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Cost of being an intraguild predator in predatory ladybirds

Satoru Sato,[1,*] Rie Jimbo,[1] Hironori Yasuda[1] and Anthony F. G. Dixon[2]

[1] Faculty of Agriculture, Yamagata University; Tsuruoka, Yamagata 997–8555, Japan
[2] School of Biological Sciences, University of East Anglia; Norwich, NR4 7TJ, UK

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Abstract
Survival and growth efficiency of fourth-instar larvae of two species of aphidophagous ladybirds, *Coccinella septempunctata brucki* Mulsant and *Harmonia axyridis* Pallas were determined when fed aphid, *Acyrthosiphon pisum* Harris, or intraguild prey, another species of aphidophagous ladybird, *Propylea japonica* Thunberg. The percentage of fourth instars fed intraguild prey that completed their development was 42.9% for *C. septempunctata brucki* and 100% for *H. axyridis*, respectively. All fourth-instar larvae of both species fed aphids completed their development. The average growth efficiency (increase in body weight/weight of prey consumed) of fourth instars of *H. axyridis* was significantly lower than that of *C. septempunctata brucki* when fed aphids. In contrast, when fed intraguild prey, it was significantly higher than that of *C. septempunctata brucki*. Adaptive significance and determinants of prey specialization in aphidophagous ladybirds are discussed.

Key words: *Coccinella septempunctata brucki*; *Harmonia axyridis* Pallas; intraguild predator; growth efficiency; prey specialization

INTRODUCTION

All predator species exploiting the same prey resource form its predator guild. Predation between guild members, i.e. intraguild predation, is widely reported in various groups of predator species, such as vertebrates, insects and microbes, and is thought to play an important role as a determinant of its guild structure (Polis et al., 1989). Although the adaptive significance of being an intraguild predator, such as eliminating competitors, has been well described, its negative aspect is poorly understood.

Aphidophagous ladybird species exploiting the same aphid colonies also form its predator guild (e.g. Maredia et al., 1992; Lamana and Miller, 1996; Brown and Miller, 1998; Sakuratani et al., 2000; Wright and DeVries, 2000; Burkness et al., 2001), and they are often engaged in intraguild predation; e.g. larvae occasionally consume eggs, larvae and pupae of other species (Yasuda and Shinya, 1997; Cottrell and Yeargan, 1998; Sakuratani et al., 2000). However, since the consumption of other predator species, i.e. intraguild predation, tends to adversely affect the survival and development of larvae (Yasuda and Ohnuma, 1999; Sato and Dixon, 2004), they are reluctant to consume immature stages of other predators (e.g. Agarwala and Dixon, 1992; Agarwala et al., 1998; Hemptinne et al., 2000). For example, the survival and development of larvae of *Coccinella septempunctata brucki* worsens after consuming larvae (Yasuda and Ohnuma, 1999) and eggs (Sato and Dixon, 2004) of other species of ladybirds, which might make intraguild predation by larvae of *C. septempunctata brucki* rare in the field (Sato, 2001), and might indicate that *C. septempunctata brucki* is not well adapted for intraguild predation.

Conversely, if the performance of larvae is not affected adversely by consuming other species, then they should be less reluctant to consume other species. In fact, intraguild predatory ability varies among species. For instance, the survival and development of *Harmonia axyridis* Pallas are not adversely affected after consuming other species of ladybird (Yasuda and Ohnuma, 1999; Cottrell,

* To whom correspondence should be addressed at: E-mail: satorus@tds1.tr.yamagata-u.ac.jp
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2004; Sato and Dixon, 2004). In addition, in the field, larvae of *H. axyridis* frequently consume eggs, larvae and pupae of other species (Yasuda and Shinya, 1997; Sakuratani et al., 2000), such as *Propylea japonica* (Sato, 2001). Therefore, *H. axyridis* is likely to be well adapted for intraguild predation (Sato et al., 2003; Sato and Dixon, 2004) and is a top predator among ladybirds (Dixon, 2000). Although, in general, prey availability markedly affects the performance of ladybirds (Kawauchi, 1979), aphid abundance is affected by various intrinsic and extrinsic factors (Powell and Parry, 1976; Dixon, 1998, 2000). Consequently, the temporal availability of aphids for predators is likely to change dramatically, and intraguild predation could be advantageous as it increases the overall availability of prey.

