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Parasitism and Host-Location Preference in *Habrobracon hebetor* (Hymenoptera: Braconidae): Role of Refuge, Choice, and Host Instar

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ABSTRACT *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) is a cosmopolitan insect infesting a broad range of commodities, including raw or processed cereal. It has a high fecundity and short generation time, making it a useful tool in testing host–parasitoid hypotheses. The current study examined the interactions between trophic levels during parasitism and host location by *Habrobracon hebetor* Say (Hymenoptera: Braconidae) within a closed environment by carrying out multiple tests to evaluate the role of refuge and host instar, on the mortality of *P. interpunctella* and on the emergence of *H. hebetor*. Results showed that *H. hebetor* was able to parasitize all instars (first through fourth) of *P. interpunctella*, but significantly fewer early instars (first through fourth) were parasitized. Parasitized third and fourth instars were more profitable to *H. hebetor*, irrespective of refuge or choice factors, as significantly more adult parasitoids emerged from third and fourth instars. *H. hebetor* females consistently showed a preference for fourth instars of *P. interpunctella* when they were offered a choice between early and late host instars in arenas both with and without a refuge. Generally, parasitization of early instars was higher in no-choice than in choice tests. The behavior of *H. hebetor* in relation to host choice and its influence on the pest mortality are discussed.

KEY WORDS choice, *Habrobracon hebetor*, host instar, parasitoid, *Plodia interpunctella*

The Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), is a cosmopolitan insect infesting a broad range of commodities, including raw or processed cereal and leguminous products, dried fruits, and animal feeds. Its activities in infested commodities usually lead to serious losses in stored produce (Madrid and Sinha 1982, Arbogast et al. 2000). Recently, biological control techniques such as the use of parasitoids have been used as a replacement for nonenvironmentally friendly synthetic chemical pesticides, which are widely used in managing this moth (Milonas 2005).

The gregarious parasitoid *Habrobracon hebetor* Say (Hymenoptera: Braconidae) is a natural enemy of late larval stages of several field and stored-product lepidopterous pests, including *P. interpunctella* (Milonas 2005), *Ephestia cautella* (Walker) (Press et al. 1982), *Ephestia kuehniella* Zeller (Strand et al. 1989, Darwish et al. 2003), and *Galleria mellonella* L. (Awadallah et al. 1985). *H. hebetor* can be found parasitizing its hosts in both grain storages and field habitats (Puttarudriah and Channabasavanna 1956).

Numerous studies have been conducted on the ability of parasitoids to locate, attack, and successfully develop on different stages of the same host (Vinson 1976, Bellows and Hassell 1988, Mattiacci and Dicke 1995b, Sait et al. 1997, Canale and Loni 2006). While foraging, parasitoids may encounter different host developmental stages, which are vulnerable to attack. These hosts may differ in their profitability in terms of fitness, so that parasitoids become selective for particular stages of their hosts (Godfray and Hunter 1994). Host instars could influence the duration of host location by parasitoids, mortality of host or parasitoid, fecundity of parasitoid or size of its progeny (Sait et al. 1995). Refuge, a physical barrier within host's habitat that protects a proportion of the host population from foraging parasitoids, is another important factor that can either positively or negatively affect parasitism or host location in parasitoids (Sait et al. 1995).

In this study, we report the results of laboratory experiments in which four different *P. interpunctella* larval stages (with or without refuge) were offered to *H. hebetor*, in simple choice and no-choice tests. Our objectives were to determine how refuge, or host developmental stage (instar), would affect parasitism of *P. interpunctella* by *H. hebetor* or parasitoid emergence, and how the interactions of these factors could affect the foraging behavior of *H. hebetor*.

Materials and Methods

All insects used in this study were cultured and studied in a climate room at 29 ± 1°C, 60–70% RH, and a photoperiod of 14:10 (L:D) h.

