LADYBIRDS AND THE BIOLOGICAL CONTROL OF APHID POPULATIONS

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Although *Rodolia* and other ladybirds have been successfully used to control pest coccids they have not proved effective in classical biological control programmes against aphids. A better understanding of the foraging behaviour of ladybirds and a more realistic theory of insect predator- prey dynamics are beginning to reveal the reason for this.

Aphidophagous ladybirds exploit patches of aphid prey for feeding and reproduction. As suitable nurseries for their offspring patches of aphid prey generally only persist for about the same period of time as it takes the larvae of these ladybirds to complete their development. This is the case even in the absence of natural enemies. Thus aphids become scarce within a patch just when the food requirements of the ladybirds are greatest. Optimal foraging theory predicts that ladybirds should lay a few eggs early in the development of a patch and empirical data indicates that ladybirds appear to forage optimally.

There have been several studies on the cues used by ladybirds when selecting patches of prey for oviposition. This review will consider how the responses shown by ladybirds may have shaped what has become known as the "egg window", how cannibalism may regulate the number of ladybirds within a patch, and the consequences of this for classical biological control.

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THEORY

In classical insect predator-prey population dynamics organisms in two trophic levels interact; prey and predator (Fig. 1A).

A plant through it's morphology and chemistry can directly affect the well being of herbivores, and they similarly can affect predators. That is, in addition to their effects on one another's abundance a plant can have a direct effect on a herbivore, which can have a direct effect on a predator, and *vice versa*. In addition to these direct effects there is a growing literature that claims predators and parasitoids are attracted by volatiles emitted by plants under attack by herbivores. This is regarded as a mutualism, in which the effectiveness of the searching behaviour of the natural enemy is enhanced and the herbivore pressure on the plant reduced (PRICE et al. 1980; Fig 1B). Predators are considered to be part of a plant's defence. When attacked by herbivores some plants emit volatiles that are attractive to natural enemies, which has resulted in them being likened to "body guards" and the use of emotive phraseology like " the enemy of my enemy is my ally" (DICKE & SABELIS 1988; SABELIS et al. 2001). That ladybirds respond to these volatiles is supported by technically elegant studies in which gas chromatography of plant volatiles was directly coupled with recordings from the olfactory organs of a ladybird. Herbivore damaged plants emit (Z)-jasmone, which is attractive to adult *Coccinella septempunctata* (BIRKETT et al. 2000; NINKOVIC et al. 2001). The central tenet of the mutualism hypothesis is that herbivore-induced plant volatiles enable natural enemies to more easily find their prey and so reduce herbivore pressure.

Claims that such signals are so used by parasitoids was scrutinized by Vinson (1999) and van der Meijden & Klinkhammer (2000), who found no field evidence for this.

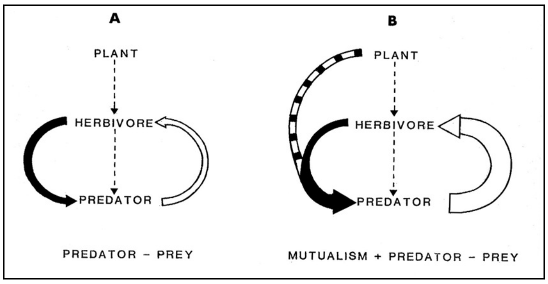

Fig. 1. The direct and indirect effects on one another of plants, herbivores and predators in classical insect population dynamics (A) and plant predator mutualisms (B).

Although there is no doubting that the volatiles (synomones - Dicke & Sabelis 1988) released by plants when attacked by herbivores are attractive to predators and parasitoids, the way in which they affect their searching behavior and the distance over which they operate still needs to be resolved. Discussions of this problem (e.g. Janssen et al. 2002) tend to follow Price et al. (1980) and only consider the adaptive significance of herbivore-induced plant volatiles in terms of plant fitness. It is generally assumed it is advantageous for natural enemies to respond to such signals. However, it is pertinent to ask - What advantages would a predator gain by responding to these signals? Here we consider only ladybird beetles, but the principles are likely to apply to all natural enemies.

