

Predation and oviposition by predatory *Stethorus japonicus*, *Oligota kashmirica benefica*, and *Scolothrips takahashii* in egg patches of various spider mite species

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Abstract

Predation and oviposition by three predacious insects [*Scolothrips takahashii* Priesner (Thysanoptera: Thripidae), *Stethorus japonicus* H. Kamiya (Coleoptera: Coccinellidae), and *Oligota kashmirica benefica* Naomi (Coleoptera: Staphylinidae)] were examined using egg patches of three spider mite species [*Amphitetranychus viennensis* (Zacher), *Tetranychus urticae* Koch, and *Panonychus mori* Yokoyama (all Acari: Tetranychidae)] that are pest species on Japanese pear [*Pyrus serotina* Rehder (Rosaceae)]. *Scolothrips takahashii* females consumed more prey and laid more eggs in *A. viennensis* and *T. urticae* egg patches than in *P. mori* egg patches. Females also left *P. mori* egg patches sooner than they left other egg patches even at high prey density. Predation and oviposition of *S. takahashii* in a prey patch were greatly enhanced by the complicated webs produced by *A. viennensis*. *Stethorus japonicus* females consumed significantly more prey and laid more eggs in *A. viennensis* egg patches than in *P. mori* egg patches, with intermediate values in *T. urticae* egg patches, reflecting the quality of each spider mite species as prey. *Oligota kashmirica benefica* females consumed more prey and laid more eggs in *A. viennensis* and *T. urticae* egg patches than in *P. mori* egg patches, particularly at high prey density. However, predation and oviposition by *O. kashmirica benefica* increased greatly with increasing prey density, even in *P. mori* egg patches, indicating that prey density was the most important factor in predation and oviposition by this species. These results are discussed in relation to the potential effect of each predator on the suppression of different spider mite species on Japanese pear.

Introduction

On deciduous fruit trees such as Japanese pear [*Pyrus serotina* Rehder (Rosaceae)], a wide variety of genera and species of spider mites occur, including *Amphitetranychus viennensis* (Zacher), *Tetranychus urticae* Koch, *Panonychus citri* (McGregor), and *Panonychus mori* Yokoyama (all Acari: Tetranychidae), and they can cause serious damage in Japan (Ehara & Shinkaji, 1975). These spider mites are difficult to control solely by means of agrochemicals as

in other horticultural crops, because of their ability to rapidly develop resistance to various insecticides. In the past few decades, pesticide applications have gradually been replaced by the use of multiple-mating-disruption technology to control major lepidopteran pests in deciduous fruit tree orchards (e.g., Izawa et al., 2000). This reduction in pesticides has also led to increased populations of native natural enemies of spider mites in the affected orchards (e.g., Izawa et al., 2000). Thus, the use of biological control agents against spider mites has become more feasible. To make effective use of this approach to control spider mites, it therefore would be necessary to evaluate the influence of each natural enemy on different spider mite species.

Three predacious insects native to Japan, namely, *Scolothrips takahashii* Priesner (Thysanoptera: Thripidae), *Stethorus japonicus* H. Kamiya (Coleoptera: Coccinellidae),

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and *Oligota kashmirica benefica* Naomi (Coleoptera: Staphylinidae), are considered to be prospective natural enemies of spider mites because of their voracity and reproductive capacity (Shimoda et al., 1993; Gotoh et al., 2004a,b; Mori et al., 2005). These insects are specialized predators of spider mites, but have wide prey ranges among spider mite species (Chazeau, 1985; Amano, 1996). In Japanese pear orchards, they often occur simultaneously irrespective of the dominant spider mite species (Takahashi et al., 2001; Kishimoto, 2002). However, Kishimoto & Adachi (2006) found that the above-mentioned predators could prey on *A. viennensis* and *T. urticae* even when densities of these spider mites were low, although they suppressed *P. citri* only at high prey density. These observations suggest that different predators are likely to respond differently depending on spider mite species and their densities.

