



Assessment of prey preference by the mass-produced generalist predator, *Mallada basalis* (Walker) (Neuroptera: Chrysopidae), when offered two species of spider mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae), on papaya

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ABSTRACT

We investigated potential prey preference of the mass-produced generalist predator *Mallada basalis* (Walker) when offered two mites, *Tetranychus kanzawai* Kishida and *Panonychus citri* (McGregor), both important pests on papaya. Laboratory choice tests revealed that none of the three larval instars of *M. basalis* showed a preference for either species of mite or discriminated among the four mite life stages. Direct observations also showed that lacewing larvae mostly consumed whichever mite was encountered. Previous feeding experience on one mite species did not influence subsequent prey choice when lacewings were presented with both mite species. High acceptability of all life stages of both mite pests suggests that mass-produced *M. basalis* has potential as an effective biological control agent for *T. kanzawai* and *P. citri* when the two mites occur simultaneously or sequentially in papaya plantations.

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1. Introduction

Tetranychus kanzawai Kishida and *Panonychus citri* (McGregor) (Acari: Tetranychidae) are important mite pests of papaya in Taiwan. *Tetranychus kanzawai* is a widely-distributed pest throughout East and Southeast Asia, attacking over a hundred species of plants, including many food crops and ornamental plants (Bolland et al., 1998; Zhang, 2003). It is normally an outdoor species, but can attack greenhouse plants as well. *Panonychus citri* has a worldwide distribution and feeds on over 80 plant species, including citrus, rose, almond, pear, castor bean, and several broadleaf evergreen ornamentals (Bolland et al., 1998; Zhang, 2003).

Presently, control of these two mite pests depends mainly on chemical applications. However, the intensive application of miticides in combination with short life cycles and high reproductive rates have led to the development of resistance in these two pests to many registered miticides (Furuhashi, 1994; Masui et al., 1995; Goka, 1998; Aiki et al., 2005). In addition, many miticides produce

unacceptable phytotoxicity to papaya (Lo, 2002). It is therefore necessary to search for alternative approaches for controlling these mites on papaya.

The lacewing *Mallada basalis* (Walker) (Neuroptera: Chrysopidae) is a common predator in agricultural fields in Taiwan. The larvae of this lacewing are generalist predators, whereas the adults feed on nectar, honeydew, and pollen (Wu, 1995). This predator has been shown to have potential as a biological control agent for *P. citri* on citrus (Wu, 1992, 1995) and on Indian jujube (Hao, 2002), and for *T. kanzawai* and *T. urticae* on strawberry (Chang and Huang, 1995), as well as for *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), *Aphis* spp. (Hemiptera: Aphididae), *Nipaeccoccus filamentosus* (Cockerell) (Hemiptera: Pseudococcidae), and *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) on citrus (Wu, 1992; Lo, 1997) and *Aphis gossypii* Glover (Hemiptera: Aphididae) on sweet pepper (Lu and Wang, 2006). Moreover, *M. basalis* can be successfully mass-produced in a cost-effective manner using a microcapsulated artificial diet (Lee, 1994, 1995, 2003), and cold storage techniques have been established for various life stages, which facilitates the scheduling of shipments and releases (Wu, 1992). In addition, research has demonstrated that *M. basalis* has some tolerance to selected insecticides, fungicides, and acaricides (Tzeng and Kao, 1996; Lo, 2002). All of these findings suggest that

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M. basalis may be a suitable candidate for augmentative biological control, and may be compatible for use in integrated pest management programs.

Previously, we investigated aspects of the feeding behavior of mass-produced *M. basalis*, including foraging schedules, prey acceptance, handling times, and consumption rates, on each of the two major mite pests of papaya, *T. kanzawai* and *P. citri* (Cheng et al., 2009). However, these two mites can occur simultaneously at the same papaya plantation and on the same papaya leaves. This might complicate the use of *M. basalis* for biological control because generalist predators may exhibit prey preference in the presence of mixed prey species (Dicke et al., 1989; Nordlund and Morrison, 1990; Hanna and Wilson, 1991; Hazzard and Ferro, 1991; Legaspi et al., 1994). Prey preference by biological control agents can affect their ability to effectively control target pests (Nordlund and Morrison, 1990; Legaspi et al., 2006; Provost et al., 2006). However, little is known about prey preference in *M. basalis*. Therefore, the primary objective of this study was to determine whether mass-produced *M. basalis* exhibit a preference for either species of pest mite. Because prey preference may be a learned response (Houck, 1986), tests were also done to determine whether prey preference was linked to the lacewing's previous feeding experience on either of the two mite species. Prey size in relation to that of the predator also may influence prey preference (McKamey et al., 2003; Troost et al., 2008). Therefore, for each mite species we tested for prey stage preference in each *M. basalis* larval instar.

