Intra-guild predation and variation in egg defence between sympatric and allopatric populations of two species of ladybird beetles

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Abstract. 1. Ladybird eggs are defended chemically against intra-guild predation, and are unsuitable to varying degrees as food for other ladybirds.

2. Ladybird eggs [*Coccinella septempunctata* (Cs) and *Harmonia axyridis* (Ha); Coleoptera: Coccinellidae] from local Japanese versus North American populations were compared as food for two ladybirds (Cs and Ha) co-occurring in Japan.

3. Larvae of Cs exhibited high mortality, slow development, and reduced egg consumption and weight gain when they fed on Ha versus conspecific eggs, especially when Ha eggs were from the local (Japanese) population versus a distant (North American) population of Ha.

4. Larvae of Ha survived equally well on a diet of Cs or conspecific eggs, but developed more slowly and gained less weight on Cs eggs. Ha larvae were more reluctant to eat eggs from the local (Japanese) population of Cs than eggs from the distant (North American) population of Cs; however, other measures of performance did not differ significantly.

5. These results indicate greater egg chemical defence of Ha eggs against Cs larvae than vice versa, as expected from field observations of greater temporal overlap between Cs larvae and Ha eggs than between Ha larvae and Cs eggs. Furthermore, results also indicate that local populations of eggs are better defended than eggs from elsewhere against locally occurring intra-guild predators. Thus, it appears that the effectiveness of chemical defence of ladybird eggs reflects the degree to which specific pairings of ladybirds have the potential to interact in nature through egg predation.

Key words. *Coccinella septempunctata*, Coccinellidae, coevolution, geographic variation, *Harmonia axyridis*, intraguild predation, local adaptation.

Introduction

While exploiting a common prey, predators often interact with each other through intra-guild predation (Polis *et al.*, 1989; Rosenheim *et al.*, 1995). Such interactions, especially when fre-

quent and intense, may lead to adaptations protecting individual species from each others' attacks (Dixon, 2000; Sato & Dixon, 2004; Sato *et al.*, 2005). For example, multiple species of ladybirds congregate to forage and reproduce at aphid populations of high density in many agricultural and natural settings. Intraguild predation has the potential to be a major source of egg mortality among these ladybirds, and chemical defence of eggs appears important often in reducing the incidence of such intraguild predation (e.g. Agarwala & Dixon, 1992, 1993a; Yasuda & Shinya, 1997; Schellhorn & Andow, 1999; Hemptinne *et al.*, 2000a, b; Agarwala & Yasuda, 2001; Cottrell, 2004, 2005; Sato & Dixon, 2004).

Intriguingly, the degree to which eggs of a given ladybird species are toxic is species dependent (e.g. Sato & Dixon, 2004); not only does toxicity of eggs vary among ladybird species, but

the impact of that toxicity on the intra-guild predator (i.e. larva of a ladybird species) varies across species. One hypothesis is that this variation reflects the degree and intensity with which any two species may interact through intra-guild predation (Sato & Dixon, 2004). Interacting pairs of species, furthermore, often overlap only incompletely in their geographic ranges, raising the possibility of significant spatial variation in selective pressure for chemical protection against each other's attacks (Thompson, 1994). Here, laboratory experiments are presented that investigate geographic variation in chemical protection. Specifically, these studies address whether chemical defence of ladybird eggs is more effective against intra-guild predators when the eggs are produced by individuals from the same locale as the predators versus when the eggs are produced by individuals from a geographically distant population.