The responses of predators to prey are affected by products and residues associated with the prey, as well as by prey density and quality. Spider mites are characterized by their web-spinning behavior, but the thread structures vary among species: for example, *Amphitetranynchus* and *Tetranychus* species produce complicated webs, whereas *Panonychus* species never construct webs and use threads only as lifelines and egg covers (Saito, 1983). In phytoseiid mites, which are also important predators of spider mites, foraging behaviors are affected by the complicated webs: they hinder most phytoseiid mites from foraging (e.g., Takafuji & Chant, 1976; Osakabe, 1988), but encourage attack by some phytoseiid mites that are specialist or selective predators of *Tetranychus* species (e.g., Hoy & Smilanick, 1981). In contrast, the effects of web structure on predacious insects remain to be clarified.

In this study, we attempted to clarify the mechanisms that determine how well the three above-mentioned predacious insect species suppress various spider mite species on Japanese pear. To do so, we first compared predation and oviposition by these insects during their residence in egg patches of each spider mite species. Then, we examined the effects of complicated webs on the predation and oviposition by the predacious insects.

Materials and methods

Predacious insects and prey spider mites

The predatory insects used in this study (*S. takahashii*, *S. japonicus*, and *O. kashmirica benefica*) were collected from a Japanese pear orchard at the National Institute of Fruit Tree Science, Tsukuba, Japan (36°3'N, 140°6'E), in September 1997. They were reared on lima bean [*Phaseolus lunatus* L. (Fabaceae)] leaf discs populated by sufficient prey (*T. urticae*) in the laboratory at 20 °C and

L16:D8 photoperiod. Each bean leaf was placed on a pad of cotton wool saturated with water in a Petri dish (9 cm in diameter × 1.4 cm in depth). The leaf discs were then placed in screened containers (30 × 20 × 6 cm) to prevent the predators from flying away.

Three species of spider mites from different genera (*A. viennensis*, *T. urticae*, and *P. mori*) were chosen as prey. *Panonychus citri* was the dominant species in this genus in pear orchards in a previous study (Kishimoto, 2002). However, this species was inconvenient for experimental use, because its population increase on pear leaves does not occur until mid summer (Gotoh & Kubota, 1997). Thus, we replaced it by a closely related species (*P. mori*) that was formerly considered to be the diapausing strain of *P. citri* (Ehara & Gotoh, 1992). *Panonychus mori* is easier to be reared on Japanese pear leaves in the laboratory than *P. citri*. *Panonychus mori* was collected as overwintering eggs from a Japanese pear orchard in Daiei, Tottori Prefecture (35°29'N, 133°45'E), in March 1998. *Tetranychus urticae* and *A. viennensis* were collected from Japanese pear orchards at the National Institute of Fruit Tree Science, Tsukuba, in August and October 1997, respectively. Because Japanese pear is a deciduous tree, we cannot collect abundant Japanese pear leaves for rearing spider mites throughout the year, in particular, in autumn and winter. Thus, *A. viennensis* and *P. mori*, which were oligophagous species, were reared on Japanese pear leaf discs at 23 °C and L16:D8 photoperiod, whereas *T. urticae*, which was a polyphagous species, was reared on lima bean leaf discs.

Evaluation of predation and oviposition by predacious insects in prey egg patches

We used Japanese pear leaf discs to host the prey patches, and placed only one species of spider mite on each leaf disc. We prepared patches with low and high prey density for each predator species (Table 1). The numbers of eggs in the low- and high-density prey patches were determined based on the quantity of prey consumed during 0.5 days and 2 days, respectively, by an adult female of each predator species (Nakagawa, 1988; Shimoda et al., 1993; Gotoh et al., 2004a). Prey patches were prepared as follows: 5–100

Table 1 Numbers of spider mite eggs per prey patch for three predacious insect species

Predacious species	Low prey density patch	High prey density patch
<i>Scolothrips takahashii</i>	30	120
<i>Stethorus japonicus</i>	150	600
<i>Oligota kashmirica benefica</i>	70	300

