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Larvae of two ladybirds, *Phymatosternus lewisii* and *Scymnus posticalis* (Coleoptera: Coccinellidae), exploiting colonies of the brown citrus aphid *Toxoptera citricidus* (Homoptera: Aphididae) attended by the ant *Pristomyrmex pungens* (Hymenoptera: Formicidae)

Shuji Kaneko[*,†]

Shizuoka Prefectural Citrus Experiment Station; Shimizu, Shizuoka 424–0905, Japan

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Abstract

The distribution of two small coccinellids, *Phymatosternus lewisii* and *Scymnus posticalis*, across colonies of the aphid *Toxoptera citricidus* in relation to ant-attendance of the colonies and ant species, behavioral interactions between the coccinellid larvae and ants, and the overlap in the larval distribution of the two coccinellids were examined in a citrus grove in Japan. *P. lewisii* larvae were found frequently in aphid colonies attended by the ant *Pristomyrmex pungens* but rarely in colonies attended by another ant, *Lasius japonicus*, and in ant-excluded colonies. A number of *S. posticalis* larvae were also recorded in *P. pungens*-attended colonies and some larvae in ant-excluded colonies. A few *P. lewisii* adults were noted only in *P. pungens*-attended colonies, whereas some *S. posticalis* adults were observed in ant-excluded colonies. In most encounters, *P. pungens* workers tapped *P. lewisii* larvae with their antennae but showed no aggressive behavior; otherwise, *P. pungens* workers ignored the larvae. *P. pungens* exhibited the same behavior when encountering *S. posticalis* larvae. The proportion of *P. pungens*-attended aphid colonies where the larvae of both coccinellids occurred did not significantly differ from the probability of both coccinellids occurring in the same colonies given their random distribution across the colonies. Thus, larvae of the two coccinellids exploited aphid colonies attended by a particular ant, *P. pungens*, and the larval distribution of the two species may be independent of each species.

Key words: *Phymatosternus lewisii*; *Scymnus posticalis*; aphids; ant-attendance; behavioral interaction

INTRODUCTION

Ants attending honeydew-producing homopterans heavily attack and repel many species of arthropod predators and parasitoids that approach ant-attended homopteran colonies (e.g., Bartlett, 1961; Banks, 1962; Bristow, 1984; Cushman and Whitham, 1989; Vinson and Scarborough, 1991; Jiggins et al., 1993; Itioka and Inoue, 1996). However, some species of predators, chiefly their larvae, and parasitoids are able to exploit the homopterans that ants are guarding, through behavioral, chemical and/or morphological adaptations to avoid ant aggression (Pontin, 1959; Eisner et al., 1978; Takada and Hashimoto, 1985; Majerus, 1989; Völkl, 1992, 1995; Völkl and Vohland, 1996; Sloggett et al., 1998; Völkl and Mackauer, 2000; Barzman and Daane, 2001; Kaneko, 2002). It can be expected that two or more species of "ant-adapted" predators and parasitoids utilize ant-attended colonies of a single homopteran species. Recently, Kaneko (2007) indicated that a predator species and a parasitoid species foraged frequently in ant-attended colonies of an aphid, and experimentally revealed a negative effect of the predator on emerging parasitoid numbers in ant-attended aphid colonies. On the other hand, the co-occurrence of multiple predator species in ant-attended homopteran colonies has not yet been demonstrated. In addition, interspecific relationships between ant-adapted predators have not been examined. Furthermore, Kaneko (2007) suggests that

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[*] E-mail: kaneshu@ja2.so-net.ne.jp

[†] Present address: Shizuoka Prefectural Agricultural Experiment Station, Tomigaoka, Iwata 438–0803, Japan

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the strength of the interaction between the predator and the parasitoid in ant-attended aphid colonies is affected by ant species attending aphids because the level of aggressiveness towards the predator and the parasitoid, and the resulting efficiency of excluding enemies differ between the attending ant species, as documented in other systems (e.g., Addicott, 1979; Buckley and Gullan, 1991; Itioka and Inoue, 1999; Kaneko, 2003a). Therefore, the abundance of ant-adapted predators and their interrelationship may vary between homopteran colonies attended by different ant species.