Geographic variation in chemical protection among ladybirds was evaluated by considering the interaction between two species [*Coccinella septempunctata* L. (Cs) and *Harmonia axyridis* Pallas (Ha), Coleoptera: Coccinellidae] that dominate the spring-early summer guild of aphidophagous predators associated with hibiscus trees in Japan. Arriving and initiating reproduction earliest, Cs subsequently becomes vulnerable in its larval and pupal stages to asymmetric intra-guild predation by larvae of the more aggressive, later-arriving Ha (Yasuda & Shinya, 1997). Furthermore, previous research (Sato & Dixon, 2004) has shown that the eggs of Ha are highly toxic to (i.e. are well-defended against) larvae of Cs, whereas eggs of Cs are more weakly toxic to larvae of Ha (from which these eggs largely escape in time). This line of research is extended here to consider the possibility of local adaptation. Thus, data presented test whether eggs produced locally by one species (the intra-guild prey) are more toxic to, and less readily attacked by, the local population of larvae of the second species (intra-guild predators) than are eggs produced by a geographically distant population of the intra-guild prey. Based on the findings of Sato and Dixon (2004), such might be most expected for eggs of Ha as they are attacked by Cs.

Materials and methods

Adults of *H. axyridis* and *C. septempunctata brucki* Mulsant (a subspecies of *C. septempunctata* L. endemic to Japan) were collected at and near the Yamagata University Farm at Tsuruoka, Yamagata Prefecture, Japan, during the summer of 2004. They were separated by sex, and were maintained on a diet of cowpea aphids [*Aphis craccivora* Koch; reared on bean (*Vicia faba* L.)], at 22 °C, 16:8 LD for several weeks. Thereafter, these adults were paired to induce mating and egg laying. The offspring produced by these adults were used in the experiments described below, and are referred to as eggs or larvae of the Yamagata populations of *H. axyridis* (Ha-Y) and *C. septempunctata* (Cs-Y).

Adults of *H. axyridis* and *C. septempunctata septempunctata* L. (the subspecies of *C. septempunctata* L. found in North America) were also collected during the summer of 2004 near Logan, Utah, U.S.A. These adults were derived from populations of these species established in North America from the Old World in previous decades (e.g. Schaefer *et al.*, 1987; Tedders &

Schaefer, 1994). The beetles were held at 10 °C, 16:8 LD for several weeks before being transported to Tsuruoka, where they also were held as pairs at 22 °C, 16:8 LD, and provided with cowpea aphids. The offspring produced by these adults were used in the experiments, and are referred to below as eggs of the North American populations of *H. axyridis* (Ha-NA) and *C. septempunctata* (Cs-NA).

Experiments were conducted at 17 °C, 16:8 LD. In these experiments, eggs of Ha or Cs were placed individually in wells of a tissue culture plate (Becton Dickinson/Falcon™, Catalog no. 351 172; 96 wells, each well sized 6.4 × 11 mm, Becton, Dickenson & Company, Franklin Lakes, NJ;). Upon hatching, first instars often fed on the egg cuticle. Thereafter, within 24 h, they were provided with either conspecific or heterospecific eggs. In all cases, eggs were provided in excess of larval consumption. Each first instar was provided with three (or four, as the larva matured and egg consumption increased) conspecific or heterospecific eggs daily. Care was taken to avoid providing sibling eggs to individual larvae (see Agarwala & Dixon, 1993b; Joseph *et al.*, 1999), and to provide eggs no greater than 48 h old. Care was also taken to ensure that during an experiment, each larva was provided with eggs produced by several conspecific or heterospecific females.

In addition to rates of survival on different egg diets, data collected for each experiment included the developmental time and weight gain for larvae, and the daily rates with which eggs were attacked and consumed. Individual larvae were weighed to the nearest 0.01 mg at the outset of an experiment (i.e. within 24 h of hatching). They were reweighed within 24 h of molting to the second stadium. During an experiment, the larvae were checked every 12 h to determine when they molted, and to determine how many eggs they attacked and consumed. Eggs that were attacked were scored as being consumed in their entirety (i.e. only the egg cuticle and ≤20% of egg contents remained), partially consumed (i.e. 21–89% of egg contents remained), or only slightly damaged (i.e. ≥90% of egg contents remained).

