Effects of prey species and its density on larval performance of two species of hoverfly larvae, *Episyrphus balteatus* de Geer and *Eupeodes corollae* Fabricius (Diptera: Syrphidae)

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Abstract
Functional response and effects of prey species, *Acyrtosiphon pisum* (Harris) and *Aphis craccivora* Koch, and its density on larval performance such as survival rate and development time in addition to adult weight gain of the two predatory hoverflies, *Episyrphus balteatus* de Geer and *Eupeodes corollae* Fabricius, were examined in the laboratory. Our study revealed that prey density positively influences larval performance and the adult weight of the two hoverfly species. However, the effects of prey species on survival rate and development time differed: *A. pisum* was better food for *E. balteatus*, while the larval performance of *E. corollae* was enhanced by *A. craccivora*. In addition, the effect of prey density differed with development stage, since voracity increased with larval development. Both hoverfly species tended to eat a larger number of preys with lower quality, which in turn resulted in lower performance. The functional response differed between species involved and among development stages. During the third-instar stage, both species showed linear relationships as a functional response, while Holling's Type II response was observed during the young instar phase. *E. balteatus* tended to have linear relationships than *E. corollae*, and this would be caused by the larger size of *E. balteatus*, which in turn consumed more aphids than did *E. corollae*. This study suggests that the differences in the effects of prey species and its density on the larval performance of the two hoverflies are attributable to the differences in the range of food habit and body size.

Key words: *Episyrphus balteatus*; *Eupeodes corollae*; functional response; prey density; prey species

INTRODUCTION

Larval and adult performances of predatory insects are constrained by both prey quality and quantity. Some studies have highlighted that prey abundance improves the larval performance of different taxonomic groups of predatory insects (e.g., Kawauchi, 1977; Yasuda, 1995; Lee and Kang, 2004), and others have revealed that poor prey quality often results in high larval mortality (e.g., Okamoto, 1978; Sugiura and Takada, 1998; Sadeghi and Gilbert, 2000). Although these two factors are both important to understand the fate of predatory insects, there are few studies that simultaneously reveal the effects of the two factors on larval performance of predatory insects.

Aphids are one of the most devastating insect pests for many agricultural crops and fruits due to the characteristic sucking of plant phloem sap and transmission of plant viruses (Power, 1987; Werker et al., 1998; Dusi and Peters, 1999; Elibuyuk, 2003; Fiebig et al., 2004; Rassaby et al., 2004), and they easily develop insecticide resistance (Herron et al., 2001; Kift et al., 2004). Nowadays, environmental hazards due to regular and rather intensive chemical insecticide spraying is a growing concern. Thus, biological control of aphids using natural enemies, allowing the amount of insecticides to be reduced, is needed to create sustainable agriculture development.

Ladybirds, hoverflies, lacewings, flower bugs, and aphidophagous midges are well known aphid

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predators (Rotheray, 1989). We know that these predators play an important role in the suppression of aphid abundance (Dixon, 1970; Wratten, 1973; Chambers and Adams, 1986; Lucas et al., 1997; Zhang and Hassan, 2003; Lee and Kang, 2004). However, most studies have focused on the impact of ladybirds over aphids, and few experimental studies have been completed on other aphid predators.

The hoverfly in addition to ladybirds has been nominated as a candidate for controlling the aphid population, since it is a voracious species (Gilbert, 1993; Tenhumberg, 1995), and the adults tend to lay eggs at an earlier developmental phase of aphid colonies (Kan and Sasakawa, 1986; Kan, 1988a, b), suggesting their ability to reduce aphid abundance. In order to use predatory hoverflies as a candidate for biological control agent to reduce aphid abundance, more information is required in terms of functional response in addition to the effects of prey quality and quantity on larval performance. Since hoverfly larvae are slow-moving predators, prey availability in a given area on a plant might become an important factor to influence larval performance. In addition, Sadeghi and Gilbert (2000) suggested that prey quality affects the larval performance of hoverflies. However, our understanding of how these factors influence the fate of hoverfly larvae remains incomplete.

Hoverfly larvae tend to construct an aphidophagous insect guild with several other hoverfly species (Mizuno et al., 1997). In the farm at Yamagata University, there are at least more than six hoverfly species (Kusibuchi, unpublished data). In our study, two species of hoverfly, *Episyrphus balteatus* de Geer and *Eupeodes corollae* Fabricius, were chosen since they differ in size and food habit. The former species is larger and a generalist predator (Gilbert and Owen, 1990), while the latter tends to be more specialist (Mizuno et al., 1997). In this study, we hypothesize that the difference in size and food habit of hoverflies in addition to prey quality and quantity might influence prey consumption, which in turn would lead to differences in larval performance between predator species.

