

Oviposition and Reproductive Performance of *Habrobracon hebetor* (Hymenoptera: Braconidae) on Six Different Pyralid Host Species

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ABSTRACT *Habrobracon hebetor* Say (Hymenoptera: Braconidae) is a gregarious ecto-parasitoid that attacks larvae of several species of Lepidoptera, mainly pyralid moths infesting stored products. Host quality strongly influences the reproductive success of the parasitoid. In this study, we assessed the reproductive performance of the parasitoid, *H. hebetor* in a series of laboratory experiments using six different pyralid host species: Indianmeal moth, *Plodia interpunctella* (Hübner), Mediterranean flour moth, *Ephestia kuehniella* (Zeller), almond moth, *Ephestia cautella* (Walker), rice moth, *Corcyra cephalonica* (Stainton), navel orangeworm, *Amyelois transitella* (Walker), and greater wax moth, *Galleria mellonella* L. Experiments were conducted using petri dishes (100 by 15 mm) as experimental arenas at $29 \pm 1^\circ\text{C}$, $65 \pm 5\%$ relative humidity, and a photoperiod of 14:10 (L:D) h. Two-day-old *H. hebetor* females were introduced singly into experimental arenas and given a single host larva every day throughout their lifetime. The numbers of hosts paralyzed and parasitized, numbers of eggs laid each day on each host, egg-to-adult survivorship, and progeny sex ratio were used as parameters for assessing host suitability. Paralysis of hosts by *H. hebetor* females was significantly affected by host species. *H. hebetor* paralyzed >95% of the preferred host larvae that were offered and also used $\approx 90\%$ of those for oviposition. Daily fecundity was highest on *G. mellonella* (22.1 ± 0.4) and *C. cephalonica* (21.6 ± 0.3), and lowest on *E. cautella* (13.4 ± 0.2). The egg-to-adult survivorship and progeny sex ratio were also significantly affected by the host species. The highest percentage of parasitoid survival was on *A. transitella* (75.7 ± 2.0) and *C. cephalonica* (75.4 ± 2.5), and lowest on *G. mellonella* (49.7 ± 4.8). Our studies clearly showed that *H. hebetor* females can paralyze and lay eggs on several pyralid species, but it cannot necessarily develop and reproduce optimally on all host species that it can paralyze and parasitize.

KEY WORDS stored-product pest, biological control, parasitoid, reproduction, host quality

The use of biological control agents in food storage situations is not a new concept, but it has long been neglected because of the potential contamination of food products by introducing natural enemies and the low tolerance limit for pest insect damage (Arbogast 1983). Recently attention has been focused on nonchemical methods of stored-product protection, including biological control of stored-product pests, due to negative impacts of pesticides, such as restrictions on the use of certain pesticides and the evolution of insecticide resistance in pest populations (Arbogast 1984, Hagstrum et al. 1999, Phillips et al. 2000, United Nations Environment Program 2006). The use of beneficial insects in stored-product systems received government approval as a pest mitigation practice in the United States, and is exempted from a requirement for minimum tolerance levels (Environmental Protection Agency [EPA] 1992). All genera of parasitoids and predators that are known to attack stored-product

insects are exempted for their use and occurrence in stored raw commodities and processed food (Brower et al. 1996). Thus, biological control can be a legal, safe, and viable method of stored-product protection.

Stored-product pyralid moths (Lepidoptera: Pyralidae; Phycitinae) are among the most destructive pests of stored-food commodities because their larvae infest the value-added, finished food products that are packaged and ready for retail use. The Indianmeal moth, *Plodia interpunctella* (Hübner), Mediterranean flour moth, *Ephestia kuehniella* (Zeller), almond moth, *Ephestia cautella* (Walker), navel orangeworm, *Amyelois transitella* (Walker), tobacco moth, *Ephestia elutella* (Hübner), and the raisin moth, *Ephestia figuliella* (Gregson) are among a cosmopolitan group of stored-product pests in the subfamily Phycitinae, including the rice moth, *Corcyra cephalonica* (Stainton) and the greater wax moth, *Galleria mellonella* L. in the subfamily Galleriinae (Lepidoptera: Pyralidae) (Simmons and Nelson 1975; Chauvin and Chauvin 1985; Vick et al. 1987; Cox and Bell 1991; Johnson et al. 2000, 2002).

Habrobracon hebetor Say (Hymenoptera: Braconidae) is a gregarious, idiobiont, ectoparasitic wasp that

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attacks larvae of several species of Lepidoptera, mainly, pyralid moths infesting stored products (Brower et al. 1996). *H. hebetor* is considered one of the potential biological control agents for stored-product pests because of its cosmopolitan distribution and ability to regulate populations of stored-product moths (Simmons and Nelson 1975; Hagstrum and Smittle, 1977, 1978; Krombein et al. 1979; Press and Flaherty 1981; Brower et al. 1996). *H. hebetor* females first paralyze their host larva by stinging and then laying variable numbers of eggs on or near the surface of paralyzed hosts (Antolin et al. 1995). The paralyzed host larvae are then used as food sources for both developing wasps and also adult females. Normally the female *H. hebetor* paralyzes several larvae and returns afterwards to find and oviposit on some immobile larvae (Ullyett 1945). *H. hebetor* females paralyze many more hosts than needed for oviposition, and paralysis is always fatal, though life may continue for nearly a month if not parasitized by wasp larvae. Under the natural conditions, only a small proportion of the paralyzed larvae are actually used for oviposition (Doten 1911, Richards and Thomson 1932).