In the first experiment, Cs-Y first instars were fed Ha-Y, Ha-NA, or Cs-Y eggs ($n = 30$ first instars for each predator-prey combination). This experiment followed an initial trial, in which 16 and 18 Cs-Y first instars were provided with Ha-Y and Ha-NA eggs, respectively. In the initial trial, Cs-Y first instars were provided with eggs until they molted or died prior to molting (all individuals had died or molted after 21 days). Larvae were not weighed during this initial trial. During the full experiment with larger sample sizes, first instars were provided with eggs for 15 days (after which time, only a few, moribund individuals that had been fed Ha eggs remained as first instars). Individuals that had failed to molt previously were weighed on the 10th day.

In the second experiment, Ha-Y first instars were fed with eggs of Cs-Y ($n = 30$ first instars), Cs-NA ($n = 20$), or Ha-Y eggs ($n = 30$). The second experiment was conducted in the same fashion as the first experiment.

Differences in rates of survival among ladybird larvae consuming eggs of different sources were compared using the χ^2-test. Other measures of larval ladybird performance (development time, weight gain, and number of eggs attacked and consumed) were compared by one-way anova. These anovas included orthogonal linear contrasts (Sokal & Rohlf, 1995) to evaluate specific hypotheses regarding larval performance both on diets

of heterospecific versus conspecific eggs, and on diets of heterospecific eggs from Yamagata versus North America. All statistical tests were conducted using SAS (SAS Institute Incorporated, 2002).

Results

Experiment 1: Cs-Y larvae fed Ha-Y, Ha-NA, or Cs-Y eggs

Eggs of Ha were poor food for the Cs-Y larvae. In the full experiment, all 30 Cs-Y larvae that fed on conspecific eggs (Cs-Y) succeeded in molting to the second instar, and did so after 4.6 ± 0.1 days (mean $\pm$ SE). In contrast, by the end of the full experiment (mid-day on day 14), only five out of 60 Cs-Y larvae succeeded in molting on a diet of Ha eggs ($\chi^2 = 70.71$, $P < 0.0001$; Ha-Y and Ha-NA egg diets combined), and did so after a significantly longer period of development [12.2 ± 0.7 days (mean $\pm$ SE for Ha-Y and Ha-NA egg diets combined); Table 1]. Similarly, when fed conspecific eggs, Cs-Y larvae gained significantly more weight (0.97 ± 0.05 mg during the first stadium) than did Cs-Y larvae that fed on Ha eggs [0.44 ± 0.04 mg by day 10 (Ha-Y and Ha-NA egg diets combined); Table 1].

Ha-Y eggs were even less suitable than Ha-NA eggs. In the initial trial, all Cs-Y larvae that fed on Ha-Y eggs had died by mid-day on day 11 without molting to the second instar, versus 50% of larvae that fed on Ha-NA eggs (Fig. 1a; $\chi^2 = 10.88$, $P = 0.001$). Similarly, in the full experiment, larvae that fed on Ha-Y eggs died (without molting) at an especially high rate, although they succeeded in surviving longer on this diet than in the initial trial (Fig. 1b). By the end of the full experiment (mid-day on day 14), 83% of Cs-Y larvae that fed on Ha-Y eggs had died compared with only 60% of those feeding on Ha-NA eggs (Fig. 1b; $\chi^2 = 4.02$, $P = 0.045$). Furthermore, those first instars that fed on Ha-Y eggs tended to gain less weight than those that fed on Ha-NA eggs (0.35 ± 0.07 vs 0.50 ± 0.03 mg by day 10; Table 1). For both the full experiment and initial trial combined, fewer Cs-Y larvae survived to molt to the second instar on a diet of Ha-Y eggs (one out of 46 Cs-Y larvae; after 12.5 days) than those feeding on a diet of Ha-NA eggs [six out of 48 Cs-Y larvae; after 13.0 ± 1.5 days (mean $\pm$ SE)] ($\chi^2 = 3.63$, $P = 0.056$).

