

Life Tables of *Habrobracon hebetor* (Hymenoptera: Braconidae) Parasitizing *Anagasta kuehniella* and *Plodia interpunctella* (Lepidoptera: Pyralidae): Effect of Host Density

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ABSTRACT The reproductive performance of the parasitoid *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) against the moths *Anagasta kuehniella* Zeller and *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) was studied in the laboratory. The analysis was based on the comparison of parasitoid's life table parameters related to those of its hosts at various conditions of host density (daily supply of 1, 5, 15, and 30 full-grown host larvae). The estimated parameters were the intrinsic rate of natural increase (r_m), the net reproductive rate (R_o), the mean generation time (G), the finite capacity of increase (λ), the gross reproductive rate (GRR), the doubling time (DT), the reproductive value (V_x), and the life expectancy (e_x). The r_m of *H. hebetor* proved to be significantly higher than those of its hosts at all host densities. When only one host per day was supplied, the wasp had the lowest reproductive potential, whereas it was maximized when 15 hosts per day were exposed. Maximum values of R_o and GRR were obtained at densities ≥ 15 host larvae per day. Any increase in host supply above this threshold did not cause significant changes in life table parameters. Variation of r_m as a function of host density can be described by the linear regression. Sex ratio of wasp progeny (females/total) ranged from 0.36 to 0.42, irrespective of host density or species. Newly emerged adults recorded maximum e_x and V_x . The results of this study can be used to improve mass rearing programs and inoculative release applications of *H. hebetor* against moth pests of stored products.

KEY WORDS *Habrobracon hebetor*, *Anagasta kuehniella*, *Plodia interpunctella*, life tables, biological control

Over the past few decades, life tables have become an indispensable tool for biological control workers, especially in evaluating a parasitoid against a host under various climate conditions and host habitats (Birch 1948, Leslie and Park 1949, Messenger 1964, Jarvis and Copland 1996). Such demographic data can be very useful for choosing the most effective biocontrol agents, designing mass rearing programs as well as deciding the timing of introduction in inoculative releases.

Biological control has gradually come to occupy a significant part in stored product integrated pest management (IPM) because of its advantages over traditional chemical methods, pest resistance to conventional pesticides, the phase-out of methyl bromide, the favorable conditions of the stored-product environment for beneficial insects, and its compatibility with other IPM methods (Arbogast 1984, Brower et al. 1996, Schöller et al. 1997, Schöller and Flinn 2000).

Many hymenopterous parasitoids have potential as biocontrol agents against stored products pests. *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) is a gregarious, idiobiont (prevents any fur-

ther development of the host after initial parasitization), cosmopolitan, ectoparasitoid attacking many lepidopterous larvae, mainly moths in the family Pyralidae. Effects of temperature (Ahmed et al. 1985, Kim et al. 2000), relative humidity (Farghaly and Ragab 1984), adult nutrition (Güel and Gündüz 2004), host species (Taylor 1988a, 1988b; Magro and Parra 2001; Güel and Gündüz 2004), host size (Taylor 1988a, 1988b; Güel and Güel 1995), and host density (Yu et al. 2003) on its biology and ecology have been thoroughly studied. Effective control of pyralid moths by *H. hebetor* has been reported in a few field studies (Press et al. 1982, Cline et al. 1984, Cline and Press 1990, Grieshop et al. 2006). However, all the aforementioned studies have not dealt with any life table comparison between the wasp and its hosts or the effect of host density on the reproductive performance of *H. hebetor*.

Benson (1973, 1974) studied the population dynamics of the *H. hebetor*-*Ephestia cautella* (Walker) (Lepidoptera: Pyralidae) interaction, providing life table data and a classic key-factor analysis. Benson's detailed work determined that key factors for *H. hebetor* under the conditions tested were related to competition, whereas for the parasitoid, unexplained variation in fecundity was the key factor. In this study, we estimate and compare specific life table parameters

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between the wasp and its host as a basis for improving mass rearing and release programs of *H. hebetor* against moth pests of stored products. Our approach allowed us to examine effects of host density on parasitoid fecundity and sex ratio.

Materials and Methods

Insect Cultures. Stock cultures of *Anagasta kuehniella* Zeller and *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) originated from a flourmill in Athens, Greece, and a fig warehouse in Kalamata, respectively. They were reared in incubators at 25°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h. The stock cultures were maintained in clear plastic boxes (17 by 11 by 5 cm) each containing 150–200 eggs of the moths and 200–250 g of semolina, which provided the larvae with excess food throughout their larval development.