Here, we reveal functional response, the effects of prey species and its density on food consumption and the body weight in addition to larval performance such as survival rate and development time.

MATERIALS AND METHODS

Insects rearing. The stock culture of hoverflies, *E. balteatus* and *E. corollae*, was initiated with larvae caught from the Yamagata University Research Farm (38°43′N, 139°49′E), Tsuruoka, Yamagata Prefecture. After adult emergence, similar numbers of females and males (30 individuals in total) were reared in a wire frame cage (60×60×70 cm each) covered with nylon screen. Crushed-pollen (Tennen kafun, Youhouen Co.) was placed in a Petri dish (5 cm in diameter and 1 cm in height) as adult food. In addition, a 500 ml plastic bottle filled with water was prepared for providing water and honey for adults. An aluminum stick (40 cm in length and 2 mm in diameter) was inserted into the bottle through a small hole punctured in the cap. A thin layer of honey was placed on the upper section and the lower section was half covered by a kitchen paper towel that had been soaked in water. This allowed adults access to the honey and water. When some females and males were seen in pairs, a cutting-bean plant infested with *Acyrtosiphon pisum* (Harris) and *Aphis craccivora* Koch was introduced into the cage to collect eggs.

The rearing of insects and all experiments were done in a room at 23°C and 75% RH under a 16L : 8D photoperiod.

Impacts of prey species and its density on larval performance. To determine the impact of prey species and its density on the larval performance of hoverflies, five treatments corresponding to five prey densities were conducted, in which 3, 10, 20, 30, and 40 individuals of *A. craccivora* or *A. pisum* were provided to a single larva of both hoverfly species in a Petri dish (5 cm in diameter and 1 cm in height). Similarly sized individuals of the two aphid species with different instars were provided as daily food for the hoverfly larvae because of the difference in size between the two aphid species. In addition, while the hoverfly larvae grew in size, we provided older preys. For example, we provided first-instar nymphs of *A. pisum* (0.07±0.01 mg, $n=20$) and second-instar nymphs of *A. craccivora* (0.07±0.01 mg, $n=20$) to feed the first instar of hoverfly larvae. Then, as the larvae grew, we provided second-instar (0.18±0.02 mg, $n=20$) or early third-instar nymphs of *A. pisum* (0.51±0.10 mg, $n=20$) and early (0.19±0.01 mg, $n=20$) or late third-instar nymphs of *A. craccivora* (0.48±

0.02 mg, $n=20$) for second- and third-instar hoverfly larvae. As the hatched larvae were limited in terms of mobility to forage and attacking moving aphids, a pea leaf with aphids was provided to the first-instar larva of the hoverfly within 12 h of hatching. After they developed into second-instar larvae, the aphids were provided without the pea leaf. The number of replicates was 15–20 for each treatment. The number of prey consumed per day was recorded. The molting of the hoverfly larva was observed every 12 h. Petri dishes were replaced every 24 h together with the replacement of prey, except for the first-instar larvae, which was done every 3 d to avoid the mortality of larvae due to manipulation. In order to understand the effects of prey species and its density on the development time and adult weight, we analyzed the data only for prey densities of 20, 30 and 40, since the larvae reared with the prey densities of 3 and 10 mostly died before and/or during the third-instar stage. The new adults were weighed to the nearest 0.01 mg just after emergence using a Sartorius Microbalance R200D.

Statistical treatments. Chi-square test was used to compare the survival rate of hoverfly species fed on *A. craccivora* and *A. pisum* at each prey density, and to compare the survival rate among prey densities for each prey species. Two-way ANOVA was used to determine the impact of prey species and its density on the development time and adult weight of the hoverfly species, and mean differences were separated using the Tukey post-hoc test or paired *t*-test (Sokal and Rohlf, 1995).

