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Feeding Potential and Prey Acceptance of *Podisus maculiventris* (Hemiptera: Pentatomidae): Implications for Biological Pest Control

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Abstract

Determination of feeding potential and prey acceptance of natural enemies is crucial to assure that natural enemies can control target pest species. This study was conducted to investigate feeding potential and prey acceptance of a generalist predator, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae). A series of laboratory experiments were conducted to quantify feeding potential of *P. maculiventris* by measuring daily feeding amount and to determine prey acceptance by analyzing feeding behavior of *P. maculiventris* on various types of prey. The result of this study showed that the amount of prey consumption differed significantly (F = 38.48; d.f. = 5, 44; P <0.05) among stages of *P. maculiventris*. *P. maculiventris* attempted to attack *Halyomorpha halys* (Hemiptera: Pentatomidae), but could not sustain effective feeding due to behavioral and chemical defense of the prey. *P. maculiventris* showed significantly (P < 0.05) less effective feeding on prey with spines or hairs such as *Evergestis rimosalis* (Lepidoptera: Crambidae) and *Hyphantria cunea* (Lepidoptera: Arctiidae). Utilization of *P. maculiventris* for controlling various types of pests for augmentative biological control is discussed in this article.

Introduction

Since the first successful biological control using vedalia beetles to control cottony cushion scale in the United States, many specialist and generalist predators have been used for biological control of insect pests [1]. Specialist predators have a high degree of prey specificity and are considered appropriate to use to reduce a specific pest population below economic injury level [2]. Historically, the view among biological control practitioners was that generalist predators are less important than specialist predators, but recently the importance of generalist predators has been emphasized [3]. Edwards *et al.* [4] and Chiverton [5] showed that generalist predators in certain manipulated systems could be as important as specialist predators in other systems. These generalist predators include carabids [6], coccinellids [7], neuropterans [8], and predatory hemipterans [9].

Major advantages of using generalist predators is their ability to control multiple insect pests and survive on plant material or alternative prey even when their major prey is scarce or absent [8,10]. For example, the multicolored Asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) can survive by feeding on pollen and eggs of beetles and moths when its major prey (i.e. aphids) is scarce in the field [11]. Therefore, the presence of alternative prey or food sources in a crop field could improve biological control using generalist predators [12]. Although generalist predators have such advantages, they generally have different degrees of acceptance to various types of prey [13]. Prey characteristics, such as host breadth, prey chemistry, and prey behavior and morphology, can play important roles in the acceptance of prey [14]; for example, predatory hemipterans are known to exhibit prey preferences based on differences in prey mobility [12], size [15], and prey species [16]. In addition to prey acceptance, understanding feeding capacity of different stages of generalist predators is crucial to aid mass rearing and release in biological control programs. Because younger predators tend to feed less than mature predators, quantification of feeding potential of younger stages of a predator relative to older ones will help determine the number of predators to release to control pests in the field and deciding the optimal amount of prey needed for mass rearing of the predators.

The spined soldier bug *Podisus maculiventris* (Hemiptera: Pentatomidae) is a generalist predator feeding on more than 70 species of insects [17], mostly immature stages of insects in the orders of Lepidoptera and Coleoptera [18,19]. *P. maculiventris*can inhabit various agricultural ecosystems (i.e. crop fields, forests, and grasslands) and plays a key role in the control of major insect pests [17,20]. Specifically, *P. maculiventris* is an important predator of field crop pests [18] including many larvae of noctuids (Lepidoptera: Noctuidae) and Colorado potato beetles (Coleoptera: Chrysomelidae). In addition, *P. maculiventris* has high potential for augmentative biological control because it has a high reproduction rate making mass production easier [21].

This study was conducted to investigate the feeding potential and prey preference of *P. maculiventris* for augmentative biological control. The objectives of this study were determining feeding potential of different *P. maculiventris* stages/instars for a mass rearing system (Experiment 1) and investigating prey acceptance and efficacy of *P. maculiventris* as a generalist predator (Experiments 2 and 3).

Materials and Methods

Experimental conditions and insects

This study was conducted at a constant temperature (22 ± 1.7°C), relative humidity (60 ± 8.5%), and photoperiod (15:9 L:D). All *P. maculiventris* used in the experiment were obtained from colonies that have been maintained in the entomology laboratory at West Virginia University (Morgantown, WV) by using the yellow mealworm *Tenebrio molitor* (Coleoptera: Tenebrionidae) as prey. Young *T. molitor* (third instars) were purchased from New York Worms (Long

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Island, New York, NY) and reared them in the laboratory to fifth instars and pupae that were used in this study.