H. hebetor was collected in a culled fig warehouse near Kalamata. It was reared in similar plastic boxes to those used for moths. Approximately, 200 fifth instars from the host stock culture were placed in each box together with five pairs of adult wasps. This procedure was repeated every 3–5 d. The boxes were left until the next generation of wasps emerged. All experiments were carried out in incubators at 25°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h.

Experimentation with Hosts. To estimate host life table parameters 40 eggs of each host were placed individually in petri dish (9 cm in diameter) containing 20 g of semolina and left undisturbed to complete development. Air circulation was achieved through a hole (diameter 4 cm) in the lid, covered with nylon mesh. After pupation, dishes were checked daily and the number and sex ratio of emerging moths were recorded. Newly emerged female and male moths were paired and placed into a large modified petri dish (12 cm in diameter) containing 30 g of semolina, for egg laying. Each moth pair was transferred daily to another petri dish identical to the previous one to continue oviposition, until female's death. Egg batches from each day were left undisturbed in the dish to complete development. Dishes were checked daily for moth eclosion. Newly emerged moths were sexed and counted.

Experimentation with Parasitoid. Preliminary experiments were conducted to estimate the duration and survival of *H. hebetor* during the preimaginal period. Approximately 100 full-grown larvae of each host were placed with five pairs of wasps for parasitization for 2–3 h. After parasitization 35 parasitized larvae were collected and placed individually into a petri dish (90 mm in diameter). Only one wasp egg was left on each host. Development of wasp larvae was checked daily, and number and sex ratio of progeny was recorded upon emergence.

To estimate life table parameters under various conditions of host density, 1, 5, 15 and 30 full grown (fifth instar) host larvae were introduced into a large modified petri dish containing 30 g of semolina and left undisturbed to settle for 6–12 h. One pair of newly emerged parasitoids (age <24 h) was introduced and allowed to oviposit for 24 h. Wasps had access to honey

Table 1. Development of *H. hebetor* (25°C, 65% RH, photoperiod of 16:8 [L:D] h, one egg per host larva)

Parameter	<i>A. kuehniella</i> mean ± SE (n)	<i>P. interpunctella</i> mean ± SE (n)
Developmental time (egg to adult)	12.85 ± 1.21a (28)	13.16 ± 1.43a (25)
Survival to adult eclosion (%)	80.0	71.4
Sex ratio (♀/♂ + ♀)	0.46	0.44

Means followed by the same letter are not significantly different ($P < 0.05$; Tukey–Kramer honestly significant difference test). n is number of replicates.

smear on the inside of the dish. In case the male was found dead, it was replaced by another of similar age. Each pair was transferred daily to another petri dish identical to the previous dish. Larvae in the previous dish were transferred at 25°C to large glass jars containing excess food medium to complete development. The number and sex ratio of emerging parasitoids was recorded daily. The procedure was carried on until the female parental wasp died. Each host density was replicated for 10 times for each host.

Life Table Construction. The estimated parameters were the intrinsic rate of natural increase (r_m), the net reproductive rate (R_o), the mean generation time (G), the finite capacity of increase (λ), the gross reproductive rate (GRR), the doubling time (DT), the reproductive value (V_x) and the life expectancy (e_x). For life table construction and r_m comparison, the methodology and equations of Eliopoulos (2006) were adopted. For all estimated parameters the raw data were used. Based on preliminary experiments, wasp development was predicted to last 13 d. Developmental data were subjected to analysis of variance (ANOVA), with $\alpha = 0.05$. Means were separated using the Tukey–Kramer honestly significant difference (HSD) test (Sokal and Rohlf 1995). Statistical analysis was performed using the statistical package JMP version 4.0.2 (SAS Institute 2000).

Results

The duration of development of *H. hebetor* did not differ significantly between the two hosts (Table 1) ($F = 0.6958$; $df = 1, 51$; $P = 0.4081$). As was clearly shown, wasp development lasted almost 13 d in both hosts. This is the reason why we assumed that all wasps emerged on thirteenth day after oviposition during life table construction.