2. Materials and methods

2.1. Arthropod and plant cultures

2.1.1. Papayas

Papaya seedlings (*Carica papaya* L., 'Tainung No. 2') were purchased from a commercial nursery 3–4 weeks after germination. The seedlings were then transferred individually to 9-cm diameter pots, and maintained in a room at 26 ± 2 °C, $70 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) with fluorescent lights at 7000 lux until they were approximately 25 cm tall and suitable for rearing mites. The seedlings were watered twice a week, but without any fertilization.

2.1.2. Green lacewings

The *M. basalis* used for this study were from a laboratory colony that has been maintained since 1999 at 26 ± 2 °C, $70 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) with fluorescent lights at 500 lux. No wild individuals have been introduced into the colony since then. Lacewing larvae were reared on a microencapsulated artificial diet developed by Lee (1994, 1995).

The larvae were reared in plastic pans of $40 \times 30 \times 10.5$ cm ($L \times W \times H$). Corrugated paper rolls (10 cm diameter and 1.5 cm thick) were first placed side-by-side in the pan, and then two tablespoons of sawdust, 25 ml of microencapsulated diet, and approximately 1000 green lacewing eggs were added. Subsequently, diet was added three more times at 3-day intervals in the following amounts: 75, 100, and 25 ml. These amounts corresponded to the relative feeding rates of larval instars during growth and development. A piece of 200-mesh white screen was taped on the top of the rearing pan to prevent the escape of lacewing larvae and the invasion of their predators (ants, spiders, etc.). Most larvae pupated on or inside the corrugated paper rolls.

After the majority had pupated, pupae along with the paper rolls were removed and placed in a black acrylic box ($45 \times 45 \times 45$ cm) at the top of which was attached a clear acrylic cylinder (15 cm diameter \times 20 cm high). Upon emergence, adult

lacewings would fly up into the clear cylinder due to their attraction to light. The adults were then transferred to another acrylic cylinder which had a piece of white paper attached to the wall. The paper served as an oviposition site and was changed daily. Brewer's yeast and honey (1:1) were mixed, stuck on a piece of plastic slide, and hung inside the cylinder for adult food. Water was also provided with a wetted cotton ball.

2.1.3. Mites

Tetranychus kanzawai were collected from papaya plantations in and around Nantou, Taiwan in 2003 and maintained in a rearing room on papaya seedlings kept on shelves at 26 ± 2 °C, $70 \pm 10\%$ RH, and a photoperiod of 14:10 (L:D) with fluorescent lights at 4000 lux. *Panonychus citri* were also collected from the same fields at the same time and maintained under similar conditions as *T. kanzawai*, but in a walk-in growth chamber. The temperature was slightly lower (25 ± 1 °C) with light intensity at 5000 lux. Both mite colonies were regenerated every 3–4 weeks, when the old papaya seedlings were ~40 cm high (a height that reached the lights suspended above the shelves), by transferring several pieces of mite infested papaya leaves to the new seedlings.

2.2. Preference of larval *M. basalis* for different life stages of either *T. kanzawai* or *P. citri*

To evaluate whether *M. basalis* larval instars exhibited a preference for various life stages of *T. kanzawai* and *P. citri*, and whether preference differed with predator life stage, separate experiments were conducted with each mite species. Experiments were done as choice tests and consisted of exposing a lacewing larva from one of the three instars (all three tested separately) to 100 prey of each of the following mite life stages: egg, larva, nymph, adult from a single prey species; this resulted in their exposure to 400 total prey per test. This was repeated for both prey species. Prior to each test, mites were transferred to a piece of papaya leaf (~270 mm²), which was floated on water (~4 ml) in a Petri dish (5 cm diameter) with the undersurface of the leaf facing up. One *M. basalis* larva was then introduced onto the leaf. This method confined the lacewing and the mites on the leaf throughout the experiment. Although the density of 400 prey per 270 mm² leaf area was extremely high compared to possible field densities, this was used to allow lacewings equal opportunity to encounter various life stages of the mites. Lacewings used for this test were in the second day of each instar, and were fed the microencapsulated artificial diet until tests began to avoid possible effects on prey preference due to hunger.

