ECOLOGY AND POPULATION BIOLOGY

Demography of *Habrobracon hebetor* (Hymenoptera: Braconidae) on Two Pyralid Hosts (Lepidoptera: Pyralidae)

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ABSTRACT Demography of *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) on two pyralid host species [*Galleria mellonella* (L.) and *Ephestia kuehniella* Zeller] (Lepidoptera: Pyralidae) was studied at 28°C in the laboratory. Data were analyzed based on an age-stage, two-sex life table, to take both sexes and variable development into consideration. The intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), gross reproductive rate (GRR), and mean generation time (T) of *H. hebetor* on *G. mellonella* were 0.1520 d^{-1}, 1.1640 d^{-1}, 12.5 offspring, 50.1 offspring, and 16.8 d, respectively. These values were not significantly different from the values obtained for *E. kuehniella*, i.e., 0.1375 d^{-1}, 1.1473 d^{-1}, 11.9 offspring, 54.9 offspring, and 18.2 d. The life expectancy of an *H. hebetor* egg was 10.6 d on *E. kuehniella* and 10.4 d on *G. mellonella*. On both host species, the maximum reproductive value of female *H. hebetor* occurred on the 12th day.

چکیده: جدول زندگی زنبور ***Habrobracon hebetor* (Say) (Hym.: Braconidae)** روی دو میزبان (لارو پروانه موم‌خوار ***Galleria mellonella* L.** و لارو شب‌پره آرد ***Ephestia kuehniella* Zell.**) از خانواده **Pyralidae** در دمای ۲۸ درجه سانتی‌گراد در شرایط آزمایشگاهی مطالعه شد. در هر دو میزبان، داده‌های بدست آمده بر اساس جدول زندگی دو جنس (نر و ماده)، مراحل رشدی- سنی، با در نظر گرفتن تغییرات رشد افراد و جنسیت آنها، تجزیه و تحلیل گردیدند. نرخ ذاتی افزایش جمعیت (r)، نرخ متناهی افزایش جمعیت (λ)، نرخ خالص تولید مثل (R_0)، نرخ ناخالص تولید مثل (GRR) و متوسط مدت زمان نسل (T) زنبور پارازیتویید ***H. hebetor*** روی لارو پروانه موم‌خوار به ترتیب ۰/۱۵۲ روز$^{-۱}$، ۱/۱۶۴ روز$^{-۱}$، ۱۲/۵۰ نتاج ماده، ۵۰/۱ تخم ماده و ۱۶/۸ روز برآورد گردید. پارامترهای فوق‌الذکر برای زنبورهای پرورش یافته روی شب‌پره آرد به ترتیب ۰/۱۳۷ روز$^{-۱}$، ۱/۱۴۷۳ روز$^{-۱}$، ۱۱/۹۰ نتاج ماده، ۵۴/۹ تخم ماده، ۱۸/۲ روز بودند و تفاوت معنی‌داری بین پارامترهای محاسبه شده در زنبورهای پارازیتویید پرورش یافته روی لارو پروانه موم‌خوار و لارو شب‌پره آرد مشاهده نشد. امید زندگی تخم های تازه گذاشته شده زنبور پارازیتویید روی لارو شب‌پره آرد ۱۰/۶ و روی لارو پروانه موم‌خوار ۱۰/۴ روز بود. در هر دو میزبان، حداکثر مقدار تولید مثل زنبور های ماده در روز دوازدهم دیده شد که رابطه نزدیکی با طول دوره پیش از تخم ریزی (از تولد تا تخم ریزی)، آنها دارد.