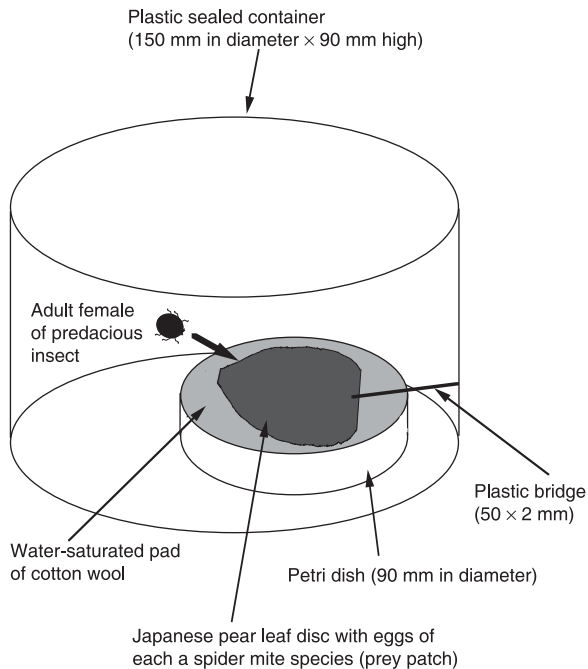


Figure 1 Experimental set-up used for monitoring the responses of predacious insect species to prey patches of spider mites.

adult females of each spider mite species, depending on the number of eggs needed per prey patch (Table 1), were allowed to oviposit on Japanese pear leaf discs at 25 °C and L16:D8 photoperiod. After 24 h, the females were removed but the webs and threads were left intact, and the numbers of eggs were adjusted carefully so as not to damage the webs and threads. We then set the leaf disc in a screened plastic container (15 cm in diameter × 9 cm in depth), and connected the edge of the patch to the wall of the container with a plastic bridge (50 × 2 mm in diameter; Figure 1). After the predator left a patch by crossing the bridge, it reached the wall of the container and usually walked upwards. Thus, we could prevent the predator from returning to the patch soon. We introduced one mated adult female of each predator species (about 3–7 days after start of oviposition) into a prey patch. Then, we set the container in a climate-controlled room at 25 °C. Every 30 min, we monitored whether the predator had left the prey patch, and measured the residence time from the introduction of the predator until the predator left the patch. Using a stereomicroscope, we then counted the number of prey that had been consumed and the number of eggs that had been deposited during the predator's residence in the patch. For counting the number of eggs of *S. takahashii*, we set the leaf directly on a stereomicroscope and observed through transmitted light, because this species deposit the

eggs into the leaf tissue. Each experiment was replicated 21 times.

The mean residence time and the mean numbers of prey consumed and eggs deposited were analyzed using two-way multiple analysis of variance (MANOVA) with two factors (prey species and prey density). We performed subsequent univariate two-way ANOVAs for individual responses. As interactions between the two factors were not significant in the results of a MANOVA on the responses of *S. takahashii* and *S. japonicus*, and in the result of an ANOVA on each response of *O. kashmirica benefica* ($P > 0.05$; Tables 2 and 3), we performed pairwise comparisons of the means using the Tukey–Kramer honestly significant difference (HSD) test for the prey species and one-way ANOVA for prey density independently. Statistical tests were conducted using JMP version 5.0.1 J (SAS Institute, 2002). To stabilize the variance, residence time was \ln transformed, whereas numbers of prey consumed and eggs deposited were $\sqrt{(x + 0.5)}$ transformed, as recommended by Yamamura (1999).

Effects of complicated spider mite webs on predation and oviposition by predacious insects

To evaluate the effects of the complicated webs produced by spider mites on predation and oviposition by each predator, we covered *P. mori* egg patches (which have no web cover in nature) with the complicated webs produced by *A. viennensis*. Adult females of *P. mori* were allowed to oviposit on Japanese pear leaf discs at 25 °C and L16:D8 photoperiod. After 24 h, the females were removed and the number of eggs on the leaf disc was adjusted to a low prey

Table 2 Results of a two-way multiple analysis of variance (MANOVA) testing the effects of prey species and prey density on the responses of (A) *Scolothrips takahashi*, (B) *Stethorus japonicus*, and (C) *Oligota kashmirica benefica*

	d.f.	Wilks' λ	F	P
A. <i>Scolothrips takahashii</i>				
Prey species	6,236	0.592	11.795	<0.001
Prey density	3,118	na ¹	23.156	<0.001
Prey species × density	6,236	0.902	2.076	0.057
B. <i>Stethorus japonicus</i>				
Prey species	6,236	0.248	26.934	<0.001
Prey density	3,118	na ¹	17.300	<0.001
Prey species × density	6,236	0.919	1.695	0.123
C. <i>Oligota kashmirica benefica</i>				
Prey species	6,236	0.751	6.046	<0.001
Prey density	3,118	na ¹	66.179	<0.001
Prey species × density	6,236	0.863	3.018	0.007

¹Not applicable.