RESULTS

Prey consumption of the two hoverflies fed on different prey species and densities

The larvae of the two species showed different voraciousness in relation to their development (Fig. 1). In general, the third-instar larvae of the two hoverflies had similar voracity with a linear functional response irrespective of prey species. For the second-instar larvae, *E. corollae* showed the response of Holling's Type II, while the response of *E. balteatus* was a linear relationship on both prey
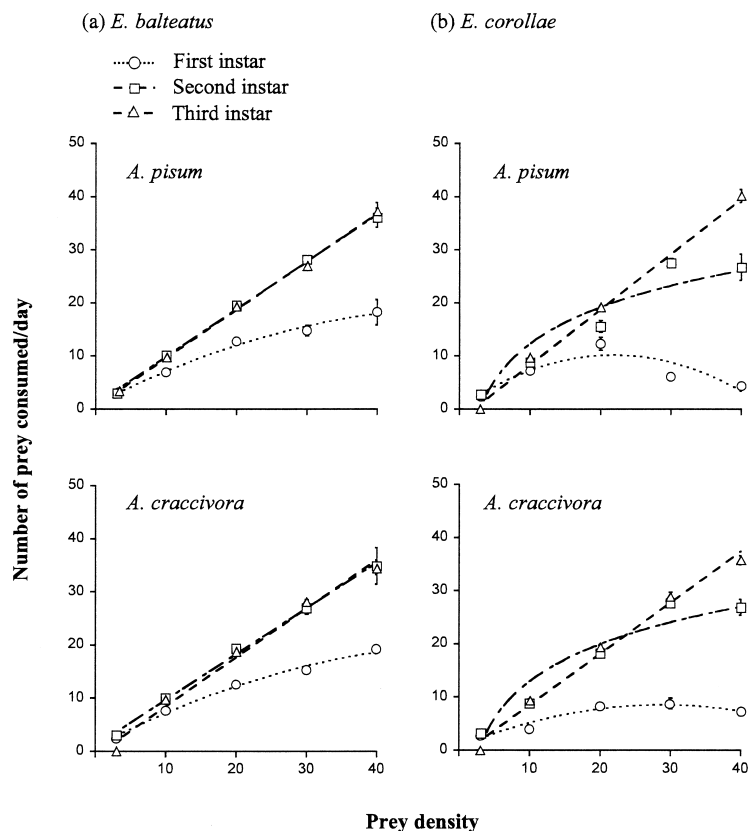

Fig. 1. Relationships between aphid density and number (Mean±SE) of aphids consumed per day by single larva of (a) *E. balteatus* and (b) *E. corollae* when reared on *A. pisum* or *A. craccivora*.
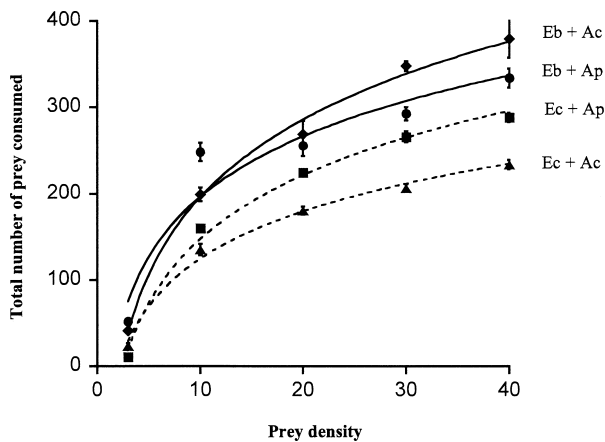
Fig. 2. Relationships between prey density and total number (Mean±SE) of prey consumed by single larva of *E. balteatus* (Eb) and *E. corollae* (Ec) when reared on *A. pisum* (Ap) or *A. craccivora* (Ac) throughout the larval period.

species. However, during the first-instar stage, a unimodal relationship was observed for the response of *E. corollae*, while *E. balteatus* had a Holling's Type II response. Both hoverfly species consumed more prey at higher prey densities through their larval periods (Fig. 2). In addition, *E. balteatus* tended to consume more *A. craccivora* than *A. pisum*, while *E. corollae* larvae consumed more *A. pisum* than *A. craccivora*.

Survival rates of the two hoverflies fed on different prey species and densities

Table 1 shows the impacts of prey density and species on the survival rates of *E. balteatus* and *E. corollae*. In general, the survival rates of the two species tended to increase with prey density up to 30, although both hoverfly larvae failed to develop into pupae at prey densities of 3 and 10. Furthermore, the impact of prey species on the total survival rate of each hoverfly species differed. The rates of *E. balteatus* tended to be higher when fed *A. pisum* than when fed *A. craccivora* (Table 1a), although they were not significantly different except at a prey density of 20. On the other hand, *E. corollae* had a significantly higher survival rate when fed *A. craccivora* than when fed *A. pisum* at prey densities of 20 and 30 (Table 1b).