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Collection and Rearing of Test Insects. *P. interpunctella* was originally obtained during October 2005 from infested dried peanuts stored in the research and teaching warehouse of Huazhong Agricultural University (Wuhan, China). Since then, the strain has been maintained on artificial diet consisting of cracked wheat (1,000 g), wheat shorts (1,000 g), wheat germ (100 g), brewer's yeast (80 g), sorbic acid (4 g), methyl-*p*-hydroxybenzoate (4 g), glycerine (240 ml), pure honey (240 ml), and 120 ml of water (McGaughey and Beeman 1988). *P. interpunctella* adults (1–2 d old) were collected from the stock culture and held in 500-ml glass jars filled with artificial diets for 24 h for oviposition. The resulting first through fourth instar larvae were used for bioassays. The mean head capsule width (Yu et al. 2003) and weight of the instars (Cloutier et al. 2000) were used in determining instar stages. Head capsules were collected, placed into a gel cup, and then measured using a digital length measuring unit (WX-130, Shanghai Equipment Company, Shanghai, China).

H. hebetor was procured from Xinjiang Agricultural Academy (Xinjiang, People's Republic of China) in April 2006. This strain was previously used for many generations in biocontrol of *Helicoverpa armigera* (Hübner) and has since been maintained in our laboratory on honey and *P. interpunctella* larvae. Adult parasitoids were released into glass jars (diameter, 14 cm; height, 16 cm) containing *P. interpunctella* late larvae and covered with white muslin cloth. After 24 h of exposure to parasitoids, the parasitized larvae were removed and kept on paper discs (6 by 4 cm) inside glass vials for further development.

To obtain the newly emerged parasitoid, 20 *P. interpunctella* larvae (fourth instar) were introduced into petri dishes (diameter, 9 cm) containing 10 g of artificial diet. One pair (female and male) of newly emerged (0–12-h-old) *H. hebetor* was released into each petri dish and allowed to attack the hosts for 24 h. Each parasitized larva was incubated separately and the resulting adult parasitoids were used in the experiments.

Experimental Procedures. *P. interpunctella* larvae were introduced into a glass arena (height 10 cm, diameter 4.5 cm) containing either 0.5 cm in depth (no refuge) or 1.0 cm in depth (with refuge) of the artificial diet described above, followed by a mated female parasitoid (4–5 d old). It was then covered with an organdy screen. The parasitoid was left to freely locate and attack the host for either a 24- or 48-h oviposition period. Control treatment was done without the addition of parasitoid. There were five replicates in each case and control. It should be noted that a 1.0-cm depth of host diet is an effective refuge for all larval stages, and only hosts that move into the top 0.5 cm from the surface of the diet are within range of parasitoid's ovipositor (Sait et al. 1997). The arenas were monitored daily for host mortality (parasitism) and or parasitoid mortality as well as the number of emerging wasps. Parasitized larvae were counted and incubated separately to evaluate number of wasps emerging.

Table 1. Analysis of variance for instar and refuge factors on percentage of *P. interpunctella* larvae parasitized by *H. hebetor*, in choice and no-choice experiments

Variable	Choice exp			No-choice exp		
	F	df	*P*	*F*	df	*P*
24-h oviposition period						
Instar	3.495	3	0.027*	21.03	3	0.00***
Refuge	10.839	1	0.002**	1.88	1	0.180 NS
Instar × refuge	0.117	3	0.949 NS	0.23	3	0.874 NS
48-h oviposition period						
Instar	9.177	3	0.000***	17.34	3	0.00***
Refuge	54.336	1	0.000***	1.33	1	0.258 NS
Instar × refuge	1.684	3	0.190 NS	0.06	3	0.981 NS

For each experiment, a matrix featuring 40 values for each variable was obtained: four host-instar stages × two refuge conditions × five replicates. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

No-Choice and Choice Experiments. In the choice experiment, a female parasitoid was confined in individual glass arenas (height, 10 cm; diameter, 4.5 cm) with 12 *P. interpunctella* larvae (three individuals of each of the four instars), whereas in the no-choice experiment, the parasitoid was confined with 12 individuals of a single instar (first through fourth). So, the choice offered to the parasitoid is the choice of instar. For the choice and no-choice experiments, emergence data were collected from a total of 160 treatment combinations with four instars × two refuge conditions × two choice conditions × two oviposition periods × five replicates. Data from treatments with no parasitoid were dropped before analysis for percentage of parasitism and number of emerging wasps, because in arenas with no parasitoid, no parasitism or emergence was observed.