KEY WORDS life table, reproduction, stored product pest, parasitoid

Habrobracon hebetor (Say) (=*Bracon hebetor*) (Hymenoptera: Braconidae) is a cosmopolitan ectoparasitoid that has been studied as a control agent of various lepidopteran pests in China (Huang 1986), Bulgaria (Balevski 1984), the former Soviet Union (Adashkevich et al. 1981, Kovalenkov and Meshcheryakova 1983), the Middle East (Harakly 1968, Hussain and Jafar 1969, Gerling 1971), and the United States (Keever et al. 1986, Cline and Press 1990, Youm and Gilstrap 1993, Quicke 1997, Hopper 2003). In 1962,

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H. hebetor was introduced to Taiwan for the control of the sugarcane pink borer (Cheng 1991). Two pyralid species, *Galleria mellonella* (L.) and *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), are commonly used for mass rearing of *H. hebetor;* both are suitable for development and reproduction (Astanov 1980; Adashkevich and Saidova 1984, 1987; Kurbanov and Kuliev 1984; Rasnitsyna and Gordeichuk 1985). In Iran, *H. hebetor* has been evaluated for controlling *Heliothis*/*Helicoverpa* spp. (Lepidoptera: Noctuidae), and a mass rearing program has been initiated (Attaran 1996).

Demographic information for *H. hebetor* is currently unavailable. However, such information can be useful for projecting population growth, timing pesticide applications, and designing insect mass rearing programs. In traditional life tables (Lewis 1942; Leslie 1945, 1948; Birch 1948), only female individuals are taken into consideration, and the means of the durations of developmental stages are used to construct age-specific survival rates and age-specific fecundity for the "female" population (Birch 1948, Pianka 1994). Youm and Gilstrap (1993) studied the life table of *B. hebetor* based on the traditional female age-specific life table. Variation in developmental rates among individuals is commonly observed in most organisms, and ignoring such variation may result in errors in life table analysis (Chi 1988, Chi and Yang 2003). Ignoring the sex of individuals can also result in errors (Chi 1988). Chi and Liu (1985) and Chi (1988) developed an age-stage, two-sex life table model incorporating variable developmental rates and both sexes. In this study, we investigated life tables of *H. hebetor* reared on two host species, *G. mellonella* and *E. kuehniella.* We also calculated a number of demographic parameters by using the age-stage, two-sex life table model.

Materials and Methods

G. mellonella and *E. kuehniella* were reared in an incubator at 28 ± 0.5°C with a photoperiod of 16:8 (L:D) h and 65 ± 5% RH. Cultures were maintained in clear plastic boxes (25 by 20 by 7 cm) containing 1 kg of diet for 250–300 pyralid eggs. The diet for *E. kuehniella* contained 970 g of wheat flour and 30 g of brewer's yeast (Attaran 1996). The diet for *G. mellonella* contained 443 g of wheat flour, 229 g of honey, 182 g of glycerol, 45 g of wax, and 110 g of brewer's yeast (Mohaghegh and Amir-Maafi 2001).

A colony of *H. hebetor* was established using several hundred pupae from parasitized *Heliothis* spp. collected in tomato fields near Salmas city, Azarbayjan-Gharbi Province, Iran. This colony was then divided into two groups, one reared on *G. mellonella* and the other group on *E. kuehniella.* Fifth instars of *G. mellonella* and *E. kuehniella* were used for both colony maintenance and experiments. For the life table study, 150 *G. mellonella* larvae and 200 *E. kuehniella* larvae parasitized within a 1-h period were collected. One *H. hebetor* egg was left on each larva, and the remaining eggs were removed. Parasitized larvae were transferred individually to plastic petri dishes (1.5 cm in height, 10 cm in diameter). Petri dishes with parasitized larvae were kept in incubators under the same conditions as described above. The developmental stage of each individual was recorded daily. As adult wasps emerged, males and females were paired in plastic vials (5.7 cm in diameter, 6.5 cm in height) (Fig. 1, modified from Attaran 1996) and provided with honey and water. Two fifth instars of the designated host were supplied daily for oviposition. The daily survival of each individual and fecundity of each female were recorded. Adults were kept in incubators under the same conditions as described above.