Development time of the two hoverflies fed different prey densities and species

Two-way factorial ANOVA showed that prey species and its density significantly influenced the total development time of the two hoverflies from first instar to adult emergence (for *E. balteatus* with prey species, $F_{1,46}=10.2$, $p<0.05$, with prey density, $F_{1,46}=17.9$, $p<0.001$, with species and density interactions, $F_{1,46}=0.5$, $p>0.05$; for *E. corollae* with species, $F_{1,46}=29.3$, $p<0.001$, with density, $F_{1,46}=21.5$, $p<0.001$, with species and density interactions, $F_{1,46}=2.5$, $p>0.05$). In general, the total development time of both hoverflies tended to be shorter when fed higher prey densities (Table 2). However, the effects of prey species on the total development time differed between the two hoverflies. *E. balteatus* tended to develop in shorter time when fed *A. pisum* than when fed *A. craccivora* (with prey density of 30, $t=3.39$, $p<0.05$, df=7), while development time of *E. corollae* was shorter when fed *A. craccivora* than when fed *A. pisum* (with prey density of 20, $t=5.00$, $p<0.05$, df=1, with prey density of 30, $t=4.68$, $p<0.05$, df=7), although a significant difference was not found when both species were fed at a prey density of 40 (for *E. balteatus*, $t=0.36$, $p>0.05$, df=9, for *E. corollae*, $t=1.32$, $p>0.05$, df=9).

Adult weight of the two hoverflies fed different prey densities and species

Prey density had a significant impact on the adult weight of *E. balteatus*, while there was no significant difference in the weight due to prey species (with prey density, $F_{1,39}=43$, $p<0.001$; with prey species, $F_{1,39}=0.9$, $p>0.05$; with species and density interactions, $F_{1,39}=2.4$, $p>0.05$), showing that *E. balteatus* gained more body weight when fed at higher prey densities (Table 3a). In addition, there were similar tendencies for the effects of prey species and its density on the weight of *E. corollae* (with prey density, $F_{1,44}=72.5$, $p<0.001$; with prey species, $F_{1,44}=0.9$, $p>0.05$; with prey species and density interactions, $F_{1,44}=5.0$, $p<0.05$; Table 3b). In general, females tended to be bigger than males in both species (for *E. balteatus*, $t=8.77$, $p<0.001$, df=20, for *E. corollae*, $t=19.07$, $p<0.001$, df=17), and *E. balteatus* was bigger than *E. corollae* (for female, $t=6.23$, $p<0.001$, df=21; for male, $t=4.4$, $p<0.01$, df=17).

DISCUSSION

Our study revealed that prey density had a posi-

Table 1. Survival rates of the two species of hoverfly larvae, *E. balteatus* and *E. corollae*, when reared on different prey densities of *A. pisum* and *A. craccivora*

(a) *E. balteatus*

Aphid density	Species	Survival rate (%)					*n*
		1st instar	2nd instar	3rd instar	Pupa	Total[a]	
3	*A. pisum*	100 ns[b]	83.3**	0	—	0	18
	A. craccivora	100	0	—	—	0	18
10	*A. pisum*	100 ns	88.9 ns	0	—	0	18
	A. craccivora	100	100	0	—	0	17
20	*A. pisum*	100 ns	94.7ns	38.9*	100	36.8*	19
	A. craccivora	94.4	100	0	—	0	18
30	*A. pisum*	100 ns	100 ns	70 ns	92.9 ns	65 ns	20
	A. craccivora	88.9	100	87.5	71.4	55.6	18
40	*A. pisum*	100 ns	100 ns	64.7 ns	90.9 ns	58.8 ns	17
	A. craccivora	100	100	68.4	76.9	52.6	19
	A. pisum	ns[c]	**	*	ns	*	
	A. craccivora	**	**	**	ns	**	

(b) *E. corollae*

Aphid density	Species	Survival rate (%)					*n*
		1st instar	2nd instar	3rd instar	Pupa	Totala	
3	*A. pisum*	50 ns	0**	—	—	0	18
	A. craccivora	37.5	100	0	—	0	16
10	*A. pisum*	100 ns	64.7*	0**	—	0	17
	A. craccivora	100	100	60	0	0	15
20	*A. pisum*	93.7 ns	73.3*	45.5*	40*	12.5**	16
	A. craccivora	100	100	88.9	75	66.7	18
30	*A. pisum*	88.9 ns	87.5 ns	85.7 ns	66.7*	44.4*	18
	A. craccivora	100	100	100	100	100	18
40	*A. pisum*	94.1 ns	75 ns	83.3 ns	100 ns	58.8 ns	17
	A. craccivora	100	100	100	80	80	15
	A. pisum	*	*	*	**	**	
	A. craccivora	**	ns	*	*	*	

[a] Total means total survival rates from first instar to adult stage.