Data Analysis. Statistical analyses were performed with SPSS 11.0 software (SPSS, Inc., 2007) and XL Stat software (XLSTAT, 1995–2007). Analysis of variance (ANOVA) procedures were performed to test the significance of host instar, refuge, and their interactions on larval mortality and parasitoid emergence. Tukey's b tests also were performed to compare parasitism and emergence rates for each host instar. Two-sample *t*-tests were performed to test the existence of significant differences in parasitism and parasitoid emergence between larvae from choice and no-choice conditions.

Results

Effect on Parasitism. After a 24-h oviposition period, under choice condition, host instar, and refuge significantly affected the percentage of *P. interpunctella* parasitized by *H. hebetor* (Table 1). The interaction between instar × refuge on percentage of parasitism was not significant. In the no-choice experiment, only instar had a significant effect on parasitism. The effects of refuge and instar × refuge were not significant. A similar trend was observed for the percentage *P. interpunctella* parasitized after a 48-h oviposition period.

After a 24-h oviposition period in the no-choice experiment, the percentage of first and second instars parasitized was higher than observed for the same

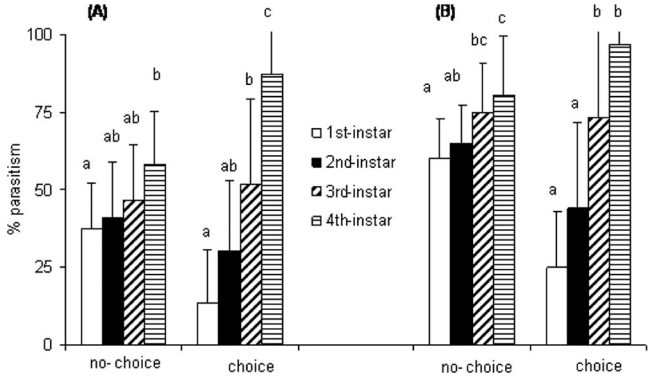

Fig. 1. Effect of host instars on percentage (mean ± SD) *P. interpunctella* larvae parasitized by *H. hebetor*. (A) Within a 24-h oviposition period. (B) Within a 48-h oviposition period. In the choice experiment, a female parasitoid was confined in individual glass arenas with 12 *P. interpunctella* larvae (three of each four instars), whereas in the no-choice experiment, the parasitoid was confined with 12 individuals of a single instar (first through fourth). The bars within each experiment (choice or no-choice) with the same letter(s) are not significantly different ($P > 0.05$; Tukey's b test).

larvae stages in the choice experiment (Fig. 1A and B). This trend also occurred in the test using a 48-h oviposition period. In the no-choice experiment, more first instar larvae were parasitized than when the parasitoid had a choice between larval stages. Generally, parasitism seemed to increase with the increase in oviposition period. Significantly more fourth instar larvae were parasitized than other larvae from the other stages irrespective of the duration of exposure (Fig. 1A and B).

Level of refuge (diet depth of 0.5 versus 1.0 cm) had significant effect on parasitism by *H. hebetor* at both 24- and 48-h oviposition exposure times under choice condition. A lower percentage of hosts were parasitized in the presence of a refuge (1.0-cm diet depth) than in the absence of a refuge (0.5-cm diet depth). In contrast, parasitism was not significantly affected by refuge in the no-choice tests Fig. 2A and B).

The nonsignificant interaction between instar × refuge indicated that, irrespective of the presence of refuge, percentage of host parasitized by *H. hebetor* increased with increase in larval stage.

