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Full Length Article

Reproductive Potential and Biological Fitness of *Bracon hebetor* **Parasitizing the Hosts,** *Corcyra cephalonica* **and** *Ephestia kuehniella*

Muhammad Sajjad Khalil^{1,2,3*}, Abu Bakar Muhammad Raza^{2,4}, Huma Khalil^{2,3}, Muhammad Afzal^{2,5}, Naeem Abbas^{1*}, Muhammad Anjum Aqueel⁴ and Thierry Hance³

¹Department of Plant Protection, College of Food and Agriculture Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Saudi Arabia

²Department of Entomology, University of Sargodha, 40100, Sargodha, Pakistan

³Earth and Life Institute, Biodiversity Research Centre, UCL, Belgium

⁴Department of Entomology, Faculty of Agriculture and Environment Sciences, The Islamia University of Bahawalpur, Pakistan ⁵Baba Guru Nanak University, Nankana Sahib, Pakistan

*Correspondence authors: khan87350@gmail.com

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Abstract

Knowledge of the reproductive biology parameters of a parasite on its insect hosts is necessary for successful mass rearing and augmentative release. Here, we examine the fitness-related traits and life-history parameters of the parasitoid Bracon hebetor living on two hosts Ephestia kuehniella and Corcyra cephalonica. Results showed that oviposition period, fecundity, production of immature stages, adult emergence, female longevity, and egg-to-adult survivorship were significantly higher in B. hebetor individuals on E. kuehniella compared with those on C. cephalonica. Mean lifetime egg production of B. hebetor was higher on E. kuehniella (429.4 eggs) compared with C. cephalonica larvae (157.5 eggs). The egg-adult development time on E. kuehniella was 10.85 days and on C. cephalonica 12.11 days. Host species greatly influenced egg-to-adult survivorship of B. hebetor progeny, with the percentage survival greater on E. kuehniella larvae (64.81%) than on C. cephalonica (55.37%). The highest daily mean fecundity on E. kuehniella was observed in week 4 (12.81) followed by C. cephalonica at weeks 2 and 3 (7.13 and 7.15, respectively). Overall mean weekly production of B. hebetor immature stages and adult emergence were also significantly higher on E. kuehniella than on C. cephalonica. The intrinsic rate of increase and finite rate of increase in *B. hebetor* were similar on both hosts, while net reproductive rate and generation time were higher on *E.* kuehniella compared with C. cephalonica. Adult B. hebetor fitness traits such as tibia size and wing area increased more significantly with the passage of time on C. cephalonica compared with those on E. kuehniella. The largest tibia size and wing area of B. hebetor males were observed on C. cephalonica. Significantly higher dry masses of B. hebetor females were associated with E. kuehniella compared with C. cephalonica. In conclusion, the biological parameters, fitness-related traits (wing area, tibia size and dry mass) and egg-to-adult development time of *B. hebetor* progeny were enhanced in individuals living on E. kuehniella. This demonstrates that the E. kuehniella larvae were the most suitable hosts for in vivo rearing of B. hebetor in terms of population increase and commercial use of B. hebetor. © 2022 Friends Science Publishers

Keywords: Braconidae; Parasitoid; Pyralidae; Fitness traits; Life table

Introduction

Insect pests are responsible for damage to stored products such as nuts, dried fruits, oilseeds, legumes, and cereals, which can suffer both qualitative and quantitative losses. Post-harvest losses due to stored-product pests range from 5–10% in developed countries such as the United States to 20% in developing countries (Adams 1977; Boxall 2001). Seed viability and nutritional and market values can all decline as a result of insect infestation. Among stored-grain insect pests, Coleoptera and Lepidoptera are economically important orders, with approximately 600 species of beetles and 70 species of moths associated with damage to stored products worldwide (Cox and Bell 1991; Rajendran and Sriranjini 2008). Pyralid moths including the Mediterranean flour moth *Ephestia kuehniella* Zeller and the rice moth *Corcyra cephalonica* (Stainton) are usually proposed for industrial rearing and are among the most destructive pests in milled products. They are also widely considered destructive in stored products, with larvae causing substantial losses through feeding and mold development (Ghimire and Phillips 2014).