Colonies of the brown citrus aphid *Toxoptera citricidus* on young citrus shoots are often attended by one of two species of ants, *Lasius japonicus* and *Pristomyrmex pungens* (Kaneko, 2003b). The two ants exclude many species of large predators such as coccinellids, chrysopids and syrphids from aphid colonies that they attend through aggressive behavior, and differ in exclusion ability (Kaneko, 2003a, b). Two species of small ladybird beetles, *Phymatosternus lewisii* and *Scymnus posticalis* (both Coleoptera: Coccinellidae), prey on the aphid *T. citricidus* (Kaneko, 2003b). Thus, in this system (Fig. 1), we can examine the occurrence of the two predator species in aphid colonies attended by different ant species and the relationship between these predators in ant-attended colonies.

In this paper, it is first shown that larvae of the two coccinellids, *P. lewisii* and *S. posticalis*, exploit *T. citricidus* colonies attended by a particular ant, *P. pungens*, by describing the distribution of larvae and adults of the two coccinellids across *T. citricidus* colonies in relation to the presence of ants attending the colonies and the ant species, *P. pungens* and *L. japonicus*. Behavioral interactions between larvae of the two coccinellids and attending workers of the ant *P. pungens* in their encounters in aphid colonies are then represented. Finally, the interrelationship between the two coccinellids is assessed by analyzing the overlap in the larval distribution of the two species across aphid colonies attended by *P. pungens*.

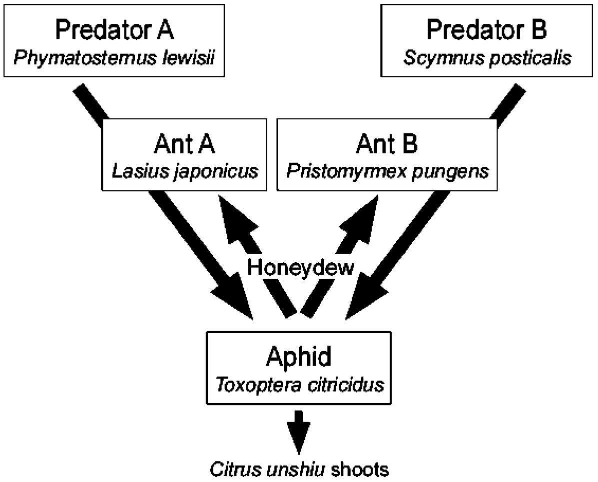

Fig. 1. The studied system consisting of the aphid *Toxoptera citricidus* on citrus shoots, the two ants attending the aphid, *Lasius japonicus* and *Pristomyrmex pungens*, and the two coccinellid predators attacking the aphid, *Phymatosternus lewisii* and *Scymnus posticalis*.

MATERIALS AND METHODS

Study site and organisms. Field experiments and observations were carried out in a no-pesticide grove (approximately 700 m^2 in area) cultivating Satsuma mandarin, *Citrus unshiu*, located in Shizuoka Prefectural Citrus Experiment Station in Shimizu City, central Japan in 1998. The grove supported 25 twenty-year-old trees and 20 ten-year-old trees. No pesticide had been applied there for 20 years.

The brown citrus aphid *T. citricidus* has a restricted host range, exclusively infesting citrus spp. (Moritsu, 1983). It feeds on the phloem sap of young citrus shoots and forms dense colonies that consist of nymphs and adults, chiefly on the lower surface of the expanding leaves and the apical portion of the stems (Korenaga et al., 1992).

Two species of ants, *L. japonicus* (formerly described as *L. niger* in Japan) and *P. pungens*, actively attended *T. citricidus* colonies in the citrus grove during the summer (Kaneko, 2003b). Since the co-occurrence of the two ants in a single aphid colony was never found, the effect of each ant species could be assessed independently.

Larvae and adults of the two species of small coccinellids, *P. lewisii* and *S. posticalis*, attacked *T. citricidus* in the citrus grove. Both coccinellids are common and widely distributed in Japan, except the Ryukyu Islands for both species and Hokkaido Island for *P. lewisii* (Kurosawa et al., 1985). The adult body length is 2.9–3.7 mm in *P. lewisii* and 1.9–2.8 mm in *S. posticalis*. In these coccinellids, the larvae have peculiar features: *P. lewisii* larvae have a flat, broad oval-shaped body, with the dorsum weakly convex and the entire outer margin very thin, i.e., coccid-like shape (Sasaji and Tsubokawa, 1983), and the dorsum of *S. posticalis* larva is covered densely with fleecy, waxy secretions (Sasaji, 1998).