Lacewing feeding behavior was observed under a stereomicroscope illuminated at an intensity of ~95 lux. During observations, the numbers of each prey life stage encountered and consumed by the lacewing were recorded. Each test was terminated when a predator had consumed 20 mites, the point after which first instar lacewings would become satiated. For this reason, we used 20 mites as the standard in all tests. Individual tests were mostly completed within 30 min for second and third instar predators, and within 2 h for the first instars. Mites were not replaced throughout the test. However, the initial numbers provided greatly exceeded the 20 mites actually needed and made the change in encounter rates of the lacewing with the mites due to prey depletion negligible. Tests with each *M. basalis* larval stage against each mite species were replicated 10 times.

The relative prey encounter rates were expressed as percentages, and were computed by dividing the number of each mite life stage encountered by the total number of mites of all life stages encountered \times 100. The relative prey consumption rate was measured as the percentage of the individual life stage of the mites consumed in relation to total mites consumed (i.e., the number

of the individual life stage of the mite consumed divided by the total number of mites consumed during each observation $\times 100$). Prey acceptability for each prey life stage was measured as the percentage of encountered prey of each individual life stage that was consumed (i.e., for each individual mite life stage, the number consumed over the number encountered $\times 100$).

2.3. Preference of *M. basalis* for *T. kanzawai* and *P. citri* nymphs and effect of previous feeding experience

Based on the results of the tests described above, we chose to conduct species preference tests with mites in the nymphal stages only. The arena and experimental conditions were the same as in the previous experiment. Leaves were infested with 200 total nymphs of *T. kanzawai* and *P. citri*. We defined preference as taking a greater proportion of a particular food than is available in the environment. To test the robustness of preference, we made prey available in three different ratios: 160:40, 100:100, and 40:160 of *T. kanzawai* to *P. citri*. One 2-day-old *M. basalis* 2nd instar larva was used per test. This stage was selected because it is an intermediate larval stage, has a feeding period and stadia length that exceeds the test period, and allowed prior feeding experience before tests. *Mallada basalis* were tested under three sets of feeding experience: (1) directly from artificial diet; (2) after feeding on *T. kanzawai* from hatching until tests were initiated (ca. 4 days);

and (3) after feeding on *P. citri* for the same amount of time. To initiate a test, one lacewing larva was introduced onto the leaf and the numbers of each species of mite encountered and consumed by the lacewing were observed and recorded under a stereomicroscope. Tests ended when a total of 20 mites were consumed. Tests with each predator treatment by mite ratio combination were repeated 10 times. As in the previous experiment, providing a surplus of each species of mite allowed *M. basalis* to exhibit preference without a limitation of prey.

2.4. Data analyses

Relative encounter and consumption rate data for *M. basalis* were analyzed with χ^2 goodness of fit tests (Zar, 1984). The Mann–Whitney *W* test (for two-sample comparisons) and Kruskal–Wallis test (conducted with STATGRAPHICS Centurion XV, Software, 2005 (Statpoint, Inc.) were used to analyze prey acceptability data because these data were not normally distributed. Means were separated for significance using Fisher's protected LSD procedure.

3. Results

Mallada basalis larvae exhibited little or no preference for different life stages of the two mites. Although there were some signif-