However, the efficient conversion of intraguild prey possibly involves costs. Rana et al. (2002) showed that after artificially selecting two spot ladybirds, *Adalia bipunctata* (L.), for improved performance on the black bean aphid, *Aphis fabae* Scopoli, over several generations, their performance on that aphid improves but worsens on another aphid species, *Acyrthosiphon pisum* Harris. This suggests that specialization in a certain type of prey results in improved performance on that prey but reduced flexibility in exploiting other types of prey. By definition, the food of aphidophagous ladybirds is aphids; therefore, it is likely that their ability to exploit prey other than aphids, i.e. intraguild prey, is determined by the extent to which they are specialized in exploiting aphids. Thus, the relative performance of aphidophagous ladybirds when fed aphids and intraguild prey may indicate their potential as intraguild predators. If so, it is likely that better performance on intraguild prey affects their performance on aphids.

In the present laboratory study, the survival and growth efficiency of larvae of two species of aphidophagous ladybirds, *C. septempunctata brucki* and *H. axyridis*, were determined when fed on the aphid *A. pisum*, or intraguild prey, *P. japonica*. The significance of the results for intraguild predation and the structure of aphidophagous guilds is discussed.

MATERIALS AND METHODS

Ladybirds. Several species of ladybird make up the aphidophagous ladybird guild on shrubs from mid-spring to early summer in Yamagata, Japan. This guild is co-dominated by *C. septempunctata brucki* and *H. axyridis*, and *P. japonica* is the intraguild prey in over 50% of intraguild predation (Sato, 2001); therefore, in the present study, larvae of *P. japonica* were used as the intraguild prey.

Adults of these three species, *C. septempunctata brucki*, *H. axyridis* and *P. japonica*, were collected on an experimental farm of Yamagata University, Tsuruoka, Japan, from April to June 2003. Several pairs of each species were kept in Petri dishes (9 cm diameter) and daily fed an excess of *A. pisum*. Egg clusters were removed and kept singly in other Petri dishes (9 cm diameter) until the eggs hatched. Hatchling larvae of each species were also daily fed an excess of *A. pisum* and checked at 12-hour intervals until they moulted to the fourth instar.

Experimental procedures. Fourth instars of *C. septempunctata brucki* and *H. axyridis* were weighed less than 12 hours after moulting to the fourth instar larvae (initial body weight). These larvae were kept singly in Petri dishes (5 cm diameter) and daily fed 15 adult *A. pisum* or 5 standard-sized fourth instar larvae of *P. japonica* until they pupated or died. The number of prey left from the previous day was recorded 24 hours later. Survival and development of *C. septempunctata brucki* and *H. axyridis* were checked every 12 hours, and adults were weighed and sexed within 12 hours of emergence (final body weight). The *P. japonica* larvae and *A. pisum* used in these experiments were all recently moulted fourth instar larvae or adults, respectively. In addition, the legs of *P. japonica* larvae were removed so that they could be easily caught and eaten by fourth instar larvae of *C. septempunctata brucki* and *H. axyridis*.

Growth efficiency. In the present study, growth efficiency is the growth/consumption ratio, i.e. increase in body weight of fourth instars, which was measured as the body weight of adults minus the initial body weight of fourth instars, divided by the weight of prey consumed. The weight of prey consumed was the total number of prey consumed multiplied by the average weight of the prey individual, which was either that of 30 randomly selected adults of *A. pisum* or fourth instars of *P. japonica* (*A. pisum*: 2.6±0.4 mg; *P. japonica*: 8.0±0.2 mg).

Statistical analysis. Survival was compared using the chi-square test, and all other comparisons were made using the Mann-Whitney *U*-test.

RESULTS

The percentage of fourth instars that completed their development after consuming intraguild prey was significantly lower in *C. septempunctata brucki* than in *H. axyridis* ($\chi^2=17.1$, $p<0.0001$; Fig. 1), while no larvae of either species died when fed aphids. The results for larvae that completed their development were used to determine prey consumption, increase in body weight, and growth efficiency, except for the prey consumption of fourth instars of *C. septempunctata brucki* that died before pupation in Fig. 2.