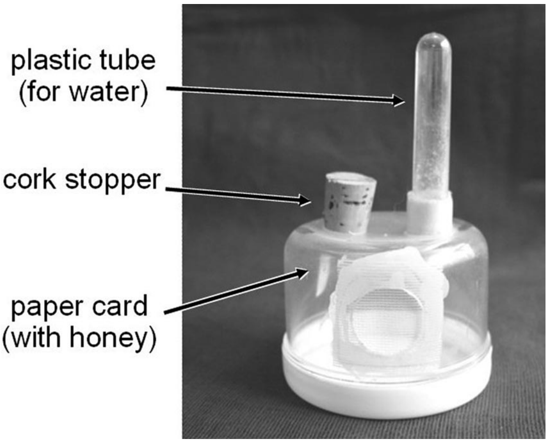

Fig. 1. Plastic vial for rearing adult parasitoids (modified from Attaran 1996).

Resulting data were analyzed based on the age-stage, two-sex life table model developed by Chi and Liu (1985) and Chi (1988). Means and standard errors of population parameters were estimated using the jackknife method (Sokal and Rohlf 1995). A computer program, TWOSEX-MSChart (Chi 2005), was developed for data analysis and jackknife estimation in Visual BASIC for the Windows operating system. This program is available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu.tw/wes/chi.html (Illinois Natural History Survey). TWOSEX-MSChart groups the raw data and calculates a number of life table parameters: age-stage specific survival rates (s_{xj}) (where x is the age and j is the stage), age-stage specific fecundity (f_{xj}), age-specific survival rates (l_x), age-specific fecundity (m_x), the intrinsic rate of increase (r), the finite rate of increase (λ), the gross reproductive rate (GRR), the net reproductive rate (R_0), and the mean generation time (T). The intrinsic rate of increase is calculated iteratively from the Euler–Lotka equation

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$

with age indexed from 0 (Goodman 1982). The Student's t-test was used to determine differences in population parameters, developmental times, and fecundities between *H. hebetor* reared on *G. mellonella* and *E. kuehniella* (Zar 1999).

Table 1. Basic statistics (mean ± SE) of life history data of *H. hebetor* at 28°C on *G. mellonella* and *E. kuehniella*

Statistics	Stage or sex	Host species		t	df	P
		G. mellonella mean ± SE (n)	*E. kuehniell* mean ± SE (n)			
Developmental time (d)	Egg	1.25 ± 0.04 (150)	1.27 ± 0.03 (200)	0.3496	348	0.7268 (>0.05)
	Larva	3.04 ± 0.08 (55)	2.69 ± 0.06 (81)	3.4772	134	0.0007 (<0.05)
	Pupa	6.77 ± 0.14 (44)	7.03 ± 0.08 (67)	1.6818	109	0.0954 (>0.05)
Total preadult duration (d)	Female	10.96 ± 0.16 (24)	10.83 ± 0.16 (36)	0.5329	58	0.5962 (>0.05)
	Male	10.80 ± 0.20 (20)	10.81 ± 0.21 (31)	0.0210	49	0.9833 (>0.05)
Adult longevity (d)	Female	17.42 ± 1.37 (24)	17.25 ± 1.20 (36)	0.0902	58	0.9284 (>0.05)
	Male	19.40 ± 1.88 (20)	13.71 ± 1.45 (31)	2.4157	49	0.0194 (<0.05)
APOP (d)	Female	2.04 ± 0.44 (24)	1.39 ± 0.15 (36)	1.6327	58	0.1080 (>0.05)
TPOP (d)	Female	13.00 ± 0.52 (24)	12.22 ± 0.18 (36)	1.6212	58	0.1104 (>0.05)
Fecundity (eggs)	Female	78.3 ± 9.3 (24)	66.3 ± 7.4 (36)	1.0224	58	0.3108 (>0.05)

Results and Discussion

Juvenile Parameters. The duration of the egg and pupal stages of *H. hebetor* reared on *G. mellonella* did not differ significantly from those on *E. kuehniella* when using the *t*-test at the 5% significance level (Table 1). However, there were significant differences in larval duration. The total preadult duration ranged from 10.80 to 10.96 d, and there was no significant difference in total preadult duration between *H. hebetor* reared on *E. kuehniella* and *G. mellonella.* Jackson and Butler (1984) reported that the developmental time of *B. hebetor* reared on the pink bollworm, *Pectinophora gossypiella* (Saunders), was 10.8 d at 25°C. Attaran (1996) reported a developmental time of 10 d for both female and male parasitoids at 30°C reared on *G. mellonella* and *E. kuehniella.* The stage durations of parasitoids in our study are within the range of these reports.