Host quality strongly influences the main components of parasitoid fitness, such as fecundity, developmental time, survivorship, secondary sex ratio, and size of the emerging adult wasps (Vinson and Iwantsch 1980, Charnov 1982, Godfray 1994). Successful identification of host quality, and adjusting the clutch size accordingly, has important consequences for the fitness of a gregarious parasitoid (Godfray 1987, Taylor 1988). Several studies have shown that the clutch sizes of gregarious parasitoids are correlated with the size of the hosts at oviposition (Hardy et al. 1992, Zaviezo and Mills 2000). Therefore, attacking large hosts and provisioning the host with optimum clutch size maximizes the female parasitoid's reproductive success and is considered adaptive in terms of parasitoid fitness. In contrast, recent work has shown that host size at the time of oviposition may have little influence on the fitness functions in some of the koinobiont species (Harvey 2000, Harvey et al. 2004). However, little information is available on whether such a situation occurs in *H. hebetor*, a gregarious idiobiont ectoparasitoid of lepidopterous moth pests of stored-food products. The experiments presented here compare and examine the effects of six pyralid host species from two different subfamilies, with considerable variation in larval body size, on several reproductive parameters of *H. hebetor*. Basic and applied aspects of parasitoid biology are discussed relative to optimization of efficacy for the biological control and management of stored-product moths.

Materials and Methods

Parasitoid Origin and Rearing. The *H. hebetor* used in this study originated from feral adults collected from grain bins at the Stored Products Research and Education Center, Oklahoma State University, Stillwater, OK, in November 2003 and were associated with an infestation of the Indianmeal moth, *P. interpunctella*.

Table 1. List of host species (Lepidoptera: Pyralidae) used in this study and their average larval body weight (mg \pm SE; $n = 12$)

Subfamily	Common name	Scientific name	Larval weight
Phycitinae	Navel orangeworm	<i>A. transitella</i>	55.00 \pm 1.90
	Almond moth	<i>E. cautella</i>	18.66 \pm 1.31
	Mediterranean flour moth	<i>E. kuehniella</i>	24.56 \pm 0.96
Galleriinae	Indianmeal moth	<i>P. interpunctella</i>	20.15 \pm 0.92
	Rice moth	<i>C. cephalonica</i>	48.89 \pm 1.66
	Greater wax moth	<i>G. mellonella</i>	262.78 \pm 15.17

punctella. The parasitoids were then cultured and mass-reared on full-grown larvae of *P. interpunctella* in the laboratory at a temperature of 29 \pm 1°C, 65 \pm 5% relative humidity (RH), and a photoperiod of 14:10 (L:D) h. Full-grown larvae of *P. interpunctella* were obtained from a laboratory culture that was reared on a standardized diet of corn meal, chick laying mash, chick starter mash, and glycerol (Phillips and Strand 1994) at a volumetric ratio of 4:2:2:1, respectively, at a temperature of 28 \pm 1°C, 65 \pm 5% RH, and a photoperiod of 14:10 (L:D) h.

Host Species. Four species of phycitine pyralids and two species of nonphycitine pyralids were studied in these experiments (Table 1). The larvae of phycitine pyralids were obtained from laboratory colonies at Oklahoma State University. The initial culture of *G. mellonella* was obtained from a local pet store that was supplied through Timberline Live Pet Foods Inc., Marion, IL. The initial culture of *A. transitella* was obtained from the U.S. Department of Agriculture, Agriculture Research Station, Commodity Protection and Quality Laboratory at Parlier, CA. The culture of *C. cephalonica* was obtained from Insects Limited Inc, Westfield, IN.

The larvae of phycitine species except those of *A. transitella* were reared on the same diet as used for rearing *P. interpunctella*, and these were all maintained at the same environmental condition (see Parasitoid Origin and Rearing). *A. transitella* was reared on a mixture of 11.355 liter of flakey red food bran, 900 ml of honey, 800 ml of deionized water, 100 gm of brewer's yeast, and 10 ml of Vanderzants vitamins solution (1%). *G. mellonella* was reared on a mixture of wheat flour, honey, glycerol, bee wax, and brewer's yeast at a weight basis ratio of 0.44:0.23:0.18:0.04:0.11, respectively. *C. cephalonica* was reared on a mixture of wheat bran, wheat germ, rolled oats, glycerin, and brewer's yeast at a ratio of 1:1:1:1:0.5, respectively. All the cultures were maintained at the similar growth chamber environment as used for rearing of *P. interpunctella*.