Experiment 1: Feeding Potential of Different *P. maculiventris* stages

An experiment was conducted to quantify daily feeding amount of *P. maculiventris* expressed as weight loss of prey. *T. molitor* was used as prey in this study because it is common prey used for mass rearing of *P. maculiventris*. All predacious stages of *P. maculiventris* were used in this study (i.e. all but egg and first instar). One *T. molitor* pupa was weighed by using an electronic balance (PB 303-S/Fact, Mettler-Toledo Inc., Columbus, OH) and placed in a cup (4-cm diameter) (Solo®, Solo Cup Company, Urbana, IL) along with one *P. maculiventris* (second instar, third instar, fourth instar, fifth instar, or adult). After 24 hr, the weight of the *T. molitor* pupa was measured again to determine the amount of weight loss due to *P. maculiventris* feeding. All *P. maculiventris* used in this study were starved for 24 hr, allowing access to water only. This experiment was repeated 30 times for each *P. maculiventris* instar/stage (i.e. four different instars and two different sexes of adults) and no insect was used more than one time. Because weight loss of *T. molitor* by feeding of younger *P. maculiventris* was too small to measure, we combined and measured the weight loss of three *T. molitor* pupae together. A total of 30 *T. molitor* were used as a control (i.e. without *P. maculiventris* in a cup). Differences in weight loss of *T. molitor* pupae due to *P. maculiventris* feeding compared to the control were analyzed with paired t-test [22].

To compare feeding potential of different stages of *P. maculiventris*, we adopted the concept of injury equivalency proposed by Hutchins *et al.* [23]. The term injury equivalency was used originally to quantify the overall amount of plant injury caused by multiple pest species with different feeding potential. Feeding equivalency can be presented as feeding equivalency coefficient that measures relative feeding potential by setting the amount of feeding by a certain insect or a stage of insect as 1.0. In our study, feeding equivalency coefficient was calculated by setting the amount of feeding by the second instar as 1.0. Data on weight loss of *T. molitor* was analyzed with ANOVA and difference in means due to feeding for second–fifth instars and adults (male and female) were compared with Tukey's HSD test at 5% error rate [22].

Experiment 2: Prey acceptance and feeding effectiveness of *P. maculiventris* on different types of prey

An experiment was conducted to determine prey acceptance and feeding effectiveness of *P. maculiventris* on different types of prey. A total of six different prey types in six different families and four different orders were used in this study. The prey were fully grown larvae or nymphs including the cabbage worm *Pieris rapae* (Lepidoptera: Pieridae) (1.9–2.4 cm in length), the cross-striped cabbage worm *Evergestis rimosalis* (Lepidoptera: Crambidae) (1.7–2.4 cm in length), the Colorado potato beetle *L. decemlineata* (Coleoptera: Chrysomelidae) (0.8–1.2 cm in length), the fall web worm *Hyphantria cunea* (Lepidoptera: Arctiidae) (1.9–2.5 cm in length), the Mexican bean beetle *Epilachna varivestis* (Coleoptera: Coccinellidae) (0.6–0.8 cm in length), and the brown marmorated stink bug *Halyomorpha halys* (Hemiptera: Pentatomidae) (1.0–1.2 cm in length). The prey were collected from cabbage (*Brassica oleracea*), kale (*Brassica oleracea*), potato (*Solanum tuberosum*), black cherry (*Prunus serotina*), soybean (*Glycine max*), and corn (*Zea mays*). The prey was maintained in the laboratory on leaves of their host plants until the experiment was started.

One species of prey was placed in a Petri dish (5.5-cm diameter) (Lab-Tech Plastic Petri Dish, Miles Laboratories Inc., Naperville, IL) along with one *P. maculiventris* (third instar, fifth instar, or adult). To collect data more accurately and precisely, the feeding activity of *P. maculiventris* in the arena was videotaped for 24 hr using infrared cameras (The Hawk Eye Nature Cam, West Linn, OR) connected to a 4-channel DVR (Falco Model LX-4PRO, Falco Pro Series, Taiwan). This experiment was repeated 12 times for each stage/instar of *P. maculiventris* with each prey species. All insects were used only once in this study. From the video footage, two behaviors were quantified to determine prey acceptance and effectiveness of *P. maculiventris*: numbers of each prey killed by *P. maculiventris* feeding and the number of attacks required prior to successful feeding by *P. maculiventris* for each prey. Data were analyzed with ANOVA and effectiveness of *P. maculiventris* killing six different prey species were compared with Tukey's HSD test at 0.05% error rate [22].

