POPULATION ECOLOGY

A Comparison of Artificial Diet and Hybrid Sweet Corn for the Rearing of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) Based on Life Table Characteristics

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ABSTRACT   The demographic characteristics of *Helicoverpa armigera* (Hübner) reared on hybrid sweet corn (*Zea mays* L. variety *saccharata*) (hybrid super sweet corn KY bright jean) and on an artificial diet were compared by using the age-stage, two-sex life table. Because the hatch rate of eggs varies with maternal age, age-specific fecundity was calculated based on the numbers of hatched eggs to reveal the biological characteristics of *H. armigera* accurately. The intrinsic rate of increase (r), finite rate (λ) and mean generation time (T) of *H. armigera* were 0.0853 d^{-1}, 1.0890 d^{-1}, and 46.6 d, respectively, on *Z. mays* and 0.1015 d^{-1}, 1.1068 d^{-1}, and 46.3 d, respectively, on the artificial diet. There were significant differences in the intrinsic rate of increase and finite rate between two treatments. The age-stage life expectancy and reproductive value also were calculated. The relationships among the net reproductive rate, the mean female fecundity, the number of emerged females, and the total number of individuals used in the life table study are consistent with theoretical expectations. We recommend the age-stage, two-sex life table for use in insect demographic studies to incorporate both sexes and the variation in developmental rate among individuals and to obtain accurate population parameters. The artificial diet is more suitable for the mass rearing of *H. armigera*.

KEY WORDS   *Helicoverpa armigera*, *Zea mays*, life table, artificial diet

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a cosmopolitan pest feeding on >170 plant species (Zalucki et al. 1994), including cotton, corn (*Zea mays* L.), tomato (*Solanum lycopersicum* L.), legumes, asparagus (*Asparagus officinalis* L.), and other vegetable crops. The larvae of *H. armigera* prefer to eat the reproductive organs of plants (Fitt 1989, Zalucki et al. 1986). Polyphagy, high mobility, high fecundity, and facultative diapause enable this pest to survive in various habitats, to adapt to seasonal changes, and thus to achieve pest status (Fitt 1989). Capinera (2008) reported that sweet corn (*Zea mays* variety. *saccarata*) is more susceptible to *Helicoverpa* spp. than field corn. Several hybrid sweet corn varieties have been developed for more uniform maturity, improved quality with 5–20% sugar content and disease resistance. Because it is used for human consumption, the price of sweet corn is ≈2.5 times that of other varieties. The high potential profit margin encourages farmers to use pesticide-free management methods, especially in organic farming, to supply pesticide-free corn ears.

The life table is a powerful, necessary tool for analyzing and understanding the effect of external factors and host plants on the growth, survival, reproduction, and intrinsic rate of increase of insect populations (Chi and Su 2006). Based on the life table, population projections can be performed using computer simulation (Chi 1990). Life tables have been used in diverse types of studies related to population ecology, such as the population biology of invasive species (Sakai et al. 2001); conservation strategies (Wilcox and Murphy 1985); demographic ecotoxicology (Stark and Banks 2003); harvesting theory (Chi and Getz 1988, Chi 1994); and pest control timing (Chi 1990).

Numerous life table studies of *H. armigera* have been performed under varying conditions, including constant and alternating temperatures (Mironidis and Savopoulou-Soultani 2008); different host plants (Liu et al. 2004); and ambient and elevated CO_2 levels (Yin et al. 2009, 2010). However, most of these studies, with the exception of Yin et al. (2009, 2010), are based on an age-specific female life table that ignores the overlap of developmental stages in *H. armigera* populations or calculates age-specific fecundity based on the "adult age". Yu et al. (2005) indicated that an erroneous relationship among gross reproductive rate, net reproductive rate, and preadult survivorship is obtained when an age-specific female life table is applied to a two-sex population. Huang and Chi (2011) discussed many of the problems that occur when using female age-specific life tables. To overcome the short-

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falls in life table construction that arise owing to the neglect of the variation in developmental rates among individuals, the erroneous calculation of fecundity and the exclusion of males, Chi and Liu (1985) and Chi (1988) developed an age-stage two-sex life table theory. Age-stage two-sex life table theory has been applied to insect pests (Gabre et al. 2005; Silva et al. 2006; Yin et al. 2009, 2010; Bailey et al. 2010; Huang and Chi 2011); mites (Kavousi et al. 2009); predator life table and predation rate studies (Chi and Yang 2003, Yu et al. 2005, Mo and Liu 2006); life tables of parasitoids and parasitism rate (Amir-Maafi and Chi 2006, Chi and Su 2006); temperature-dependent demography (Yang and Chi 2006, Tsai and Chi 2007); and ecotoxicological studies (Schneider et al. 2009).

