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Environmental and maternal effects on host selection and parasitism success of *Bracon hebetor*

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Abstract The biological control programs supporting the native species of natural enemies are far more sustainable than those which use exotic enemies of the target pest. Little is known about the effects of the surrounding environment on host selection behavior of *Bracon hebetor* Say (Hymenoptera: Braconidae). In the present study, the effects of the origin of the parasitoid populations, host species and parasitoid rearing history on host selection and parasitism success of *B. hebetor* were investigated. Several life-history parameters, including the frequency of parasitism, percentage parasitism, egg load, survival rate and the offspring sex ratio of the parasitoid were measured. In terms of both selection and parasitism success, *B. hebetor* preferred *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) over *Apomyelois ceratoniae* Zeller (Lepidoptera: Pyralidae) and

Helicoverpa armigera Hübner (Lepidoptera: Noctuidae), and *A. ceratoniae* over *H. armigera*. When different populations of *B. hebetor* were compared, the *B. hebetor* population originated from orchard was the most successful compared with the field and store populations. In addition, the rearing history was influential on the parasitism preference and success: a better performance of the parasitoid was obtained when it was reared on its original host compared with an intermediate host, *E. kuehniella*. The causes and consequences of these findings were further discussed in relation with mass rearing of this parasitoid for biological control programs.

Keywords Parasitism · Experience · Rearing history · Population · Hymenoptera · Braconidae

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Introduction

The biological control programs supporting the native species of natural enemies are far more sustainable than those which use exotic enemies of the target pest (Losey and Vaughan 2006; Zehnder et al. 2006). In order to enhance the efficacy of native natural enemies, investigations on the demographic characteristics, such as sex ratio and experience, are of prime importance (Cobbold et al. 2009; Heimpel and Lundgren 2000). There is evidence suggesting that parasitoids regulate their clutch size based on the size or quality (*i.e.*, the

nutritional value) of their hosts (Godfray 1994; Taylor 1988). In a multitrophic context, the effects of resource variation may cascade up to higher trophic levels, influencing the fitness and performance (such as survival, development, size, longevity, fecundity and sex ratio) of natural enemies (Karimzadeh and Wright 2008; Karimzadeh et al. 2013). It is likely that a tritrophic (resource-herbivore-parasitoid) system is greatly affected by the surrounding environment: apart from the indirect effects (mediated by lower trophic levels) of the ecosystem on parasitoids, the direct impact of the environment on parasitoids is more evident (Ohgushi 1995).

Parasitoids' searching behavior can be influenced by experience at different stages of their life: some cues were learned by immature states (an early experience; Takasu and Lewis 1995) and other cues were learned in the adult stage (a late experience; King 1987). Both the information from host-related cues and the nutritional resources of the parasitoid are determinative in its foraging behavior. Even unrecognized stimuli might be learned by the parasitoid through linking these new stimuli to contact stimuli (King 1987). The process would lead to formation of a preference for the parasitoid choices. Indeed, the experience not only causes more alerts and interactions with the host (Darwish et al. 2003), but it also affects the parasitoid preference while encountering the host (Papaj and Lewis 1993).

The interactions between external cues emitted by the host and internal factors generated by physiological conditions of the parasitoid may influence female choices when probing (Lewis and Tumlinson 1988; Turlings et al. 1990). The nature of the host-parasitoid interactions greatly affects the success of biocontrol programs. For this purpose, many host-parasitoid systems have been investigated in great detail (Baker and Fabrick 2000; Karimzadeh et al. 2004; Salvador and Consoli 2008).

In order to have an efficient production of a biocontrol agent, it is necessary to obtain the knowledge of the physiologically- and biochemically-mediated host-parasitoid interactions (Karimzadeh and Wright 2008; Nakamatsu and Tanaka 2003). Patterns of parasitoid foraging are determined by the interactions of genetic, physiological, environmental and experiential factors. In order to get a high rate of parasitism, it is suggested that females of *Bracon*

hebetor Say (Hymenoptera: Braconidae) must have prior experience on the host before being released for biological control purposes (Nakamatsu and Tanaka 2003).