When reared on *G. mellonella,* 24 of 150 eggs emerged as females and 20 emerged as males. Among these 150 eggs, 63.3% died in the larval stage and 7.3% in the pupal stage. On *E. kuehniella,* out of 200 eggs, 36 emerged as females and 31 emerged as males. Among these 200 eggs, 59.5 and 7% died in the larval and pupal stage, respectively. In our study, only one egg was left on a host and all eggs hatched successfully; however, because of high mortality in the larval stage, adult emergence rates were 0.29 on *G. mellonella* and 0.34 on *E. kuehniella.* The preadult survival rates are lower than those reported by Cerutti et al. (1992) and Yu et al. (2003). Variation in preadult mortality among different studies might be because of different host species and/or different rearing conditions.

Adult Parameters. Mean lifetime fecundities of *H. hebetor* were 78.3 eggs/female on *G. mellonella* and 66.3 eggs/female on *E. kuehniella* (Table 1). These values are much lower than the 253 eggs/female on *Anagasta kuehniella* (Zeller) (Clark and Smith 1967), 326.4 eggs on *P. gossypiella* (Saunders) (Jackson and Butler 1984), and 116.5 eggs on *G. mellonella* (Adashkevich and Atmirzaev 1986). Taylor (1988a) studied the functional and ovipositional responses of *B. hebetor* at three parasitoid densities (one, two, and four per arena) and different host–parasitoid ratios; they showed that the number of eggs laid per wasp was independent of the densities both of parasitoids and available hosts. Because only *B. hebetor* females of 48–72 h old were used in their study, the effect of female age on fecundity was not studied and no lifetime fecundity was available. In this study, we studied the parasitism rate based on the life table of the parasitoid and noticed that the age-specific fecundity of females varied with the age (discussed in the following paragraph). The low lifetime fecundity observed in this study was possibly a consequence of supplying only two fifth instars per parasitoid for oviposition

The age of first reproduction by females has an important effect on population growth, and many researchers have defined the adult preoviposition period (APOP) as the time between adult emergence and first oviposition. Ignoring the length and variation of

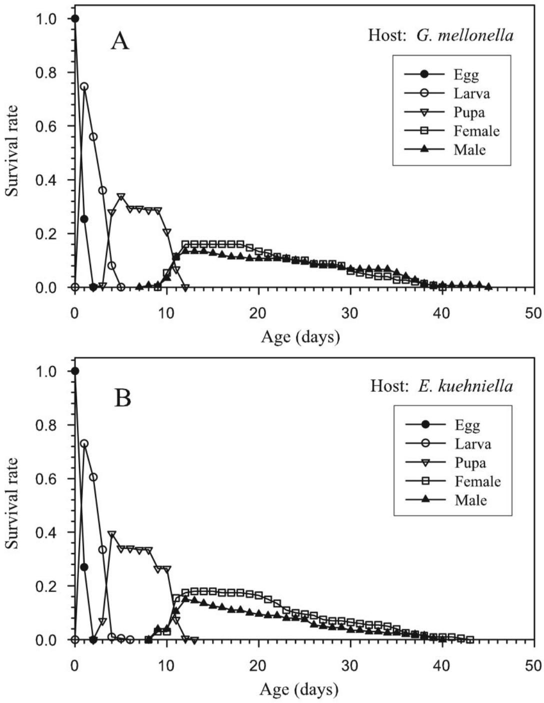

Fig. 2. Survival rate curves (s_{xj}) of *H. hebetor* reared on *G. mellonella* (A) and *E. kuehniella* (B).