It seems likely that the quantity of volatile material released by a plant depends on the intensity of herbivore attack, i.e., density-dependent. If this is true then aphid-infested plants are likely to be at their most attractive for ladybirds when aphids are most abundant. However, at this stage in the infestation it is highly likely that ladybird larvae will already be present. Therefore, responding to a strong cue that a plant is under attack by aphids is not necessarily advantageous. In addition, as not all aphids are equally suitable as prey for ladybirds (Rana et al. 2002) it is relevant to ask: - Is the synomone emanating from a plant specific for a particular species of aphid or a general response to aphid infestation? Similarly, is the synomone produced by a plant in response to being eaten by lepidopterous larvae different from that produced when infested with aphids? Therefore, in addition to determining whether the odour originates directly from the prey (prey pheromone hypothesis) or indirectly - after feeding by the prey - from the plant (plant synomone hypothesis) there is an urgent need to determine whether the signals are prey specific and how they affect predators' searching behaviour. It is well documented that bark beetles aggregate in response to volatiles produced by trees and attractant pheromones produced by the beetles, and so overcome the host's defences by a mass attack, but avoid heavily attacked trees, when the beetles present produce deterrent pheromones (Wood 1982; Raffa 2001). That is, if chemical signaling by plants significantly influences ladybird foraging then it is likely the signal is complex, as in bark beetles.

Alternatively one can ignore plants when considering predator-prey interactions, which is the case in most mathematical models of population dynamics. These have been widely used to predict the behavior of predator-prey systems, in particular their stability and the outcome of introducing natural enemies on the abundance of pests (Beddington et al. 1976, 1978; Hassell 1978; Murdoch 1994). In spite of the great and long-standing interest in these models, there has been little success in using them to account for why insect predators, compared to parasitoids, have generally not been very effective in suppressing the numbers of their prey (DeBach 1964).

Our studies on the way insect predators, and ladybirds in particular, forage, led to an appreciation of the ecological significance of the difference in mobility of juvenile and adult insects; the latter can fly while the former cannot (Fig. 2). That larvae generally stay within a prey patch while adults may not was incorporated into a model. Patch in this sense means the space that a larva can explore by walking, usually one or only a few adjacent plants, or even only part of an individual plant as in the case of trees. Three factors are likely to determine the reproductive strategy of ladybirds to a much greater extent than availability of food, which is the usual assumption of models of predator-prey systems: (1) Ladybird developmental time is much longer than that of its aphid prey and comparable with the average duration of a patch of prey (Fig. 3; Hemptinne et al. 1990; Hemptinne & Dixon 1991). Thus it is maladaptive for a ladybird to lay eggs in an old prey patch, as they are unlikely to complete their development before the aphids disappear. (2) As shown by Kindlmann & Dixon (1993), there should be a selective advantage in optimizing the number of eggs laid in a patch. This is because - as stated above - ladybird developmental time is similar to the duration of a patch of aphids. If many eggs are laid, the ladybird larvae may reduce the rate of increase of the aphids, cause an earlier decline in aphid abundance, and thus food may become scarce well before the larvae complete their development (Fig. 3). (3) Cannibalism is common in aphidophagous ladybirds and in nature often reduces juvenile survival dramatically, as only about 1% of the eggs laid in a patch survive (Dixon 2000). Cannibalism may be selected for (see below) and even sibling cannibalism may have a selective advantage, if prey becomes scarce (Osawa 1992). To avoid cannibalism, adults should avoid patches of aphids where ladybird larvae are already present.

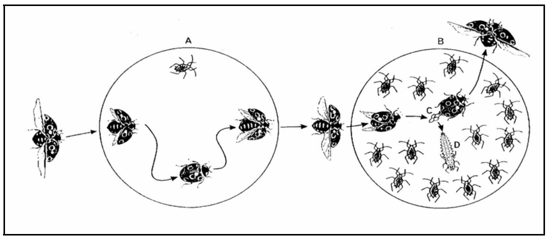

Fig. 2. Aphidophagous ladybirds quickly leave patches where aphids are scarce (A) but oviposit in patches where prey is abundant (B). The larvae (D) that hatch from the eggs (C) are confined to the patch, and have to pursue and subdue the aphids they need for their development.