Because insecticidal application on stored food products comes with negative consequences for human

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health, biological control is the preferred alternative for the management of stored-product pests. However, successful release of natural enemies requires mass rearing on alternative hosts to reduce the costs of production. Among potential natural parasites, the highly polyphagous ecto-parasitoid idiobiont *Bracon hebetor* Say (Braconidae: Hymenoptera) is a promising biological agent for controlling members of the pyralid family in stored products. The pyralid moths, *E. kuehniella* and *C. cephalonica* are considered potential hosts and have been proposed for industrial rearing. They are widely used in many biological control programs to rear both predators and parasitoids (Clercq *et al.* 2005; Kim and Riedl 2005; Hamasaki and Matsui 2006).

The quality of the host used for rearing influences the biological fitness traits of a parasitoid and its efficacy in biological control (Khalil *et al.* 2016). The biological parameters of *B. hebetor* reared on different hosts including *E. kuehniella* and *C. cephalonica* were studied from different countries (Faal-Mohammad-Ali and Shishehbor 2013; Imam 2013; Farag *et al.* 2015). But the biological and demographic parameters of *B. hebetor* reared on these host species were not explored comprehensively in Pakistan. Therefore, we analyzed various life-history traits such as immature development, fecundity, and longevity in *B. hebetor* living on *E. kuehniella* and *C. cephalonica* to determine the most promising host for mass rearing under laboratory conditions and for commercialized management of stored pests.

Materials and Methods

Insects and rearing

E. kuehniella and *C. cephalonica* colonies were cultured separately on wheat- and rice-flour diets in plastic boxes ($25 \times 17 \times 8$ cm). *E. kuehniella* larvae were reared on a wheat (300 g) and maize (300 g) mixture while the *C. cephalonica* colony was maintained on rice flour (600 g) for larval feeding. Both cultures were maintained at a temperature of 25–26°C and a relative humidity (RH) of 25–35%.

Three consecutive generations of B. hebetor were reared on each of the two pyralid host species separately to synchronize the populations prior to experimentation at the Earth and Life Institute of the Biodiversity Research Centre, Université Catholique de Louvain, Belgium. The initial B. hebetor culture was obtained from parasitized larvae of the wax moth Galleria mellonella (L.) from infected honeybee combs at the College of Agriculture, University of Sargodha, Pakistan. Infected larvae were transferred to a clean sterilized plastic vial (7×3.5 cm in diameter) for adult emergence. Species identity was confirmed on the basis of morphological characteristics by utilizing Shaw and Huddleston (1991) keys and further confirmed by DNA sequencing (Hajibabaei et al. 2006). After the emergence of adult wasps, each pair was introduced to a separate plastic vial with a droplet of 50% honey solution. After copulation, five host larvae of *E. kuehniella* and *C. cephalonica* were separately introduced into the vial for ovipositioning on a daily basis. The same procedure was following for several generations of the parasitoids on their respective hosts' larvae. All insects were reared under laboratory conditions: $25 \pm 1^{\circ}$ C, $70 \pm 5\%$ RH and 16:8 h light-dark photoperiod.

Life parameters of *B. hebetor* from parasitized *E. kuehniella* and *C. cephalonica*

Ten freshly emerged *B. hebetor* females (< 24 h old) were separately mated with a male and kept in a separate plastic vial (7 \times 3.5 cm in diameter) containing five fully grown fifth-instar larvae of each tested host species. This stage was confirmed as the preferential stage for the parasitoid (Taylor 1988). Every day, a new set of five fifth-instar larvae of each host was provided to replace previous larvae until the female parasitoid died. We recorded daily ovipositioning per female, numbers of larvae, pupae, sex ratios, dry mass, tibia size, and wing area of adult parasitoids at emergence. The life table data were calculated from daily observations of both immature and adult stages. The completely randomized design (CRD) was used for the experiment and was replicated three times.