Experiments. Experiments were conducted in the laboratory in a no-choice design using plastic petri dishes (100 by 15 mm) as experimental arenas with a single larva of each host species. The last instar, wandering stage larvae were used in this experiment because it has been shown that *H. hebetor* females preferred to attack wandering larvae at a rate 10-fold more than they attack young larvae (Hagstrum and Smittle 1977). Before the experiment, a relative sample of last instar of each host species were randomly

taken from the rearing jars and larval fresh weights were measured ($n = 12$) by placing an individual larva on an M-220 electronic balance (± 0.01 mg, Denver instruments, Denver, CO; Table 1). *H. hebetor* females within 24 h after emergence were kept with males for another 24 h in a 500-ml glass jar for mating. We assume ample opportunity for mating was provided as 80% of virgin *H. hebetor* females mate within the first 15 min of being in the presence of male (Ode et al. 1995). After 24 h, *H. hebetor* females were isolated from the males and introduced individually into experimental arenas containing a single last instar host larva. After 24 h, females were carefully moved to a new experimental arena containing a fresh larva of a given host species. This procedure was repeated until parasitoids died. There were 12 replicates for each host species and all 12 replicates of all the host species were run at the same time. Experiments were conducted in a growth chamber at a temperature of $29 \pm 1^\circ\text{C}$, $65 \pm 5\%$ RH, and a photoperiod of 14:10 (L:D) h. Observations were taken consistently on 24-h period for each female parasitoid until their death, and included the number of hosts paralyzed, parasitized (oviposited on), number of eggs laid on each host, progeny development time, longevity of female parents, lifetime fecundity, egg-to-adult survivorship, and secondary sex ratio (proportion of females in a clutch surviving to adult progeny). Development time was the duration from the egg stage within 6 h of oviposition on individual host larvae by single female *H. hebetor* until emergence of adult parasitoids. Adult emergence was measured twice daily from the beginning of adult parasitoid emergence until emergence stopped (≈ 3 wk).

Statistical Analysis. The influence of host species on the paralysis and oviposition were determined by analysis of variance (ANOVA; PROC MIXED procedure, SAS Institute 2005). A DIFF option was used to analyze the differences among the means ($\alpha = 0.05$). Data on the development time of both sexes were pooled together, as no statistically significant difference between male and female development time was found, and subjected to one-way ANOVA procedures. Oviposition period, postoviposition period, longevity of females, lifetime fecundity, total adult progeny, and egg-to-adult survivorship were determined by one-way ANOVA (PROC MIXED procedure; SAS Institute 2005). The differences in age-specific daily oviposition, adult progeny, and secondary sex ratio (proportion of females) were determined by two-way repeated measure ANOVA (PROC MIXED) assuming an autoregressive covariance structure (Littell et al. 1996). The age of *H. hebetor* females by host species interaction was analyzed within LSMEANS statement and a SLICE option was used to test the overall simple effects of the factor in question.

Results

All six species of pyralid hosts exposed to *H. hebetor* females were paralyzed and used for oviposition (parasitization; Fig. 1). However, proportions of *C. cepha-*

lonica and *G. mellonella* larvae (0.94 and 0.96, respectively) paralyzed by *H. hebetor* females, though relatively high, were significantly lower ($F = 6.94$; $df = 5, 3324$; $P < 0.00001$) than those for *A. transitella*, *E. kuehniella*, or *E. cautella* (Fig. 1). In contrast, proportions of parasitism were significantly higher ($F = 10.24$; $df = 5, 3323$; $P < 0.00001$) on *G. mellonella* (0.93 ± 0.01) than that of *E. kuehniella*, *A. transitella*, or *E. cautella* (Fig. 1).

The egg-to-adult developmental duration for *H. hebetor* progeny varied significantly with host species (Table 2). The shortest total egg-to-adult developmental times were observed on *E. cautella* and *P. interpunctella* (9.7 ± 0.2 and 9.9 ± 0.2 d, respectively), which were not different than those on *E. kuehniella* and *C. cephalonica*. The egg-to-adult developmental time was longest on *G. mellonella* (12.6 ± 0.3 d; Table 2). The total oviposition period for *H. hebetor* females also varied significantly with host species (Table 2). The longest oviposition period was observed on *E. cautella*, *E. kuehniella*, and *A. transitella* at 49.2 ± 3.1 , 48.7 ± 3.8 , and 41.4 ± 2.5 d, respectively, and the shortest was on *C. cephalonica*, *P. interpunctella*, and *G. mellonella* at 33.7 ± 2.8 , 34.7 ± 2.8 , and 36.9 ± 5.0 d, respectively (Table 2). Similarly, postoviposition period for *H. hebetor* females was observed significantly longer on *E. kuehniella* (11.4 ± 3.1) than that of all other host species (2.5 ± 0.4 – 6.1 ± 1.3 d; Table 2). Longevity of *H. hebetor* females was significantly higher on *E. kuehniella* and *E. cautella* larvae (60.3 ± 4.2 and 55.3 ± 3.5 d, respectively) than compared with that on *C. cephalonica*, *P. interpunctella*, and *G. mellonella* (37.9 ± 3.5 , 38.0 ± 2.8 , and 39.4 ± 4.1 d, respectively; Table 2).