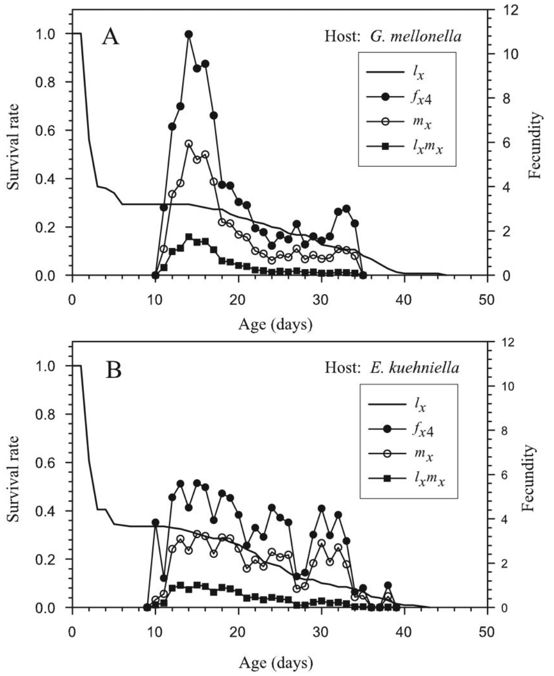

Fig. 3. Age-specific survival rate (l_x), female age-stage-specific fecundity (f_{x4}), age-specific fecundity (m_x), and age-specific maternity (l_xm_x) of *H. hebetor* reared on *G. mellonella* (A) and *E. kuehniella* (B).

preadult stages, APOP for *H. hebetor* reared on *E. kuehniella* was 1.39 ± 0.15 d (mean ± SE) and 2.04 ± 0.44 d on *G. mellonella* (Table 1).

Population Parameters. Age-stage-specific survival rates (s_{xj}) of *H. hebetor* were similar for the two host species (Fig. 2). The survival rate s_{xj} represents the probability that an egg will survive to age *x* while in stage *j*. This parameter gives a detailed description not only of survival but also of stage transitions. Because s_{xj} takes into account variation in developmental rates among individuals, we are able to depict stage overlap during the development of a cohort. Age-specific survival (l_x), female age-specific fecundity (f_{x4}), age-specific fecundity of the total population (m_x) and age-specific maternity (l_xm_x) of *H. hebetor* are illustrated in Fig. 3. A peak of age-specific fecundity for *H. hebetor* reared on *G. mellonella* was obvious at 14 d after birth. There was no obvious reproductive peak for *H. hebetor* reared on *E. kuehniella.*

The means and standard errors of *r*, λ, R_0, *GRR*, and *T* estimated by using the jackknife method are shown in Table 2. The intrinsic rate of increase for *H. hebetor* was 0.1520 d^{-1} on *G. mellonella* and 0.1375 d^{-1} on *E. kuehniella. GRR*, R_0, and *T* for *H. hebetor* on *G. mellonella* were 50.1 offspring, 12.5 offspring, and 16.8 d, respectively. On *E. kuehniella, GRR*, R_0, and *T* were 54.9 offspring, 11.9 offspring, and 18.2 d, respectively. No differences were found in any of the population parameters for *H. hebetor* reared on the two host species using a *t*-test at the 5% significance level (Table 2). Youm and Gilstrap (1993) reported that r_c and the net reproductive rate for *B. hebetor* reared on the millet head caterpillar, *Heliocheilus albipunctella* de Joannis (Lepidoptera: Noctuidae), were 0.26 and 86.5, respectively. Youm and Gilstrap (1993) constructed the survival curve (l_x) and fecundity curve (m_x) based on adult age, and used R_0 and the mean generation time T_c ($= \Sigma x l_x m_x / \Sigma l_x m_x$) to estimate r_c ($=$ (log R_0) / T_c). In our study, we used the Euler–Lotka equation to calculate the intrinsic rate of increase. The differences between our results and that of Youm and Gilstrap (1993) may be because of the different host, different analytical method, and/or different life table theory.