Distribution of the two coccinellids. Thirty-seven citrus trees were selected in the grove, including trees on which workers of either ant species were foraging, on July 10, 1998. The following day, a single growing shoot on each tree was randomly chosen and *T. citricidus* colonies were artificially established on the shoots, using aphids that had been collected in the field in June and had been reared on potted *C. unshiu* trees in a plant-growth chamber. Introduction of the aphids onto the chosen shoots followed the procedure by Kaneko (2002). The initial number of aphids was counted on July 17 and each shoot was infested with 60–200 aphids. The aphids feeding on a single shoot were regarded as forming a single colony. For ant-exclusion treatments, 17 of the 37 trees were randomly selected. A 5-cm-wide band of sticky barrier (tanglefoot) was applied around the trunk of each selected tree and any lower branches touching the ground were removed, so that no ant could reach the aphid colonies introduced on the trees (hereafter called ant-excluded aphid colonies). The trunks of the remaining trees were left untreated, so that ants of either species could freely visit the aphid colonies introduced onto the trees; *L. japonicus* workers attended the aphid colonies on eight trees and *P. pungens* attended the aphid colonies on 12 other trees (hereafter called *L. japonicus*-attended or *P. pungens*-attended colonies). The species of attending ants did not change on these trees during the experimental period. From July 18 to August 17, at intervals of 2–3 days, the number of foraging or feeding larvae of the two coccinellids, *P. lewisii* and *S. posticalis*, and adults of the two coccinellids in each of the aphid colonies were counted.

Behavioral interactions between coccinellid larvae and ants. Behavioral interactions between honeydew-collecting workers of the ant *P. pungens* and foraging larvae (mainly second- or third-instar larvae) of the coccinellids *P. lewisii* and *S. posticalis* were observed in ant-attended aphid colonies. When a coccinellid larva was found, its behavior was recorded during two to three encounters with ants. During encounters with a foraging or feeding coccinellid larva in aphid colonies, the ants displayed the following two distinct behaviors: *ignoring*—the ant made physical contact with the coccinellid but otherwise did not respond to it; and *antennal tapping*—the ant made physical contact with the coccinellid and tapped the coccinellid with its antennae for a short time.

Coccinellid larvae responded to an encountered ant with the following two different behaviors: *ignoring*—the coccinellid continued its activities, foraging or feeding, after contact with the ant; and *cowering*—the coccinellid pressed its body tightly against the plant surface when touched by the ant and then showed no movement (remained motionless).

Overlaps in the larval distribution of the two coccinellids. The degree to which larvae of the two coccinellids, *P. lewisii* and *S. posticalis*, overlapped in their distributions across *P. pungens*-attended aphid colonies was analyzed. First, the proportion of the number of *P. pungens*-attended colonies in which larvae of either or both of the two coccinellids were present to the total number of surviving *P. pungens*-attended colonies was calculated on each monitoring date. The expected probability of both coccinellids occurring in the same *P. pungens*-attended colonies, given that the two species were randomly distributed across *P. pungens*-attended colonies, was defined and calculated as the product of the proportion of *P. pungens*-attended colonies in which each coccinellid species was present. Finally, the expected probability was compared with the proportion of colonies in which both coccinellids actually co-occurred on each date by Fisher's exact test.

RESULTS

Distribution of the two coccinellids

Many larvae of the coccinellid *P. lewisii* were found in *P. pungens*-attended aphid colonies, with a peak number in the middle of the experimental period, whereas larvae were rarely noted in *L. japonicus*-attended colonies and no larvae in ant-excluded colonies (Fig. 2a). A number of larvae of another coccinellid, *S. posticalis*, were also observed in *P. pungens*-attended colonies throughout the experiment, and the larvae were recorded in small numbers in ant-excluded colonies during the first half of the experiment and few larvae in *L. japonicus*-attended colonies (Fig. 2b).