Table 3 Results of a two-way analysis of variance (ANOVA) testing the effects of prey species and prey density on the responses of (A) *Scolothrips takahashii*, (B) *Stethorus japonicus*, and (C) *Oligota kashmirica benefica* in terms of residence time, number of prey consumed, and number of eggs laid

	Residence time			Number of prey consumed			Number of eggs deposited		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
A. <i>Scolothrips takahashii</i>									
Prey species	2,120	31.281	<0.001	2,120	12.794	<0.001	2,120	18.880	<0.001
Prey density	1,120	27.941	<0.001	1,120	55.842	<0.001	1,120	24.455	<0.001
B. <i>Stethorus japonicus</i>									
Prey species	2,120	36.561	<0.001	2,120	19.175	<0.001	2,120	84.532	<0.001
Prey density	1,120	18.933	<0.001	1,120	42.765	<0.001	1,120	36.718	<0.001
C. <i>Oligota kashmirica benefica</i>									
Prey species	2,120	14.683	<0.001	2,120	3.877	0.023	2,120	10.172	<0.001
Prey density	1,120	101.806	<0.001	1,120	193.647	<0.001	1,120	107.774	<0.001
Prey species*density	2,120	1.136	0.325	2,120	2.957	0.056	2,120	1.558	0.215

density using the densities specified in Table 1. Then, we introduced newly emerged adult females of *A. viennensis* onto the leaf discs. Gotoh & Takayama (1992) reported that newly emerged females of *A. viennensis* do not begin laying eggs within 24 h, and only produce their complicated webs on the leaves. To control the amount of web, the numbers of *A. viennensis* adult females introduced per leaf disc equaled those corresponding to low-density prey patches for each predator. After 24 h, the *A. viennensis* females were carefully removed, without damaging their webs. Because predation and oviposition by *S. takahashii* greatly increased in the above patch, we tested whether the webs or some effect of infestation, such as chemical traces left by the mites, was the primary factor in this response by preparing additional patches for this predator. These additional patches consisted of leaves with *P. mori* eggs that were infested by releasing *A. viennensis* females onto the egg patches for 24 h and then removing both females and their webs. We introduced one mated adult female of each predator species into the prey patches (Figure 1), and then recorded their residence time and the numbers of prey consumed and eggs deposited, in the same manner as described above. Each experiment was replicated 21 times.

The results in these 'false' patches were compared with those in the original patches of *A. viennensis* eggs (with the complicated webs) and *P. mori* eggs (with no webs) using one-way MANOVA and one-way ANOVA. Then, we performed pairwise comparisons of the means using the Tukey–Kramer HSD test. All statistical analyses used JMP version 5.0.1 J (SAS Institute, 2002). To stabilize the variance, the data were transformed using $\ln x$ or $\sqrt{(x + 0.5)}$, as described above.

Results

Predation and oviposition by predacious insects in prey patches

In all three predacious insect species, both prey species and prey density were found to have large effects both on the response of females in the MANOVA (Table 2) and on all individual responses (i.e., residence time, predation, and oviposition) in the ANOVA (Table 3). However, the effects of prey species and prey density on individual responses differed among the three predacious insects (Figure 2).

In *S. takahashii*, females stayed longer, consumed more prey, and laid more eggs in *A. viennensis* or *T. urticae* egg patches than in *P. mori* egg patches, particularly at high prey density (Figure 2A). In addition, females in *A. viennensis* or *T. urticae* egg patches greatly increased their residence time, prey consumption, and oviposition with increasing prey density, whereas prey density had little effect on the response of females in *P. mori* egg patches (Figure 2A).

In *S. japonicus*, females stayed longer, consumed more prey, and laid more eggs in *A. viennensis* egg patches than in *P. mori* egg patches at each prey density level, with intermediate values in *T. urticae* egg patches (Figure 2B). Females in *A. viennensis* or *T. urticae* egg patches also greatly increased their residence time, prey consumption, and oviposition with increasing prey density (Figure 2B). In contrast, values of all three parameters were significantly lower in *P. mori* egg patches, and prey density had only a slight effect on the responses in patches of this species (Figure 2B).