Experiment 3: Feeding preference of *P. maculiventris* on three different prey types

An experiment was carried out to determine the feeding preference of three different stages of *P. maculiventris* (i.e. third instar, fifth instar, and adult) on three different types of larvae. We chose *H. cunea*, *E. rimosalis*, and *E. varivestis* as prey in this study because they were accepted by *P. maculiventris* as prey (see Results of Experiment 2) and they exhibited different types of body surface; *H. cunea* has a hairy body surface, *E. rimosalis* has a smooth body, and *E. varivestis* has a spiny body surface. One *H. cunea* (1.8–2.5 cm in length), one *E. rimosalis* (1.9–2.4 cm in length) and one *E. varivestis* (0.6–1.1 cm in length), was randomly assigned to one quadrant of a Petri dish (9-cm diameter) (Pyrex Petri Dishes, Science Kit and Boreal Laboratories, Tonawanda, NY). Then, one *P. maculiventris* was introduced into the remaining quadrant of the Petri dish. The experiment was videotaped for 24 hr using infrared cameras and a 4-channel DVR. The experiment was repeated 20-22 times for each *P. maculiventris*. All *P. maculiventris* used in this study were starved for 24 hr before the experiment and all insects were used only once. From the video footage, two different data were collected: prey that *P. maculiventris* initially attacked and prey that was fed upon successfully. Attacking behavior was indicated by *P. maculiventris* protruding its proboscis toward prey and initiating feeding, but not killing the prey. Successful feeding behavior was indicated by *P. maculiventris* feeding upon and killing prey after attacking. Data were analyzed using chi-square test [22] to determine the feeding preference of *P. maculiventris* based on the types of prey for initial attacking and successful feeding.

Results

Experiment 1: Feeding Potential of Different *P. maculiventris* stages

The weight loss of *T. molitor* by *P. maculiventris* feeding was significantly higher than that of the control ($t = 6.74–11.80$; d.f. = 18; $P < 0.05$). Also, there was a significant difference in feeding amount among different stages of *P. maculiventris* ($F = 38.48$; d.f. = 5, 44; $P < 0.05$) (Table 1). The fifth instar *P. maculiventris* caused the largest amount of weight loss of *T. molitor* pupae and the second instar fed the least amount. When feeding equivalency for the second instar of *P. maculiventris* was designated as 1.0., feeding equivalencies for

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nymphs and adults were 1.83–9.45 and 5.67–6.21, respectively (Table 1).

Experiment 2: Prey acceptance and Feeding effectiveness of *P. maculiventris* on different types of prey

Overall, *P. maculiventris* caused the highest mortality to *P. rapae* larvae (Table 2), and the lowest mortality to *H. halys.* The number of attacks required prior to effective feeding upon different prey species differed significantly for the third instar *P. maculiventris* (F = 8.05; d.f. = 4, 27; $P < 0.05$). Third instar *P. maculiventris* required six attacks to effectively feed on *H. cunea* and *E. varivestis* larvae (Figure 1). However, there were no effects of prey species on the number of attacks required prior to effective feeding for fifth instar (F = 1.88; d.f. = 4, 27; $P > 0.05$) and adult *P. maculiventris* (F = 1.70; d.f. = 4, 38; $P > 0.05$). *P. maculiventris* attempted to attack *H. halys* continuously throughout the experimental period, but it could not complete any effective feeding on *H. halys*at all due to the prey's high mobility and chemical defense.