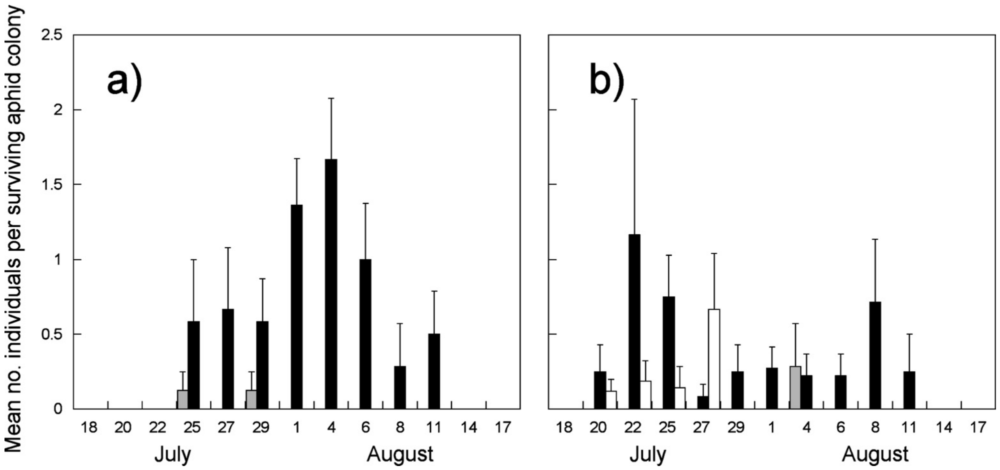

Fig. 2. Changes in the mean number of foraging larvae of the two coccinellids, *Phymatosternus lewisii* (a) and *Scymnus posticalis* (b), per surviving colony of the aphid *Toxoptera citricidus* through time in *Lasius japonicus*-attended (▨), *Pristomyrmex pungens*-attended (■) and ant-excluded (□) colonies. Vertical bar illustrates + 1 SE.

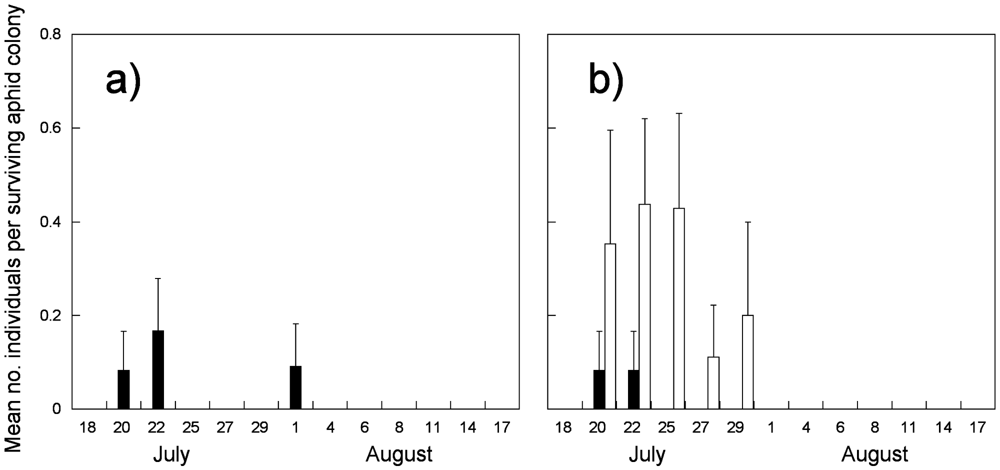

Fig. 3. Changes in the mean number of foraging adults of the two coccinellids, *Phymatosternus lewisii* (a) and *Scymnus posticalis* (b), per surviving colony of the aphid *Toxoptera citricidus* through time in *Lasius japonicus*-attended (▨), *Pristomyrmex pungens*-attended (■) and ant-excluded (□) colonies. Vertical bar illustrates + 1 SE.

A few *P. lewisii* adults were found only in *P. pungens*-attended aphid colonies (Fig. 3a), whereas some *S. posticalis* adults were noted in ant-excluded colonies and a few adults in *P. pungens*-attended colonies (Fig. 3b).

Thus, many larvae of *P. lewisii* and *S. posticalis* exploited aphid colonies attended by *P. pungens* workers.