In both types of prey, the average amount of prey consumed by fourth instars did not differ significantly between *C. septempunctata brucki* and *H. axyridis* (aphid: Mann-Whitney $U=137.0$, $p>0.05$, intraguild prey: Mann-Whitney $U=77$, $p>0.05$; Fig. 2). In addition, fourth instars of *C. septempunctata brucki* that died before pupation also consumed a similar amount of intraguild prey com-

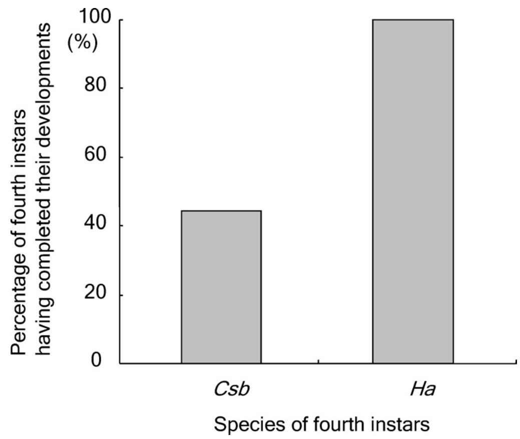

Fig. 1. Percentage of fourth instars of *C. septempunctata brucki* and *H. axyridis* that completed their development after consuming intraguild prey. *Csb* and *Ha* are *C. septempunctata brucki* and *H. axyridis*, respectively.

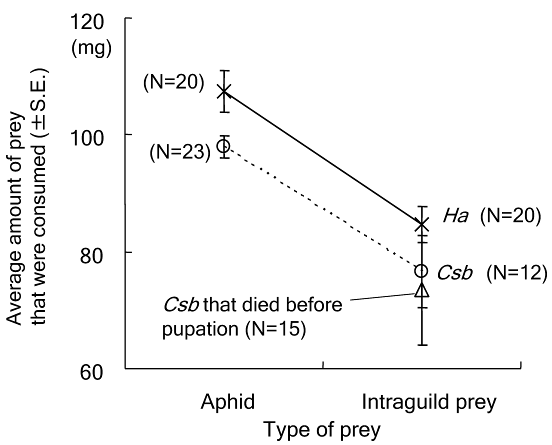

Fig. 2. Average amount of prey consumed by fourth instars of *C. septempunctata brucki* and *H. axyridis* when fed aphid or intraguild prey. *Csb* and *Ha* are *C. septempunctata brucki* and *H. axyridis*, respectively.

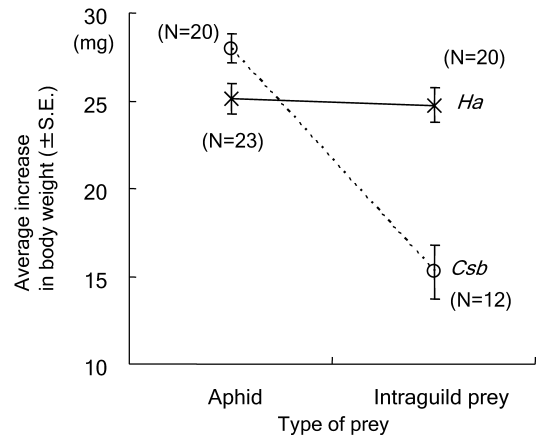

Fig. 3. Average increase in body weight of fourth instars of *C. septempunctata brucki* and *H. axyridis* after consuming aphid or intraguild prey. *Csb* and *Ha* are *C. septempunctata brucki* and *H. axyridis*, respectively.

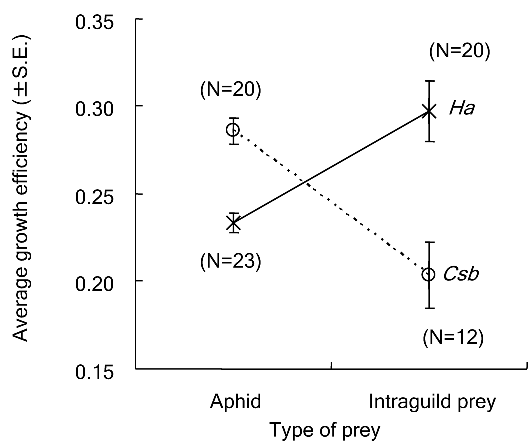

Fig. 4. Average growth efficiency of fourth instars of *C. septempunctata brucki* and *H. axyridis* after consuming aphid or intraguild prey. *Csb* and *Ha* are *C. septempunctata brucki* and *H. axyridis*, respectively.

pared with those that completed their development after consuming intraguild prey (Mann-Whitney $U=89.0$, $p>0.05$).