The Cs-Y larvae attacked similar numbers per day of conspecific and Ha eggs (Ha-Y and Ha-NA combined) (Fig. 2a, Table 1). However, there was a strong difference in the fate of those attacked eggs. The Cs-Y larvae consumed in their entirety 12 times as many conspecific as Ha eggs (Fig. 2a, Table 1). At the same time, they partially consumed approximately one-third, and only slightly damaged approximately one-fifth, as many conspecific as Ha eggs (Fig. 2a, Table 1). The same tendency of Cs-Y larvae to only partially consume or slightly damage (versus entirely consume) Ha eggs was also evident in the initial trial (Fig. 2b).

In the initial trial, Cs-Y larvae attacked significantly more Ha-NA than Ha-Y eggs (Fig. 2b; ANOVA; $F_{1,32} = 6.49$, $P = 0.016$). In particular, Cs-Y larvae consumed in their entirety ($F_{1,32} = 12.76$, $P = 0.001$), and partially consumed ($F_{1,32} = 4.36$, $P = 0.045$), significantly more Ha-NA eggs than Ha-Y eggs, but did not differ in the number of Ha-NA and Ha-Y eggs that they slightly damaged ($F_{1,32} = 0.01$, $P = 0.91$) (Fig. 2b). Similar (but not significant) tendencies of Cs-Y larvae were observed in the full experiment (Fig. 2a, Table 1).

Table 1. One-way ANOVA for measures of performance of *Coccinella septempunctata brucki* (Cs-Y) and *Harmonia axyridis* (Ha-Y) first instars feeding on eggs. Results are for linear contrasts of performance on heterospecific eggs (Yamagata and North America combined) versus conspecific eggs, and for heterospecific eggs from Yamagata (Y) versus North America (NA), for experiment 1 (full experiment only) and experiment 2.

| Experiment 1: Cs-Y larvae	Ha eggs versus Cs-Y eggs		Ha-Y eggs versus Ha-NA eggs	
	F (d.f.)	P	F (d.f.)	P
Development time (days)	637.90 (1,33)	<0.0001	—	—
Gain in weight (mg)	76.78 (1,60)	<0.0001	3.16 (1,60)	0.0806
No. eggs per day:				
Attacked	1.48 (1,87)	0.2271	1.68 (1,87)	0.1988
Consumed in entirety	324.40 (1,87)	<0.0001	0.44 (1,87)	0.5080
Consumed partially	97.78 (1,87)	<0.0001	3.03 (1,87)	0.0854
Slightly damaged	26.98 (1,87)	<0.0001	1.03 (1,87)	0.3121
	Cs eggs versus Ha-Y eggs		Cs-Y eggs versus Cs-NA eggs	
Experiment 2: Ha-Y larvae	F (d.f.)	P	F (d.f.)	P
Development time (days)	59.84 (1,77)	<0.0001	0.01 (1,77)	0.9317
Gain in weight (mg)	49.53 (1,77)	<0.0001	0.39 (1,77)	0.5356
No. eggs per day:				
Attacked	0.09 (1,77)	0.7645	40.07 (1,77)	<0.0001
Consumed in entirety	33.89 (1,77)	<0.0001	7.23 (1,77)	0.0088
Consumed partially	14.32 (1,77)	0.0003	10.74 (1,77)	0.0016
Slightly damaged	7.99 (1,77)	0.0060	1.66 (1,77)	0.2021
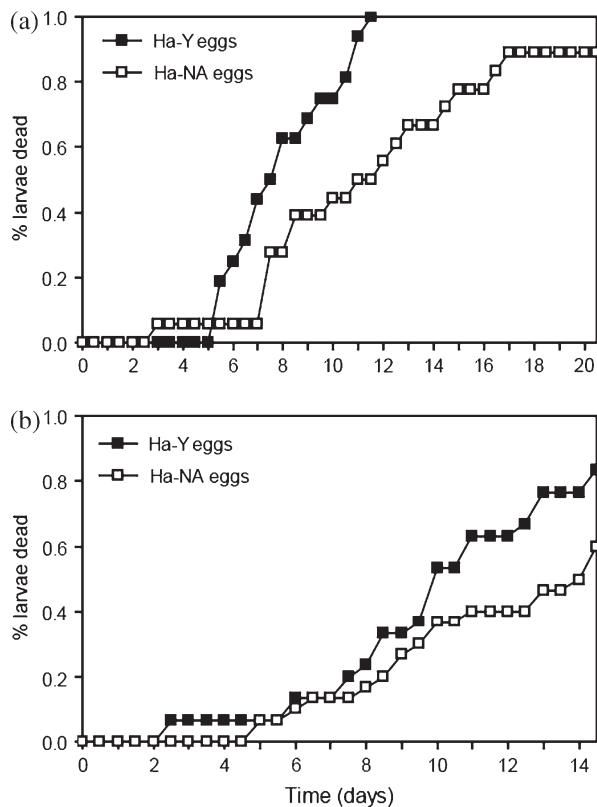
Fig. 1. The cumulative percentage of first instars of *Coccinella septempunctata brucki* from Yamagata (Cs-Y) that had died at successive censuses during the first experiment when these larvae were provided with a diet of eggs of *Harmonia axyridis* from Yamagata (Ha-Y) or from North America (Ha-NA) (a: initial trial; b: full experiment).