Demographic parameters of cohorts of *H. hebetor* adults reared at different conditions of host density are presented in Table 2 and Figs. 1 and 2. Increasing host density from 1 to 15 host larvae per day resulted in significantly higher values of the intrinsic rate of increase (Table 2). Nonsignificant changes of r_m ($\approx 3.5\%$) were recorded for both hosts when host density increased from 15 to 30 host larvae.

The intrinsic rate of increase of *H. hebetor* was significantly higher than that of its host at all host densities (Table 2). The variation of *H. hebetor* r_m as

Table 2. Life table parameters of *H. hebetor* and its hosts (25°C, 65% RH, photoperiod of 16:8 [L:D] h)

Host density	<i>A. kuehniella</i>									<i>P. interpunctella</i>						
	<i>n</i>	Sex ratio	r_m	R_o	GRR	<i>G</i>	<i>DT</i>	λ	<i>n</i>	Sex ratio	r_m	R_o	GRR	<i>G</i>	<i>DT</i>	λ
1	10	0.3728	0.1217aA	11.59	42.00	20.14	5.70	1.13	10	0.3732	0.1092aB	9.09	37.70	20.21	6.34	1.12
5	10	0.4141	0.1631bA	30.33	113.63	20.92	4.25	1.18	10	0.4260	0.1507bA	22.00	97.91	20.51	4.60	1.16
15	10	0.3649	0.1918cA	44.70	150.64	19.81	3.61	1.21	10	0.4109	0.1838cA	37.78	171.67	19.75	3.77	1.20
30	10	0.3459	0.1850cA	40.00	142.56	19.94	3.75	1.20	10	0.3989	0.1859cA	41.14	187.96	19.99	3.72	1.20
Host	15	0.5166	0.0545dA	88.81	113.44	82.33	12.72	1.06	14	0.4918	0.0697dB	97.88	75.84	65.75	9.94	1.07

r_m values of same column followed by the same lowercase letter are not significantly different. r_m values of same row followed by the same uppercase letter are not significantly different. *n* is number of replicates.

a function of host density is depicted in Fig. 3. Relationship between r_m and the natural logarithm of host density can be described very well by linear regression [$r_m = 0.020 \times \ln(\text{host density}) + 0.126$, $R^2 = 0.914$ for host *A. kuehniella*; $r_m = 0.023 \times \ln(\text{host density}) + 0.111$, $R^2 = 0.971$ for host *P. interpunctella*].

Maximum values for R_o and GRR were obtained at densities of 15 and 30 host larvae for adults parasitizing *A. kuehniella* and *P. interpunctella*, respectively. Values of *G* and λ did not show any noteworthy change when host density increased, and the value differentiation did not exceed 5.3 and 6.6%, respectively. Adults supplied with only one host per day showed the longest *DT*. When wasps had access to more larvae of *A. kuehniella* or *P. interpunctella*, *DT* was shortened up to ≈ 25 –36 and 27–41%, respectively, depending on host density. The sex ratio was apparently stable because 37 to 42% of total progeny was female irrespective of host density or species. *H. hebetor* presented higher GRR and λ and lower R_o , *DT*, and *G* than those of its hosts at all host densities.

Life expectancy (e_x) of newly emerged adults ranged between 16.30 and 16.90 with *P. interpunctella* and between 16.60 and 18.40 with *A. kuehniella* as host, and it decreased thereafter at all host densities (Figs. 1 and 2). The same pattern was recorded in reproductive value (V_x) given that *H. hebetor* presented maximum V_x in the age of one (newly emerged adults) (Figs. 1 and 2) and increased when more host larvae were supplied. The only exception was the wasps having access to 15 larvae of *A. kuehniella*, which showed a 9.97% decrease of V_x when host density increased to 30. Both e_x and V_x of *H. hebetor* were higher than those of its moth hosts at all cases (Figs. 1 and 2).

Discussion

Despite the fact that life history parameters are determined under artificial laboratory conditions, they remain a useful tool for evaluating a parasitoid against its hosts under the more complex and fluctuating conditions of their natural environment (Birch 1948, Leslie and Park 1949, Jervis and Copland 1996).

The r_m of *H. hebetor* is significantly higher than those of its hosts at all host densities, as pointed out by the jackknife statistical procedure (see Eliopoulos 2006 for detailed description). Specifically, it is 2.2–3.5 and 1.6–2.7 times higher than *A. kuehniella* and *P. interpunctella*, respectively. Theoretically, this should ensure that *H.*

hebetor would be able to control these moths and thus provide adequate biological control for them. However, this may not be so in natural settings where the insects are less confined and densities of hosts are lower, thereby reducing host discovery rates.