Mean lifetime fecundities of *H. hebetor* females were significantly higher on *A. transitella*, *G. mellonella*, *E. kuehniella*, and *C. cephalonica* larvae (810.1 ± 46.0 , 808.0 ± 96.5 , 800.0 ± 65.8 and 728.4 ± 69.6 eggs per female, respectively) than when parasitizing *P. interpunctella* larvae (538.3 ± 50.6 eggs per female; Table 2). A similar trend was observed in terms of the mean number of adult progeny produced from larvae of each hosts species, except for the *G. mellonella* (Table 2). The mean number of adult progeny produced by *H. hebetor* females in their lifetimes on *A. transitella*, *E. kuehniella*, and *C. cephalonica* larvae (616.9 ± 42.6 , 568.2 ± 43.2 , and 551.8 ± 60.6 adults per female, respectively) were significantly higher than when using *G. mellonella*, *P. interpunctella*, and *E. cautella* larvae (369.2 ± 39.1 , 372.6 ± 35.6 , and 426.5 ± 31.5 adults per female, respectively; Table 2). Egg-to-adult survivorship of *H. hebetor* progeny was significantly influenced by the host species. The egg-to-adult survivorship of *H. hebetor* progeny was highest on *A. transitella* ($75.7 \pm 2.0\%$) followed by *C. cephalonica* ($75.4 \pm 2.5\%$), *E. kuehniella* ($71.7 \pm 1.80\%$), and *P. interpunctella* ($70.3 \pm 3.3\%$), and lowest on *G. mellonella* larvae ($49.7 \pm 4.8\%$; Table 2).

Age-specific daily fecundity was significantly affected by the host species ($F = 13.33$; $df = 5, 55$; $P < 0.00001$), age of female wasp ($F = 47.02$; $df = 8, 2805$; $P < 0.00001$), and by the interaction between host

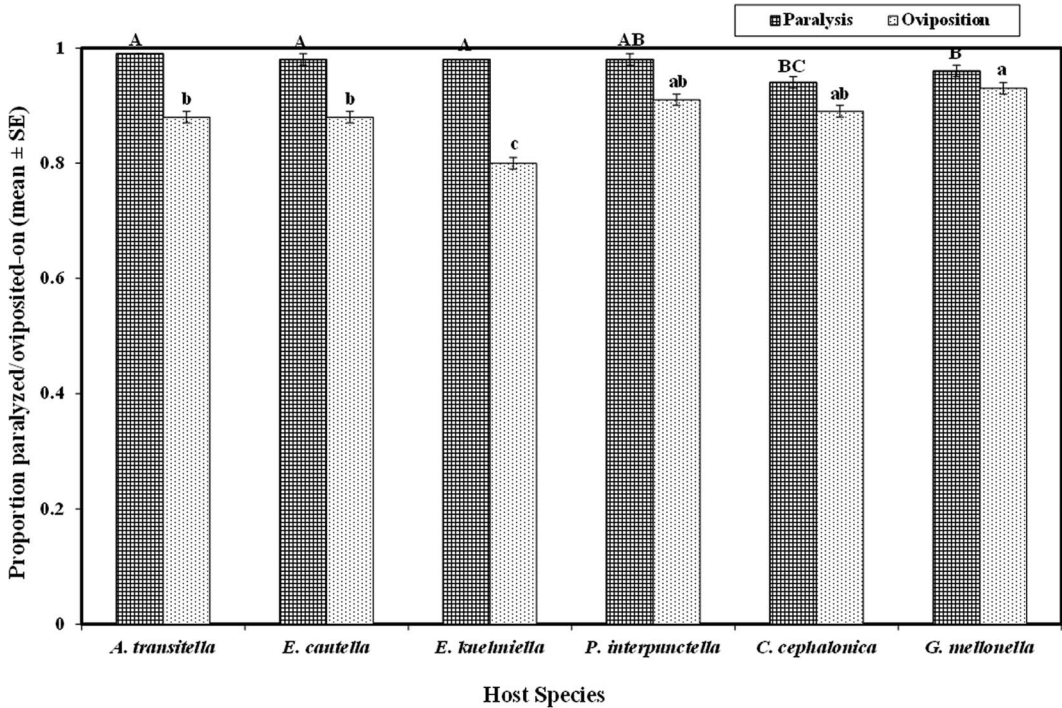


Fig. 1. Proportion of hosts that were paralyzed and parasitized (oviposited on) by *H. hebetor* females throughout their lifetime. Bars of the same type followed by the same lowercase (oviposition) or uppercase (paralysis) letters are not significantly different at $\alpha \geq 0.05$ using least significant difference (LSD) procedures.

species and age of the female wasps ($F = 9.27$; $df = 35, 2805$; $P < 0.0001$). Overall, age-specific daily fecundity was higher for the first 5 wk of oviposition and gradually declined until reproduction ceased (Fig. 2). The daily fecundity was highest in *G. mellonella* in week 2 (27.3 ± 0.7 eggs) followed by *C. cephalonica* in week 5 (24.7 ± 0.8 eggs) and *A. transitella* in week 1 (22.9 ± 0.8 eggs; Fig. 2).