[b] Chi-square test was performed to find the difference in survival rates between prey species at each prey density.

[c] Chi-square test was performed to find the difference in survival rates between prey species for each prey density.

ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$.

tive influence on larval performance and adult weight of the two hoverfly species. However, the effects of prey species on survival rates and development times differed: *A. pisum* was better food for *E. balteatus*, while larval performance of *E. corollae* was enhanced by *A. craccivora*. In addition, the effects of prey density differed with development stage, since voracity increased with larval development as shown in previous studies (Yasuda,

1995; Omkar and Srivastava, 2003; Omkar and James, 2004).

It is well known that different prey species have different influences on the larval performance of aphid predators (Sadeghi and Gilbert, 2000; Bilde and Toft, 2001; Rana et al., 2002; Omkar and James, 2004) and other predatory insects (Bilde et al., 2000; Stamp and Meyerhoefer, 2004). For instance, the survival rates from hatching to adult

eclosion of two predatory ladybirds were more than 90% when fed on suitable prey species, while poor prey quality resulted in low survival rates (Sugiura and Takada, 1998). In our results, *E. corollae* presented better performance when preyed

upon *A. craccivora* than *A. pisum*. In contrast, *E. balteatus* showed higher survival rates and shorter development times when fed upon *A. pisum* than *A. craccivora*, which is similar to the results reported by Sadeghi and Gilbert (2000). In addition, our findings indicate that the increase in the survival rate of *E. corollae* was more significant than that of *E. balteatus* when the larvae were provided with suitable prey. Previous studies revealed that *E. balteatus*, contrary to *E. corollae*, which tended to be a specialist, had a wider range of preys (Mizuno et al., 1997; Sadeghi and Gilbert, 2000). Therefore, in general, as a trade-off between the range of food and better performance obtained, generalist predators might lose the best performance due to a lack of the best prey species since they adapt a wide range of food. On the other hand, the performance of specialist predators increases when they consume the best food because of the adaptation for the food, as shown in the present study.

Interestingly, our results revealed that both hoverfly species tend to eat a larger number of preys of lower quality, which in turn results in lower per-

Table 2.   Mean developmental time from first instar to adult emergence in days ($\pm$SE) of the two hoverflies, *E. balteatus* and *E. corollae*, when reared on different prey densities of *A. pisum* or *A. craccivora*

Aphid density	Species	Developmental time	
		E. balteatus	*E. corollae*
20	*A. pisum*	23.6$\pm$1.5 a[a]	22.5$\pm$0.5 a
	A. craccivora	—	19.7$\pm$0.2 a
30	*A. pisum*	19.5$\pm$0.5 b	20$\pm$0.5 a
	A. craccivora	21.2$\pm$0.2 a	17.4$\pm$0.1 b
40	*A. pisum*	17.9$\pm$0.4 b	18.1$\pm$0.8 b
	A. craccivora	19.0$\pm$0.6 b	17.0$\pm$0.0 b

[a] Different letters following means in the column indicate significant differences among densities by Tukey post-hoc test ($p<0.05$) or paired *t*-test ($p<0.05$) for *E. balteatus* with *A. craccivora*.

Table 3.   Adult weight of the two hoverflies, *E. balteatus* and *E. corollae*, when reared on different prey densities of *A. pisum* or *A. craccivora*

(a) *E. balteatus*

Aphid density	Species	Weight (in mg)			
		Female	*n*	Male	*n*
20	*A. pisum*	13.7$\pm$0.2 a[a]	2	11.2$\pm$0.3 a	5
	A. craccivora	—		—	
30	*A. pisum*	14.9$\pm$0.5 b	6	12.7$\pm$0.2 a	7
	A. craccivora	15.0$\pm$0.3 a	5	12.6$\pm$0.3 a	5
40	*A. pisum*	19.4$\pm$0.9 c	5	15.5$\pm$0.3 b	5
	A. craccivora	20.0$\pm$0.9 b	6	15.7$\pm$0.3 b	5