The emergence rate was used to estimate larval-pupal mortality for each replicate. A parasitoid was considered as surviving when it emerged completely from the pupae. To test for possible variation in parasitoid longevity, 10 newly emerged females were kept at 25°C with a 50% honey solution and survival was checked twice daily until the last parasitoid died.

B. hebetor fitness indicators (dry mass, wing area, tibia size) from parasitized *E. kuehniella* and *C. cephalonica*

From each day of emergence, five males and females that appeared to be physically fit in appearance were selected from both host species and collected in separate Eppendorf tubes containing 70% ethanol prior to dry mass measurements. Adults were dried in an oven at 60°C for 3 days and then weighed on a Mettler Me22 electro-balance (sensitivity: $1 \mu g$) to measure dry mass (mg).

According to Godfray (1994), parasitoid standard size can be estimated by measuring the length of the hind tibia. We therefore randomly selected 10 adults (males and females) each day for measurements of tibia length (mm) and wing area (mm²). A digital camera (SONY SSC-DC198P) mounted on a stereomicroscope was used to photograph the tibia and wings. The pictures were analyzed with ImageJ, version 1.46r (Wayne Rasband National Institutes of Health, USA).

The mean number of eggs, larvae, pupae, adults to emerge, egg-to-adult development time, percentage survivorship, sex ratio and longevity were used as response variables to evaluate the suitability of *E. kuehniella* and *C. cephalonica* larvae for the reproduction and development of

Host species	Oviposition period (days)	Fecundity (eggs/female)	Number of larvae	Number of pupae	Egg-adult development time (days)
C. cephalonica	$21\pm2.18~b$	$158 \pm 22.12 \text{ b}$	$122\pm19.18b$	$102 \pm 17.15 \text{ b}$	12 ± 0.33 a
E. kuehniella	$36 \pm 2.88a$	429 ± 41.39 a	363 ± 35.57 a	332 ± 31.72 a	$11 \pm 0.26 \text{ b}$
Means in the colum	nn followed by the same letters are	e not significantly different (LSD	$P \le 0.05$		

Table 1: Reproductive and developmental parameters of B. hebetor reared on two hosts

Table 2: The adult emergence of B. hebetor and egg-adult survivorship (%) on two hosts

Host species	Number of adults emerged	Number of males	Number of females	M:F ratio	Female longevity (days)	Egg-adult survivorship
C. cephalonica	87 ± 13.13 b	$59\pm7.83~b$	29 ±3.49 b	2:1	$27 \pm 2.01 \text{ b}$	55 ± 2.68 b
E. kuehniella	278 ± 23.39 a	155 ± 10.49 a	124 ± 8.25 a	1:1	$46 \pm 1.82 \text{ a}$	$65 \pm 1.59 \text{ a}$
Means in the colun	nn followed by the same letters are	not significantly differed	nt (LSD, $P \le 0.05$)			