The mean number of adult progeny produced per day from eggs laid in a given week on a given host was significantly affected by the host species ($F = 14.29$; $df = 5, 55$; $P < 0.0001$), age of female wasp ($F = 23.31$; $df = 8, 2805$; $P < 0.0001$), and by the interaction between host species and age of the female wasps ($F = 9.97$; $df = 35, 2805$; $P < 0.0001$). The highest number of *H. hebetor* adults was produced from *C. cephalonica* (19.5 ± 0.9 adults) in week 4 followed by *A. transitella* (18.3 ± 0.6 adults) in week 1 and *G. mellonella* (16.4 ± 0.9 adults) in week 2 (Fig. 3).

The sex ratio (proportion of the female progeny) of emerging adults was not significantly affected by the host species ($F = 1.61$; $df = 5, 55$; $P = 0.1725$). However, it was significantly affected by age of the female wasps ($F = 145.01$; $df = 9, 2632$; $P < 0.0001$) and interaction between host species and age of female wasps ($F = 4.81$; $df = 34, 2632$; $P < 0.0001$). The sex ratio of emerging adults was significantly female biased during the first 3 wk of oviposition, it remained ≈ 0.5 during week 4, and then switched to male-biased progeny from the oviposition resulting from >4 -wk-

old females (Fig. 4). However, in the case of *G. mellonella*, female bias progenies were observed only during the first 2 wk (0.73 ± 0.03 and 0.71 ± 0.03 for week 1 and 2, respectively) and then declined sharply to male bias progeny (Fig. 4).

Discussion

H. hebetor females first paralyze their hosts by injecting venom through the host cuticle with the ovipositor and then lay a variable number of eggs on or near the surface of paralyzed host larvae (Hagstrum and Smittle 1978). In the current study, *H. hebetor* females were able to paralyze and subsequently oviposit on or parasitize most individuals of all the host species that were offered to them (Ghimire and Phillips 2010). Although *H. hebetor* females paralyzed $>90\%$ of all host species, their reproductive performance was significantly higher with phycitine species, which were *P. interpunctella*, *E. kuehniella*, *E. cautella*, and *A. transitella*, as compared with nonphycitine species, *C. cephalonica* and *G. mellonella* (Fig. 1; Table 2). In contrast to paralysis, for the case of the proportion of hosts parasitized, *H. hebetor* females performed better with nonphycitine species as compared with phycitine species, except in *P. interpunctella* (Fig. 1). The possible explanation for this could be difference in size of the host species because full-grown larvae of nonphycitine species were larger than full-grown larvae of phycitine species, except *A. transitella* (Table 1), and

Table 2. Developmental and reproductive statistics (mean ± SE) of *H. hebetor* on six different pyralid host species

Host species	Developmental time (d)	Oviposition period (d)	Postoviposition period (d)	Longevity of females (d)	Lifetime fecundity	Total adult progeny	Egg-to-adult survival (%)
<i>A. transitella</i>	10.5 ± 0.2b (9.5–11.5)	41.4 ± 2.5ab (25–53)	5.5 ± 2.3b (1–27)	46.9 ± 2.8bc (26–60)	810.1 ± 46.0a (461–1069)	616.9 ± 42.6a (307–840)	75.7 ± 2.0a (65.3–83.9)
<i>E. cautella</i>	9.7 ± 0.2a (9.5–10.5)	49.2 ± 3.1a (23–61)	6.1 ± 1.3b (1–13)	55.3 ± 3.5ab (24–69)	653.9 ± 51.6ab (249–896)	426.5 ± 31.5b (201–545)	66.9 ± 3.3b (37.6–80.7)
<i>E. kuehniella</i>	10.3 ± 0.2ab (9.5–12.5)	48.7 ± 3.8a (21–64)	11.4 ± 3.1a (1–31)	60.2 ± 4.2a (22–82)	800.0 ± 65.8a (325–1219)	568.2 ± 43.2a (255–828)	71.7 ± 1.8ab (61.9–83.9)
<i>P. interpunctella</i>	9.9 ± 0.2a (9.5–11.5)	34.7 ± 2.8b (14–44)	3.3 ± 0.4b (1–6)	38.0 ± 2.8c (18–46)	538.3 ± 50.6b (216–754)	372.6 ± 35.6b (137–554)	70.3 ± 3.3ab (40.7–87.5)
<i>C. cephalonica</i>	10.2 ± 0.2ab (9.5–11.5)	33.7 ± 2.8b (13–46)	4.2 ± 1.1b (1–13)	37.9 ± 3.5c (14–56)	728.4 ± 69.6a (278–1081)	551.8 ± 60.6a (245–836)	75.4 ± 2.5a (60.8–88.1)
<i>G. mellonella</i>	12.6 ± 0.3c (12.0–14.5)	36.9 ± 5.0b (9–60)	2.5 ± 0.4b (1–4)	39.4 ± 4.1c (13–61)	808.0 ± 96.5a (259–1243)	369.2 ± 39.1b (130–545)	49.7 ± 4.8c (32.1–82.6)
F	20.05	4.28	3.36	6.76	2.77	6.28	10.42
df	5, 52	5, 66	5, 66	5, 66	5, 66	5, 66	5, 55
P	<0.0001	0.0023	0.0091	<0.0001	0.0247	<0.0001	<0.0001
n	66–148	12	12	12	12	12	12

Means in a column for a given value followed by same letters are not significantly different at α ≥ 0.05 using LSD procedures. Range of data (minimum to maximum) is given in the parenthesis.

thus may have presented a greater stimulus for oviposition. A similar explanation was given by Ghimire and Phillips (2007) for the solitary ectoparasitoid *Anisopteromalus calandrae* Howard parasitizing cowpea weevil. Although better performance (more adult progeny, higher fecundity, more longevity, etc.) occurred with *P. interpunctella* because the wasps used were from a long-term colony reared on *P. interpunctella*, and presumably adapted to *P. interpunctella*, other hosts were actually “better.”