Experiment 3: Feeding preference of *P. maculiventris* on three different prey types

Overall, adult *P. maculiventris* significantly ($\chi^2 = 13.30$; d.f. = 2; $P < 0.05$) preferred to initially attack smooth prey (i.e. *E. rimosalis*) (Figure 2A). The pair-wise comparison for the first attack showed that adult *P. maculiventris* significantly preferred smooth prey over spiny prey (i.e. *E. varivestis*) ($\chi^2 = 4.26$; d.f. = 1; $P < 0.05$), smooth prey over hairy prey (i.e. *H. cunea*) ($\chi^2 = 11.60$; d.f. = 1; $P < 0.05$), and spiny prey over hairy prey ($\chi^2 = 2.66$; d.f. = 1; $P < 0.05$). Fifth instar *P. maculiventris* showed a significant ($\chi^2 = 6.63$; d.f. = 2; $P < 0.05$) preference to initially attack smooth prey. Pair-wise comparisons indicated that fifth instar *P. maculiventris* significantly preferred smooth prey over spiny ($\chi^2 = 4.75$; d.f. = 1; $P < 0.05$) or hairy prey ($\chi^2 = 4.75$; d.f. = 1; $P < 0.05$). However, fifth instar *P. maculiventris* did not show significant difference in preference between spiny and hairy prey ($\chi^2 = 0.11$; d.f. = 1; $P > 0.05$). Third instar *P. maculiventris* showed a significant ($\chi^2 = 9.33$; d.f. = 2; $P < 0.05$) preference to first attack smooth prey. Pair-wise comparisons revealed that third instar *P. maculiventris* had significant preference to initiateattack on smooth prey over spiny ($\chi^2 = 0.81$; d.f. = 1; $P < 0.05$) or hairy prey ($\chi^2 = 7.00$; d.f. = 1; $P < 0.05$). Third instar did not show significant ($\chi^2 = 2.50$; d.f. = 2; $P > 0.05$) difference in preference to first attack between spiny and hairy prey.

Table 1: Amount of weight loss (mean ± SEM) of *T. molitor* by *P. maculiventris* feeding and feeding equivalency when the feeding amount by second instar is set as 1.00. Note that first instar is not predacious.

***P. maculiventris* stage**	**N**	**Weight loss of *T. molitor* per day (g)**	**Feeding equivalency**
2nd instar	30	0.003 ± 0.001 c*	1.00
3rd instar	30	0.006 ± 0.002 c	1.83
4th instar	30	0.019 ± 0.006 b	5.13
5th instar	30	0.035 ± 0.011 a	9.45
Adult male	15	0.023 ± 0.010 ab	6.21
Adult female	15	0.021 ± 0.009 b	5.67

* Mean weight loss followed by the same letters is not significantly different ($P > 0.05$; Tukey's HSD test).

Table 2: Mortality of different prey species caused by third instar, fifth instar, and adult *P. maculiventris* feeding. Note that some *P. maculiventris* could feed and kill more than one type of larvae.

Prey species (Order: Family)	***P. maculiventris* stage**		
	3rd instar (N = 12)	5th instar (N = 12)	Adult (N = 12)
P. rapae(Lepidoptera: Pieridae)	91.7%	58.3%	91.7%
E. rimosalis (Lepidoptera: Crambidae)	91.7%	75.0%	91.7%
L. decemlineata (Coleoptera: Chrysomelidae)	66.7%	25.0%	58.3%
E. varivestis (Coleoptera: Coccinellidae)	8.3%	58.3%	83.3%
H. cunea (Lepidoptera: Arctiidae)	8.3%	41.7%	8.3%
H. halys (Hemiptera: Pentatomidae)	0%	0%	0%

