved only predators. The reductions in host density below the enemy free value (q value) by parasitoids are reported (2) to be an order of magnitude greater than by predators.

The famous exception is the control of the cottony-cushion scale, *Icerya purchasi*, by the ladybird beetle, *Rodolia cardinalis*. This outstanding success resulted in the widespread and haphazard introduction of natural enemies, which has been referred to as the period of the 'ladybird fantasy'(3). Many ladybirds were introduced during this period and apart from the above success this was possibly also due to the way these beetles have been perceived for centuries. The prevalence of holy attributes in their common names, in all European languages, might be seen to indicate divine intervention in pest aphid control.

Population Dynamics of Aphids and Ladybirds

Aphid populations characteristically show dramatic changes in abundance in time, with the species peaking in abundance at different times. That is, the prey of aphidophagous ladybirds occurs in patches that vary in quality both in space, and above all in time. Early studies revealed that the survival of the first instar larvae of ladybirds is dependent on an abundance of young aphids. This defines the aphid population density below which any eggs the ladybirds lay are unlikely to survive. The time from egg hatch to pupation in ladybirds spans more than one generation of aphids and is similar in duration to the period for which colonies or patches of aphids contain sufficient prey to sustain ladybird larvae. In addition to feeding on aphids ladybird larvae and adults will readily eat conspecific eggs and larvae. Both egg (5) and larval (6) cannibalism have frequently been observed in the field especially when prey is scarce. Field studies indicate that ladybirds tend to lay their eggs early in the development of an aphid colony and their larvae pupate just prior to the aphids in the patch becoming scarce.

Optimal Foraging by Ladybirds

A simulation model of the interaction between aphids and ladybirds, which takes the minimum aphid population density requirements of the first instar larvae of ladybirds 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 (7). If they lay their eggs later the larvae will not mature before the prey becomes scarce. In addition, if many eggs are laid, the larvae reduce the rate of increase of the aphid colony and cause an earlier decline in abundance. If this happens the larvae resort to cannibalism to survive. This results in the production of a few small adults, which are unlikely to overwinter successfully and have a low potential fecundity (8). That is, if ladybirds are to maximise their fitness they should lay a few eggs early in the development of an aphid colony (Fig. 1).

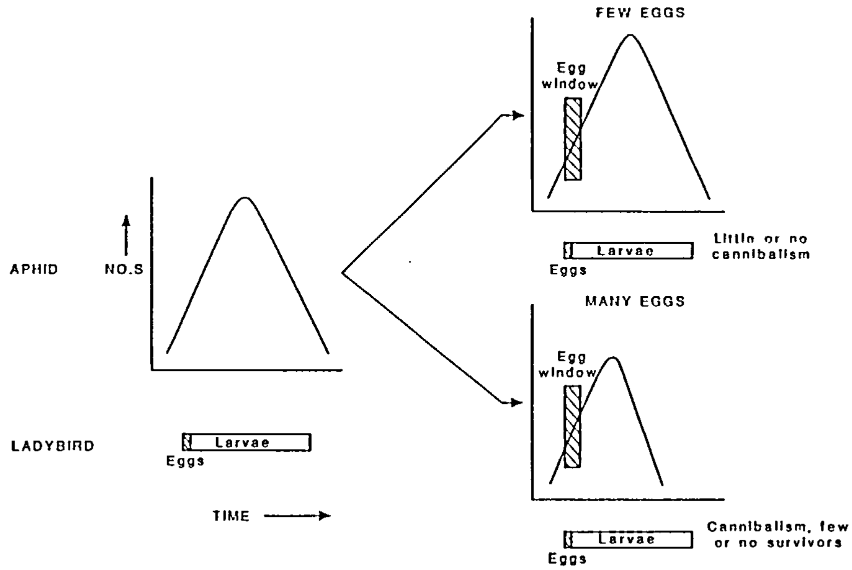

Fig. 1. Diagram illustrating when in the existence of a patch of aphids ladybirds should lay eggs, and how many they should lay in order to maximise their fitness.

What evidence is there that ladybirds forage optimally? *A. bipunctata* lays eggs on apple trees, nettles and wheat in this sequence as the aphid populations develop on these plants (9). In these different habitats most of the eggs are laid over a short period of time before each of these aphids peak in abundance (10). What causes the adults to cease laying eggs when the aphids are still increasing in abundance? 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, they are extremely reluctant to lay eggs and attempt to leave the area even though aphids are abundant. The females are responding to the chemical tracks left by the larvae, which appear to be acting as an 'oviposition inhibiting pheromone'. It is likely that the adaptive significance of this response is that it reduces the incidence of cannibalism. The consequence of this response is that fewer eggs are laid, which restricts their effectiveness as biocontrol agents.

Biological Control

The above we believe is characteristic of predators that are long lived relative to their prey. In the case of the ladybird, *Rodolia cardinalis*, an egg is laid under an adult female scale or its egg mass, and the lava completes its development by consuming the scale and its eggs (11). That is, the generation time of *Rodolia* and its prey are comparable. In the field, ladybirds in general are successful in controlling univoltine scales (1), but not polyvoltine aphids (12) and mites (13).

Thus instead of parasites vs predators there is a continuum of ratios of the generation times of the natural enemies to those of their prey (GTR), which is correlated with the q-values. In natural enemy/prey systems where the GTR is much larger than 1, the corresponding q-values are large. In parasite/host, predatory mite/herbivorous mite and *Rodolia cardinalis* /scale systems, the GTR is close to 1 and the corresponding q-values are small. Ladybirds successfully control their prey when the GTR is small and not so when the GTR is large as is the case for all aphidophagous ladybirds.

Conclusions

Thus ladybirds and other insect predators are unlikely to reduce greatly the rate of population increase in aphids. This leaves only one other means of reducing aphid rate of increase, which is to reduce the quality of the host plant for aphids. Most crops can be selected or genetically engineered to be considerably more resistant to aphids. The prospect of using plant resistance to reduce pest aphid abundance is much more promising and largely unexploited.

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