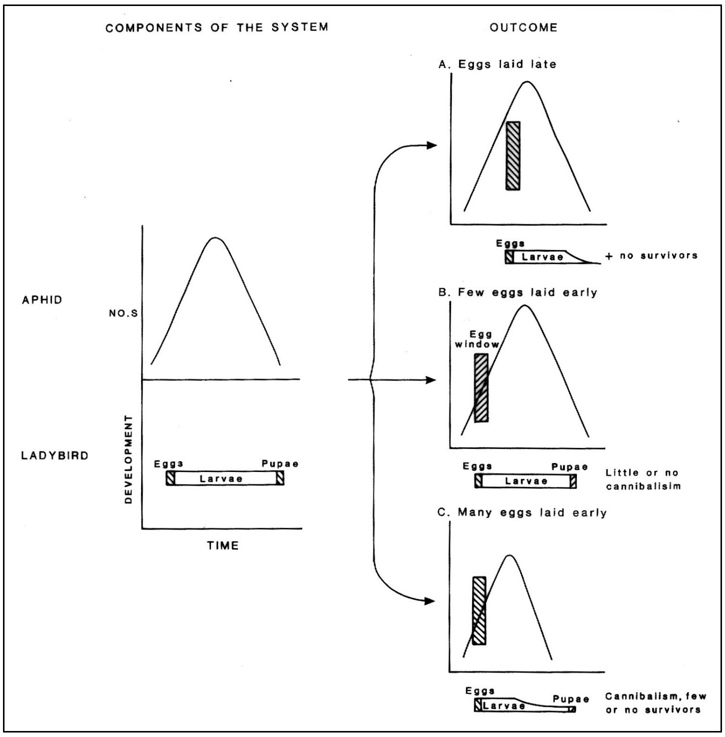

Fig. 3. Graphical presentation of the components of the ladybird-aphid interaction: temporal changes in the abundance of aphids and relative developmental time of the ladybird, and the outcome if (A) the eggs are laid late, (B) a few eggs are laid early, or (C) many eggs are laid early.

Assuming that the proportion of conspecifics in the diet of ladybirds is proportional to their relative abundance then if prey abundance is kept constant the incidence of cannibalism increases with increase in predator abundance. That is, cannibalism is likely to act as a density dependent mortality factor. Alternatively if the number of predators is kept constant and that of their prey is varied the incidence of cannibalism decreases with increase in the abundance of prey (Fig. 4).

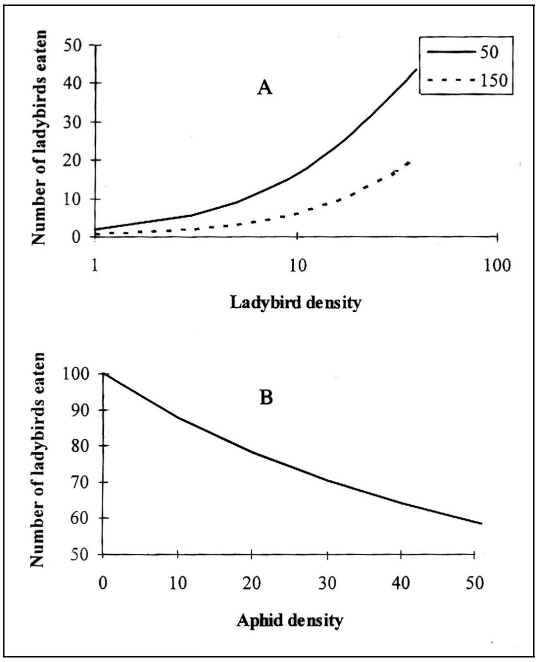

Fig. 4. The predicted (A) increase in cannibalism with increase in predator density, 50 and 150, and (B) the decrease in cannibalism with increase in aphid density when predator density is kept constant assuming that: $f(x, y) = ay/(x+y)$, where x is the number of prey, y is the number of ladybirds and a is a scaling constant.

This is referred to as the "meet and eat" hypothesis and accounts for the incidence of cannibalism in time (DIXON 2000). However, it is just as plausible that the latter is due to the occurrence in time of certain vulnerable stages - eggs/hatchling larvae and pre-pupae/pupae, which are unable to avoid or defend themselves against active larvae. Whatever the reason for the temporal incidence of cannibalism the outcome is the same: cannibalism is proportional to the relative abundance of the predator and therefore likely to be density dependent.