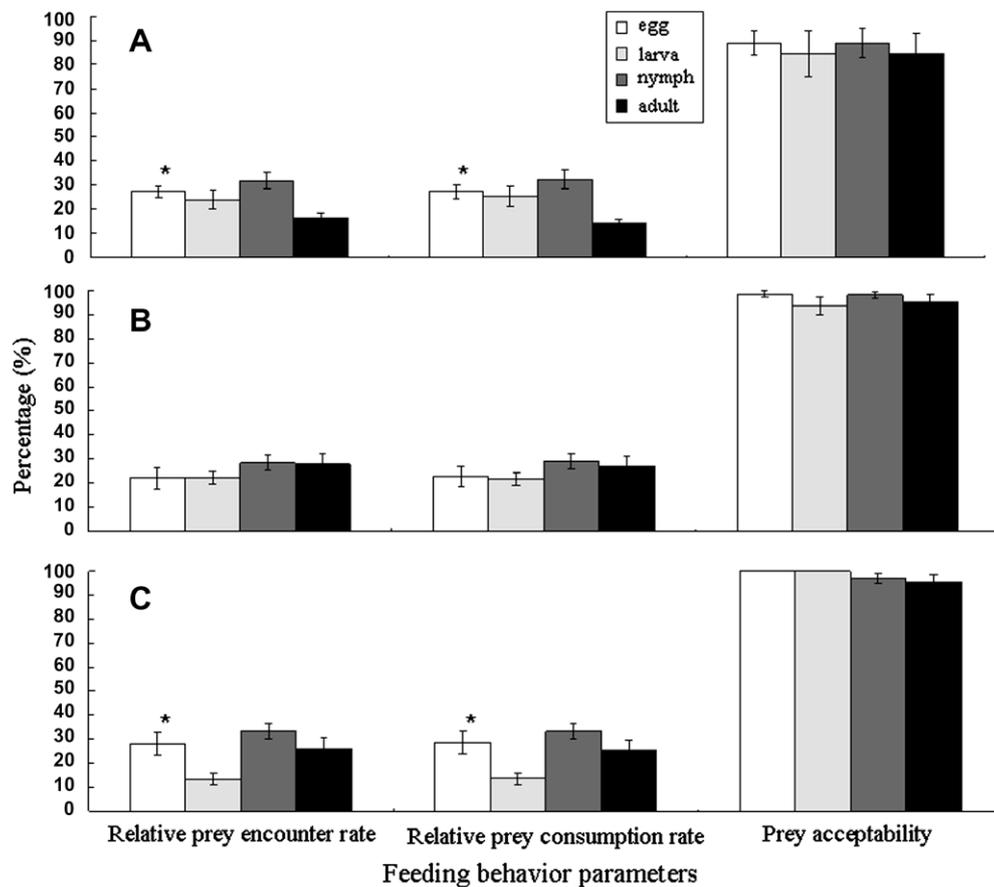


Fig. 1. Relative prey encounter and consumption rates, and prey acceptability of *M. basalis* (A) 1st instar; (B) 2nd instar; (C) 3rd instar to a mixture of various life stages of *T. kanzawai*. Relative prey encounter rate ($n \geq 200$) = the number of the specific mite life stage encountered divided by the total number of the mites encountered during the observation $\times 100$; relative prey consumption rate ($n = 200$) = the number of the specific mite life stage consumed divided by the total number of the mites consumed during the observation $\times 100$; prey acceptability ($n = 10$) = the number of the specific mite life stage consumed divided by the number of the specific mite life stage encountered during the observation $\times 100$. Asterisk indicates a significant difference from the expected 25% in relative prey encounter and consumption rates among the four prey instars ($P < 0.05$, χ^2 goodness of fit tests; Zar, 1984). There were no significant differences in prey acceptability ($P > 0.05$, Kruskal–Wallis tests; STATGRAPHICS Centurion XV, 2005) of *M. basalis* among various life stages of the mites. Error bars represent \pm SEM. Actual number of mites of specific life stage encountered = percentage $\times 20$ (total number mites consumed to terminate a test)/prey acceptability, and consumed = percentage $\times 20$.

ificant differences in the relative encounter and consumption rates of various life stages of each mite species by *M. basalis* when all prey instars were offered simultaneously ($\chi^2 = 9.23\text{--}76.31$, $P < 0.05$, $df = 3$, $n \geq 200$; Figs. 1 and 2), the encounter and consumption rates corresponded to one another. In addition, there were very few significant differences in prey acceptability of *M. basalis* among the various prey instars, except that first instar *M. basalis* exhibited lower prey acceptability of *P. citri* adults than of the earlier life stages ($H = 10.94$, $P = 0.01$, $df = 3$; Kruskal–Wallis test) (Fig. 2).