The increase in body weight of the fourth instars of *C. septempunctata brucki* averaged over 1.1 times that for *H. axyridis* after consuming aphid (aphid: Mann-Whitney $U=123.5$, $p<0.05$; Fig. 3), whereas it averaged about 0.6 times that for *H. axyridis* after consuming intraguild prey (Mann-Whitney $U=21.5$, $p<0.0001$; Fig. 3).

The average growth efficiency of the fourth instars of *C. septempunctata brucki* fed aphids was over 1.2 times that for *H. axyridis* (Mann-Whitney $U=47.5$, $p<0.0001$; Fig. 4). In contrast, when fed intraguild prey, growth efficiency for *H. axyridis* was over 1.4 times that for *C. septempunctata brucki* (Mann-Whitney $U=35.0$, $p<0.001$; Fig. 4).

DISCUSSION

In general, ladybird survival is affected adversely after consuming intraguild prey (e.g. Dixon, 2000). Also, in the present study, over half of fourth instars of *C. septempunctata brucki* died after consuming intraguild prey. Although the actual mechanism of this mortality remained unknown in the present study, the fact that both fourth instars of *C. septempunctata brucki* that pupated and those that died before pupation consumed a similar amount of intraguild prey suggests that its suitability as a prey resource varied in the two groups of fourth instars, e.g. intraguild prey may have been less suitable for the dead larvae than the survivors.

The results of a previous study suggest that flexibility in processing various types of prey is determined by the degree of prey specialization (Rana et al., 2002). Therefore, it is suggested that the performance of ladybird larvae fed intraguild prey is likely to be negatively associated with that when fed aphids. The present results indicate that larvae of *H. axyridis* are better adapted to feed on intraguild prey than those of *C. septempunctata brucki*, as suggested by Yasuda and Ohnuma (1999). In addition, as predicted above, when fed aphids, performance was poorer in *H. axyridis* than in *C. septempunctata brucki*; that is, the performance of the larvae of these two species of ladybirds when fed intraguild prey reflects the extent to which they have specialized in aphids or vice versa.

Factors determining prey specialization in ladybirds are unknown; however, Rana et al. (2002) suggested that the degree of specialization in exploiting a certain type of prey can be increased by natural selection driven by its availability in the field; for example, when aphids are abundant, ladybird larvae do not have to exploit alternative prey, which may adversely affect their performance (Agarwala and Dixon, 1992; Agarwala et al., 1998; Yasuda and Ohnuma, 1999; Hemptinne et al., 2000; Sato and Dixon, 2004). Thus, ladybirds should specialize in aphids when aphids are abundant. In contrast, when aphids are scarce, ladybirds should exploit intraguild prey to survive and develop. Since intraguild predation generally adversely affects the performance of ladybird larvae (e.g. Agarwala and Dixon, 1992), for species that are likely to experience frequent low levels of aphid abundance, it is advantageous to be more effective at converting intraguild prey; that is, it is likely that prey specialization is determined by the relative availability of aphids and intraguild prey. In fact, larvae of *H. axyridis* are more likely to suffer from the limited availability of aphids compared with those of *C. septempunctata brucki* in the field (Yasuda and Shinya, 1997; Sato, 2001), suggesting that larvae of *H. axyridis* are more likely to consume intraguild prey to complete their development compared with those of *C. septempunctata brucki*. This may imply that further adaptation to intraguild prey is advantageous for *H. axyridis*, although it may diminish their flexibility against various types of prey (Rana et al., 2002); however, in the field, as the availability of potential intraguild prey varies from year to year (Sato, 2001), further specialization in intraguild prey may not be advantageous for *H. axyridis*.

The present study shows that the performance of ladybirds on intraguild prey is likely to reflect their performance on aphids and vice versa. Consequently, being an efficient intraguild predator is costly in terms of the effectiveness of converting aphids into the ladybird body, which has not previously been reported for aphidophagous ladybirds. Resource utilization is usually viewed in terms of food species size (Schoener, 1974), with each species in a predator guild adapted to exploit a particular-sized species of prey. Large species of predator exploit large species of prey and vice versa. In aphidophagous insects, there appears to be no association between the size of an aphidophagous predator and that of their prey aphid (Stewart et al., 1991). Aphid colonies, which are usually monospecific, generally increase, peak and decline in abundance, and are exploited by a sequence of predators, which is consistent from year to year (Dixon, 2007). Factors that determine the growth stage of an aphid colony at which particular predators lay their eggs in the colony is only just beginning to be studied. For example, immature stages of syrphids, smaller than ladybirds, occur in aphid colonies earlier in spring in temperate regions, which may be associated with a lower developmental threshold of syrphids smaller than ladybirds (Dixon et al., 2005; Dixon, 2007). Thus, the life history strategies of various predators in a guild have to be taken into consideration when studying prey specialization or intraguild predation and the structure of aphidophagous guilds.