Consideration of the above leads to the prediction that there should be a strong selection for ladybirds to lay eggs only in patches in the early stages of development and avoid those containing conspecific larvae (KINDLMANN & DIXON 1993; DOSTALKOVA et al. 2002). Thus in assessing the potential effectiveness of a predator for biological control one should take into account that selection maximizes predator fitness, not its effectiveness as a biocontrol agent (KINDLMANN & DIXON 1999a). In aphidophagous ladybirds the major determinant of their reproductive strategy is that their prey develops much faster then they do (DIXON et al. 1995; DIXON & KINDLMANN 1998; KINDLMANN & DIXON 1999b). Therefore, the potential fitness of an adult depends mainly on the future trends in resource availability for its larvae, which unlike the adult are confined to a patch (Fig. 2). This leads to the following predictions. In arthropod predator-prey systems in which the predator has a long generation time relative to that of its prey (ladybird/aphid systems), predator reproduction should be correlated with the age of a prey patch rather than the numbers of prey present, and top-down regulation is unlikely. However, in ladybird/ coccid systems, where both prey and predator have similar developmental times, ladybird reproduction is likely to be correlated with prey abundance and top-down regulation is possible (KINDLMANN & DIXON 2001). In addition there is evidence that specificity may also be an important attribute of a biological control agent. The coccidophagous ladybirds that feed on Margarodidae, the group of coccids that includes *Icerya*, are generally more specific than those that feed on other groups of coccids. In terms of successful control ladybirds have been used 20 times more successfully to control Margarodidae than other groups of coccids (DIXON 2000).

EXPERIMENTAL EVIDENCE FOR OPTIMAL FORAGING IN LADYBIRDS

What evidence is there that selection maximizes predator fitness? Below is presented the results of studies undertaken to assess this in the case of aphidophagous ladybirds. In particular, this will be done by examining the evidence for an egg window, mechanisms for avoiding cannibalism and the proposed consequences for aphid abundance.

Egg Window

Experimental and field studies indicate there is a density below which ladybirds are unlikely to lay eggs (DIXON 1959; WRATTEN 1973; HONĚK 1978). In addition, in the field ladybirds tend to lay their eggs well before aphid populations peak in abundance (Fig. 5; HEMPTINNE et al. 1992). That is, there is a window in the development of a patch of aphids when ladybirds are most likely to lay their eggs. The opening of the window is possibly determined by the minimum density of aphids required for the survival of the first instar larvae (DIXON 1959). The closing of the window appears to be initiated by adults responding to the presence of conspecific larvae (HEMPTINNE et al. 1992).

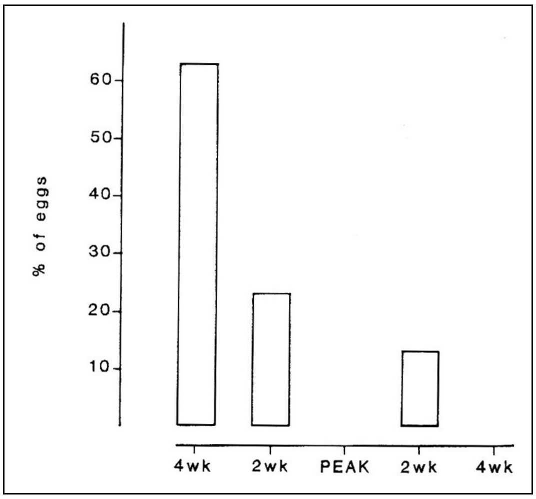

Fig. 5. Distribution in time, relative to peak aphid abundance of the laying of eggs by *Adalia bipunctata* on lime trees. Development of aphid populations expressed in weeks before and after the recorded peak in aphid abundance in each year. (After HEMPTINNE et al. 1992)

In the presence of conspecific larvae and/or their tracks gravid females of *Adalia bipunctata, Coccinella septempunctata, Cycloneda limbifer, Harmonia axyridis,* and *Semiadalia undecimnotata* become very active and if prevented from leaving the area refrain from laying eggs for a few hours (HEMPTINNE et al. 1992; DOUMBIA et al. 1998; YASUDA et al. 2000; RŮŽIČKA 2001b). Similar responses are observed when females of *A. bipunctata* are placed on plants in the field experimentally infested with aphids and contaminated with larval tracks. (Fréchette, unpublished). Although some species of ladybird respond to the tracks left by larvae of other species the response is generally statistically insignificant and much weaker than that to conspecific larvae or their tracks (HEMPTINNE et al. 1992; YASUDA et al. 2000; RŮŽIČKA 1997b, 2001a, b). This is expected because the greatest threat to the survival of a ladybird in its preferred habitat, where it is likely to be the most abundant ladybird, are individuals of the same species. In addition, ladybirds appear to be well defended chemically against intraguild predation (AGARWALA & DIXON 1992; HEMPTINNE et al. 2000). The deterrent effect of larval tracks is density dependent and mediated via a pheromone present in the tracks. In the case of *A. bipunctata* the cue consists of a cocktail of alkanes, which spread easily on the hydrophilic cuticle of plants and so leave a large signal. In addition the oviposition-deterring pheromone is very stable lasting for at least 10 days (DOUMBIA et al. 1998; HEMPTINNE et al. 2001).