Mallada basalis exhibited no preference for either *T. kanzawai* or *P. citri*. When diet-fed lacewings were offered mixtures of various ratios of the nymphal stage of the two mite species, the percentage of each mite species encountered and consumed corresponded with the proportion of each mite in the mixtures ($\chi^2 = 0.10\text{--}2.53$, $P > 0.05$, $df = 1$, $n \geq 200$) (Table 1). *Mallada basalis* larvae did not change prey preference with different feeding experiences. When lacewings were fed on either one of the two mite species prior to the tests, the encounter and consumption rates were still proportional to the relative abundance of the mites in the mixtures ($\chi^2 = 0.32\text{--}3.13$, $P > 0.05$, $df = 1$, $n \geq 200$) (Table 1). Moreover, prior feeding experience did not influence percentage acceptability (range of means: 95.5–100%), as there were no significant differences between the two mite species (W ranging from -6.0 to 6.0 ; $P > 0.05$; Mann–Whitney W test) (Table 1). Direct observations showed that lacewings mostly consumed any mite they encountered.

4. Discussion

Green lacewings are generalist predators, but some species are known to exhibit preferences for particular prey when they are simultaneously offered a number of different species. For example, in the presence of mixed pests, *Chrysopa* (= *Chrysoperla*) *carnea* Stephens attacked aphids first, then thrips, and finally tetranychid mites (Tulisalo, 1984). In *Chrysoperla rufilabris* (Burmeister), larvae showed a preference for *Heliothis virescens* (F.) (bollworm) larvae over the cotton aphid, *A. gossypii*; but they preferred *A. gossypii* over *H. virescens* eggs (Nordlund and Morrison, 1990). Even when prey life stages are the same, lacewings may show interspecific feeding preferences. For example, larvae of *C. rufilabris* preferred eggs of *Sitotroga cerealella* (Olivier) and *Helicoverpa zea* (Boddie) over eggs of *Manduca sexta* (Linnaeus) and *Bemisia tabaci* (Gennadius) (Legaspi et al., 1994). However, in the current study, mass-produced *M. basalis* showed a similarly high degree of prey acceptability for nymphs of both species of papaya mites, and encounter and consumption rates of *M. basalis* were proportional to the relative abundance of the two mite species in the mixture. These results are consistent with our previous finding on the prey acceptability of *M. basalis* when the two mite species were offered in no-choice tests (Cheng et al., 2009). We observed that *T. kanzawai* and *P. citri* are approximately the same in terms of size, mobility, and ability to escape predators. These factors may account for the similarities in their acceptance by lacewing larvae. Other