Because the growth and development of insects are affected by their host plants and various abiotic factors, an ecologically-based pest management program for *H. armigera* requires life tables constructed under different conditions and using different food sources. Because this approach potentially will be used in biological control programs, especially in organic farming, collecting these life table data are especially important. For all of these, it is crucial to choose the age-stage, two-sex life table to obtain comprehensive, precise, and meaningful analytical results. In this study, we compare the demographic characteristics of *H. armigera* reared on hybrid sweet corn and on an artificial diet by using the age-stage, two-sex life table theory. The constructed life tables will be used in the development of a mass-rearing program for the production of *H. armigera* to be used in study of entomopathogenic fungi and bioassay.

Materials and Methods

Hybrid Sweet Corn. The cobs of the KY bright jean variety of hybrid super sweet corn (*Zea mays*) were obtained from plants grown in the field without any application of pesticides. During the experimental period (March through June 2010), mixed fertilizers (Compound-Fer 43, N:P:K:Mg = 15:15:15:4, Taiwan Agricultural Biotechnology Co., Ltd) were applied twice at an interval of 4 wk, and weeds were removed by hand. The healthy cobs with immature grains were collected and stored in a deep freezer at −20°C. Before the cobs were supplied to *H. armigera* as food, they were defrosted at room temperature.

Artificial Diet. For rearing *H. armigera* in this study, we prepared the artificial diet modified from Kao (1995). It consists of the following ingredients: 150 g of bean powder (sterilized sieved mixture of kidney bean and soy bean), 55 g of wheat germ, 60 g of yeast powder, 0.6 g of L-cysteine, 6 g of ascorbic acid, 1.5 g of sorbic acid, 1.75 g of Methyl-p-hydroxybenzoate, 37.5 g of agarose and 1,300 ml of water.

H. armigera. The colony of *H. armigera* originally was collected from a corn field in Taichung County and maintained in the Microbial Control Laboratory, Department of Entomology, National Chung Hsing University Taichung, Taiwan. The colony is periodi-cally supplemented with larvae collected from the field to maintain its genetic variability.

Life Table Study. Before the life table study, the insects were reared on the respective diets (hybrid sweet corn and artificial diet) for one generation in a growth chamber at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 14:10 (L:D) h. Newly emerged adults were paired and kept in pairs in an individual oviposition container (a plastic cup of 9 cm in diameter by 5.5 cm in height, with paper towel lining). Each day, the adults were given a cotton ball saturated with 30% honey solution. Eggs from each female were collected in petri dishes (9 cm in diameter) and kept separately in the growth chamber mentioned above. In total, 120 eggs (10 eggs from each female) were used for the life table study on hybrid sweet corn and the artificial diet, respectively. The hatch rates of eggs were observed daily. The newly hatched larvae were individually transferred to petri dishes (9 cm in diameter) by using a fine brush and reared in groups up to the second instar. The third and older instars were reared individually in 30-well plates. In the experiment with hybrid sweet corn, the first and second instars were reared on corn silk, whereas the third and older instars were reared on immature corn seed. The individual larvae were observed daily for molting and survivorship. The diet was replaced every other day. The larvae entering the prepupal stage were given decomposed peat-based compost (Blocking Compost by Plantflor Humus Verkaufs GmbH, D 49377 Vechta, Germany) for pupation. Each pupa was sexed, weighed, and kept in an individual plastic cup (9 cm in diameter by 5.5 cm in height). Newly emerged adults were paired in oviposition containers lined with paper towels. Each day, adults were checked for oviposition and transferred to a new container after the eggs were collected. The eggs laid by each female at different ages were kept separately to record the hatch rates. Survival and fecundity were recorded for each individual until death. If any moth died earlier than its mate, a replacement would be supplied from the mass-rearing colony. The data on these recruited individuals were excluded from analysis.