Behavioral interactions between coccinellid larvae and ants

A total of 33 encounters between honeydew-collecting *P. pungens* workers and foraging or feeding *P. lewisii* larvae were recorded in aphid colonies attended by the ants. In 10 (30%) encounters, an ant ignored a *P. lewisii* larva and the larva also ignored the ant, continuing its activities. In 22 (67%) encounters, an ant tapped a *P. lewisii* larva with its antennae and showed no aggressive behavior, and the larva ignored the ant. In one (3%) encounter, an ant tapped a larva with its antennae and the larva cowered, pressing its body tightly against the plant surface and remaining motionless; the ant continued antennal tapping for a while and then walked away without exhibiting any aggressive behavior.

A total of 36 encounters between *P. pungens* workers and *S. posticalis* larvae were noted. In 15 (42%) encounters, an ant ignored a foraging or

Table 1. Proportion of the number of *P. pungens*-attended aphid colonies in which larvae of either or both of the coccinellids, *P. lewisii* and *S. posticalis*, were present to the total number of surviving *P. pungens*-attended colonies, and the probability that larvae of both coccinellids occur in the same colonies, given that each coccinellid is randomly distributed across the colonies

Date	Total no. aphid colonies	Proportion of *P. lewisii*-present colonies (No. colonies)	Proportion of *S. posticalis*-present colonies (No. colonies)	Proportion of both spp-present colonies (No. colonies)	Probability that both spp are present in the same colonies
July 18	12	0.000 (0)	0.000 (0)	0.000 (0)	0.000
July 20	12	0.000 (0)	0.167 (2)	0.000 (0)	0.000
July 22	12	0.000 (0)	0.333 (4)	0.000 (0)	0.000
July 25	12	0.250 (3)	0.500 (6)	0.083 (1)	0.125
July 27	12	0.333 (4)	0.083 (1)	0.000 (0)	0.028
July 29	12	0.333 (4)	0.167 (2)	0.000 (0)	0.056
Aug. 1	11	0.818 (9)	0.273 (3)	0.273 (3)	0.223
Aug. 4	9	0.778 (7)	0.222 (2)	0.111 (1)	0.173
Aug. 6	9	0.556 (5)	0.222 (2)	0.000 (0)	0.123
Aug. 8	7	0.143 (1)	0.429 (3)	0.000 (0)	0.061
Aug. 11	4	0.500 (2)	0.250 (1)	0.250 (1)	0.125
Aug. 14	1	0.000 (0)	0.000 (0)	0.000 (0)	0.000
Aug. 17	1	0.000 (0)	0.000 (0)	0.000 (0)	0.000

feeding *S. posticalis* larva and the larva also ignored the ant. In 21 (58%) encounters, an ant tapped a *S. posticalis* larva with its antennae and showed no aggressive behavior, and the larva ignored the ant.

Thus, foraging larvae of both *P. lewisii* and *S. posticalis* were not treated aggressively by aphid-attending *P. pungens* workers.

Overlaps in the larval distribution of the two coccinellids

Larvae of the two coccinellids rarely co-occurred in the same *P. pungens*-attended aphid colonies during the experimental period (Table 1). The proportion of *P. pungens*-attended colonies in which larvae of both coccinellids were foraging did not significantly differ from the expected probability of both coccinellids occurring in the same *P. pungens*-attended colonies, given that the two species were randomly distributed across *P. pungens*-attended colonies, on each monitoring date ($p>0.05$).

DISCUSSION

The present study documented that larvae of the two coccinellids, *P. lewisii* and *S. posticalis*, utilized colonies of the aphid *T. citricidus* attended by the ant *P. pungens* (Fig. 2). Thus, multiple species of predators attack ant-attended colonies of an aphid species. Kaneko (2007) reported that both *S. posticalis* larvae and the parasitoid wasp *Lysiphlebus japonicus* exploited colonies of the spirea aphid *Aphis spiraecola* attended by either ant, *P. pungens* or *Lasius japonicus*. These results suggest that ant-attended aphid colonies may be shared by multiple enemy species more commonly than previously thought. Different ant-adapted enemy species may interact competitively with each other in ant-attended homopteran colonies and these interactions may affect their survival, foraging or oviposition strategies, and population dynamics (Kaneko, 2007). More attention, therefore, should be paid to the co-occurrence of ant-adapted enemies in ant-attended homopteran colonies. In addition, the co-occurrence of the two coccinellids was detected only in aphid colonies attended by *P. pungens*, not in colonies attended by another ant, *L. japonicus* (Fig. 2). Thus, the effect of ant species attending homopterans on the co-occurrence of ant-adapted enemies and their interactions also needs to be considered, as demonstrated by Kaneko (2007).