Bracon hebetor is a cosmopolitan and gregarious ectoparasitoid that attacks the larval stage of several species of Lepidoptera. This parasitoid is considered as one of the best potential biological control agents for lepidopteran stored-product pests (Brower and Press 1990; Chen et al. 2013). It also attacks some insect pests in the field (Gothilf 1996). The females first paralyze the last-stage larvae of their host, and then deposit variable numbers of eggs on the paralyzed host. Several characteristics, such as the broad host range, high reproductive rate and short generation time of *B. hebetor* make it an excellent candidate for biological control of many insect pests (Dweck et al. 2010).

Due to the fact that *B. hebetor* is a polyphagous parasitoid with a wide range of hosts, it is very important to understand the variation in preference and performance of the host-specific strains of this parasitoid. One of the most famous hosts of *B. hebetor* is the carob moth, *Apomyelois ceratoniae* Zeller (Lepidoptera: Pyralidae), which is a key pest of pomegranate worldwide (Al-Izzi et al. 1985; Nay and Perring 2005). The present study aimed to evaluate the effect of different ecosystems on some *B. hebetor* behavioural ecology related to parasitism success, in favour of optimizing mass production of the parasitoid in biological control programs. It is possible that different ecosystems, in which different populations of *B. hebetor* live, influence the behavioral ecology of the wasp in response to the environment. The specific objective was to investigate parasitism success of *B. hebetor* on *A. ceratoniae* under different situations (*i.e.*, different origin, host and rearing history of *B. hebetor*) in order to select the best conditions adapted for mass rearing and an efficient biological control. Before starting the experiments, all the three populations of *B. hebetor* were determined by Dr. Klaus Horstmann (Biozentrum, Wuerzburg, Germany) as *B. hebetor*. A preliminary test then was performed to find out if the populations can interbreed. The results showed that all three populations can successfully mate together and produce fertile offspring. This indicated that these populations from the different origins (field, orchard or store) are not sibling species and can interbreed successfully in the laboratory.

Materials and methods

Host rearing protocol

Apomyelois ceratoniae was originally collected from infested fruits of pomegranate orchards in Najafabad county (Isfahan, Iran) in July 2012. The larvae were separated from infested fruits, moved to ventilated cages (40 × 60 × 50 cm) and reared on fresh pomegranate fruits. After emergence, the adults were moved to oviposition cages (80 × 50 × 100 cm) for mating and laying eggs. The appeared neonate larvae were then placed in individual Petri dishes (5 cm dia.) containing 1 g of a specific diet (glycerol 130 ml, distilled water 120 ml, yeast 9 g, sugar 80 g, wheat bran 300 g and tetracycline 0.66 g as an antibiotic; Mediouni and Dhouibi 2007), and kept under standard environmental conditions (29 ± 1 °C, 75 ± 5 % RH and L:D 16:8 h; Kishani Farahani et al. 2012). The stock culture of *Ephesia kuehniella* Zeller (Lepidoptera: Pyralidae) was originally initiated with samples taken from the infested wheat flour in a bakery in Karaj (Alborz, Iran) in May 2012. The larvae were reared on two different foods, (1) on wheat flour, and (2) on an artificial diet (wheat flour and yeast as 3:1 w/w; Cerutti et al. 1992), and kept under standard environmental conditions (27 ± 1 °C, 55 ± 5 % RH and L:D 16:8 h; Cerutti et al. 1992). The stock culture of *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) was originally initiated from samples taken from the infested tomato field in Tabriz (East Azerbaijan, Iran) in July 2012. After emergence, the adults were moved to oviposition cages (cylindrical containers, 20 cm dia. and 30 cm height), and the eggs were then placed in individual ventilated Petri dishes (5 cm dia.), containing 1 g of an artificial diet (cowpea powder 205 g, powdered agar 14 g, ascorbic acid 3.5 g, sorbic acid 1.1 g, methyl-4-hydroxybenzoate 2.2 g, yeast 35 g, wheat germ powder 30 g, formaldehyde 37 % 2.5 ml, vegetable oil 5 ml and distilled water 650 ml) and kept under standard environmental conditions (25 ± 1 °C, 55 ± 5 % RH and L:D 6:8 h; Naseri et al. 2009). To ensure that the host larvae are synchronized for the experiments, the 4th instar larvae were selected based on the larval molting and the observation of 3rd head capsule exuviae.