Weeks	Number of eggs/female		Num	ber of larvae	Num	Number of pupae	
	C. cephalonica	E. kuehniella	C. cephalonica	E. kuehniella	C. cephalonica	E. kuehniella	
Week 1	$4.39\pm0.49~b$	$7.57 \pm 0.64 \text{ c}$	$3.25\pm0.40b$	$6.28\pm0.58~d$	$2.68\pm0.35~b$	$5.87 \pm 0.58 \text{ c}$	
Week 2	7.13 ± 0.53 a	11.69 ± 0.63 ab	$5.30 \pm 0.48 \text{ a}$	$9.97 \pm 0.60 \text{ ab}$	$4.40 \pm 0.43 \text{ ab}$	$9.17 \pm 0.60 \text{ ab}$	
Week 3	7.15 ± 0.83 a	$10.61 \pm 0.75 \text{ b}$	5.73 ± 0.75 a	$8.51\pm0.64~bc$	$4.67 \pm 0.69 \text{ a}$	$7.94\pm0.63~b$	
Week 4	$4.42\pm0.94~b$	12.81 ± 0.85 a	$3.63 \pm 0.85 \text{ ab}$	10.91 ± 0.81 a	3.28 ± 0.82 ab	10.21 ± 0.81 a	
Week 5	5.47 ± 2.11 ab	$11.87 \pm 0.86 \text{ ab}$	$4.47 \pm 1.95 \text{ ab}$	10.33 ± 0.79 ab	$4.00 \pm 1.87 \text{ ab}$	9.42 ± 0.74 ab	
Week 6	0.00	8.37 ± 0.84 c	0.00	$7.18 \pm 0.79 \text{ cd}$	0.00	$5.98 \pm 0.71 \text{ c}$	
Overall mean	$5.83\pm0.36\ B$	$10.52\pm0.32~A$	$4.51\pm0.32~B$	$8.89\pm0.30\ A$	$3.78\pm0.29~B$	$8.14\pm0.29~A$	
Moone in the colum	n followed by the small s	imilar lattars are not signifi	contly different (ISD P	(0.05)			

Means in the column followed by the small similar letters are not significantly different (LSD, $P \le 0.05$) Means in the row followed by the capital similar letters are not significantly different (LSD, $P \le 0.05$)

B. hebetor. Analysis of variance was used to calculate the average responses of the parasitoid on the two host species at different days and a least significant difference test was used for mean separation (Stell *et al.* 1980). Regression and correlation was also used to study the average change in dry mass, tibia size, and wing area of *B. hebetor* at different days on *E. kuehniella* and *C. cephalonica.* The life table parameters of all individuals were analyzed according to a method described by Farag *et al.* (2015). Intrinsic rates of increase were estimated using the iterative bisection method from the Euler-Lotka formula, $\sum_{x=0}e^{-(x+1)}mx = 1$.

Results

The mean oviposition periods of *B. hebetor* females on fully grown fifth-instar larvae of *C. cephalonica* and *E. kuehniella* were 20.6 and 36 days, respectively. Mean lifetime egg production of *B. hebetor* was higher on *E. kuehniella* (429.4 eggs) compared with *C. cephalonica* larvae (157.5 eggs). The egg-adult development time on *E. kuehniella* was 10.85 days and on *C. cephalonica* 12.11 days (Table 1).

The mean number of adult progenies produced by *B. hebetor* females over their lifetimes on parasitized *E. kuehniella* larvae was higher than on *C. cephalonica*. A significantly higher longevity of 46.4 days was recorded for females on *E. kuehniella* compared with *C. cephalonica*. Host species greatly influenced egg-to-adult survivorship of *B. hebetor* progeny, with the percentage survival greater on *E. kuehniella* larvae (64.81%) than on *C. cephalonica* (55.37%) (Table 2).

The highest daily mean fecundity on *E. kuehniella* was observed in week 4 (12.81) followed by *C. cephalonica* at weeks 2 and 3 (7.13 and 7.15, respectively). A similar trend

was observed in parasitoid larval and pupal development stages, with highest larval (10.91) and pupal (10.21) numbers observed at week 4 on *E. kuehniella*. For *C. cephalonica*, the highest larval population was observed at weeks 2 (5.3) and 3 (5.73), respectively, and a significantly higher pupal population was observed at week 3 (4.67) (Table 3).

Significant numbers of *B. hebetor* adult progeny were produced at week 4 (8.69) on *E. kuehniella* compared with *C. cephalonica* at week 3 (4.14). A similar trend was observed for the emergence of male parasitoids from both host species at week 4 (4.99) and week 3 (3.65). Variations were observed in female emergence, with maximum progenies observed during weeks 2 (4.4) and 4 (3.7) on *E. kuehniella*, while no significant female emergence was observed on *C. cephalonica* from all five weeks (Table 4).