In summary, there is good field evidence that aphidophagous ladybirds, as predicted by theory, lay their eggs early in the development of patches of aphids, and laboratory and field experiments reveal the possible mechanisms by which this is achieved.

Cannibalism

Cannibalism is widely recorded for aphidophagous ladybirds, but rarely mentioned in the literature on coccidophagous species. Theory predicts that it should occur when the relative abundance of ladybirds is high and/or is associated with an asymmetry between cannibal and victim. The victim is usually at a vulnerable stage in its development (Agarwala & Dixon 1992), i.e., in the egg or pupal stage, or is smaller or about to moult or pupate. That is, cannibalism should be highest in the egg and pupal stages, and in the fourth instar larval stage when prey is likely to be scarce, and decrease with increase in aphid abundance (Fig. 4). Life table studies done on field populations and laboratory studies (Fig. 6) support these predictions (Agarwala & Dixon 1992; Yasuda & Shinya 1997).

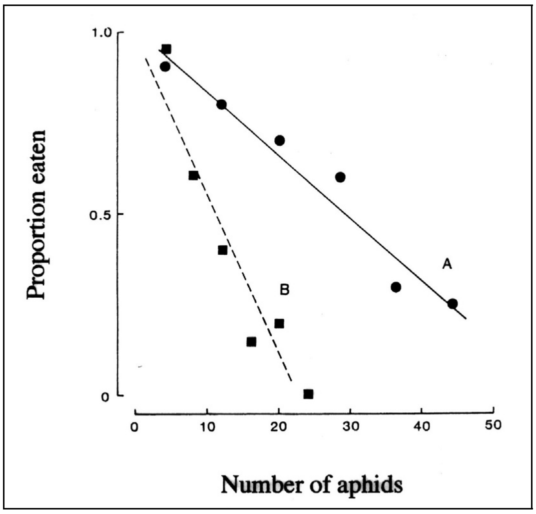

Fig. 6. The incidence of cannibalism in the laboratory of clutches of eggs (A) and larvae (B) of Adalia bipunctata in relation to aphid abundance (After Agarwala & Dixon 1992)

In the grain beetle *Tribolium* there are strains that show either a high or a low level of cannibalism, which is genetically determined (Stevens 1992). This has also been shown for *H. axyridis* (Wagner et al. 1999). Thus, selection should favour an optimum level of cannibalism in a given environment. That is, a species may be more or less cannibalistic than one would expect on the basis of the predicted frequency of encounters between conspecifics outlined above. Is there any evidence for this? Clearly some species are more difficult to rear collectively because they show higher levels of cannibalism than other species (unpublished results). A recent study of cannibalism in the aphidophagous ladybird *H. axyridis* indicates it prefers to eat conspecifics (Gagné et al. 2002). Thus cannibalism would appear to have been selected for in the individuals of *H. axyridis* used in this study.

Not only does the high probability of egg cannibalism make it advantageous for ladybirds to avoid ovipositing in patches of prey already occupied by conspecific larvae field, but evidence indicates that cannibalism, as predicted by theory, serves subsequently to regulate the numbers of ladybird larvae within a patch (Fig. 7).

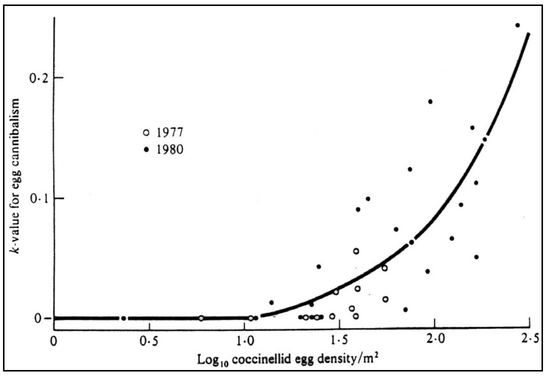

Fig. 7. The relationship between egg cannibalism and the number of eggs of Adalia bipunctata per unit area of lime foliage in relation to aphid abundance in the field (After Mills 1982)

That is, cannibalism is strongly density dependent and capable of regulating the abundance of ladybird larvae within patches (Kindlmann & Dixon 2001).

In summary, there is good field evidence that cannibalism is widespread and an important mortality factor potentially capable of regulating the abundance of aphidophagous ladybird larvae in a patch.

