

## FIELD TEST OF THE EFFECTIVENESS OF LADYBIRDS IN CONTROLLING APHIDS

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### ABSTRACT

Some experiments indicate the ability of coccinellids to significantly suppress aphid abundance. Exclusion of predators by caging aphid-infested plants has repeatedly resulted in higher aphid populations and greater aphid population growth rates. However, aphidophagous coccinellids have never proved effective in controlling aphid populations in the field. To resolve this apparent contradiction, a field experiment was used to determine the effectiveness of two coccinellids, *Coccinella septempunctata bruckii* and *Harmonia axyridis* in suppressing populations of the aphid, *Aphis gossypii*, on shrubs of *Hibiscus syriacus* under natural conditions. Instead of caging some of the shrubs, the effect of each species of coccinellid on aphid population dynamics was estimated by direct counts and a manipulative experiment, in which all the eggs of *C. septempunctata bruckii* were removed from 8 shrubs, all those of *H. axyridis* from another 8 shrubs, all those of both species from an additional 12 shrubs, and no eggs were removed from 6 control shrubs. The predators did not have a negative effect on the peak numbers of their prey. This is in full accord with the GTR hypothesis, according to which long-lived predators cannot be effective in controlling a short-lived prey.

## INTRODUCTION

Aphidophagous coccinellids are probably the most abundant generalist predators of aphid populations. Some experiments indicate they significantly suppress aphid abundance. Exclusion of predators by caging aphid-infested plants has repeatedly resulted in significantly higher aphid populations (Brown 2004; Chambers *et al.* 1983; Michels *et al.* 2001) and greater aphid population growth rates (Elliott and Kieckhefer 2000), indicating that coccinellids markedly reduce aphid abundance. However, aphidophagous species of ladybirds have never proved effective in controlling aphid populations (e.g., van den Bosch and Messenger 1973).

The apparent contradiction of the results of the exclusion experiments and attempts to use coccinellids in the large-scale biocontrol of aphids may be explained as follows: when access of predators to aphids is excluded by caging the aphid-infested patches, aphids cannot react to their own increasing local density by emigration, which causes large aphid density in caged patches. Thus, there are more aphids in caged patches because they cannot leave the patch, not because predators reduce aphid numbers in non-caged patches. To test this hypothesis, field experiments were used to determine the effectiveness of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to suppress populations of the aphid *Aphis gossypii* Glover (Homoptera: Aphididae) on small shrubs of *Hibiscus syriacus* L. under natural conditions. Instead of caging infested shrubs, the effect of each species of ladybird on aphid population dynamics was estimated by direct counts on naturally infested shrubs and in a manipulative experiment, in which the eggs of one or both predators were removed from the shrubs.

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## METHODS

The study site was on the Yamagata University farm (Tsuruoka, Yamagata pref., Japan, 38° 43' N, 139° 49' E). It consisted of about 100 shrubs of *Hibiscus syriacus* L., which is the primary host of the aphid *Aphis gossypii* Glover. This aphid is attacked by two coccinellids: *Coccinella septempunctata bruckii* and *Harmonia axyridis*.

In the years 1993-1996, a total of 30 shrubs naturally infested with aphids and their predators were monitored from mid May to mid July. The numbers of coccinellid eggs, larvae, and of aphids were counted daily. To evaluate the effect of the number of aphids at the beginning of the season,  $x$ , the number of egg batches of *C. septempunctata bruckii*,  $c$ , and the number of egg batches of *H. axyridis*,  $h$ , on the peak number of aphids,  $Y$ , a stepwise regression, descending method, was applied to the data from 1993-1996. As aphids multiply exponentially, and therefore linear dependence of the logarithm of the peak on other variables was expected, the same methodology was applied to the data set with  $\log(Y+1)$  instead of  $Y$ .

It is difficult to identify coccinellids at the egg stage because they are often similar in size, color and number in a batch. In 1993, eggs were identified to species using the larvae that hatched from them. In the following years, a few eggs were removed from each egg mass and placed in Petri dishes at 25 °C and a 14L:10D photoperiod in the laboratory, and identified when the larvae hatched. Eggs reared in the laboratory hatched earlier than those left on the shrubs, which enabled the removal of the eggs before they hatched.