Experiment 2: Ha-Y larvae fed Cs-Y, Cs-NA, or Ha-Y eggs

In all cases, first instars of Ha-Y survived to molt when consuming either conspecific (Ha-Y) or Cs eggs. However, the Ha-Y larvae developed more slowly on a diet of Cs (Cs-Y and Cs-NA combined) versus Ha eggs [4.7 ± 0.1 vs 4.1 ± 0.1 (mean $\pm$ SE for developmental time for the first instar in days); Table 1]. The Ha-Y larvae also gained significantly less weight as first instars on a diet of Cs (Cs-Y and Cs-NA combined) versus Ha eggs (0.98 ± 0.03 vs 1.35 ± 0.04 mg; Table 1). First instars of Ha-Y that consumed Cs-Y versus Cs-NA eggs did not differ significantly in either developmental time (4.7 ± 0.1 vs 4.7 ± 0.1 days; Table 1) or weight gain (0.96 ± 0.03 vs 1.00 ± 0.06 mg; Table 1).

Ha-Y larvae did not differ significantly in the number of conspecific versus Cs eggs (Cs-Y and Cs-NA combined) that they attacked daily (Fig. 3, Table 1). In a similar (although less pronounced) fashion to that of Cs-Y larvae above, however, they consumed significantly more conspecific eggs than Cs eggs in their entirety each day, and partially consumed or slightly damaged significantly fewer conspecific than Cs eggs (Fig. 3, Table 1).

Ha-Y larvae attacked significantly fewer Cs-Y than Cs-NA eggs (Fig. 3, Table 1). In addition, significantly fewer Cs-Y than
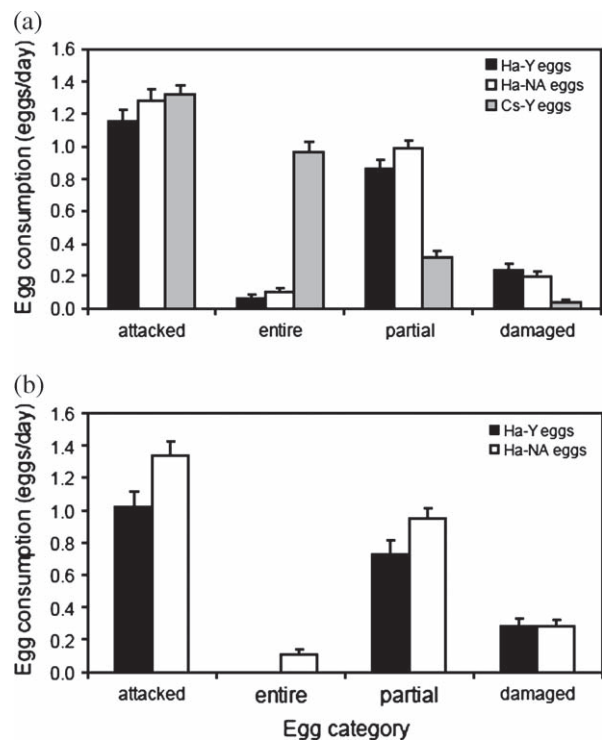