Life table parameters for *B. hebetor* were notably superior for parasites on *E. kuehniella* in terms of intrinsic rate of increase (0.14), finite rate of increase (1.14), net reproductive rate (42.10), and generation time (34.56) compared with those of parasites living on *C. cephalonica* (Table 5). A regression equation showed a 0.0028% and 0.0013% change in female and male *B. hebetor* dry mass, respectively, with unit change in number of days (Table 6).

Newly emerged *B. hebetor* male and female tibia size (mm) and wing area (mm²) gradually increased each day for individuals on *C. cephalonica* while decreases were observed in those on *E. kuehniella* (Fig. 1 and 2). A regression analysis showed positive change in tibia size and wing area in both male and female *B. hebetor* adults from *C. cephalonica* compared with *E. kuehniella*, with unit change in number of days. *B. hebetor* female and male adult dry masses were significantly higher on *E. kuehniella* compared with *C. cephalonica* (Fig. 3).

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Number of adults emerged		Numl	per of males	Numb	Number of females	
C. cephalonica	E. kuehniella	C. cephalonica	E. kuehniella	C. cephalonica	E. kuehniella	
2.28 ± 0.32 b	5.10 ± 0.53 de	$1.88 \pm 0.25 \text{ c}$	$2.49 \pm 0.25 \text{ c}$	0.39 ± 0.11 a	$2.61 \pm 0.36 c$	
3.69 ± 0.40 ab	$8.56 \pm 0.55 \text{ ab}$	3.34 ± 0.32 ab	$4.16\pm0.30~ab$	0.34 ± 0.14 a	$4.40 \pm 0.46 \text{ a}$	
4.14 ± 0.62 a	$7.10 \pm 0.60 \text{ bc}$	3.65 ± 0.52 a	4.21 ± 0.37 ab	0.48 ± 0.14 a	2.89 ± 0.34 bc	
2.84 ± 0.71 ab	8.69 ± 0.75 a	2.28 ± 0.56 bc	4.99 ± 0.49 a	0.56 ± 0.22 a	3.7 ± 0.43 ab	
3.11 ± 1.49 ab	6.64 ± 0.63 cd	$2.16 \pm 1.09 \text{ bc}$	4.30 ± 0.45 ab	0.95 ± 0.45 a	2.34 ± 0.32 c	
0.00	$4.55 \pm 0.62 \text{ e}$	0.00	3.52 ± 0.51 bc	0.00	1.03 ±0.25 d	
$3.23\pm0.26~B$	$6.82\pm0.26~A$	$2.77\pm0.21~\mathrm{B}$	$3.95 \pm 0.17 \; A$	$0.46\pm0.07~B$	$2.87\pm0.16~A$	
		C. cephalonica E. kuehniella 2.28 ± 0.32 b 5.10 ± 0.53 de 3.69 ± 0.40 ab 8.56 ± 0.55 ab 4.14 ± 0.62 a 7.10 ± 0.60 bc 2.84 ± 0.71 ab 8.69 ± 0.75 a 3.11 ± 1.49 ab 6.64 ± 0.63 cd 0.00 4.55 ± 0.62 e 3.23 ± 0.26 B 6.82 ± 0.26 A	C. cephalonica E. kuehniella C. cephalonica $2.28 \pm 0.32 b$ $5.10 \pm 0.53 de$ $1.88 \pm 0.25 c$ $3.69 \pm 0.40 ab$ $8.56 \pm 0.55 ab$ $3.34 \pm 0.32 ab$ $4.14 \pm 0.62 a$ $7.10 \pm 0.60 bc$ $3.65 \pm 0.52 a$ $2.84 \pm 0.71 ab$ $8.69 \pm 0.75 a$ $2.28 \pm 0.56 bc$ $3.11 \pm 1.49 ab$ $6.64 \pm 0.63 cd$ $2.16 \pm 1.09 bc$ 0.00 $4.55 \pm 0.62 e$ 0.00 $3.23 \pm 0.26 B$ $6.82 \pm 0.26 A$ $2.77 \pm 0.21 B$	C. cephalonica E. kuehniella C. cephalonica E. kuehniella $2.28 \pm 0.32 b$ $5.10 \pm 0.53 de$ $1.88 \pm 0.25 c$ $2.49 \pm 0.25 c$ $3.69 \pm 0.40 ab$ $8.56 \pm 0.55 ab$ $3.34 \pm 0.32 ab$ $4.16 \pm 0.30 ab$ $4.14 \pm 0.62 a$ $7.10 \pm 0.60 bc$ $3.65 \pm 0.52 a$ $4.21 \pm 0.37 ab$ $2.84 \pm 0.71 ab$ $8.69 \pm 0.75 a$ $2.28 \pm 0.56 bc$ $4.99 \pm 0.49 a$ $3.11 \pm 1.49 ab$ $6.64 \pm 0.63 cd$ $2.16 \pm 1.09 bc$ $4.30 \pm 0.45 ab$ 0.00 $4.55 \pm 0.62 e$ 0.00 $3.52 \pm 0.51 bc$ $3.23 \pm 0.26 B$ $6.82 \pm 0.26 A$ $2.77 \pm 0.21 B$ $3.95 \pm 0.17 A$	C. cephalonicaE. kuehniellaC. cephalonicaE. kuehniellaC. cephalonica $2.28 \pm 0.32 b$ $5.10 \pm 0.53 de$ $1.88 \pm 0.25 c$ $2.49 \pm 0.25 c$ $0.39 \pm 0.11 a$ $3.69 \pm 0.40 ab$ $8.56 \pm 0.55 ab$ $3.34 \pm 0.32 ab$ $4.16 \pm 0.30 ab$ $0.34 \pm 0.14 a$ $4.14 \pm 0.62 a$ $7.10 \pm 0.60 bc$ $3.65 \pm 0.52 a$ $4.21 \pm 0.37 ab$ $0.48 \pm 0.14 a$ $2.84 \pm 0.71 ab$ $8.69 \pm 0.75 a$ $2.28 \pm 0.56 bc$ $4.99 \pm 0.49 a$ $0.56 \pm 0.22 a$ $3.11 \pm 1.49 ab$ $6.64 \pm 0.63 cd$ $2.16 \pm 1.09 bc$ $4.30 \pm 0.45 ab$ $0.95 \pm 0.45 a$ 0.00 $4.55 \pm 0.62 e$ 0.00 $3.52 \pm 0.51 bc$ 0.00 $3.23 \pm 0.26 B$ $6.82 \pm 0.26 A$ $2.77 \pm 0.21 B$ $3.95 \pm 0.17 A$ $0.46 \pm 0.07 B$	

Table 4: Mean (± SEM) weekly production of adults of B. hebetor on two hosts over six weeks period

Means in the column followed by the small similar letters are not significantly different (LSD, $P \le 0.05$). Means in the row followed by the capital similar letters are not significantly different (LSD, $P \le 0.05$).

Table 5: Life table parameters of B. hebetor reared on C. cephalonica and E. kuehniella under laboratory conditions

Host species	Intrinsic rate of natural increase (r_m)	The finite rate of increase (λ)	Net reproductive rate (R0)	Mean generation time (T)
E. kuehniella	0.14	1.14	42	35
C. cephalonica	0.13	1.14	25	29

Table 6: Influence of C. cephalonica and E. kuehniella hosts on fitness consequences of female B. hebetor parasitoids