Benson (1973) showed that the size of the surviving progeny of *B. hebetor* decreased as parasitoid density per host increased. Taylor (1988b) showed that the mean size of emerging adult *B. hebetor* was strongly density dependent. To minimize the density-dependent effect, only one parasitoid egg was reared on each host in this study. This manipulation, however, may also have excluded the differential effect of density on survival, development, and fecundity on the two host species, and consequently diminished the difference in population parameters between these two host species. Further study is needed to clarify the effect of host density on the survival, development, fecundity, and population parameters of *H. hebetor* on different host species. Because no differences were found in any of the population parameters of the two host species, using the cheaper host (*E. kuehniella*) rather than the more expensive host (*G. mellonella*) for mass-rearing programs would be justified economically.

Life Expectancy. The life expectancy (e_{xj}) of each age-stage group of *H. hebetor* is plotted in Fig. 4. Life expectancy represents the time that an individual of age *x* and stage *j* is expected to live. The life expectancy of an egg was 10.4 d on *G. mellonella,* which is comparable with the value of 10.6 d on *E. kuehniella.*

Table 2. Means and standard errors intrinsic rate of increase (*r*), finite rate of increase (λ), gross reproductive rate (*GRR*), net reproductive rate (R_0), and mean generation time (*T*) of *H. hebetor* reared on *G. mellonella* and *E. kuehniella* estimated by using the jackknife method

Parameter	*G. mellonella*	*E. kuehniella*	*t*	df	*P*
r (d^{-1})	0.1520 ± 0.0140	0.1375 ± 0.0104	0.8529	348	0.3943 (>0.05)
λ (d^{-1})	1.1640 ± 0.0162	1.1473 ± 0.0119	0.8510	348	0.3953 (>0.05)
GRR (offspring)	50.1 ± 10.7	54.9 ± 10.1	0.3256	348	0.7449 (>0.05)
R_0 (offspring)	12.5 ± 2.8	11.9 ± 2.2	0.1714	348	0.8640 (>0.05)
T (d)	16.8 ± 0.7	18.2 ± 0.6	1.6032	348	0.1098 (>0.05)

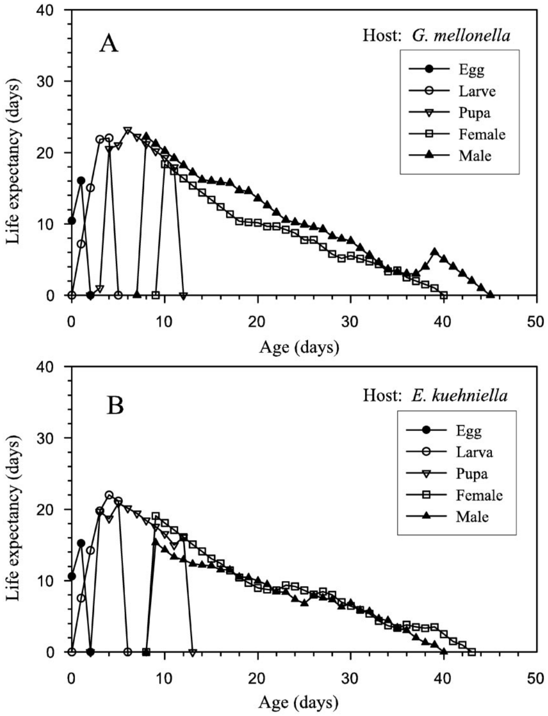

Fig. 4. Age-stage-specific life expectancy (e_{xj}) of *H. hebetor* reared on *G. mellonella* (A) and *E. kuehniella* (B).