Fig. 2. The number of eggs attacked per day (scored also as consumed in their entirety, partially consumed, or slightly damaged, as described in the text) by first instars of *Coccinella septempunctata brucki* from Yamagata (Cs-Y) when provided with a diet of eggs of *Harmonia axyridis* from Yamagata (Ha-Y) or from North America (Ha-NA), or with conspecific eggs (Cs-Y) (a: full experiment; b: initial trial conducted without including a diet of conspecific eggs).

Cs-NA eggs were consumed in their entirety, or partially consumed, by Ha-Y larvae (numbers of eggs that were slightly damaged did not differ; Fig. 3, Table 1).

Discussion

Ladybird eggs might seem ready sources of food for larvae among co-occurring species of ladybird predators. The predators aggregate to reproduce at local outbreaks of aphids (and similar prey). Thus, ladybird larvae developing from eggs laid early have ample opportunity to feed not only on aphids, but also on ladybird eggs laid later (Hemptinne *et al.*, 1992). Such temporal overlap of species is illustrated by the case of hibiscus in Japan, where Cs and Ha co-occur in exploiting the aphid *Aphis gossypii* (Yasuda & Shinya, 1997).

The experiments conducted here suggested, however, that eggs of Ha were a poor source of food for Cs larvae, most likely because these eggs are chemically well-protected. Consistent with the results of Sato and Dixon (2004), this study demonstrated that Cs-Y larvae suffered very high rates of mortality on a diet of Ha eggs, in clear contrast to their ability to survive well on a diet of conspecific (Cs-Y) eggs. Those relatively few Cs-Y first instars that were able to survive for an extended period of
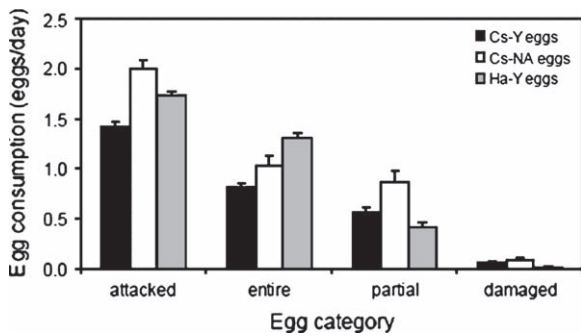
Fig. 3. The number of eggs attacked per day (scored as in Fig. 2) by first instars of *Harmonia axyridis* from Yamagata (Ha-Y) when provided with a diet of eggs of *Coccinella septempunctata* from Yamagata (Cs-Y) or from North America (Cs-NA), or with conspecific eggs (Ha-Y).

time on a diet of Ha eggs had very slow rates of development and low weight gain in comparison to Cs-Y first instars on a diet of conspecific eggs. The likely role of chemical protection through deterrence (as opposed to poor efficiency of conversion, for example) was apparent from the clear reluctance of first instars to consume Ha eggs; while they readily consumed Cs-Y eggs in their entirety, they typically only partially consumed and often simply slightly damaged the similar number of Ha eggs that they attacked. As a result, Cs-Y larvae consumed far less biomass of Ha eggs than of Cs-Y eggs.

Further, results presented here indicated that Ha-Y eggs are even less suitable for Cs-Y than are Ha-NA eggs; almost no larvae survived to the second stadium when fed Ha-Y eggs, versus approximately 12% of individuals when fed Ha-NA eggs. Weight gain during the first stadium was also lower on the Ha-Y diet than on the Ha-NA diet (the one individual that succeeded in molting on a Ha-Y diet, however, took no longer to develop during the first stadium than the mean of those individuals molting on a diet of Ha-NA). The higher survivorship and weight gain on the Ha-NA diet was also reflected in a greater number of Ha-NA than Ha-Y eggs attacked daily by Cs-Y first instars, especially during the initial trial. These results support the hypothesis that eggs produced by the local (Yamagata) population of Ha are more chemically protected against co-occurring intra-guild predators (Cs-Y) than are Ha eggs from a geographically distant location (North America). This in turn may reflect the intriguing possibility that over a long history of interaction, there has been selection for eggs of Ha-Y to become increasingly toxic to the locally occurring intra-guild predators (Cs-Y).