When only one host was exposed, *H. hebetor* presented the lowest reproductive potential, given that it recorded the lowest r_m , R_o , GRR, and λ and highest *DT*, irrespective of host species. This may be attributed to high immature mortality of *H. hebetor* due to extreme attack rates per host larva, because all wasp eggs were laid every day on only one host. Taking into consideration that *H. hebetor* not only lays an average of 12.6 eggs when it is supplied with only one host per day (Yu et al. 2003), but also records increased mortality of immature when the number of eggs laid on a single host is more than eight (Benson 1973; Yu 1999), it may be assumed that extreme immature mortality caused this significant decrease.

Previous studies have pointed out that r_m of parasitoids increases with increasing host density (Mackauer 1983, Liu 1985). This holds true for *H. hebetor* up to host density of 15 host larvae per day. As was shown for the first time by the current study, the r_m does not change significantly above that threshold even after doubling of the host density (Table 2). This phenomenon may occur because the wasp emerges with a limited number of mature eggs and continues developing eggs during its adult life (synovigenic species). Synovigenic wasps lay eggs at physiological maximum when they have access to unlimited numbers of hosts until oviposition is effectively constrained by the rate of egg maturation under the given set of conditions (Heimpel and Rosenheim 1998, Harvey et al. 2001). This phenomenon of egg limitation has been previously recorded in *H. hebetor* (Ode et al. 1997). It is evident from our findings that *H. hebetor* reaches its maximum reproductive potential when it is supplied with almost 15 hosts per day. Thus, it would be meaningless and wasteful to use higher host densities in mass rearing programs of this parasitoid.

The linear response of r_m to host density is similar to that observed for other parasitoids (Burnett 1951, Mackauer 1983). This linear relationship may prove useful for mass rearing design or inoculative release application, because an accurate estimation of r_m can be achieved when host density can be measured. However, it should be clarified that coefficients of this linear relationship may vary according to host species,