Parameters	Sex	C. cephalonica			E. kuehniella		
		Intercept	Day	R ² value	Intercept	Day	R ² value
Tibia size (mm)	М	0.72***	0.002	0.13	0.80***	-0.002***	0.40
	F	0.77***	0.0003	0.01	0.82***	-0.002*	0.15
Wing area (mm ²)	М	0.83***	0.004**	0.27	0.99***	-0.003*	0.13
	F	0.98***	0.0001	0.0002	1.08***	-0.001	0.02
Dry mass (mg)	М	0.24***	-0.00003	0.00003	0.23***	0.001	0.06
	F	0.33***	-0.0019	0.09	0.29***	0.003*	0.15

Significance at *** 0.001; ** 0.01; * 0.05



Fig. 1: Influence age-related factors of female parasitoids on newly emerged adult *B. hebetor* size, expressed as change in tibia length (mm) from *C. cephalonica* and *E. kuehniella*, respectively



Fig. 2: Influence age-related factors of female parasitoids on newly emerged adult *B. hebetor* size, expressed as change in wing area measurement (mm²) from *C. cephalonica* and *E. kuehniella*, respectively



Fig. 3: Influence age-related factors of female parasitoids on newly emerged adult *B. hebetor* dry mass (mg) from *C. cephalonica* and *E. kuehniella*, respectively

Discussion

The current study showed that host species significantly influenced the reproductive and developmental parameters of B. hebetor. Although this species is a well-known generalist parasitoid, all hosts are not equivalent in terms of population growth potential. The results of the present study are in accordance with those of Ghimire and Phillips (2014), in which the shortest egg-to-adult development time and reduced larval and pupal development period of B. hebetor progeny was observed on E. kuehniella. The developmental time of *B. hebetor* on *E. kuehniella* in the present study was in agreement with those of previous reports, including 10.83 days (Amir-Maafi and Chi 2006), 12.85 days (Eliopoulos and Stathas 2008), 10.2 days (Ghimire and Phillips 2010), and 9-12 days (Faal-Mohammad-Ali and Shishehbor 2013). E. kuehniella was the most preferred host of B. hebetor, possibly because of less vigorous defensive behavior or provision of more nourishment to developing parasitoids compared with other host species (Saadat et al. 2014a, b, 2016).

Similarly, average life-time fecundity of B. hebetor females and all immature production were significantly higher in individuals on E. kuehniella than on C. cephalonica. Overall the B. hebetor female oviposition period was significantly higher on E. kuehniella (36 days) than on C. cephalonica (20.6 days). Significantly more adults (male and females numbers)/female, female longevity, and egg-adult survivorship of *B. hebetor* was observed on *E.* kuehniella (278.3 adults/female, 46.4 days, and 64.81%, respectively) than on C. cephalonica (87.2 adults/female, 27 days, and 55.37%, respectively). These results follow the pattern reported by Ghimire and Phillips (2014), with significantly higher oviposition periods, female longevity, and egg-adult survivorship, and immature-stage populations observed on E. kuehniella compared with C. cephalonica. According to Imam (2013), similar trends were observed in the biological and developmental parameters of a closely related species, Bracon brevicornis (Wesmael), on Ephestia cautella (Walker). B. hebetor longevity approaches 60.3 days, according to Ghimire and Phillips (2014). Contrary to our results, Nikam and Pawar (1993) reported the mean longevity (37.5 days), oviposition period (34.5 days), total progeny development (258.9 adults/female) and sex ratio (1.9:1) of B. hebetor from parasitized C. cephalonica. This difference may be due to variations in experimental protocols, temperature, RH, or host density, age, size, strain, and host diet used to carry out the experiment (Harbison et al. 2001; Rohne 2002; Milonas 2005). In the present result, Bracon females' mean oviposition periods, larval and pupal stages, longevity, and male and female emergence and survival percentages of immature individuals favored Ephestia species, which may be attributable to the fact that Ephestia is the natural host of Bracon.