In *O. kashmirica benefica*, females stayed longer, consumed more prey, and laid more eggs in *A. viennensis* or/and *T. urticae* egg patches than in *P. mori* eggs patches when patch density was high (Figure 2C). When patch density

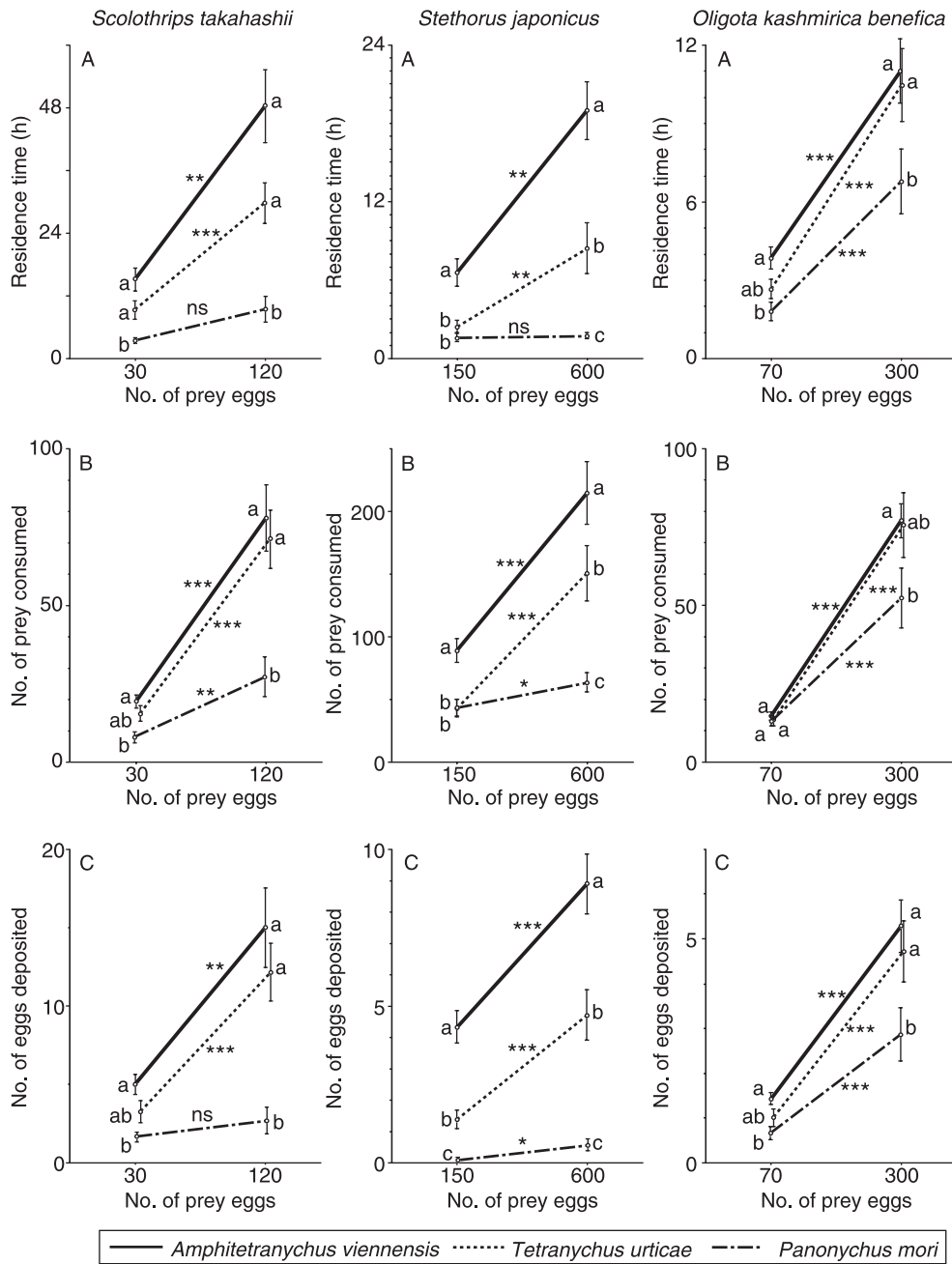


Figure 2 The response of three predacious insect species, *Scolothrips takahashii*, *Stethorus japonicus*, and *Oligota kashmirica benefica*, in prey patches of three spider mite species, *Amphitetranychus viennensis*, *Tetranychus urticae*, and *Panonychus mori*. (A) Residence time in a prey patch. (B) Number of prey consumed. (C) Number of eggs deposited during residence of the predator in the patch. Each experiment was replicated 21 times. Data represent means \pm SE. At each prey density, points labeled with different letters differ significantly among the spider mite species [Tukey–Kramer honestly significant difference (HSD) test: $P < 0.05$]. In each prey species, differences between the low and high prey densities were determined using one-way analysis of variance (ANOVA) (ns, not significant, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