Local adaptation of ladybird eggs in response to pressure from predation by ladybird larvae is a plausible explanation for our results. The general phenomenon of local adaptation is well supported, with examples that include parasites and hosts (Lively *et al.*, 2004), predators and prey (Brodie & Brodie, 1999; Brodie *et al.*, 2002), and phytophagous insects and plants (Mopper & Strauss, 1998). However, without additional experimentation we can not dismiss an alternative explanation for our results. The ladybirds Cs-NA and Ha-NA may have escaped specialised pathogens, parasites, and other enemies upon invading North America, thus allowing increased allocation of re-

sources to growth and reproduction rather than defence [i.e. the evolution of increased competitive ability (EICA) hypothesis; Blossey & Nötzold, 1995]. Such could also account for our experimental results that Cs-NA and Ha-NA were less chemically defended than their Japanese counterparts. However, in light of this it is noteworthy that eggs of Ha introduced to eastern North America appear to be very strongly defended chemically; these eggs were highly unsuitable as food for larvae of two native ladybirds [*Coleomegilla maculata* (DeGeer) and *Olla v-nigrum* (Mulsant); Cottrell, 2004 (see also Cottrell, 2007)].

Because Ha arrives later than Cs to exploit aphids and reproduce on hibiscus in Japan, Cs eggs are likely to escape in time from becoming intra-guild prey of Ha larvae (Yasuda & Shinya, 1997; Sato & Dixon, 2004). This leads to the prediction that chemical defence of Cs eggs from Ha larvae may be less pronounced than vice versa. The results presented here are consistent with previous results of Sato and Dixon (2004) in supporting this prediction. Sato and Dixon (2004) found that consumption of Cs eggs only slightly reduced survivorship of Ha first instars compared with a diet of conspecific (Ha) eggs. Here, 100% of Ha-Y first instars survived to molt to the second stadium on a diet of Cs eggs. Nonetheless, some chemical protection was suggested here; development rate and weight gain of Ha-Y larvae were reduced on a diet of Cs versus conspecific (Ha-Y) eggs. Also, similar to the case for Cs larvae attacking Ha eggs, Ha-Y larvae were reluctant to consume Cs eggs, and most frequently they only partially consumed, or simply damaged slightly, the Cs eggs that they attacked. In contrast, in most cases they completely consumed the similar number of conspecific eggs that they attacked.

Perhaps because the overall level of chemical protection of Cs eggs against Ha larvae is relatively weak, no significant differences in Ha-Y larval survivorship, development time, or weight gain, in response to a diet of Cs-Y versus Cs-NA eggs were detected. However, Ha-Y first instars did attack and eat Cs-NA eggs more readily than Cs-Y eggs. This suggests that Cs-Y eggs may indeed be more chemically protected against locally occurring intra-guild predators (Ha-Y) than are Cs eggs from elsewhere (Cs-NA).

In conclusion, results presented here support the findings of Sato and Dixon (2004) that Ha eggs are strongly protected chemically against intra-guild predation by Cs larvae. In addition, Cs eggs may also be similarly protected chemically, but more weakly so, from intra-guild predation by Ha larvae. These results are consistent with expectations suggested from field observations documenting a greater synchrony of Cs larvae and Ha eggs than of Ha larvae and Cs eggs (Sato & Dixon, 2004). Further, these results suggest the possibility of local adaptations in response to the pressure of intra-guild predation. Locally produced eggs of Ha appear to be even more strongly protected chemically against the local population of Cs larvae than are eggs produced by a geographically distant population of Ha. To a lesser degree, a similar phenomenon appears to apply to the susceptibility of eggs of Cs to intra-guild predation by Ha. In summary, it appears that the effectiveness of egg chemical defence of Ha and Cs against each other reflects the degree to which specific pairings of these ladybirds have the potential in nature to interact through egg predation.