In 2000 and 2001, the effect of the absence of each coccinellids on aphid population dynamics was estimated. For this an additional 34 shrubs were selected for a manipulative experiment. After identification to species but before hatching, all the eggs of *C. septempunctata bruckii* were removed from 8 shrubs, those of *H. axyridis* from another 8 shrubs, eggs of both species from an additional 12 shrubs, and on the remaining 6 control shrubs no eggs were removed. Sticky bands were placed at the bottom of each shrub in order to prevent colonization by larvae from other shrubs. The shrubs were monitored from mid May to mid July. The numbers of coccinellid eggs, larvae and aphids were counted daily.

## RESULTS

In the model with the peak number of aphids,  $Y$ , as the dependent variable, no independent variable demonstrated a significant effect (Table 1). If  $\ln(x + 1)$  was used instead of  $x$  and  $\ln(Y+1)$  instead of  $Y$ , as the aphids are expected to grow exponentially, at least at the beginning of the season, the equation for the reduced model was:  $\ln(Y+1) = 4.6 + 0.32 \cdot \ln(x+1) + 0.055 \cdot h$ . The selected independent variables explained 33.26% of the variability of  $\ln(Y+1)$ . There is a 4.82% risk of rejecting the hypothesis that a constant model would be better, so the selected variables make a significant contribution to the model.

The variable that explained the most of the variation was the intercept (Table 1). In neither of the models did the abundance of either predator species significantly affect the peak aphid numbers (Table 1). As there is a lot of unexplained variability in this system, a manipulative experiment was carried out in 2000-2001. On average, 12.9 egg batches of *H. axyridis* and 13.9 of *C. septempunctata bruckii* were laid per shrub during 2000 and 2001. Almost no parasitism was observed. The resulting peak numbers of aphids are shown in Fig. 1. Predators did not significantly affect the peak numbers of aphids (one-way ANOVA gives  $F = 3.71$ ,  $P = 0.67$  in 2000 and  $F = 3.24$ ,  $P = 0.37$  in 2001).

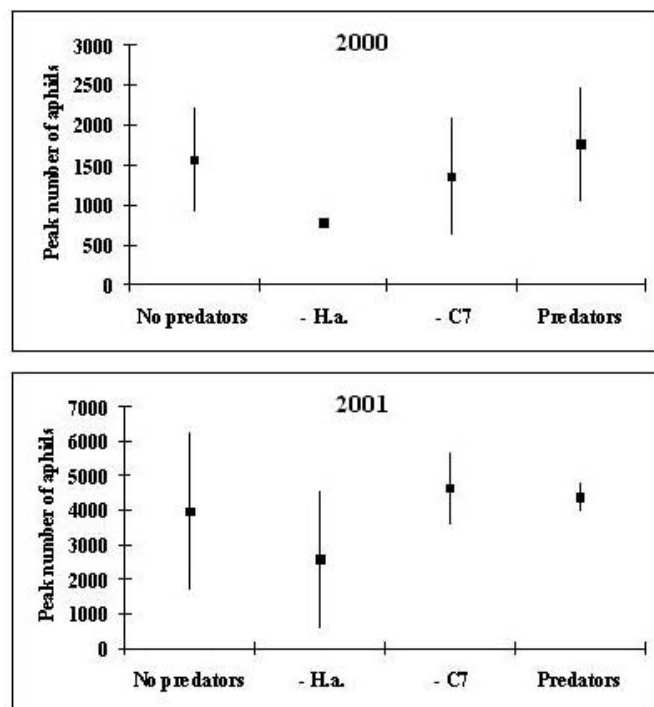
## DISCUSSION

There has only been one attempt until recently to account for the low effectiveness of insect predators: Kindlmann and Dixon (1999; 2001) proposed that the ratio of generation time of insect predators to that of their prey (generation time ratio, GTR) determines their effectiveness in suppressing prey. Kindlmann and Dixon (1999) assume that on a large spatial scale, at any instant, herbivore populations exist as patches of prey, associated with patches of good host plant quality. Predators exploit these patches, which vary greatly in number of prey both spatially and temporally (Kareiva 1990). GTR in insect predator-prey systems is often large – the developmental time of insect predators often spans several prey generations and is similar to the duration of a patch of prey (Dixon 2000). Cannibalism is common in insect predators (Agarwala and Dixon 1993; Fox 1975) and is adaptive, as eating conspecific competitors will increase the fitness of their larvae (Dong and Polis 1992). Mortality during larval stages reaches about 99% (Hironori and Katsuhiko 1997; Kindlmann *et al.* 2000; Kirby and Ehler 1977; Matura 1976; Osawa 1993; Wright and Laing 1982). Because of the enormous larval mortality, the life history strategy of these predators is likely to be selected to maximize the probability of survival of their offspring, rather than maximize the number of eggs laid. In major-

**Table 1.** Results of stepwise regression, descending method, on the effect of the number of aphids at the beginning of a season,  $x$ , the number of egg batches of *C. septempunctata bruckii*,  $c$ , and the number of egg batches of *H. axyridis*,  $h$ , on the peak number of aphids,  $Y$ , and on its logarithm,  $\log(Y)$ . Statistically significant values indicated by asterisks (\*means 5%, \*\* means 1% significance level).