Effects of Host Instar on *H. hebetor* Emergence. The difference between emergence rates of males ($P = 0.496$) and females ($P = 0.278$) was not significant. We therefore only considered the average number of *H. hebetor* adults emerged from both 24- and 48-h oviposition periods and did not consider the sex ratio of emerged wasps. Only host instar significantly affected parasitoid emergence rate (Table 2). Refuge and the interaction among the two factors did not significantly affect parasitoid emergence. However, parasitoid emergence was higher under no-choice condition than in choice (Fig. 3). There was no significant difference between the parasitoid emergence rates on third and fourth instars, but this was significantly different from parasitoid adults emerging from second instars (Fig. 3). Emergence of first instars was negligible.

Discussion

The developmental stage of *P. interpunctella* larvae as hosts had a significant effect on parasitism by *H.*

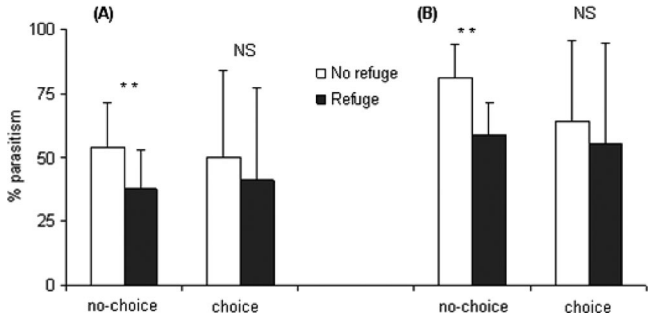

Fig. 2. Effect of refuge factor on percentage (mean ± SD) *P. interpunctella* larvae parasitized by *H. hebetor*. (A) Within a 24-h oviposition period. (B) Within a 48-h oviposition period. In the choice experiment, a female parasitoid was confined in individual glass arenas with 12 *P. interpunctella* larvae (three of each four instars), whereas in the no-choice experiment, the parasitoid was confined with 12 individuals of a single instar (first through fourth). Significant differences between means were tested by two-sample *t*-tests (pairwise comparisons: **, $P < 0.01$; NS, not significant).

Table 2. Analysis of variance for instar factor on *H. hebetor* emergence, in choice and no-choice experiments

Variable	Choice exp			No-choice exp		
	F	df	*P*	*F*	df	*P*
Instar	20.955	3	0.000***	20.33	3	0.000***
Refuge	0.282	1	0.599 NS	0.98	1	0.330 NS
Instar × refuge	0.850	3	0.477 NS	0.14	3	0.933 NS

For each experiment, a matrix featuring 40 values for each variable was obtained: four host-instar stages × two refuge conditions × five replicates. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

hebetor. Early instars are generally difficult to locate and parasitize by the parasitoid, because they feed deep within the food medium (the food medium serve as a refuge). Sait et al. (1997) reported that it was more difficult for the parasitoid *V. canescens* to locate and parasitize *P. interpunctella* second instars, which are concealed in a refuge, than fifth instars within the same environment. Other researchers have reported that host location in braconids could be achieved if mobile host larvae and food were present (Duan and Messing 2000). In the current study, *H. hebetor* apparently had difficulty in locating first and second instars of *P. interpunctella,* although they were exposed in combination with their food medium. The greater rates of parasitism in third and fourth instars as compared with first and second could reflect differences in the ability of the parasitoids to locate different instars, differences in preference for different instars, or a combination of these. Early instars could be more difficult to locate because of their size and the presence of refuge. Once located, earlier instars might be less preferred based on age-dependent cues. Meyhöfer and Casas (1999) reported that vibrations produced by hosts which were feeding or moving played a major role in host location in a number of parasitoid species. The inability of *H. hebetor* to locate and attack a higher percentage of early instars compared with later instars could result from the fewer or weaker vibrations produced by the early instars. Furthermore, *H. hebetor,* as do many parasitoids, uses chemical cues (kairomones) when searching for hosts in a concealed environment (Weseloh 1987, Vet and Dicke 1992, Lou and Cheng 2001). Although kairomonal activities were not directly evaluated in this study, release of infochemicals by early instars may be relatively low compared with those emitted by late instars, thereby making it difficult for female *H. hebetor* to locate and parasitize younger hosts (Vet and Dicke 1992).