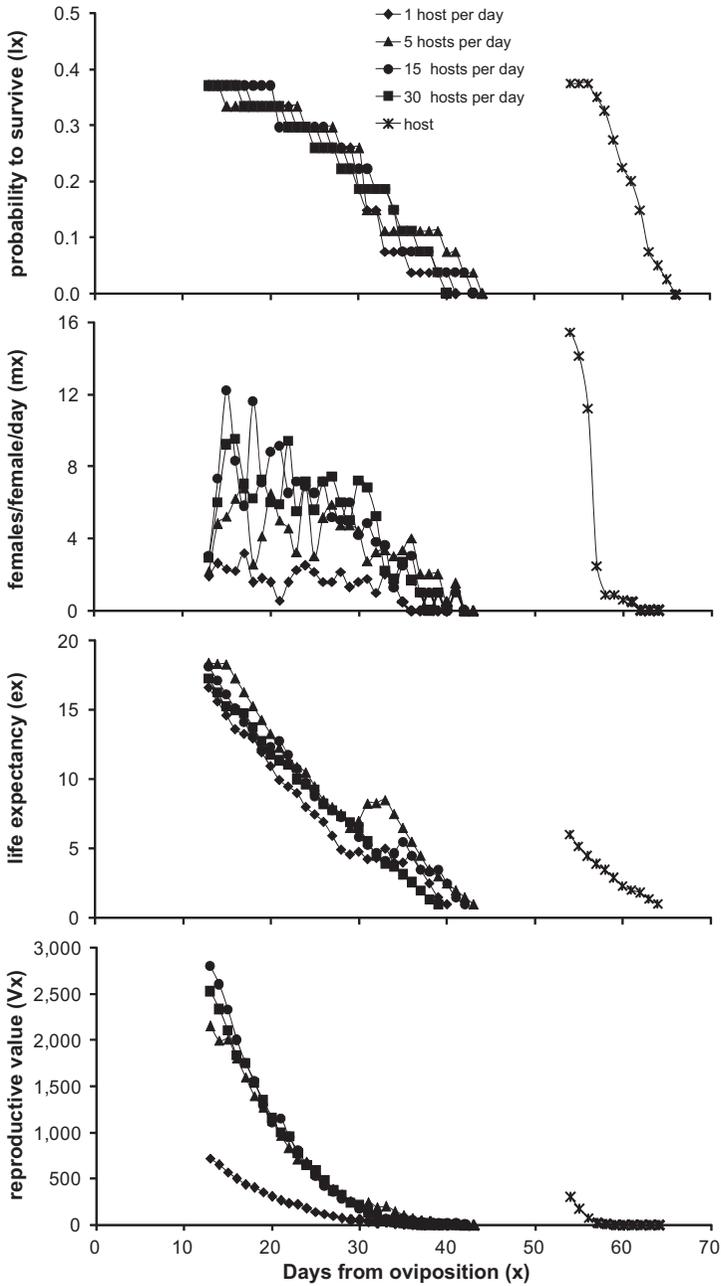


Fig. 1. Survival rate (l_x), female fecundity (m_x), life expectancy (e_x), and reproductive value (V_x) of *H. hebetor* adults and its host *A. kuehniella* at various host densities.

temperature, or other experimental parameter and should be estimated every time.

The r_m of *H. hebetor* attacking other hosts has been estimated to range from as low as 0.152 (Amir-Maafi and Chi 2006) to 0.2910 (Yu et al. 1999). Our estimates range from 0.1092 to 0.1839, depending upon host density. The variability among these reported values for r_m can be attributed to variation in biotic and abiotic factors, including temperature, relative humidity, host species, host density, host habitat, and wasp strain.

The sex ratios (females/total) we detected are within the reported range for *H. hebetor* (Reinert and King 1971, Benson 1974, Rotary and Gerling 1973, Antolin and Strand 1992, Nikam and Pawar 1993, Ohh 1993, Yu 1999, Yu et al. 2003, Gündüz and Gülel 2005). Our finding that sex ratio of *H. hebetor* was unaffected by host density disagrees with Benson (1973) who measured approximately equal numbers of both sexes when there were three eggs per host (sex ratio ≈ 0.45) but 3 to 4 times as many males as females when there