Parasitoid rearing protocol

The three different stock cultures of *B. hebetor* were established based on the populations originated from

(1) the parasitized larvae of *A. ceratoniae* in pomegranate orchards (APO population), (2) the parasitized larvae of *E. kuehniella* in stored wheat flour (EPH population), and the (3) parasitized larvae of *H. armigera* in tomato fields (HEL population). Original populations were taken from the areas in which no previous release of *B. hebetor* or pesticide application had been performed. These populations were individually reared on their own hosts under standard environmental conditions (25 ± 1 °C, 55 ± 5 % RH and L:D 16:8 h). In addition, to examine the effect of parasitoid rearing history APO and HEL populations were also cultured on *E. kuehniella* kept on the artificial diet (as mentioned above), as the intermediate host, for four generations. To avoid *Wolbachia* infections, which is likely to induce thelytoky in *B. hebetor*, all female wasps were fed on honey solution (30 %) mixed with tetracycline (50 µg l⁻¹; Rasekh et al. 2010).

Host preference and performance of different populations of *B. hebetor*

A single, mated one–two-day-old female of *B. hebetor* was released into a ventilated Perspex cylindrical container (17 cm dia. and 30 cm height), containing a Petri dish (10 cm dia.) divided into three equal parts, where each part was provided with two early 4th instar larvae of the same host species. A special net separated the Petri dish from the rest of the container. Such a net would let the parasitoid to enter the Petri dish for parasitism of the larvae but inhibited the larvae from leaving the Petri dish. After 24 h, the paralyzed larvae were replaced with fresh ones. The parasitoid behavior was monitored during the light period for 48 h such that the number of the parasitized host larvae and the number of parasitoid eggs on each host larva were recorded every 2 h. Furthermore, the parasitoid eggs were kept under standard environmental conditions (as above) to determine sex ratio [female/(male + female)] of emerged adults. Each test was replicated 14 times for each parasitoid population and the data were used as a measure of host preference. The following factors were examined for their effects on host preference of *B. hebetor*: (1) source of the parasitoid (*i.e.*, the origin of parasitoid populations, including APO, EPH and HEL), (2) host species (*A. ceratoniae*, *E. kuehniella* or *H. armigera*) and (3) experience by the parasitoid (*i.e.*, parasitoid rearing history or the

influence of the intermediate host, *E. kuehniella*; Karimzadeh et al. 2013).

Statistical analyses

Generalized linear models (GLMs) with the family Poisson (for count data, e.g., egg load) and the family Binomial (for proportional data, e.g., parasitism frequency, percentage parasitism, survival rate and sex ratio) was applied to the data. In particular, the number of deposited *B. hebetor* eggs per host larva was analyzed using log-linear models (a three-way factorial analysis of deviance with Poisson errors). In case of over dispersion, the model was refitted using quasi-Poisson rather than Poisson errors. Differences in the frequency of parasitism, percentage parasitism, survival rate and offspring sex ratio of *B. hebetor* were analyzed using logistic analysis of deviance (a three-way factorial analysis of deviance with binomial error). In case of over dispersion, the model was refitted using quasi-binomial rather than Binomial errors. To achieve the minimal adequate model, non-significant terms were removed through model simplification, in which, the original and simplified models were compared by a F-test instead of a χ^2 test. The statistical significance of minimal adequate model was then expressed as a standard normal deviate (z-value), a result of a test (Crawley 2007). All statistical analyses were completed in R 2.10.0 (R Development Core Team).

Results

The effects of host species on life-history parameters of *B. hebetor*

There were significant effects of the host species on the frequency of parasitism, percentage parasitism, the number of eggs, survival rate and offspring sex ratio of *B. hebetor* (Table 1). The mean frequency of parasitized host larva by *B. hebetor* per day was greatest (0.318), intermediate (0.268) and lowest (0.185) on *E. kuehniella*, *A. ceratoniae* and *H. armigera*, respectively (Table 2). Similarly, the mean percentage of parasitized host larvae by *B. hebetor* per day was highest (31.0), intermediate (28.0) and lowest (9.5) on *E. kuehniella*, *A. ceratoniae* and *H. armigera*, respectively. The mean

number of deposited *B. hebetor* eggs per host larva per day was significantly greater on *E. kuehniella* (0.72) compared with *A. ceratoniae* (0.61), and in turn greater on *A. ceratoniae* (0.61) compared with *H. armigera* (0.42). The mean percentage of survived *B. hebetor* adults from eggs on *E. kuehniella* (74.3) and *A. ceratoniae* (70.3) was significantly higher than that on *H. armigera* (43.4). The mean sex ratio of *B. hebetor* offspring was significantly greater on *E. kuehniella* (0.64) and *A. ceratoniae* (0.60) compared with *H. armigera* (0.29).