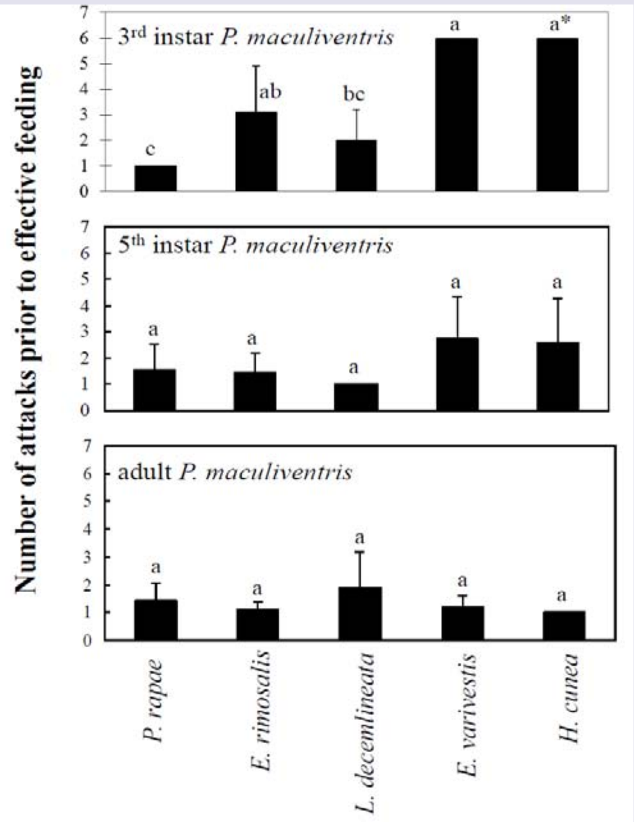

Figure 1: Number of attacks prior to effective feeding by different *P. maculiventris* stages on five different larvae. The bar indicates standard deviation and * means that the same letter are not significantly different ($P > 0.05$; Tukey's HSD test). Note that *P. maculiventris* did not complete any effective feeding on *H. halys* during the 24 hr experimental period.

The results of the feeding preference test showed that adult *P. maculiventris* significantly ($\chi^2 = 17.66$; d.f. = 2; $P < 0.05$) preferred to feed upon smooth prey (Figure 2B). Pair-wise comparisons showed that adult *P. maculiventris* preferred smooth prey over spiny prey ($\chi^2 = 4.48$; d.f. = 1; $P < 0.05$), smooth prey over hairy prey ($\chi^2 = 16.20$; d.f. = 1; $P < 0.05$), and spiny prey over hairy prey ($\chi^2 = 5.44$; d.f. = 1; $P < 0.05$). Fifth instar *P. maculiventris* showed a significant ($\chi^2 = 20.8$; d.f. = 2; $P < 0.05$) feeding preference on smooth prey over hairy and spiny prey. Pair-wise comparisons revealed that fifth instar *P. maculiventris* significantly preferred smooth prey over spiny prey ($\chi^2 = 7.2$; d.f. = 1; $P < 0.05$), smooth prey over hairy prey ($\chi^2 = 16.00$; d.f. = 1; $P < 0.05$), and spiny prey over hairy prey ($\chi^2 = 4.00$; d.f. = 1; $P < 0.05$). Third instar *P. maculiventris* had a significant ($\chi^2 = 6.72$; d.f. = 2; $P < 0.05$) preference for feeding on smooth prey. Pair-wise comparisons indicated that third instar *P. maculiventris* showed

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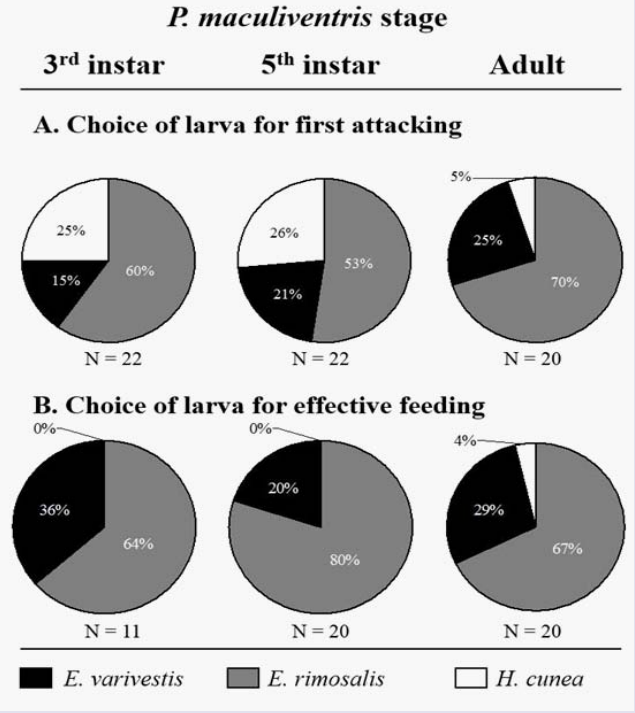

Figure 2: Frequency (%) of prey choices for initial attacks of different *P. maculiventris* stages on three different types of prey (A) and choices for effective feeding on different types of prey (B). See text for detailed statistics and note that attacking means that *P. maculiventris* fed without killing prey and successful feeding means that *P. maculiventris* fed and killed prey after attacking.

feeding preferences for smooth prey over hairy prey ($\chi^2 = 7.00$; d.f. = 1; $P < 0.05$) and spiny prey over hairy prey ($\chi^2 = 4.00$; d.f. = 1; $P < 0.05$). However, no significance was found between smooth and spiny prey ($\chi^2 = 0.82$; d.f. = 1; $P < 0.05$) for third instar *P. maculiventris*.