Data Analysis. The raw data were analyzed based on the theory of the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988). The mean of the development periods for each development stage, the longevities for adult males and females, the adult preoviposition period (APOP), the total preoviposition period (TPOP) and the female fecundity of *H. armigera* were calculated. The APOP is calculated based on the adult age, whereas the TPOP includes the preadult age in the total. The age-stage specific survival rate (s_{xj}) (where x is the age and j is the stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), and the age-specific fecundity (m_x) were calculated from the daily records of the survival and fecundity of all individuals in the cohort. The age-stage specific fecundity (f_{xj}) was calculated from the numbers of hatched eggs to represent the biological characteristics of *H. armigera* accurately.

Table 1. Basic statistics of the life history of *Helicoverpa armigera* reared on artificial diet and hybrid sweet corn

Statistics	Stage or sex	Larval Diet				P
		Hybrid Sweet Corn		Artificial diet		
		n	Mean ± SE	n	Mean ± SE	
Preadult duration (d)	Egg	98	2.56 ± 0.05	106	2.53 ± 0.05	
	First Instar	95	2.08 ± 0.03	97	2.4 ± 0.05	0.0001
	Second Instar	87	3.77 ± 0.12	89	3.38 ± 0.09	0.0114
	Third Instar	85	2.53 ± 0.11	81	4.95 ± 0.30	0.0001
	Fourth Instar	78	4.22 ± 0.32	77	4.04 ± 0.28	0.9995
	Fifth Instar	70	5.32 ± 0.34	74	4.89 ± 0.16	0.6886
	Sixth Instar	14	4.71 ± 0.54	7	3.71 ± 0.36	0.2493
	Larva	63	18.30 ± 0.48	74	19.58 ± 0.49	0.031
	Prepupa	58	4.66 ± 0.22	71	2.20 ± 0.10	0.0001
	Pupa	46	14.70 ± 0.33	60	12.77 ± 0.19	0.0001
	Egg- pupa	46	39.24 ± 0.50	60	37.10 ± 0.60	0.0025
Pupal wt (gm)	Pupa	46	0.213 ± 0.007	60	0.261 ± 0.005	<0.0001
Adult longevity (d)	Female	22	24.91 ± 2.33	29	30.17 ± 2.88	0.2090
	Male	24	16.92 ± 2.32	31	27.68 ± 2.02	0.0073
APOP (d)	Female	13	6.69 ± 0.85	19	7.16 ± 0.89	0.984
TPOP (d)	Female	13	43.38 ± 1.05	19	42.37 ± 0.58	0.367
Fecundity (F) (eggs/female)	Female	22	223.1 ± 62.9	29	381.8 ± 104.7	0.5580

All *P* values are calculated from the *U* test except the *P* value of pupal wt and TPOP.
APOP (Adult preoviposition period) and TPOP (Total preoviposition period) are calculated by using females that produced fertile eggs.

The intrinsic rate of increase was estimated by using the iterative bisection method from the Euler–Lotka formula:

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

with age indexed from 0 (Goodman 1982). The bisection method can be found in most textbooks of numerical analysis (Burden and Faires 2005). The finite rate λ is calculated as e^r. The net reproductive rate is the total offspring that an individual can produce during its life time and is calculated as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \qquad [2]$$

The mean generation time (T) is defined as the time that a population needs to increase by a factor of R_0 as the stable age-stage distribution and the stable increase rate (i.e., r and λ) are reached. The relationship defining T is $e^{rT} = R_0$ or $\lambda^T = R_0$, and the mean generation time is then calculated as $T = \ln R_0 / r$. The gross reproductive rate (*GRR*) was calculated as $GRR = \Sigma m_x$. Based on the age-stage, two-sex life table, the life expectancy for individual of age x and stage y (e_{xy}) was calculated by

$$e_{xy} = \sum_{l=x}^{n} \sum_{j=y}^{m} s'_{ij} \qquad [3]$$

where n is the last age of the cohort, m is the number of stages, and s'_{ij} is the probability that an individual of age x and stage y will survive to age i and stage j and is calculated by assuming $s'_{xy} = 1$ and following the procedures described in Chi (1988) and Chi and Su (2006). Because the unhatched eggs were excluded