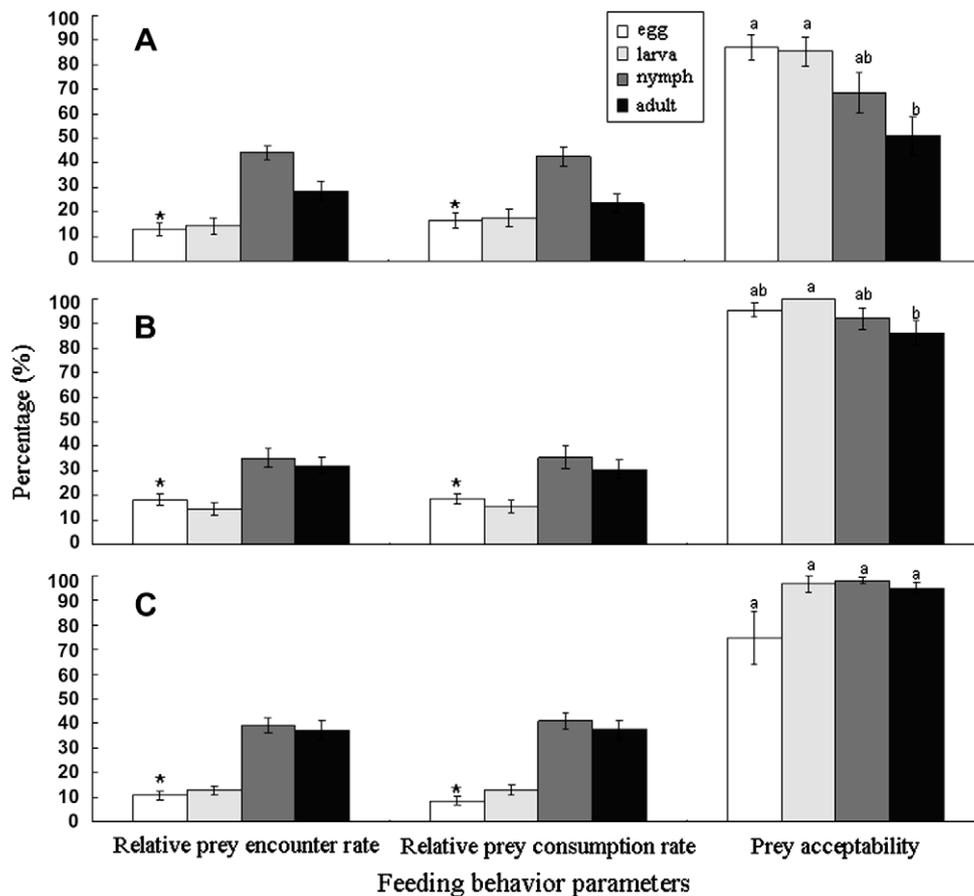


Fig. 2. Relative prey encounter and consumption rates, and prey acceptability of *M. basalis* (A) 1st instar; (B) 2nd instar; (C) 3rd instar to a mixture of various life stages of *P. citri*. Prey encounter rate, prey consumption rate, and prey acceptability were calculated using the same formulas as described in Fig. 1. Asterisk indicates a significant difference from the expected 25% in relative prey encounter and consumption rates among the four prey instars at $P < 0.05$ (χ^2 goodness of fit test; Zar, 1984). Means with different letters in prey acceptability are significantly different at $P < 0.05$ (Kruskal–Wallis test and Fisher's protected LSD procedure; STATGRAPHICS Centurion XV, 2005). Error bars represent \pm SEM. Actual number of mites of specific life stage encountered = percentage \times 20 (total number of mites consumed to terminate a test)/prey acceptability, and consumed = percentage \times 20.

Table 1

Relative prey encounter rate, prey consumption rate, and prey acceptability of second instar *M. basalis* when offered various ratios of *T. kanzawai* (Tk) and *P. citri* (Pc) nymphs after being conditioned on different foods (artificial diet, Tk, or Pc) prior to tests. The relative encounter and consumption rates of *M. basalis* to the two mites were statistically proportional to the mites ratios offered (χ^2 goodness of fit tests; Zar, 1984), and there were no significant differences in prey acceptability between the two mites at any of the ratios (Mann–Whitney *W* tests; STATGRAPHICS Centurion XV, 2005).

Previous food	Prey provided	% Encounter ^a (Mean ± SE)		% Consumption ^b (Mean ± SE)		% Acceptability ^c (Mean ± SE)	
		Tk	Pc	Tk	Pc	Tk	Pc
Diet	50% Tk and 50% Pc	46.4 ± 2.9	53.6 ± 2.9	46.5 ± 3.0	53.5 ± 3.0	97.5 ± 1.7	97.0 ± 2.1
	20% Tk and 80% Pc	20.9 ± 2.3	79.1 ± 2.3	21.0 ± 2.2	79.0 ± 2.2	100.0 ± 0.0	99.0 ± 1.1
	80% Tk and 20% Pc	75.6 ± 3.6	24.4 ± 3.6	75.5 ± 3.6	24.5 ± 3.6	98.6 ± 1.4	98.9 ± 1.1
Tk	50% Tk and 50% Pc	52.5 ± 3.6	47.5 ± 3.6	52.5 ± 3.6	47.5 ± 3.6	100.0 ± 0.0	100.0 ± 0.0
	20% Tk and 80% Pc	23.0 ± 2.3	77.0 ± 2.3	22.0 ± 2.0	78.0 ± 2.0	95.5 ± 3.0	100.0 ± 0.0
	80% Tk and 20% Pc	75.0 ± 2.6	25.0 ± 2.6	75.0 ± 2.6	25.0 ± 2.6	100.0 ± 0.0	100.0 ± 0.0
Pc	50% Tk and 50% Pc	47.9 ± 4.2	52.1 ± 4.2	48.0 ± 4.1	52.0 ± 4.1	99.3 ± 0.7	99.1 ± 0.9
	20% Tk and 80% Pc	23.7 ± 3.1	76.3 ± 3.1	24.0 ± 3.1	76.0 ± 3.1	100.0 ± 0.0	98.7 ± 0.9
	80% Tk and 20% Pc	77.8 ± 1.8	22.2 ± 1.8	78.0 ± 1.7	22.0 ± 1.7	99.4 ± 0.6	98.3 ± 1.7

Actual number mites of specific life stage encountered = percentage × 20 (total number of mites consumed to terminate a test)/prey acceptability, and consumed = percentage × 20.