The effects of *B. hebetor* population on its life-history parameters

There were significant effects of *B. hebetor* population on the frequency of parasitism, percentage parasitism, the number of deposited eggs and survival rate of *B. hebetor* (Table 1). On the contrary, there was no significant influence of *B. hebetor* population on its offspring sex ratio. The frequency of parasitism was significantly greater for HEL population (0.304) compared with EPH (0.214) population (Table 3). However, the frequency of parasitism for APO population (0.253) did not show any difference with other populations. The proportion of the host larvae parasitized by *B. hebetor* was greater for APO population (0.250) compared with HEL (0.208) and EPH (0.226) populations. In addition, the mean number of *B. hebetor* eggs deposited per host per day by APO population (0.55) was significantly less than HEL (0.58) and EPH (0.62) populations. The percentage of survived *B. hebetor* adults from eggs for EPH (81.0) and APO (69.4) populations was significantly greater compared with HEL population (45.5).

The effects of *B. hebetor* experience on its life-history parameters

Except significant effects of *B. hebetor* experience on its egg load and offspring sex ratio, no significant effect of such experience on other life history parameters was found (Table 1). The mean number of *B. hebetor* eggs deposited per host per day by experienced wasps (0.59) was significantly greater than that of naive ones (0.58; Table 4). Similarly, the experienced *B. hebetor* (60 %) produced significantly more females compared with naive ones (53 %).

Table 1 Statistical analysis (log-linear model and logistic analysis of deviance) of the effect of different factors on life history parameter of *B.hebetor*

Parameters measured ^b											
Source of variation ^a	Parasitism frequency			Percentage parasitism		Egg load		Survival rate		Sex ratio	
	df.	z value ^c	P value	z value	P value	z value	P value	z value	P value	z value	P value
H	2	-5.381	<0.001	-4.643	<0.001	-5.138	<0.001	2.618	0.008	-2.500	0.012
P	2	-5.198	<0.001	-5.418	<0.001	-2.412	0.016	-3.161	0.0015	-0.547	0.58
E	1	-0.944	0.35	-0.189	0.85	3.127	0.0018	-1.510	0.13	2.479	0.0132
H×P	4	6.883	<0.001	5.772	<0.001	6.859	<0.001	-2.491	0.012	0.366	0.71
H×E	2	0.242	0.81	-0.022	0.98	-0.100	0.92	<0.0001	0.99	0.003	0.99
P×E	2	1.18	0.23	0.115	0.91	-4.359	<0.001	2.856	0.0042	-2.436	0.0148
H×P×E	4	0.393	0.69	0.020	0.98	-0.057	0.95	<0.001	0.99	-0.011	0.99

^a H, P and E denote host, population and experience, respectively

^b Parasitism frequency: the frequency of parasitized host larvae (i.e., occurrence of parasitism) per day; Percentage parasitism: the percentage of parasitized host larvae by *B. hebetor* per day; Egg load: the number of deposited *B. hebetor* eggs per host larva per day; Survival rate: the percentage of survived *B. hebetor* adults from eggs; Sex ratio: the sex ratio [female/(male + female)] of *B. hebetor* offspring

^c z values are standard normal deviates (i.e., a number of standard deviations from the mean). In GLMs with family Binomial (i.e., logistic analysis of deviance) or Poisson (i.e., log-linear models), z values are the values of z statistic (as a result of a χ^2 test)

Table 2 The effect of host species on the life-history parameters of *B. hebetor* (n = 14)

Parameter measured ^a (mean ± SE)	Host		
	<i>H. armigera</i>	<i>A. ceratoniae</i>	<i>E. kuehniella</i>
Parasitism frequency (per day)	0.185 ± 0.021 a ^b	0.268 ± 0.024 b	0.318 ± 0.025 c
Percentage parasitism (per day)	9.5 ± 0.1 a	28 ± 0.2 b	31 ± 0.2 c
Egg load (numbers per host per day)	0.42 ± 0.06 a	0.61 ± 0.06 b	0.72 ± 0.04 c
Survival rate (%)	43.3 ± 0.2 a	70.3 ± 0.2 b	74.3 ± 0.3 b
Sex ratio (% females)	0.29 ± 0.01 a	0.60 ± 0.02 b	0.64 ± 0.02 b