The findings of the current study demonstrated that host species can have a significant effect on several aspects of a parasitoid’s reproductive parameters, such as developmental time, oviposition period, lifetime fecundity, longevity, progeny production, and egg-to-adult survivorship (Table 1). The duration of the egg-to-adult development period was longest on *G. mellonella* (12.6 d), and shortest on *E. cautella* (9.7 d) and *P. interpunctella* (9.9 d). This indicates that *H. hebetor* immatures respond differently to different host resources, both qualitatively and quantitatively, by either developing slowly and using host resources with maximum efficiency or by developing quickly and using host resources with lower efficiency (Godfray 1994). The duration of the oviposition period was longest on *E. kuehniella* (48.7 d) and *E. cautella* (49.2 d) and shortest on *C. cephalonica* (33.7 d) and *P. interpunctella* (34.7 d). A similar pattern was observed for the postoviposition period and longevity of parent females. The oviposition period found here for *H. hebetor* females reared on *P. interpunctella* is similar to that reported earlier by Ode et al. (1996).

Adult female longevity reported here when hosts were *E. kuehniella* (60.2 d) and *G. mellonella* (39.4 d) is more than three- and twofold longer, respectively, than those reported by Amir-Maafi and Chi (2006). This variation could be due to the fact that those authors used a different strain of *H. hebetor* that was associated with *Heliothis* spp. infesting tomato plants, and also there were differences in experimental procedures. Mean lifetime fecundity was generally higher on larger host larvae (*E. kuehniella*, *G. mellonella*, and *A. transitella* with values >800 eggs per female) as compared smaller host larvae such as *P. interpunctella* (538 eggs; Table 2). Furthermore, average daily fecundity was much higher on *G. mellonella* (>27 eggs) as compared with 17 eggs on *P. interpunctella* (Fig. 2). This difference may be explained by the possibility that *H. hebetor* females prefer to attack large hosts and lay more eggs on them, because large host should have more resources available to support their progeny. Increased oviposition on larger hosts could be considered adaptive in terms of parasitoid fitness, as proposed earlier by Charnov (1982) and Godfray (1994), if the host quality is not deleteriously affected by higher parasitoid oviposition rates. However, adaptive increased oviposition on large hosts is not necessarily apparent in our study because egg-to-adult survival of *H. hebetor* progeny was lowest on *G. mellonella* (<50%), though this was the largest host (263 mg) we used in this study and females experienced the greatest lifetime fecundity with them (Table 1). On aver-

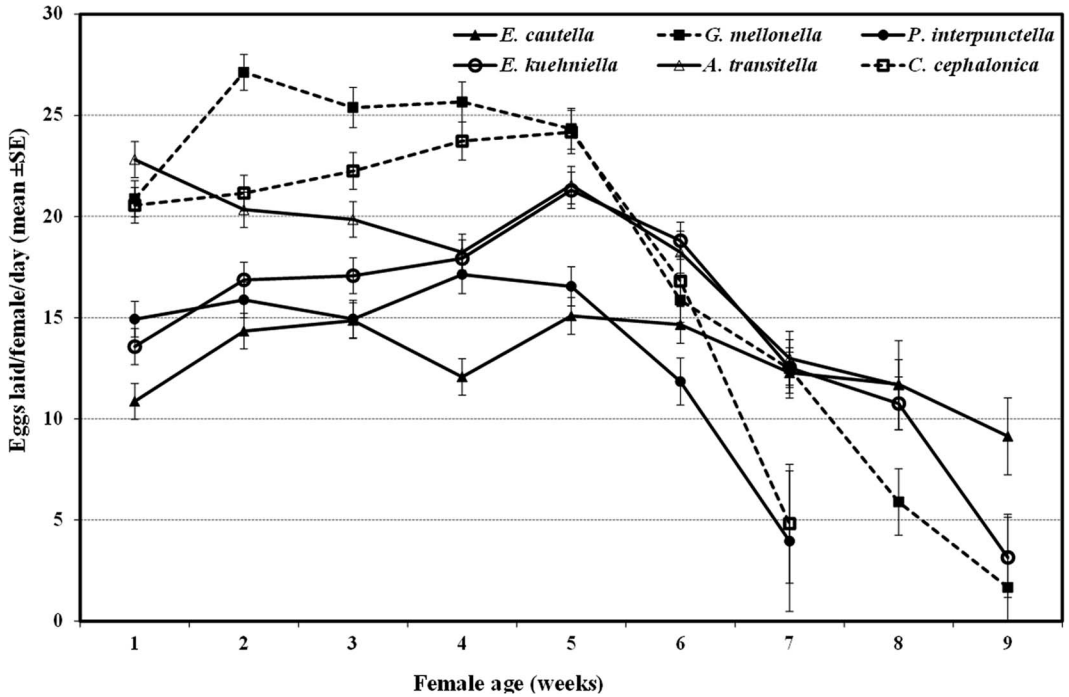


Fig. 2. Daily oviposition by female *H. hebetor* each week on six different pyralid hosts over a 9-wk period.