^a (The number of the specific mite species encountered divided by the total number of the two mite species encountered during the observation) × 100; *n* ≥ 200.

^b (The number of the specific mite species consumed divided by the total number of the two mite species consumed during the observation) × 100; *n* = 200.

^c (The number of the specific mite species consumed divided by the number of the specific mite species encountered during the observation) × 100; *n* = 10.

factors, such as the nutritional value of the prey and the long-term mass-rearing of the predator, also may have influenced our results; but we do not have data to either support or exclude these possibilities.

Changes in prey preference associated with the age of the predator have been well documented among invertebrates, including mites (Polis, 1984; Hallas, 1988; Rayor and Uetz, 1993) and insects (Thompson, 1975; McArdle and Lawton, 1979; Lockwood, 1989; McKemey et al., 2003; Troost et al., 2008). It has also been reported that mean prey size increases with body size of the predator (Hespenheide, 1973; McArdle and Lawton, 1979; Werner and Gilliam, 1984; Cisneros and Rosenheim, 1997). However, our results do not support the idea that the size of the *M. basalis* instar affected prey selection. That is, all three lacewing instars accepted all *T. kanzawai* life stages equally. For *P. citri*, first instar lacewings did not accept adults at as high a rate as eggs and larvae; this tendency diminished and was lost as predators increased in age. However, as the relative sizes of each life stage of the two mite species are very similar, we feel that some unknown factor other than size may explain the lower acceptance of *P. citri* adults compared to earlier life stages. Our previous study also showed that there was little or no difference in prey acceptability of *M. basalis* to *T. kanzawai* and *P. citri* among lacewing and among mites life stages in no-choice tests (Cheng et al., 2009). The fact that the body dimensions of all mite life stages were far smaller than those of the lacewings may have contributed to the generally high acceptance we observed in all larval instars of *M. basalis*, both in choice and no-choice tests.

Investigations of the influence of a predator's feeding experience on prey choice have not been extensive or conclusive (Houck, 1986; Rayor and Munson, 2002). Our results showed that previous feeding experience of *M. basalis* on either *T. kanzawai* or *P. citri* had no effects on subsequent prey choice between these two mites. This finding could suggest that both mite species have similar enough characteristics that a generalist predator like *M. basalis* does not discriminate.

Tetranychus kanzawai and *P. citri* are the two most important acarine pests in papaya greenhouse plantations. Both mites can occur simultaneously at the same papaya plantation and on same papaya leaves. This study documented that a domesticated line of *M. basalis* reared on an artificial diet were active and effective foragers on two species of papaya pest mites. The lacewings did not discriminate between the two mite species nor among the different mite life stages. These results suggest that mass-produced *M. basalis* may be effective in suppressing both mite pests when

they occur simultaneously in papaya plantations. Furthermore, lacewing feeding experience did not affect subsequent prey choice on the two mites. This should enable *M. basalis* to feed successively on different mite species (prey-switching) without reducing predation potential. It should also allow *M. basalis* to control the second pest mite in the beginning of its invasion since *T. kanzawai* and *P. citri* often occur sequentially in papaya plantations. However, the prey preference of a predator may also be affected by plant architecture and prey spatial distributions (Flaherty and Huffaker, 1970; Eveleigh and Chant, 1982; Gianino and Jones, 1989; Hanna and Wilson, 1991). *Tetranychus kanzawai* and *P. citri* have different spatial distribution patterns on the papaya, with *T. kanzawai* having a more clumped distribution on the older leaves, whereas *P. citri* have a more even distribution and disperse more to the young leaves (Cheng, personal observations). Therefore, prey preference of *M. basalis* for the two papaya pest mites in the field needs further investigation before we can fully determine the control efficacy of this lacewing against these two important papaya pests.

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