Results for weekly oviposition and immature stages were also in accordance with Ghimire and Phillips (2014), in which overall B. hebetor age-specific daily fecundity and immature-stage numbers were higher during the first five weeks and then decreased with the increasing age of parasitoid females until reproduction ceased. The highest mean fecundity was observed at week 5 for both E. kuehniella and C. cephalonica species, compared with our study, which week 4 on E. kuehniella and weeks 2 and 3 on C. cephalonica produced the highest fecundity. According to Ghimire and Phillips (2014), the largest numbers of adult progeny of B. hebetor were produced in week 4 on C. cephalonica followed by E. kuehniella in week 5. These results showed little variation from our results, in which C. *cephalonica* adult progeny production was significantly higher at week 3 (4.14 adults/female), compared with week 4 (8.69 adults/female) for E. kuehniella. The egg-adult developmental parameters of *B. hebetor* were significantly higher on E. kuehniella parasites, largely at week 4.

In the present study, the intrinsic rate of natural increase and finite rate of increase of B. hebetor parasites on both C. cephalonica and E. kuehniella hosts were similar, with little variation, while the net reproductive rate and mean generations time were significantly higher on E. kuehniella. Similarly, Amir-Maafi and Chi (2006) reported an r_m value of 0.14 on *E. kuehniella* fed wheat flour. In contrast to our results, the r_m for *B*. hebetor was higher on *C*. cephalonica fed sorghum flour (Nikam and Pawar 1993) compared with C. cephalonica fed wheat ($r_m = 0.21$), maize $(r_m = 0.21)$, sorghum $(r_m = 0.19)$, and rice flour $(r_m = 0.15)$ (Singh et al. 2006). Eliopoulos and Stathas (2008) reported r_m values of 0.121, 0.163, 0.191, and 0.185 on 1, 5, 15 and 30, E. kuehniella densities, respectively, for B. hebetor. Faal-Mohammad-Ali and Shishehbor (2013) estimated an r_m of 0.291 for *B. hebetor* on *E. kuehniella*. These results suggest that E. kuehniella larvae are the more suitable host in terms of population increase.

Various studies have reported that insect size at emergence is an important life-history variable that is closely associated with fitness. In parasitoids, numerous fitness indicators, such as fecundity and longevity, exhibit a positive correlation with size (Cloutier et al. 1981; Visser 1994; Ellers et al. 2001). Host age-related quality greatly affects the fitness of parasitoids (Kouamé and Mackauer 1991; Colinet et al. 2005), and our results indicated that tibia size and wing area of B. hebetor adults (males and females) were reduced on E. kuehniella but increased gradually on C. cephalonica with the passage of time. The most likely reason for this phenomenon is that competition among the plentiful numbers of immature B. hebetor on E. kuehniella ultimately resulted in a decrease in adult size compared with those on C. cephalonica (Saadat et al. 2016). In our study, a linear decrease in adult B. hebetor dry mass was observed at 25°C on C. cephalonica with the passage of time compared with those on E. kuehniella. Similarly, Saadat et al. (2014b) reported the highest dry mass of B. hebetor individuals reared on E. kuehniella compared with those reared on C. cephalonica. According to Colinet et al.

(2007) a linear decrease resulting from an increase in rearing temperature was observed in the dry mass of B. *hebetor*.

Conclusion

In conclusion, *E. kuehniella* is a more suitable host than *C. cephalonica* for rearing *B. hebetor* parasites with superior biological attributes for industrial purposes. In the future, it would be interesting to establish a phylogenetic approach that links host preference and suitability with a history of parasitism. Our hypothesis is that *E. kuehniella* is likely a primary host of *B. hebetor* with a potential for diversification.

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Author Contributions

MSK carried out research work and written original draft of the manuscript. ABMR, MA and MAA supervised the work. HK helped in carried out research work. NA improved and edited the final manuscript. Thierry Hance supervised and technically improved the final manuscript.

Conflicts of Interest

None declared.

Data Availability

All the related data reported in the manuscript will be available as requested.

Ethics Approval

The authors declare that the research was in accordance with all ethical standards.

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