was low, only females in *A. viennensis* egg patches stayed significantly longer and laid more eggs than those in *P. mori* egg patches (Figure 2C). However, unlike females of *S. takahashii* and *S. japonicus*, the effects of prey density

on female responses were similar among prey species: residence time, prey consumption, and oviposition all increased greatly with increasing prey density, regardless of the prey species examined (Figure 2C).

Effects of complicated spider mite webs on predation and oviposition by predacious insects

Residence time, predation, and oviposition by *S. takahashii* females increased significantly in *P. mori* egg patches containing complicated webs produced by *A. viennensis* compared to the original *P. mori* egg patches (with no webs), and nearly equal to the corresponding values for *A. viennensis* egg patches (Figure 3A). In contrast, residence time, predation, and oviposition by *S. takahashii* females in *P. mori* egg patches where *A. viennensis* webs had been removed were significantly lower than in *A. viennensis* egg patches and were similar to (and with the exception of oviposition, not significantly different from) those in the *P. mori* egg patches (Figure 3A). These results indicated that the response of *S. takahashii* in a prey patch was enhanced by the presence of the complicated webs produced by *A. viennensis*.

The complicated webs of *A. viennensis* had a slight effect on the responses of *S. japonicus* females. Residence time, predation, and oviposition in *P. mori* egg patches with *A. viennensis* webs were significantly lower than in *A. viennensis* egg patches (Figure 3B). Residence time and predation in *P. mori* egg patches with *A. viennensis* webs were similar to those in *P. mori* egg patches, whereas more eggs were laid in the former patches than in the latter (Figure 3B).

The complicated webs of *A. viennensis* did not significantly affect the responses of *O. kashmirica benefica* females: residence time, prey consumption, and oviposition in *P. mori* egg patches with *A. viennensis* webs did not differ significantly from the corresponding values in *P. mori* egg patches, and residence time and oviposition were significantly lower than in *A. viennensis* egg patches (Figure 3C).

Discussion

The effects of prey species and prey density on predation and oviposition differed among the three predacious insect species. Our results indicated that the relative importance of factors affecting the response in prey patches differed markedly among predators. In *S. takahashii*, prey species was the most important factor that affected predation and oviposition in prey patches: values were higher in *A. viennensis* and *T. urticae* than in *P. mori* egg patches regardless of prey density. We also showed that predation and oviposition by *S. takahashii* in a prey patch were enhanced by the presence of complicated webs produced by *A. viennensis*. In contrast, Kishimoto (2003) found little difference in prey quality of these spider mite species for *S. takahashii*, because females of this species developed and oviposited well regardless of the prey species examined.

These results suggest that *S. takahashii* responded strongly to complicated webs rather than to the prey eggs themselves, as has also been shown in *Neoseiulus womersleyi* (Furuichi et al., 2005).

Prey species was also the most important factor for *S. japonicus*. Prey consumption and oviposition were higher in egg patches of *A. viennensis* than of *P. mori*, and were intermediate in *T. urticae* egg patches, and prey density in *P. mori* egg patches had little effect on predation and oviposition. Kishimoto (2003) showed that prey quality of each spider mite species differed markedly for *S. japonicus*: *A. viennensis* was a superior prey for both development and oviposition, whereas *P. mori* was inferior. In particular, most larvae of *S. japonicus* reared on *P. mori* eggs died during the first stadium (Kishimoto, 2003). In addition, we showed that complicated webs of *A. viennensis* slightly affected predation and oviposition by *S. japonicus* females. These results indicated that the difference in predation and oviposition by *S. japonicus* in a prey patch mainly reflects the quality of each spider mite species as prey.