^a As explained in Table 1

^b The different letters within rows show a significant (P < 0.05) difference

The effects of population-host interactions on life-history parameters of *B. hebetor*

There were significant effects of the population-host interactions on the frequency of parasitism, percentage parasitism, the number of deposited eggs and survival rate of *B. hebetor* (Table 1). It can be clearly seen that the trends of decreasing or increasing of the measured values for each of the mentioned life-history parameters are not similar across the factor levels (Table 5). For example, the frequency of parasitism for APO population shows a decrease from *A. ceratoniae* (0.49) to *E. kuehniella* (0.25), and this trend continues to *H. armigera* (0.18). While the frequency of

parasitism for EPH population indicates a rise from *A. ceratoniae* (0.16) to *E. kuehniella* (0.41) and then a fall to *H. armigera* (0.07). Interestingly, the frequency of parasitism for HEL population shows a different trend, which is an increase from *A. ceratoniae* (0.15) to *E. kuehniella* (0.29), continuing to *H. armigera* (0.46).

The effects of population-experience interaction on life-history parameters of *B. hebetor*

The significant effects of the population-experience interactions on the number of deposited eggs, survival rate and offspring sex ratio of *B. hebetor* were found

Table 3 The effect of the origin and rearing history *B. hebetor* on its life-history parameters

Parameter measured ^a (mean ± SE)	<i>B. hebetor</i> populations ^b		
	HEL	APO	EPH
Parasitism frequency (per day)	0.304 ± 0.025 a ^c	0.253 ± 0.024 ab	0.214 ± 0.022 b
Percentage parasitism (per day)	20.8 ± 0.2 a	25 ± 0.2 b	22.6 ± 0.2 a
Egg load (numbers per host per day)	0.58 ± 0.01 a	0.55 ± 0.01 b	0.62 ± 0.05 ab
Survival rate (%)	45.5 ± 0.3 a	69.4 ± 0.2 b	81.0 ± 0.2 b
Sex ratio (% females)	0.38 ± 0.02 a	0.61 ± 0.02 a	0.63 ± 0.02 a

^a As explained in Table 1

^b HEL *B. hebetor* population originally obtained from rearing the parasitized larvae of *H. armigera* collected from tomato fields, and then cultured on *H. armigera* larvae; APO *B. hebetor* population originally obtained from rearing the parasitized larvae of *A. ceratoniae* collected from pomegranate orchards, and then cultured on *A. ceratoniae* larvae; and EPH *B. hebetor* population originally obtained from rearing the parasitized larvae of *E. kuehniella* collected from stored wheat flour, and then cultured on *E. kuehniella* larvae

^c The different letters within rows show a significant ($P < 0.05$) difference

Table 4 The effect of the experience on *B. hebetor* life-history parameters

Parameter measured ^a (mean ± SE)	<i>B. hebetor</i> experience ^b	
	Experienced	Naive
Parasitism frequency (per day)	0.244 ± 0.019 a ^c	0.270 ± 0.02 a
Percentage parasitism (per day)	22.8 ± 0.16 a	22.8 ± 0.19 a
Egg load (numbers per host per day)	0.59 ± 0.002 a	0.58 ± 0.003 b
Survival rate (%)	67.8 ± 0.2 a	63.1 ± 0.2 a
Sex ratio (% females)	0.60 ± 0.02 a	0.53 ± 0.01 b

^a As explained in Table 1

^b Experienced: when a *B. hebetor* population was reared from its original host (*A. ceratoniae* kept on its artificial diet, *H. armigera* kept on its artificial diet, or *E. kuehniella* kept on wheat flour); Naive: when a *B. hebetor* population was reared from the intermediate host (*E. kuehniella* kept on its artificial diet); the wasps of the 4th generation were used in the experiments

^c The different letters within rows show a significant ($P < 0.05$) difference

(Table 1). For instance, the mean number of *B. hebetor* eggs deposited per host per day by experienced wasps was significantly greater than naive ones for APO (experienced: 0.74; naive: 0.36) and EPH (experienced: 0.62; naive: 0.61) populations (Table 6). On the contrary, when HEL population was used naive wasps (0.77 egg per host per day) deposited more eggs than experienced ones (0.39 egg per host per day).