Discussion

Providing the optimum number of prey needed for rearing natural enemies is important because cannibalism among natural enemies can occur when less prey is offered [23] and it is economically impractical when excessive prey are offered. Wiedenmann and O'Neil [24] showed that the survival and fecundity of *P. maculiventris* was highly reduced if less food was offered, indicating that provision of optimal amount of prey could reduce the cost of mass rearing. In addition, adequate prey quantity is essential for optimal fitness and maximum reproductive potential for natural enemies [25]. The size of *P. maculiventris* increases with their age: 1.60, 2.95, 4.3, 5.8, 8.6, 10.0 mm in length for the first, second, third, fourth, fifth instars and adults, respectively [26]. Feeding amount also increases as *P. maculiventris* weight increases [27]. This study showed a trend that the amount of feeding by *P. maculiventris* increased with age except in the fifth instars. We attribute the higher amount of feeding by the fifth instars to the physiological requirement that the fifth instars need more energy for imminent morphological and physiological development of reproductive organs. Strohmeyer *et al.* [28] found that *P. maculiventris* females fed more than males, which is contradictory to our study. DeClercq and Degheele [29] also reported that mated *P. maculiventris* females consumed more prey than males. We hypothesize that this contradiction could be due to the mating status of the *P. maculiventris* females. *P. maculiventris* adults used in this study were virgin. Additional research would be needed to determine the effect of mating status on feeding amount of male and female *P. maculiventris.*

Possessing hairs or spines on the body is one of the major morphological defense mechanisms of some lepidoperan and coleopteran larvae against predation [30]. Our study showed that *P. maculiventris* significantly preferred to feed on smooth larvae over spiny or hairy prey. We observed that *P. maculiventris* was unable to contact larval integument with its stylet due to long hair or spines on those larvaeal though it attempted to attack hairy or spiny larvae indiscriminately. These results are congruent with Dyer [14] who reported that hairy larvae deterred feeding of *Apiomerus pictipes* (Hemiptera: Reduviidae), a generalist predator. Because hemipteran predators need to make their mouthparts contact the body of prey to feed, hairs and spines on the prey's body could make feeding difficult, resulting in less preference for hairy and spiny larvae. Fifth instar and adult *P. maculiventris* were able to feed on relatively higher numbers of *E. varivestis* larvae because spines of the prey were shorter than the mouthparts of *P. maculiventris*. The length of the mouthparts of *P. maculiventris* increases with the instars (i.e. 3–4mm, 4–5mm and 5–6mm for the third instar, fifth instar and adult, respectively). The length of *E. varivestis* spines was short which enabled the fifth instars and adult *P. maculiventris* to effectively feed upon it. Hairs of *H. cunea,* however, were long and adult *P. maculiventris* could not readily feed upon these larvae. Only fifth instar *P. maculiventris* were able to feed on higher numbers of hairy larvae because the fifth instars were more aggressive and voracious than any other stages of *P. maculiventris*.

The results of this study suggest two important considerations for using *P. maculiventris* as a generalist predator in biological control. First, the effect of *P. maculiventris* stage on feeding amount needs to be considered in mass rearing of *P. maculiventris*. This study showed a larger amount of feeding by fifth instar and adult *P. maculiventris,* indicating that age and size of *P. maculiventris* is an important factor for determining the amount of prey needed in mass rearing systems. Feeding amount of one fifth instar *P. maculiventris* is equivalent to ten second instars or five third instars. Because the feeding potential of different life stages of *P. maculiventris* could vary significantly, the feeding equivalency will also help to decide the amount of *T. molitor* that each stage of *P. maculiventris* need each day. The second, third, fourth and fifth instars of *P. maculiventris* last on average for 5.5, 5, 5 and 9.5 days, respectively [20]. Our study indicates that the mass rearing of one *P. maculiventris* from second through fifth instar will require ca. 14 *T. molitor*. Second, although *P. maculiventris* is known to prefer to feed on larvae with lower behavioral defenses [19], this study showed that morphological characteristics of prey also can deter or hinder *P. maculiventris* feeding. Although our study was not designed to investigate chemical defense of prey against *P. maculiventris*in detail, we observed that *H. halys* could avoid effective feeding by *P. maculiventris* not only because it was highly mobile but because it used chemical defenses when *P. maculiventris* tried attacking.

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