For *O. kashmirica benefica*, unlike for *S. takahashii* and *S. japonicus*, prey density greatly affected predation and oviposition in prey patches of all three prey species. Even in *P. mori* egg patches, which produced lower predation and oviposition than *A. viennensis* and *T. urticae* egg patches, prey consumption and oviposition increased greatly with increasing prey density. Kishimoto (2003) showed that most larvae of *O. kashmirica benefica* reared on *P. mori* eggs died during the first stadium. Thus, this factor may affect oviposition behavior of *O. kashmirica benefica* in *P. mori* egg patches. However, the prey quality of each spider mite species for *O. kashmirica benefica* females was not significantly different, and *O. kashmirica benefica* larvae reared on *P. mori* nymphs developed as well as those reared on *A. viennensis* and *T. urticae* nymphs in a previous study (Kishimoto, 2003). In addition, we showed that the complicated webs produced by *A. viennensis* had no effect on the response of females of *O. kashmirica benefica*. These results indicate that prey density is the most important factor for *O. kashmirica benefica* predation and oviposition.

Our study revealed the characteristics of each predacious insect species as a natural enemy for each of the three spider mite species. *Scolothrips takahashii* would be more effective in suppressing spider mites that produce complicated webs, such as *Amphitetranychus* spp. and *Tetranychus* spp., than spider mites such as *Panonychus* spp. that produce no webs. *Stethorus japonicus* is also more effective in suppressing *A. viennensis* and *T. urticae* than in suppressing *P. mori*. In contrast, *O. kashmirica benefica* seems to be an effective predator at high densities of spider mites rather than against particular spider mite species, as has