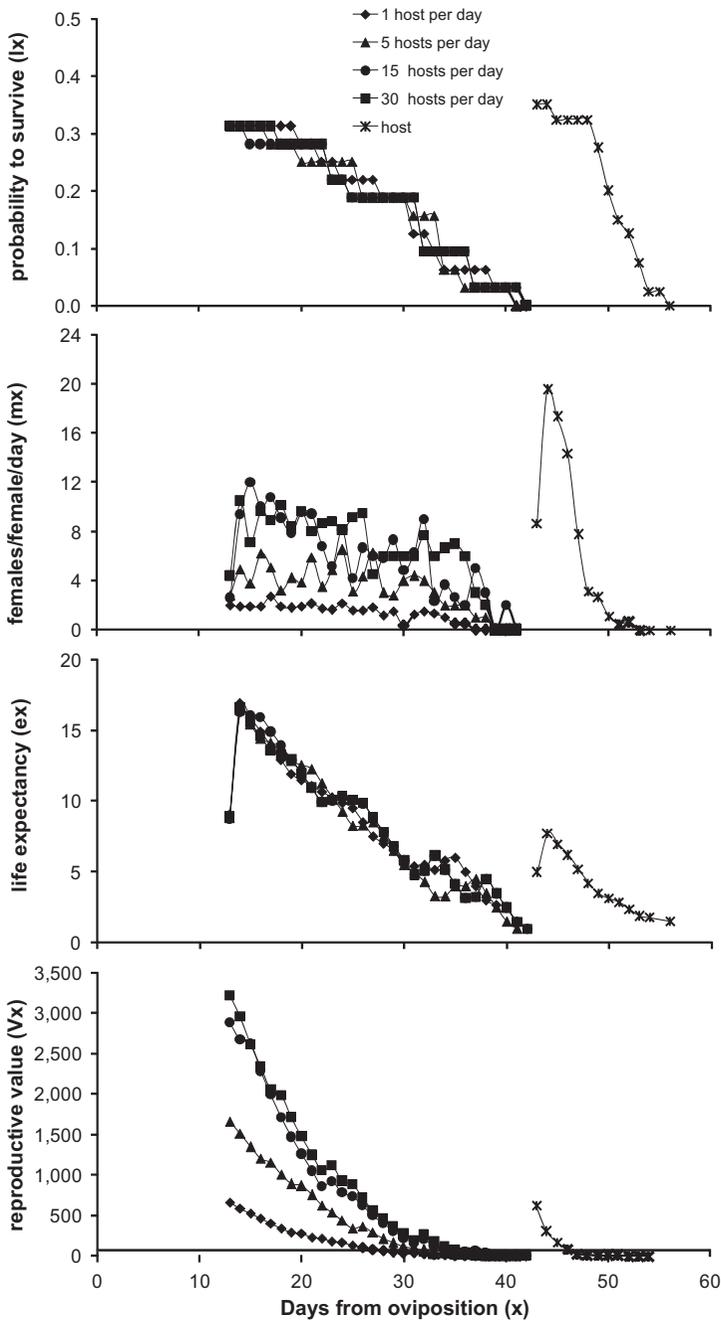


Fig. 2. Survival rate (l_x), female fecundity (m_x), life expectancy (e_x), and reproductive value (V_x) of *H. hebetor* adults and its host *P. interpunctella* at various host densities.

are 18 eggs per host (sex ratio ≈ 0.2) and attributed this change to differential mortality acting more severely to females than males. Moreover, Rotary and Gerling (1973) suggested that the male/total progeny increased when the host/parasitoid ratio decreased. The above-mentioned results are opposite to our findings, probably because of differences in strains, experimental procedure, and host species and size. Significant differences in parasitization behavior, especially dis-

tribution of eggs, among various strains of *H. hebetor* have been observed by other authors (Doutt 1959, Benson 1973).

Maximum values of both e_x and V_x were recorded for individuals of age class $x = 2$, which represent newly emerged adults. The biological meaning of this result is that these individuals are expected not only to live longer but also to offer more progeny to the next generation than their conspecifics of other classes.

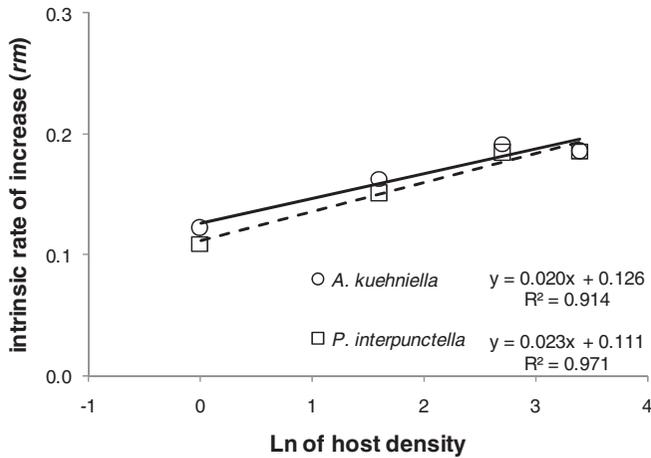


Fig. 3. Relationship between the intrinsic rate of increase (r_m) of *H. hebetor* and natural logarithm of host density.

Similar propositions have been made for other parasitoids (Morales-Ramos and Cate 1993, Doury and Rojas-Rousse 1994, Eliopoulos 2006). A practical interpretation is that newly emerged adults are the ideal individuals for inoculative release, taking into account that control is achieved not only by released wasps but mainly by their offspring.

Our results and published studies (Ohh 1993, Amir-Maafi and Chi 2006) indicate that *H. hebetor* reproductive potential is not strongly influenced by host species identity. This suggests that selection of a host for mass rearing can be based primarily on costs and other considerations that facilitate rearing. If hosts other than those that have been studied are considered for rearing, however, *H. hebetor* performance will need to be evaluated on these hosts.

H. hebetor is a commonly used biocontrol agent against storage moth pests. We have theoretically verified this fact by showing that the wasp is intrinsically capable of suppressing its hosts as revealed by the r_m comparisons. Apart from that, original findings of the current study provide information that will help to facilitate more effective mass rearing and releasing programs of *H. hebetor*. In inoculative releases, an effort should be made for the introduction of newly emerged wasps because they not only live longer but also produce more progeny than older conspecifics. Moreover, when designing mass rearing programs of the wasp it should taken into consideration that host species does not have significant effect on its reproductive potential. There is also no need to supply >15 full-grown host larvae per wasp per day given that maximum population growth is achieved at this density.

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