from the fecundity calculations, we also excluded the unhatched eggs from the parent cohort. An analysis of the raw data and an estimation of the life table parameters were performed with a user-friendly computer program, TWOSEX-MSChart (Chi 2009). This
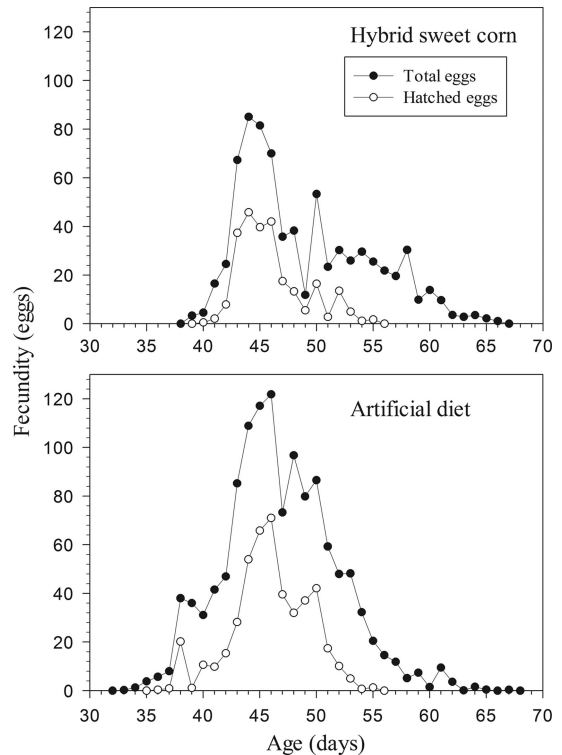

Fig. 1. Age-specific total eggs laid and age-specific hatched eggs of *H. armigera* reared on artificial diet and hybrid sweet corn.
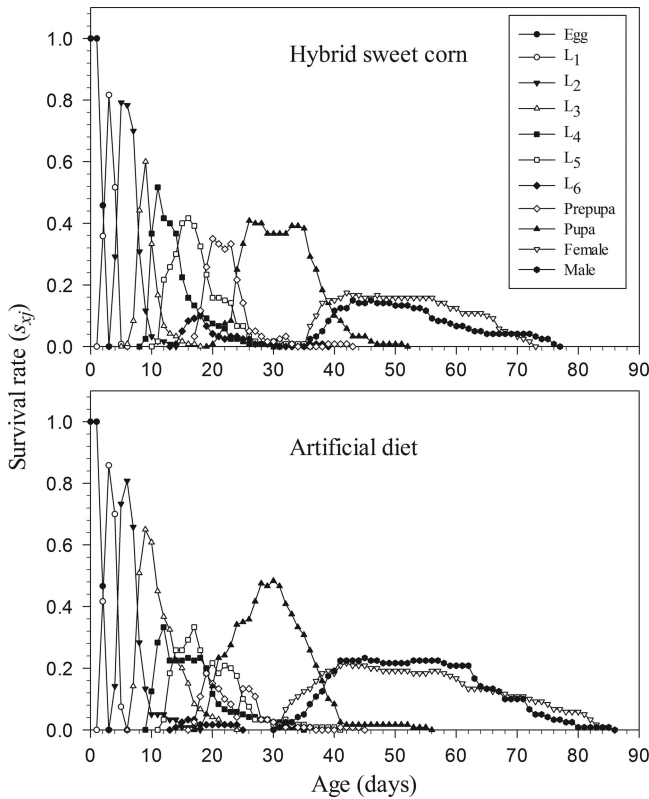
Fig. 2. Age-stage specific survival rate (s_{xj}) of *H. armigera* reared on artificial diet and hybrid sweet corn.

program also is available at http://140.120.197.173/ Ecology/Download/Twosex-MSChart.zip. The age-stage specific reproductive value (v_{xj}) also was calculated with TWOSEX-MSChart. The means and standard errors of the life table parameters were estimated by using the Jackknife technique (Sokal and Rohlf 1995) included in the TWOSEX-MSChart. The Mann–Whitney test (*U* test) (Sigmaplot 11.0, Systat Software Inc.) was used to evaluate the differences in the population parameters, development times, and fecundities of *H. armigera* reared on the artificial diet and hybrid sweet corn.