The presence of refuge resulted in low percentage host parasitism, particularly of first and second instars. The early larval stages of *P. interpunctella* are very active and move deep into the infested commodity during their feeding activity. In contrast, fifth to seventh instars wander away from the infested produce to the surface in search of pupation sites (Mbata and Osuji 1983). Thus, the presence of refuge is an advantage for early instars. This ecological behavior explains the observed refuge effect on the first and the second instars. Furthermore, the presence of refuge allows only a fraction of the host population to be vulnerable to parasitoid attack thereby reducing the overall percentage of parasitism. This could also lead to a competition for hosts among the parasitoids. When there is no refuge, more individual hosts will be accessible to the parasitoid. Conversely, the presence of refuge should decrease the accessibility to the host, increase the competition between parasitoid and decrease the percentage of the host parasitized.

This study also demonstrated that *H. hebetor* is capable of locating and attacking first to fourth instars of *P. interpunctella.* But when female *H. hebetor* were offered a choice between early and late host instars, they preferred late instars. The low preference for first and second host instars by *H. hebetor* could be due to host selectivity, which is a common phenomenon among several parasitoids (Canale and Loni 2006), including braconids (Taylor 1988a). The use of age-dependent cues has been described as one of the mechanisms parasitoids use to discriminate between different stages of the same host (Mattiacci and Dicke 1995a). One reason why *H. hebetor* would discriminate between different instars of the same host is that longer time and energy is expended while searching for first or second host instars, whereas less energy and time is required to attack late instars. Therefore, because late instars could easily be attacked, it is more

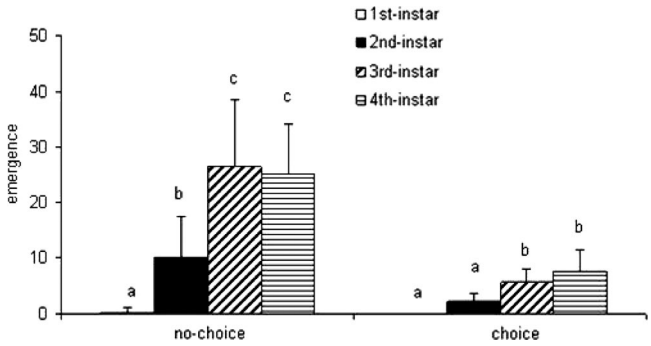

Fig. 3. Influence of host instars on the average number of *H. hebetor* adult emergence under choice and no-choice conditions. The bars within each experiment (choice or no-choice) with the same letter are not significantly different ($P > 0.05$; Tukey's b test).

profitable to the parasitoid to parasitize late larval stages of its host in a population of mixed age-group of host instars (Taylor 1988a, Mattiacci and Dicke 1995b).

Although this study showed that *H. hebetor* is capable of locating and parasitizing all larval stages of *P. interpunctella,* parasitized late instars yielded markedly more adult parasitoids than early instars. There was negligible parasitoid emergence from *P. interpunctella* first instars. *H. hebetor* is known to withhold or reduce the number of eggs laid in the presence of low-quality hosts or nonpreferred stages (Taylor 1988b, Ode et al. 1997). Competition for food among *H. hebetor* larvae developing on early host instar could have resulted in high parasitoid mortality. It was observed that survival was lower and competition more intense on smaller hosts, whereas studying the effect of host size and species on growth and development of *H. hebetor* parasitizing *P. interpunctella* (Taylor 1988a). Benson (1973) reported that larval mortality of *H. hebetor* parasitizing *Cadra cautella* (Walker) increased abruptly when the number of eggs on a host exceeded approximately eight, suggesting a scramble-like competition between the larval parasitoids.

H. hebetor could be described as a weak competitor with an opportunistic and specialized behavior. The absence of emergence in early host stage, and the decrease of parasitism when few hosts are accessible (during refuge condition) explained the weak competition capacity. The parasitism of all instars in the no-choice experiments revealed the opportunistic ability of the parasitoid. Also, the significant effect of host instar on parasitism (under both choice and no-choice conditions) illustrated the specialized behavior of *H. hebetor* on late host instars.

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