Discussion

Our experiments showed that the biological characteristics of *B. hebetor* may greatly be influenced by the host species, the wasp population and the rearing history. The marked effects of host species on the most important life-history parameters of *B. hebetor* (such as frequency of parasitism, percentage parasitism, egg load, survival rate and offspring sex ratio) highlight the primary role of the host in the efficiency of this biological control agent. A successful parasitism depends on the host selection process (including habitat preference, potential host community location, host location, host examination, ovipositor probing, ovipositor drilling and oviposition), host suitability and host regulation (Lauziere et al. 2000; Zhang and Schlyter 2004). The highest frequency of parasitism, percentage parasitism and egg load on *E. kuehniella* compared with other host species indicate the preference of *B. hebetor* for *E. kuehniella* in the host selection process.

It has been considered that polyphagous parasitoids encountering different hosts choose the host that needs less energy for parasitism (Chau and Mackauer 2001). Compared with the other two hosts, *E. kuehniella* is an easier target for *B. hebetor*. The lowest preference for *H. armigera* might be due to the vigorous behavior of its larvae as well as due to more energy costs for the parasitoid. Such a lower *B. hebetor* preference for *H. armigera* has also been observed in non-choice experiments using a wider host range (Ghimire and Phillips 2010). The parameters survival rate and

Table 5 The effect of population-host interaction on some life-history parameters of *B. hebetor*

Parameter measured ^b [mean (SE)]												
Population ^a	Parasitism frequency (per day)			Percentage parasitism (per day)			Egg load (numbers per host per day)			Survival rate (%)		
	Host ^c			Host			Host			Host		
	AC	EK	HA	AC	EK	HA	AC	EK	HA	AC	EK	HA
APO	0.49 ^d ↘ (0.05)	0.25 ↘ (0.04)	0.02 (0.01)	50.9 ↘ (2.6)	23.2 ↘ (2.7)	0.9 (0.6)	1.07 ↘ (0.10)	0.47 ↘ (0.07)	0.10 (0.05)	69.2 ↗ (4.7)	86.8 ↘ (4.5)	0.0 (0.0)
EPH	0.16 ↗ (0.03)	0.41 ↘ (0.05)	0.07 (0.02)	17.9 ↗ (2.3)	42.9 ↘ (2.5)	7.1 (1.7)	0.54 ↗ (0.08)	1.15 ↘ (0.09)	0.16 (0.04)	88.3 ↘ (4.6)	79.1 ↗ (3.9)	88.9 (3.0)
HEL	0.15 ↗ (0.03)	0.29 ↗ (0.04)	0.46 (0.05)	15.2 ↗ (2.2)	26.8 ↘ (2.8)	20.5 (2.3)	0.21 ↗ (0.03)	0.54 ↗ (0.04)	0.99 (0.11)	45.8 ↗ (3.5)	55.7 ↘ (4.7)	42.3 (4.9)

^a As explained in Table 3

^b As explained in Table 1

^c AC, EK and HA and are *A. ceratoniae*, *E. kuehniella* and *H. armigera* larvae, respectively

^d The arrows show the in-row direction of the change (increase or decrease) of a feature between the levels of a factor

Table 6 The effect of population-experience interaction on some life-history parameters of *B. hebetor*

Parameter measured ^b (mean ± SE)						
Population ^a	Egg load (numbers per host per day) ^b		Survival rate (%)		Sex ratio (% females)	
	Experience ^c		Experience		Experience	
	Experienced	Naive	Experienced	Naive	Experienced	Naive
APO	0.74 ± 0.09 ^d ↘	0.36 ± 0.04	66.1 ± 3.4 ↗	78.3 ± 3.9	0.70 ± 0.03 ↘	0.47 ± 0.03
EPH	0.62 ± 0.07 ↘	0.61 ± 0.06	77.1 ± 3.4 ↗	88.2 ± 3.7	0.65 ± 0.03 ↘	0.61 ± 0.03
HEL	0.39 ± 0.04 ↗	0.77 ± 0.07	62.1 ± 4.0 ↘	39.2 ± 3.3	0.29 ± 0.02 ↗	0.45 ± 0.02

^a As explained in Table 3

^b As explained in Table 1

^c As explained in Table 4

^d As explained in Table 5

offspring sex ratio are indicative for host suitability and host regulation. It has been documented that the progeny and oviposition of parasitoids are affected by host quality. Several studies have shown that parasitoids regulate their clutch size based on host quality and size (Taylor 1988; Milonas 2005). The sex ratio of a parasitoid refers to differences in factors such as host quality, size and age (Godfray 1994; van Alphen and Jervis 1996). The lowest sex ratio of *B. hebetor* on *H. armigera* is probably because of a low survival rate (Godfray 1994; Ghimire and Phillips 2010) or less female-based progeny (King 1987; Mody et al. 2012) on such a poor host. Given the preference of *B. hebetor* for *E. kuehniella* in the host selection process, the

highest survival rate and offspring sex ratio of *B. hebetor* on *E. kuehniella* imply a more successful parasitism on such a host species.