This study showed that foraging *P. lewisii* larvae were not treated aggressively by *P. pungens* workers. Völkl (1995) indicated that larvae of the coccinellid *Platynaspis luteorubra*, which are characterized by their flattened coccid-like shape, as well as *P. lewisii* larvae, were often found in ant-attended aphid colonies and that the larvae were ignored by aphid-attending workers of the ant *Lasius niger* even when touched by their antennae or legs. This suggests that chemical camouflage of the larvae contributes to the avoidance of ant detection. As *P. lewisii* larvae were also never attacked by *P. pungens* when tapped by their antennae, the larvae may also have chemical adaptations for avoiding ant aggression.

Völkl and Vohland (1996) documented that wax-covered larvae of *Scymnus interruptus* were often attacked by aphid-attending *L. niger* workers. The authors experimentally revealed that the wax covers mechanically protect the larval body against ant aggression. By contrast, the present study showed that *P. pungens* workers responded non-aggressively to wax-covered *S. posticalis* larvae. The observation that antennal tapping by *P. pungens* on the wax covers of *S. posticalis* larvae did not lead to ant aggression suggests that the wax covers may function as chemical camouflage or mimicry. It is necessary to verify this chemical adaptation hypothesis for larvae of *P. lewisii* and *S. posticalis* by analyzing the chemical profiles of the larval body surface and the wax cover.

Many larvae and a few adults of *P. lewisii* were found exclusively in *P. pungens*-attended aphid colonies, whereas *S. posticalis* larvae and adults foraged not only in *P. pungens*-attended but also in ant-excluded colonies (Figs. 2 and 3). This result suggests that the distribution across aphid colonies in relation to the presence or absence of attending ants differs between *P. lewisii* and *S. posticalis*; however, the number of observed adults of the coccinellids, particularly *P. lewisii*, was very small. In addition, it is possible that the sticky barrier treated on the trunks of the examined citrus trees prevented larvae and adults of the coccinellids from approaching ant-excluded aphid colonies on the trees. Therefore, the abundance of the two coccinellids in "ant-absent" aphid colonies on non-barrier trees should be investigated to determine the distribution pattern of each coccinellid species across ant-attended and unattended aphid colonies.

Few or no larvae and adults of the two coccinellids were noted in aphid colonies attended by another ant, *L. japonicus* (Figs. 2 and 3). *L. japonicus* workers are more aggressive and hence more effective in excluding predators and parasitoids from homopteran colonies that they attend, compared to *P. pungens* workers (Itioka and Inoue, 1999; Kaneko, 2003a, b). Furthermore, the defensive ability of *L. japonicus* seems to be enhanced in summer, compared to in spring, because the parasitoid *Lysiphlebus japonicus* and large predators such as coccinellids, chrysopids and syrphids were rarely recorded in *L. japonicus*-attended *T. citricidus* colonies in summer (Kaneko, 2003b). This fact implies that *L. japonicus* workers may also heavily attack and repel both larvae and adults of the two coccinellids. To reveal why larvae of the two coccinellids are not accepted by *L. japonicus* workers, it is necessary to release the larvae into *L. japonicus*-attended aphid colonies and observe their behavioral interactions with ant workers in detail.

Many studies have documented interspecific interactions, including intraguild predation and its avoidance, between aphidophagous coccinellids (e.g., Agarwala and Dixon, 1992; Rosenheim et al., 1995; Yasuda and Shinya, 1997; Agarwala et al., 2003); however, the relationship between predatory coccinellid species in ant-attended aphid colonies has not been investigated. Analysis of the overlap in the larval distribution of *P. lewisii* and *S. posticalis* across *P. pungens*-attended aphid colonies (Table 1) suggests that larvae of the two coccinellid species are distributed independently of each species. Thus, competitive interactions may rarely occur between the two coccinellids in *P. pungens*-attended aphid colonies, which might be ascribed to the low abundance of larvae of these coccinellids and their small consumption of prey in large colonies of the aphid *T. citricidus*. Interactions between larvae of the two coccinellids in relation to aphid colony size therefore need to be examined experimentally.

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