Acknowledgements

References

Agarwala, B.K. & Dixon, A.F.G. (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology*, **17**, 303–309.

Agarwala, B.K. & Dixon, A.F.G. (1993a) Why do ladybirds lay eggs in clusters? *Functional Ecology*, **7**, 541–548.

Agarwala, B.K. & Dixon, A.F.G. (1993b) Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **90**, 45–50.

Agarwala, B.K. & Yasuda, H. (2001) Overlapping oviposition and chemical defense of eggs in two co-occurring species of ladybird predators of aphids. *Journal of Ethology*, **19**, 47–53.

Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887–889.

Brodie, E.D. III & Brodie, E.D. Jr. (1999) Predator-prey arms races. *Bioscience*, **49**, 557–568.

Brodie, E.D. Jr, Ridenhour, B.J., & Brodie, E.D. III. (2002) The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. *Evolution*, **56**, 2067–2082.

Cottrell, T.E. (2004) Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control*, **31**, 362–371.

Cottrell, T.E. (2005) Predation and cannibalism of lady beetle eggs by adult lady beetles. *Biological Control*, **34**, 159–164.

Cottrell, T.E. (2007) Predation by adult and larval lady beetles (Coleoptera: Coccinellidae) on initial contact with lady beetle eggs. *Environmental Entomology*, **36**, 390–401.

Dixon, A.F.G. (2000) *Insect Predator-Prey Dynamics. Ladybird Beetles and Biological Control*. Cambridge University Press, Cambridge, U.K.

Hemptinne, J.-L., Dixon, A.F.G., & Coffin, J. (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia*, **90**, 238–245.

Hemptinne, J.-L., Dixon, A.F.G., & Gauthier, C. (2000a) Nutritive cost of intraguild predation on eggs of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **97**, 559–562.

Hemptinne, J.-L., Lognay, G., Gauthier, C., & Dixon, A.F.G. (2000b) Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). *Chemoecology*, **10**, 123–128.

Joseph, S.B., Snyder, W.E., & Moore, A.J. (1999) Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. *Journal of Evolutionary Biology*, **12**, 792–797.

Lively, C.M., Dybdahl, M.F., Jokela, J., Osnas, E.E., & Delph, L.F. (2004) Host sex and local adaptation by parasites in a snail-trematode interaction. *American Naturalist*, **164**, S6–S18.

Mopper, S. & Strauss, S.Y. (ed.) (1998) *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History, and Behavior*. Chapman & Hall, New York.

Polis, G.A., Myers, C.A., & Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20**, 297–330.

Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., & Jaffee, B.A. (1995) Intraguild predation among biological-control agents: theory and evidence. *Biological Control*, **5**, 303–335.

SAS Institute Incorporated (2002) *SAS System for Windows: Release 9.0*. SAS Institute, Inc., Cary, North Carolina.

Sato, S. & Dixon, A.F.G. (2004) Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology*, **6**, 21–24.

Sato, S., Yasuda, H. & Evans, E.W. (2005) Dropping behaviour of larvae of aphidophagous ladybirds and its effects on incidence of intraguild predation: interactions between the intraguild prey, *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecological Entomology*, **30**, 220–224.

Schaefer, P.W., Dysart, R.J. & Specht, H.B. (1987) North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. *Environmental Entomology*, **16**, 368–373.

Schellhorn, N.A. & Andow, D.A. (1999) Cannibalism and interspecific predation: role of oviposition behaviour. *Ecological Applications*, **9**, 418–428.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman and Co., New York.

Tedders, W.L. & Schaefer, P.W. (1994) Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. *Entomological News*, **105**, 228–243.

Thompson, J.N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago, Illinois.

Yasuda, H. & Shinya, K. (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*, **42**, 153–163.