Intraguild predation in aphidophagous guilds: Mechanism of being intraguild predator and its cost

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Introduction

In the field, aphid abundance is affected by various intrinsic and extrinsic factors, (Powell & Parry, 1976; Dixon, 1998; Dixon, 2000) the temporal availability of aphids for its predators is likely to change dramatically. In aphidophagous ladybirds, in general, prey availability markedly affects the performance of ladybirds, especially during their immature stages (Kawauchi, 1979). Therefore, they occasionally need to consume alternative prey, such as intraguild prey. However, in general, consumption of other species, i.e. intraguild predation, tends to affect adversely the survival and development of their larvae (e.g. Yasuda & Ohnuma, 1999; Sato & Dixon, 2004), larvae are reluctant to consume the immature stages of other predators (e.g. Agarwala & Dixon, 1992; Agarwala *et al*., 1998; Hemptinne *et al*.,2000).

Interestingly, adverse effect of intraguild predation depend on intraguild predator species; e.g. the survival and development of species like *Harmonia axyridis* Pallas are not affected adversely after consuming other species of ladybird (Yasuda & Ohnuma, 1999; Sato & Dixon, 2004; Cottrell, 2004; Yasuda *et al*., 2004). In addition, in the field, larvae of *H. axyridis* frequently consume eggs, larvae and pupae of other species (Yasuda & Shinya, 1997, Sakuratani *et al*, 2000), such as *Propylea japonica* Tunberg (Sato, 2001), suggesting that *H. axyridis* is well adapted for intraguild predation (Sato *et al*., 2003; Sato & Dixon, 2004) and that among ladybirds *H. axyridis* is a top predator (Dixon, 2000). In this circumstance, this feature of *H. axyridis* is likely to be an advantage as it increase their total availability of prey.

However, the efficient conversion of intraguild prey possibly involves costs. Rana *et al*. (2002) show that after selecting individuals of the 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 on 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 the 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 prey conversion efficiency of larvae of two species of aphidophagous ladybirds, *Coccinella septempunctata brucki* and *H. axyridis*, fed on the aphid *Acyrthosiphon pisum*, or intraguild prey, *P. japonica*, were determined. The significance of the results for intraguild predation and possibly mechanism affecting these features of the two species of ladybirds are 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. s. brucki* and *H. axyridis*, and *P. japonica* is the intraguild prey in over 50 % of the cases 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. s. brucki*, *H. axyridis* and *P. japonica*, were collected on an experimental farm of Yamagata University, Tsuruoka, Japan, from April to June in 2003. Several pairs of each species were kept in Petri dishes (9 cm diameter) and fed daily 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 fed daily an excess of *A. pisum* and checked at 12 hour intervals until they moulted to the fourth-instar.

Experimental procedures

Fourth-instar larvae of *C. s. brucki* and *H. axyridis* were weighed less than 12 hours after moulting to the fourth-instar (initial body weight). These larvae were kept singly in Petri dishes (5 cm diameter) and fed daily, 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. s. 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 the *P. japonica* larvae were removed so that they could be more easily caught and eaten by fourth-instar larvae of *C. s. brucki* and *H. axyridis*. The numbers of fourth instar larvae of *C. s. brucki* fed intraguild- or aphid prey were 28 and 20, respectively, and 20 and 23, respectively, for *H. axyridis*.

Prey conversion efficiency

The "prey conversion efficiency" is the increase in body weight of the fourth instar larvae, measured as the body weight of the adults minus initial body weight of the larvae 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, which was either that of 30 randomly selected adults of *A. pisum* or fourth instar larvae of *P. japonica* (*A. pisum*: 2.6±0.4 mg; *P. japonica*: 8.0±0.2 mg).

Results

The percentage of fourth-instar larvae that completed their development after consuming intraguild-prey was 42.9% (n = 12) in *C. s. brucki* and 100.0% in *H. axyridis* (n = 20) (Chi-square = 17.1, $P < 0.0001$). No larvae of either species died when fed aphids. The results for the larvae that completed their development were used to determine prey conversion efficiency.

For both sexes, the average prey conversion efficiency of the fourth-instar larvae of *H. axyridis* fed intraguild-prey was over 1.3 times that for *C. s. brucki* (Female: Mann-Whitney $U = 23.0$, $P < 0.05$; Male: Mann-Whitney $U = 1.0$, $P < 0.05$; Figure 1). In contrast, when fed aphids that for *C. s. brucki* was over 1.2 times that for *H. axyridis*, for both sexes (Female: Mann-Whitney $U = 5.5$, $P < 0.0001$; Male: Mann-Whitney $U = 10.0$, $P < 0.001$). That is, although prey conversion efficiency is higher in *H. axyridis* than in *C. s. brucki* when fed intraguild prey, it is lower in *H. axyridis* than in *C. s. brucki* when fed aphids.