Aphid abundance

The prediction that ladybirds that forage optimally have little affect on aphid abundance (Kindlmann & Dixon 1993) is the most contentious. The implied altruism on the part of the ladybirds and criticism of biological control practice has greatly impeded the general acceptance of this supposedly counterintuitive idea. There is good evidence that ladybirds forage in a way similar to that predicted by optimal foraging theory and they achieve this by behaviour that is clearly adaptive at the individual level. The fact that cannibalism is adaptive and strongly density dependent indicates that ladybird numbers are likely to be strongly auto-regulated. Therefore, the prediction that ladybirds should have little affect on aphid abundance is in reality also not counterintuitive.

This prediction was tested by monitoring the numbers of the aphid, *Aphis gossypii,* on 34 two metre high shrubs of *Hibiscus syriacus* in the field. All the eggs of *Coccinella septempunctata brucki* were removed from 8 of the shrubs, all those of *Harmonia axyridis* from another 8, all the eggs of both ladybirds from another 12 and no eggs were removed from the remaining 6 shrubs (control). Sticky bands were placed around the base of the stem of each shrub to prevent the immigration of larvae on to the shrubs from surrounding plants. The results were very variable but clearly indicate that the presence of aphidophagous predators on the shrubs did not significantly affect the peak number of aphids (Fig. 8).

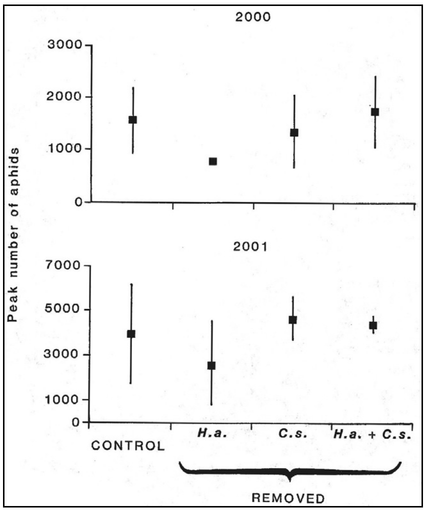

Fig. 8. The peak number of *Aphis gossypii* on *Hibiscus* shrubs in the field when aphid numbers were monitored in the presence of all the naturally occurring natural enemies (control), and when all the *Harmonia axyridis* (H.a) or *Coccinella septempuntata brucki* (C.s.) or both species of ladybird (H.a. + C.s.) were removed at the egg stage.

Unlike in other studies (e.g. ELLIOT & KIECKHEFER 2000) the shrubs were not caged, so the patches in effect were open to both immigration and emigration of both aphids and ladybirds as in natural ecosystems. That is, as predicted by theory these predators do not have a negative effect on the peak numbers of aphids in nature.

In summary, although well based theoretically and supported by a rigorous field experiment, the prediction that aphidophagous ladybirds have little affect on aphid abundance is likely to be subject to further critical experimentation before it is generally accepted.

CONCLUSIONS

Although the idea of a mutualism between plants and ladybirds is an attractive one there are no compelling theoretical reasons for, or field evidence of, such a relationship. Classical predator-prey models do not account for why insect predators are generally less effective in suppressing the abundance of pests than parasitoids. A model that includes the essential features of the foraging behavior of larvae and adults and the reproductive behavior of adult ladybirds predicts the patterns observed in the field. The major determinant of abundance in this system is the relative developmental times of the predator and prey - generation time ratio (GTR) hypothesis. If that of the predator is considerably longer than that of the prey, as in aphid/ladybird systems, than top down regulation of prey abundance is unlikely, whereas when it is of similar length, as in coccid/ladybird systems, then top down regulation is possible. The cues used by aphidophagous ladybirds to assess the quality of patches of prey have been identified and rigorously assessed. That is, in the last ten years there has been a great advance in our understanding of the patterns and processes in ladybird-prey interactions.

The GTR model should apply to all insect predators. However, as far as aphidophaga are concerned it makes a prediction: those that have longer generation times than aphids should behave similarly to ladybirds. Although this has not been studied intensively many are known to be cannibalistic and show similar reproductive behaviour. For example, the adults of some cecidomyids, chrysopids and syrphids are deterred from ovipositing by the presence of conspecific larvae or their tracks (HEMPTINNE et al. 1993; RŮŽIČKA 1994, 1996, 1997a, 1998; RŮŽIČKA & HAVELKA 1998). Thus, it is likely that the GTR hypothesis holds for all insect predators. At present the best support for this comes from studies on aphidophagous insects.

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