age, a higher proportion of parasitoids emerged when reared on *P. interpunctella*, *E. kuehniella*, *C. cephalonica*, and *A. transitella* than when reared on *G. mel-*

lonella (Table 2). However, highest lifetime fecundity and highest number of adult progeny were achieved when *H. hebetor* reared on *A. transitella*, which was the

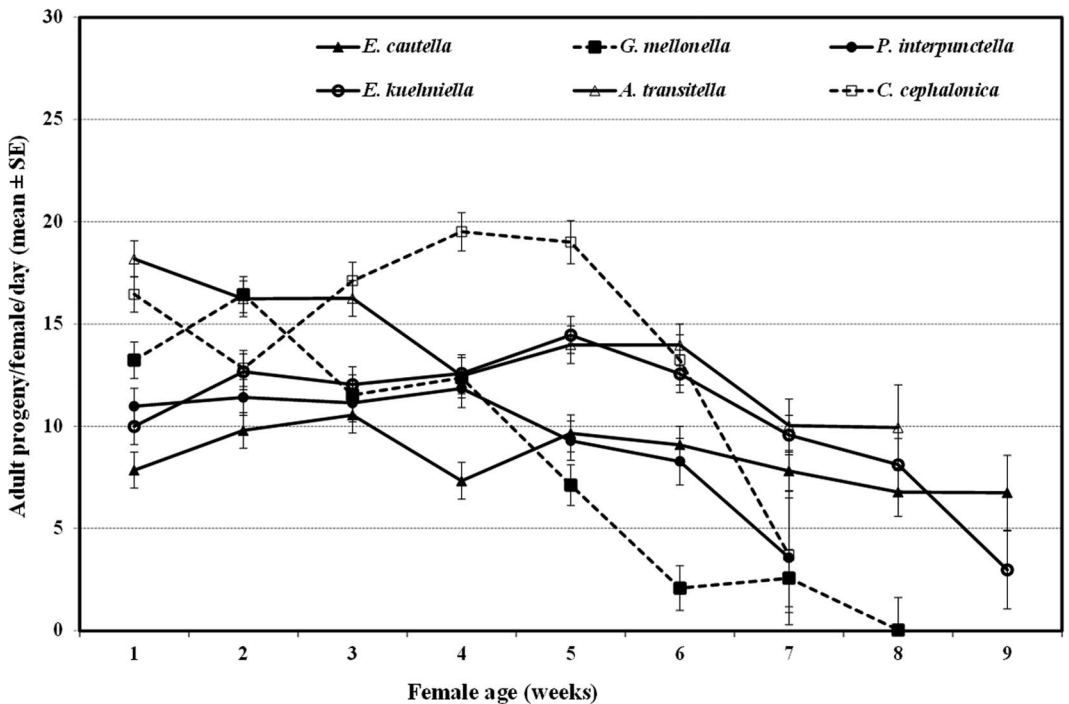


Fig. 3. Mean adult *H. hebetor* produced per day from eggs laid in a given week on six different pyralid hosts over a 9-wk period.