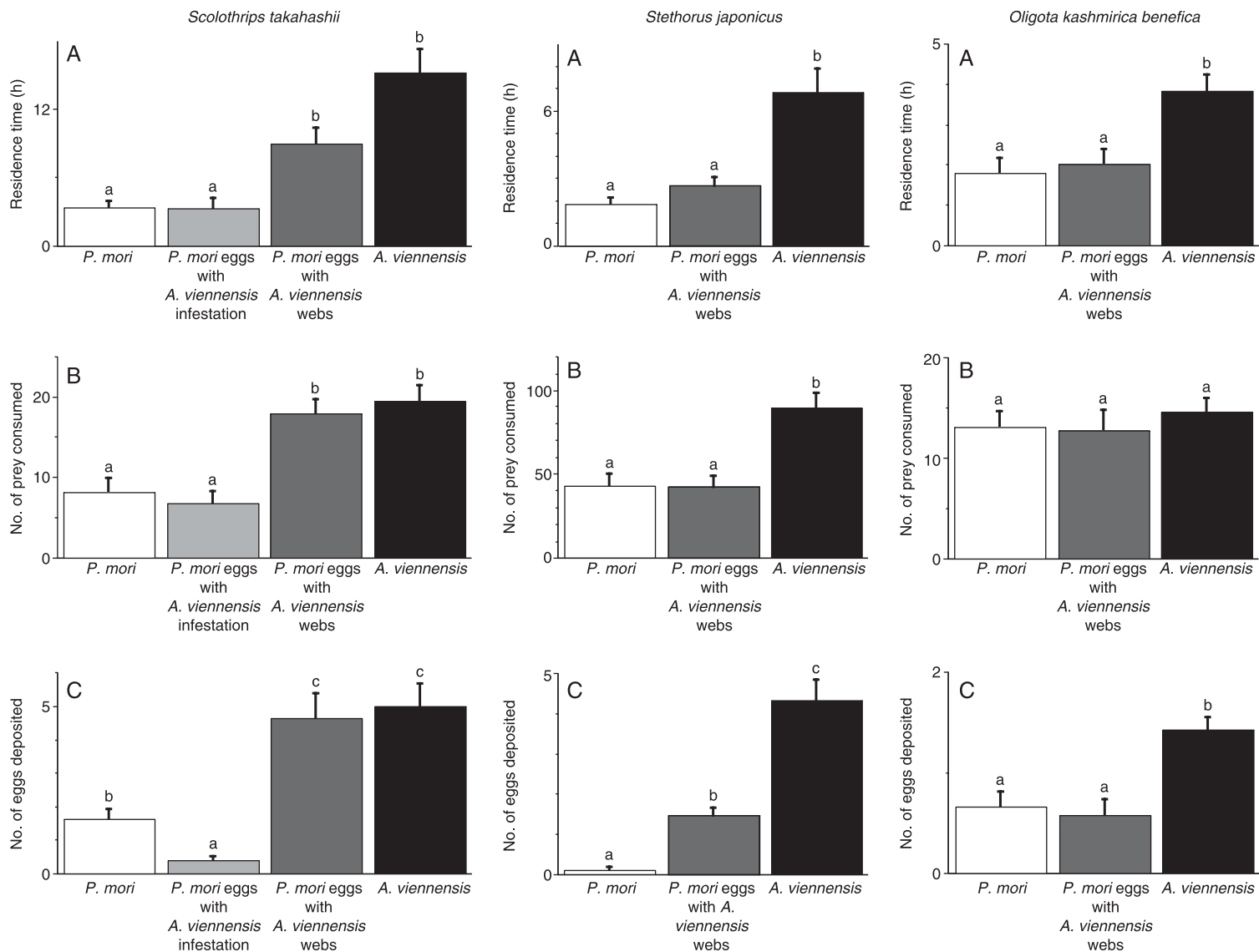


Figure 3 Effects of the complexity of the webs produced by spider mites, *Amphitetranychus viennensis*, on the responses of three predacious insect species, *Scolothrips takahashii*, *Stethorus japonicus*, and *Oligota kashmirica benefica*, in a *Panonychus mori* prey patch. (A) Residence time in a prey patch. (B) Number of prey consumed. (C) Number of eggs deposited during the residence of the predator in the patch. Each experiment was replicated 21 times. Within a graph, bars labeled with different letters differ significantly [Tukey–Kramer honestly significant difference (HSD) test following one-way multiple analysis of variance (MANOVA) and one-way ANOVA: $P < 0.05$].

earlier been suggested by Shimoda et al. (1993). *Panonychus citri* populations tend to reach a higher density than those of *A. viennensis* or *T. urticae* on Japanese pear even when predacious insects are abundant (Kishimoto, 2002). Kishimoto & Adachi (2006) demonstrated that predacious insects responded swiftly to and suppressed *A. viennensis* and *T. urticae* even when these spider mites were present at low densities, and that these insects responded to *P. citri* only when the spider mite density became high. Nevertheless, the predators, and in particular *Oligota* spp., eventually caused an abrupt decrease in *P. citri*. The results of the present study are consistent with previous field observations and experiments, and they further clarify the role of each predacious insect species in the suppression of different spider mite species. In Japan, since the 1970s, *T. urticae* has been a dominant and economically important pest species in conventionally controlled Japanese pear orchards, where natural enemies were few (Uchida, 1982; Takafuji & Kamibayashi, 1984; Gotoh, 1997). On the other hand, this study suggests that *Panonychus* species, such as *P. citri* and *P. mori*, may be abundant on Japanese pear when these predacious insects are used for biological control. Therefore, it is necessary to find other effective natural enemies for *Panonychus* species.

The three predacious insect species of the present study are known to be specialist predators of spider mites (Amano, 1996), and often occur simultaneously with spider mites on Japanese pear trees (Kishimoto, 2002). They are known to reach infested trees by flying from neighboring orchards or from surrounding vegetation, such as windbreaks and weeds near the orchards (Shimoda & Takabayashi, 2001a; Takahashi et al., 2001). However, how these predacious insects locate a patch of a spider mite species is still unclear, although *S. takahashii* and *O. kashmirica benefica* have been shown to respond to volatiles emitted by plants infested with *T. urticae* (Shimoda et al., 1997; Shimoda & Takabayashi, 2001b). Thus, to fully understand the interactions of each spider mite species and its predators on Japanese pear, further studies on the foraging behavior of the predators will be needed.

The effects of the complicated webs produced by *A. viennensis* differed among predators. These webs greatly enhanced the response of *S. takahashii* and considerably enhanced oviposition by *S. japonicus*, suggesting that complicated webs provide some benefits for these species. In contrast, neither positive nor negative effects of the webs were observed in the response of *O. kashmirica benefica*. In phytoseiid species, and especially in specialist or selective predators of *Tetranychus* spider mites, complicated webs are known to function as benefits by enhancing the foraging profitability of the predators and their offspring (Hoy & Smilanick, 1981; Gerson, 1985), by providing a more

favorable microclimate (Gerson, 1985) and by providing shelter from other predators (Roda et al., 2000). Thus, further studies will be needed to clarify the differences in the role of complicated webs for the predator species involved in the present study.

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