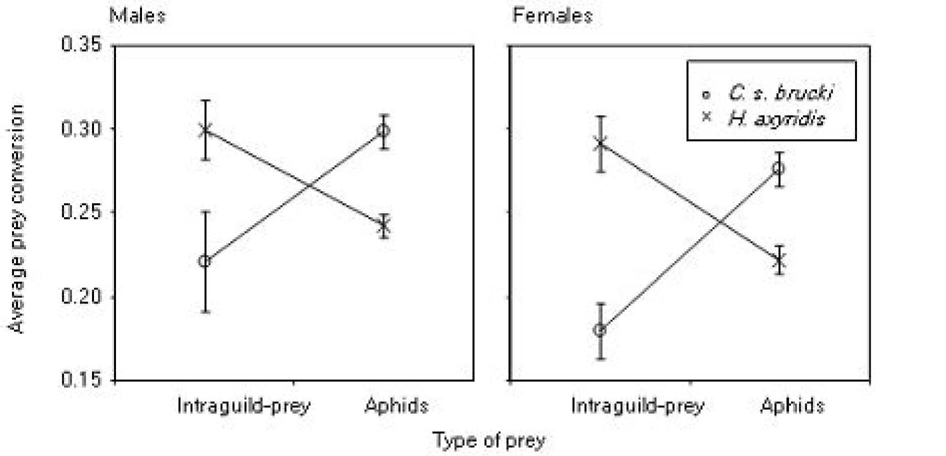

Figure 1. Average prey conversion efficiency of male and female fourth instar larvae of C. s. brucki and H. axyridis fed either aphids or intraguild-prey.

Discussion

Results of previous studies suggest that flexibility in processing various type 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. s. brucki*, as suggested by Yasuda & Ohnuma (1999). In addition, as predicted above the performance when fed aphids was poorer in *H. axyridis* than in *C. s. brucki*. That is, the performance of the larvae of these two species of ladybird when fed intraguild-prey reflects the extent to which they have specialized on aphid-prey or *vice versa*.

What determines prey specialization in ladybirds is unknown. However, Rana *et al*. (2002) suggest that the degree of specialization in exploiting aphids can be increased by selection driven by the availability of particular species of aphid 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 & Dixon, 1992; Agarwala *et al*., 1998; Yasuda & Ohnuma, 1999; Hemptinne *et al*., 2000; Sato & Dixon, 2004). Thus, ladybirds should specialize on aphids when aphids are abundant. In contrast, when aphids are scarce ladybirds should exploit intraguild prey in order to sustain their life and prolong survival. As intraguild predation generally adversely affects the performance of ladybird larvae (e.g. Agarwala & Dixon, 1992) then for species that are likely to experience frequently low levels of aphid abundance it is advantageous for them 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 ladybird larvae.

In fact, availability of aphid is likely to vary in *C. s. brucki* and *H. axyridis*. In general, duration of development of aphidophagous ladybirds is similar with longevity of aphid colony (Dixon, 2000). Therefore, if females lay their eggs early in the development of aphid abundance, their offspring are likely to complete their development prior to the extinction of aphids. However, when egg ovipositing delays offspring are unlikely to complete their development before the extinction of aphids. That is, availability of aphids in ladybird larvae is affected by timing of oviposition to development of aphid abundance. Although *C. s. brucki* and *H. axyridis* are similar in duration of development (Schanderl et al., 1985; Kawauchi, 1990), their timing of oviposition to aphid abundance dynamics varies. In Yamagata, Japan, females of *C. s. brucki* lay proportionally more eggs early in the development of aphid abundance compared with those of *H. axyridis* (Yasuda & Shinya, 1997; Sato, 2001). Consequently, larvae of *C. s. brucki* are more likely to complete their development before aphid becomes extinct compared with those of *H. axyridis*. That is, it is suggested that intraguild prey is more important prey resources for larvae of *H. axyridis* than for those of *C. s. brucki*.

In conclusion, 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 a top predator is costly in terms of their effectiveness in converting aphids into ladybird biomass, which has not previously been reported for aphidophagous ladybirds. What determines when particular predators lay their eggs in the development of an aphid colony is only just beginning to be studied. For example, the earlier appearance of the immature stages of syrphids, relative to ladybirds, in aphid colonies in spring in temperate regions, is associated with the former having a lower developmental threshold (Dixon *et al*., 2005) and of small relative to large species of ladybird with constraints associated with body size (Dixon, 2005). Thus, the life history strategies of the various predators in a guild have be taken into consideration when studying prey specialization or intraguild predation and the structure of aphidophagous guilds.

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