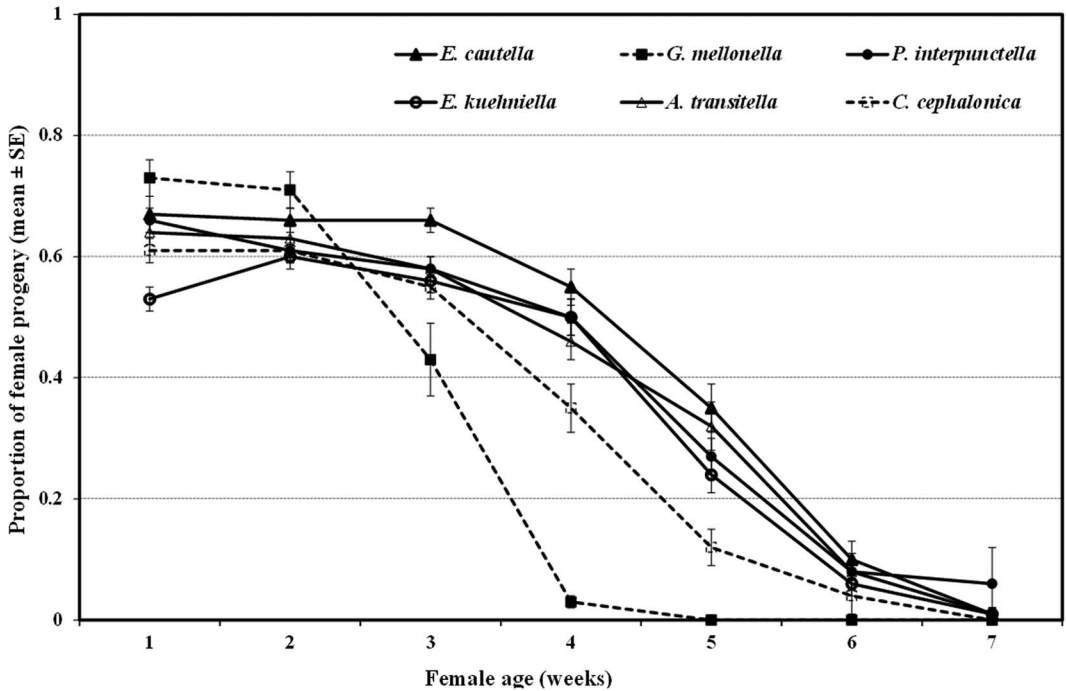


Fig. 4. Mean daily sex ratio (females by total) of *H. hebetor* progeny produced on six pyralid hosts in a given week over a 7-wk period.

second largest host studied (55 mg). Results on parasitoid success and host size indicate that other qualitative factors of hosts are more important than size of the host. These results are similar to those of Milonas (2005), who found more parasitoid survival when *H. hebetor* reared on *P. interpunctella* compared with two other tortricid moths, *Adoxophyes orana* (Fischer von Röslerstamm), and *Lobesia botrana* (Denis & Schiffermüller), which were larger.

Survival of *H. hebetor* progeny was significantly affected by the host species. Although larvae of *G. mellonella* were much larger than other hosts, the parasitoid's larval mortality was much higher in this species. We observed that *G. mellonella* larvae often had a physiological response to the attack of *H. hebetor* by developing a melanized ring at the site of feeding by the *H. hebetor* larvae. Moreover, in a few cases that the body of *G. mellonella* larvae were found turned dark brown in color and then decomposed soon after being stung by *H. hebetor* females. Parasitoid larvae could not survive on those blackened and decomposing hosts, whereas larvae of other species appeared healthy and fresh-looking for several days after paralysis and oviposition. Similar, but more substantial observations were made by Beard (1952) with *G. mellonella* larvae. Thus, although *G. mellonella* may provide a strong behavioral stimulus for female *H. hebetor* to sting it and oviposit, larvae of this moth species are apparently physiologically suboptimal as host for this parasitoid, perhaps because of a nonoptimal interaction of the wasp venom with host physiology that did not occur in the other wasp–host interactions studied here.

Sex ratio, the proportion of adult females produced by *H. hebetor*, was not influenced by the host species but it was clearly influenced by age of the female wasps. Wasps produce slightly female-biased progeny on all hosts resulting from oviposition by ≤ 3 -wk-old females and gradually switch to male-biased progeny resulting from oviposition by >4 -wk-old females. However, in the case of *G. mellonella*, female-biased progeny were produced only by ≤ 2 -wk-old females and then abruptly turned to male bias. In this case, daily fecundity peaked on week 2 and gradually started to decline. This shift in sex ratio could be explained by the fact that after oviposition of several clutches of eggs during the first few weeks, *H. hebetor* females probably became depleted of their sperm reserves from the initial mating, and thus could produce only males from unfertilized eggs. Ode et al. (1997 and 1998) observed a similar phenomenon in sex ratio shift with age beyond the last insemination. Furthermore, those authors demonstrated that *H. hebetor* females generally mate once in their lifetimes and mated females may become sperm-depleted. These females are still able lay similar numbers of eggs and produce only male progeny after depleting sperm reserves. Thus, lack of provisioning females with males later in the experimental period was not the factor for producing male-biased progeny by *H. hebetor* females later in their reproductive lifespan. Results from the current study revealed that *H. hebetor* females lay more eggs during the first 5 wk of oviposition and produced more females during that time, and then became constrained to produce only males (Figs. 2–4). A similar result was reported by Uçkan and Gülel (2002) for

another species of braconid wasp, *Apanteles galleriae* Wilkinson, a koinobiont, solitary, larval endoparasitoid reared on two lepidopteran species, *G. mellonella* and *Achoria grisella* (F.).

In conclusion, *G. mellonella* does not seem to be a very suitable host for *H. hebetor* because parasitoid larvae suffer from high juvenile mortality and the developmental period was relatively long on larvae of *G. mellonella*. This is perhaps from negative parasitoid-induced changes in host physiology. Thus, further studies are merited particularly directed in the areas of host physiological changes in response to envenomization and host-feeding by female *H. hebetor*. Nevertheless, because *G. mellonella* is relatively easy to acquire in the private market, such as pet supply stores, this species could be considered a potential supplementary host for commercial rearing of *H. hebetor*. However, *A. transitella* appears to be the most suitable host for reproductive performance of *H. hebetor*. The hosts *E. kuehniella*, *C. cephalonica*, *P. interpunctella*, and *E. cautella* are also relatively optimal for *H. hebetor* based on longer reproductive lifespan of the wasps, the relatively stable daily fecundity achieved, the higher parasitoid survival rate, and the short generation time of wasps on these hosts. Reproductive fitness of *H. hebetor* can be maximized through the utilization of hosts that allow for the highest levels of parasitoid progeny and survival, which can benefit individual *H. hebetor* wasps in their natural habitat, and which can be useful for enhanced commercial mass production of wasps for purposes of biological control of stored-product moth pests.

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