(b) *E. corollae*

Aphid density	Species	Weight (in mg)			
		Female	*n*	Male	*n*
20	*A. pisum*	5.8$\pm$0 a	2	—	
	A. craccivora	9.8$\pm$0.2 a	4	7.2$\pm$0.4 a	8
30	*A. pisum*	10.7$\pm$0.4 b	8	—	
	A. craccivora	10.8$\pm$0.5 a	10	11.3$\pm$0.3 b	8
40	*A. pisum*	15.3$\pm$0.1 c	6	12.6$\pm$1.0	4
	A. craccivora	13.2$\pm$0.1 b	6	12.8$\pm$0.4 c	6

[a] Different letters following means in the column indicate significant differences among densities by Tukey post-hoc test ($p<0.05$) or paired *t*-test (($p<0.05$) for *E. balteatus* with *A. craccivora*.

formance (*A. craccivora* for *E. balteatus* and *A. pisum* for *E. corollae*). Similar results were shown for the predatory ladybirds (Okamoto, 1978). Although the general relationship between prey preference and larval performance in predatory insects is not well known, our results suggest that the hoverfly larvae might need to consume more prey when the preys are of lower food quality.

Several studies have shown that prey density has a positive influence on larval and adult performance not only in aphid predators (Kawauchi, 1977; Dixon and Guo, 1993), but also in other predatory insects (Steffan and Evenhuis, 1981; Matsura and Morooka, 1983; Matsura et al., 1984; Yasuda, 1995). Our study supports the results of previous studies; that is, for both species, increased prey density tends to shorten the development time and increase adult weight, although the highest prey density did not always show high survival rates, which were less than 80%. This suggests that the effects of prey density function differently on larval performance, as has been shown in a predatory mosquito (Yasuda, 1995). In addition, the present study reveals that the two hoverflies failed to develop when they were provided with low prey density and needed to have more than 20 prey individuals for pupal development during the third-instar stage. However, as aphid nymphs were fed on hoverfly larvae instead of adult aphids, the expected number of prey that the larvae required to develop into pupae would be smaller than the numbers shown in this study, if the larvae consumed adult aphids.

In general, predatory insects tend to have a functional response of Holling's Type II (Spitze, 1985; Begon et al., 1996; Kohno et al., 2004). This study, however, revealed that the shapes of the curves differed between species involved and among development stages. *E. balteatus* tended to have more linear relationships than *E. corollae*, and this was caused by the larger size of *E. balteatus*, which in turn consumed more aphids than did *E. corollae*. The linear relationship shown in the third-instar larvae of *E. corollae* also supports the hypothesis that the linear functional responses in this study were mainly attributable to more prey consumption due to their large size. Indeed, *E. corollae* larvae had Holling's Type II as the functional response during the young instar.

Out of the aphid predators, hoverflies have been nominated as a candidate for controlling the aphid population because of their voracity (Gilbert, 1993; Tenhumberg, 1995) and oviposition behavior (Kan and Sasakawa, 1986; Kan, 1988a; Sadeghi and Gilbert, 2000). In addition, Michaud and Belliure (2001) provided interesting evidence on the ability of the predatory hoverfly, *Pseudodorus clavatus*, to hamper the growth of the aphid population by decreasing the production of the winged form. The present study shows that *E. balteatus* would be a better predator over *E. corollae* to reduce aphid abundance, since the former species consumes a larger number of aphids due to its large size and presents a longer development time. In addition, the wide range of food habit of the *E. balteatus* is also considered a suitable character as an aphid predator (Mizuno et al., 1997).

Large-sized ladybirds like *Harmonia axyridis* and *Coccinella septempunctata* are voracious but they tend to have summer diapause due to high temperature (Katsoyannos et al., 1997; Ohashi et al., 2003). Because these hoverfly species do not have summer diapause, it seems that they are a suitable aphid predator during the summer in particular, when the large ladybirds are less active. However, if hoverfly larvae are used as a natural enemy to reduce aphid abundance in the field, interspecific relationships between hoverfly larvae and other aphid predators, ladybirds in particular, should also be paid much attention since faster moving predators such as predatory ladybirds have a negative impact on the survival rate of slow-moving aphid predators like hoverfly larvae (Lucas et al., 1998).

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