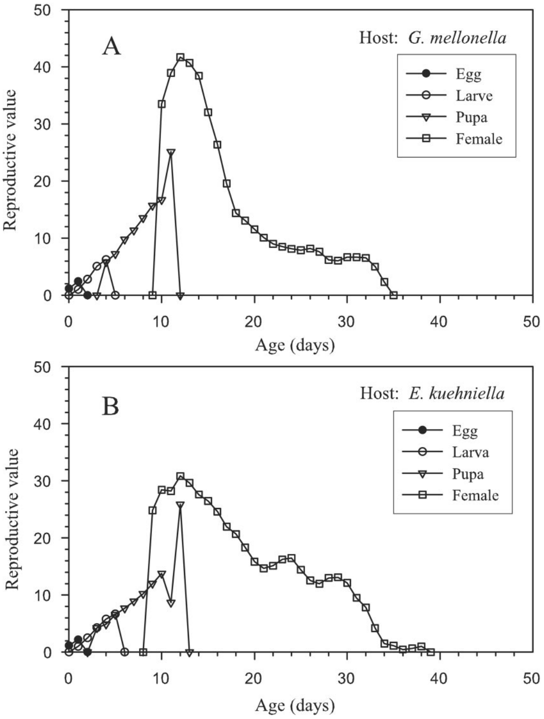

Fig. 5. Age-stage-specific reproductive value (v_{xj}) of *H. hebetor* reared on *G. mellonella* (A) and *E. kuehniella* (B).

However, when a female individual reached the adult stage, life expectancy increased to ≈18 d when reared on *G. mellonella* and 19 d when reared on *E. kuehniella.*

Reproductive Value. The reproductive value (v_{xj}) is the expectation of future offspring of individuals of age x and stage j (Fig. 5) (Fisher 1930, Pianka 1994). If the preoviposition period is counted as time from birth to first reproduction in females (TPOP), the mean TPOP for all *H. hebetor* females reared on *G. mellonella* was 13.00 ± 0.52 d (Table 1). This value is close to the age of peak reproductive value, 12 d (Fig. 5). Similarly, the peak reproductive value for *H. hebetor* reared on *E. kuehniella* was at age 12 d, which is also close to the TPOP for this host, i.e., 12.22 ± 0.18 d (Table 1). Gabre et al. (2005) found that the mean TPOP for *Chrysomya megacephala* (F.) (Diptera: Calliphoridae) was similarly close to the age of peak reproductive value.

Age-Stage, Two-Sex Life Table Justification. Ignoring differences in the preadult developmental time results in errors in the fecundity curve, and eventually will cause errors in the population parameter estimates. Errors in population parameter estimates also may result from focusing on the female sex alone, as in standard life table analysis. Most life table analyses cope with uncertainty in determining the sex of preadult by assuming a 1:1 sex ratio. Unfortunately sex ratio biases (Craig and Mopper 1993, Ode et al. 1996), sex-specific developmental rates (Gu et al. 1992, Harvey and Strand 2003, Bharthi et al. 2004), and sex-dependent mortality risk (Isenhour and Yeargan 1981, Berenbaum and Zangerl 1991) violate this assumption. In our study, we used an age-stage, two-sex life table to take both sexes into account as well as the variable developmental rate occurring among individuals. Chi (1988), Chi and Yang (2003), and Yu et al. (2005) further discuss the problem of applying standard female age-specific life tables to two-sex populations with stage structure.

In general, a life table provides a comprehensive description of the survival, development, and reproduction of a cohort of individuals. There are, however, still problems that cannot be resolved by life tables alone. For example, Ode et al. (1997) documented constrained oviposition and female-biased sex allocation in *B. hebetor.* To include such phenomena, both life table theory and data analysis may need to be modified. In addition, life table parameters often vary with different environmental variables. The effects of temperature seasonality (Johnson et al. 2000), pesticide resistance (Baker et al. 1995), and other factors on the life table of *H. hebetor* and the parasitoid's relationship to other host species (Benson 1974) are worthy of further study. These data might be useful in improving the efficacy of *H. hebetor* as a biological control agent in pest management regimes.

Acknowledgments

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