	DF	SS	MS	Fisher's F	Pr > F
Model with Y	2	5753648	2876824	2.83	0.091
Residuals	15	15264871	1017658		
Total	17	21018519			
Model with $\log(Y)$	2	20.38	10.19	3.74	0.048*
Residuals	15	40.90	2.73		
Total	17	61.28	6.00		
		Value	Std dev.	Student's t	Prob.
Model with Y	Intercept	544.3	349.2	1.56	0.14
	Initial # aphids	1.21	0.71	1.70	0.11
	<i>C. septem-punctata bruckii</i>	104.4	86.7	1.20	0.25
Model with $\log(Y)$	Intercept	4.60	0.68	6.75	0.00**
	$\ln(\text{Initial \# aphids}+1)$	0.32	0.19	1.74	0.10
	<i>H. axyridis</i>	0.055	0.043	1.27	0.22

**Figure 1.** Peak numbers ( $\pm$  SD) of aphids on shrubs from which eggs of all predators were removed (no predators), only *C. septempunctata bruckii* eggs were removed (- C7), only *H. axyridis* eggs were removed (- H.a.) and no eggs were removed (predators), in years 2000 and 2001.



ity of cases, the adults are winged and can easily move between patches, whereas the immature stages are confined to one patch throughout their development, and their survival is associated with the quality of the patch of prey in which they were born. Therefore, the fitness of most predators (especially those feeding on highly aggregated and ephemeral prey patches such as aphid colonies, like aphidophagous ladybirds and hoverflies), measured as the number of offspring that survive to reproductive age, is likely to be more closely associated with oviposition strategy (the choice of patch for laying eggs), than the trophic interactions commonly used in models of prey-predator population dynamics.

When GTR is large and cannibalism is common, eggs laid by predators late on in the existence of a patch of prey are highly likely to be eaten by larvae of predators that hatch from the first eggs to be laid. In addition, because of the large GTR, there is insufficient time for the larvae that hatch from late laid eggs to complete their development. Thus cannibalism and the ephemeral existence of patches of prey pose such constraints that females that can assess the age of a patch of prey gain an advantage. As a consequence, females oviposit in young patches (“egg window hypothesis”, Dixon 2000). The short “egg window” during which it is advantageous to lay eggs in a patch of prey in large-GTR systems reduces the number of eggs laid per patch. Incidence of cannibalism is likely to be proportional to the probability of encountering another predator, i.e., to the relative abundance of predators to prey (“meet and eat hypothesis”, Kindlmann and Dixon 2003). If this is true, then even if predators are abundant and therefore many eggs are laid in a patch of prey during the egg window, strong density dependent cannibalism greatly reduces the abundance of the predators (Mills 1982). Therefore, no matter whether abundant or not, insect predators have little impact on prey population dynamics, when GTR is large (“GTR hypothesis”, Kindlmann and Dixon 1999). A simple dynamic model published by Kindlmann and Dixon (1993) demonstrates why the verbal logic presented here is correct.

Laboratory experiments and field observations provided the foundations on which the GTR and egg window hypotheses were built. Several insect predators have evolved mechanisms that enable them to oviposit preferentially early in the development of a patch of prey and avoid patches that are already being attacked by larvae (Hemptinne *et al.* 1992; 1993; 2001). This leads to eggs being laid during the “egg window” and may lead to low effectiveness of these predator species in suppressing the numbers of their prey. However, there has not been a field test of the effectiveness of these predators.

In the coccinellid – aphid system studied here, the GTR is close to 3, and thus the GTR hypothesis would predict a low effect of predators on aphid abundance. In this study the predators did not have a negative effect on the peak numbers of their prey. On the contrary, the peak number of aphids in the control (with both predator species present) was larger, although not significantly so, than on the shrubs from which one or both predator species were removed. These conclusions only apply to predator prey systems with a large GTR and especially to predators feeding on highly aggregated and ephemeral prey patches such as aphid colonies, like aphidophagous coccinellids and syrphids. It does not follow that all insect predators are ineffective in controlling their prey as is well illustrated by the outstanding success of *Rodolia cardinalis*.

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