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REFERENCES

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

Agarwala, B. K., S. Bhattacharya and P. Bardhanroy (1998) Who eats whose eggs? Intra- versus inter-specific interactions in starving ladybird beetles predaceous on aphids. *Ethol. Ecol. Evol.* 10: 361–368.

Brown, M. W. and S. S. Miller (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomol. News* 109: 143–151.

Burkness, E. C., W. D. Hutchison, R. C. Venette and S. J. Wold (2001) In-field monitoring of beneficial insect populations in transgenic corn expressing a *Bacillus thuringiensis* toxin. *J. Entomol. Sci.* 36: 177–187.

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

Cottrell, T. E. and K. V. Yeargan (1998) Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *J. Kansas Entomol. Soc.* 71: 159–163.

Dixon, A. F. G. (1998) *Aphid Ecolog: Optimization Approach*. 2nd ed. Blackie and Son Ltd., Cornwall, UK. 300 pp.

Dixon, A. F. G. (2000) *Insect Predator-Prey Dynamics. Ladybird Beetles and Biological Control*. Cambridge University Press, London, UK. 268 pp.

Dixon, A. F. G. (2007) Body size and resource partitioning in ladybirds. *Popul. Ecol.* 49: 45–50.

Dixon, A. F. G., V. Jarosik and A. Honek (2005) Thermal requirements for development and resource partitioning in aphidophagous guilds. *Eur. J. Entomol.* 102: 407–411.

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

Kawauchi, S. (1979) Effects of prey density on the rate of prey consumption, development, and survival of *Propylea japonica* Thunberg (Col: Coccinellidae). *Kontyu* 47: 204–212.

Lamana, M. L. and J. C. Miller (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biol. Cont.* 6: 232–237.

Maredia, K. M., S. H. Gage, D. A. Landis and T. M. Wirth (1992) Ecological observations on predatory Coccinellidae (Coleoptera) in southwestern Michigan. *Great Lakes Entomol.* 25: 265–270.

Polis, G. A., C. A. Myers and R. Holt (1989) The evolution and dynamics of intraguild predation between potential competitors. *Annu. Rev. Ecol. Syst.* 20: 297–330.

Powell, W. and W. H. Parry (1976) Effects of temperature on overwintering populations of the green spruce aphid *Elatobium abietinum*. *Ann. Appl. Biol.* 82: 209–219.

Rana, J. S., A. F. G. Dixon and V. Jarosik (2002) Costs and benefits of prey specialization in a generalist insect predator. *J. Anim. Ecol.* 71: 15–22.

Sakuratani, Y., Y. Matsumoto, M. Oka, T. Kubo, A. Fujii, M. Uotani and T. Teraguchi (2000) Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. *Eur. J. Entomol.* 97: 555–558.

Sato, S. (2001) Ecology of ladybirds: factors influencing their survival. PhD thesis, University of East Anglia, UK. 120 pp.

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

Sato, S., A. F. G. Dixon and H. Yasuda (2003) Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecol. Entomol.* 28: 628–633.

Schoener, T. W. (1974) Resource partitioning in ecological communities. *Science* 185: 27–39.

Stewart, L., J.-L. Hemptinne and A. F. G. Dixon (1991) Reproductive tactics of ladybird beetles: relationship between egg size, overiole number and developmental time. *Funct. Ecol.* 5: 380–385.

Wright, R. J. and T. A. DeVries (2000) Species composition and relative abundance of Coccinellidae (Coleoptera) in south central Nebraska field crops. *J. Kansas Entomol. Soc.* 73: 103–111.

Yasuda, H. and N. Ohnuma (1999) Effect of cannibalism and predation on the larval performance of two ladybirds. *Entomol. Exp. Appl.* 93: 63–67.

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