In the present study, female wasps that had experienced the intermediate host (*E. kuehniella*) deposited less eggs compared with the naive female wasps. It is well known that the females of *B. hebetor* feed on the hemolymph of the host larvae before oviposition (Altuntas et al. 2010; Baker and Fabrick 2000). Such an influence might result from a feeding experience (Magro and Parra 2004) or an oviposition experience (Karimzadeh et al. 2013; Saour 2009) on the intermediate host larva. In addition, the experienced *B. hebetor* females produced more female

wasps than inexperienced ones. It has been considered that after an experience on the host larvae, the females of another parasitoid wasp, *Lysiphlebia mirzai* Shuja-Uddin (Hymenoptera: Aphidiidae), lay more fertilized (diploid) eggs, which produce female offspring (Pandey and Rajendra 1999).

From the pest management viewpoint, the experienced *B. hebetor* females, which produce more offspring as well as more female-based cohorts, are more useful in biological control programs. This can reduce the times and costs of release in inundative biological control. The population source of *B. hebetor* also had a strong effect on the most tested life-history parameters (such as frequency of parasitism, percentage parasitism, egg load, survival rate and sex ratio of the wasp). This indicates the paramount role of the population source in the efficiency of biological control programs involving *B. hebetor*. It has been shown that different strains or genotypes of hymenopteran parasitoids vary greatly in their searching and parasitism behaviors (Heimpel et al. 1997). In the present study, the greater percentage parasitism by the APO population, compared with other populations of *B. hebetor*, might result from more efficient host-searching behavior of the orchard population, a hypothesis that needs further investigation. The higher survival rates of APO and EPH populations, compared with the HEL population, may reflect the maternal effects (Legner and Thompson 1977). *B. hebetor* populations habituating in the field (HEL) might have problems for finding required foods for surviving to the next generation.

From the pest management point of view, the greater survival rate observed for APO and EPH populations can be important in order to build up an established population of the parasitoid in augmentation or inundative release strategies of biological control. The greater *B. hebetor* egg load from the APO population compared with that from the HEL population is possibly associated with different maternal characteristics (King 1987), which were influenced by orchard and field ecosystems. In general, it seems that the ecosystem had an influential impact on maternal characteristics, which manifested in life-history parameters such as egg load, survival rate and parasitism success of *B. hebetor*. It is believed that the reproduction level is scaled to the survival probability: the insects living in a hostile environment show higher levels of reproduction compared with

those occurring in a more benign environment (Capinera 2008). The higher survival of *B. hebetor* population living in the orchard (APO), compared with the field population (HEL), can be due to more conflicts with other natural enemies in pomegranate orchards.

The present study also showed that the effects of population and experience interact simultaneously. When natural populations of *B. hebetor* were reared on the alternative host (*E. kuehniella*) for four generations, biological parameters such as egg load, survival rate and sex ratio were influenced. It, however, showed differential effects for different populations of *B. hebetor*, such that rearing on *E. kuehniella* lowered the fitness (here, a measure that combines the values of egg load, survival rate and sex ratio) of the APO population, but it had no effect on the fitness the EPH population. On the contrary, it raised the fitness of the HEL populations.

This may have implications for maternal effects of some biological control parameters (Richards and Myers 1980). It was clear that for the APO population, which is the most effective population of *B. hebetor* for control of *E. ceratoniae* in pomegranate orchards, that a continuous culturing on its original host gives the best results. It was also found that there were interactions between hosts and populations, which demonstrated that the parasitoid populations can be adapted well on their original hosts (Heimpel et al. 1997). Here, it was demonstrated that selection of the laboratory hosts is important in increasing the efficiency of *B. hebetor* in biological control programs. In addition, the strain or sub-populations of *B. hebetor* must be carefully chosen for specific targets. It is, therefore, necessary to categorize different parasitoid strains based on their degree of host specificity before mass rearing and field release.

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