Results

The development periods for each stage, adult longevity, preoviposition period, and female fecundity of *H. armigera* reared on hybrid sweet corn and artificial diet are given in Table 1. The duration of the egg stages of *H. armigera* reared on hybrid sweet corn was not significantly different from the duration on the artificial diet. However, significant differences in total larval duration ($P = 0.043$), prepupal period ($P = 0.0001$), pupal period ($P = 0.0001$), and total preadult duration ($P = 0.0025$) were found between *H. armigera* reared on hybrid sweet corn and artificial diet. Most individuals had five larval stages, whereas a few had six larval stages. When reared on hybrid sweet corn, 20% of the fifth instars developed to the sixth

instar, whereas only 9% of the fifth instars reared on artificial diet developed to the sixth instar. The prepupal period was twice as long on hybrid sweet corn as on artificial diet, and this difference was significant ($P = 0.0001$). The pupae of *H. armigera* reared on artificial diet were significantly heavier than those reared on hybrid sweet corn ($P < 0.0001$) (Table 1).

The mean total preoviposition period (TPOP) of *H. armigera* reared on hybrid sweet corn and artificial diet was 43.38 d and 42.37 d, respectively. This difference was not statistically significant. The mean fecundity of *H. armigera* on sweet corn was 223.1 fertile eggs, a value considerably less than that on artificial diet (381.8 eggs). This difference was statistically insignificant. The numbers of age-specific total eggs and hatched eggs are shown in Fig. 1. Although the means of TPOP for hybrid sweet corn and artificial diet did not differ significantly, the cohort on artificial diet began oviposition a few days earlier than the cohort on hybrid sweet corn.

The curves of age-stage survival rate (s_{xj}) show the probability that an egg of *H. armigera* will survive to age *x* and stage *j* (Fig. 2). The overlap among the stage-specific survivorship curves is the result of the variation among individuals in the rate of development. The probability that a newly hatched larva would survive to the adult stage was 0.566 on artificial diet, considerably higher than that on hybrid sweet corn (0.469).
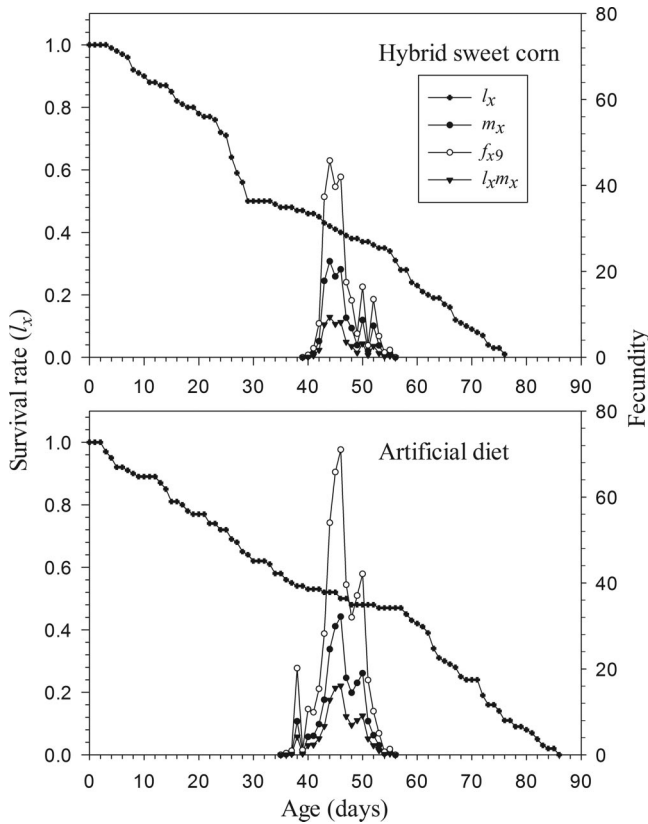
Fig. 3. Age-specific survival rate (l_x), female age-specific fecundity (f_{x9}), age-specific fecundity of total population (m_x), and age-specific maternity ($l_x m_x$) of *Helicoverpa armigera* reared on artificial diet and hybrid sweet corn.

The female age-specific fecundity (f_{x9}) shows the mean number of fertile eggs produced by the female adult (the ninth stage) at age x (Fig. 3). If all individuals of age x are included, this value expresses the age-specific fecundity of the total population (m_x). The l_x curve is the age-specific survival rate including all individuals of the cohort (Fig. 3) and ignoring the stage differentiation. It is thus a simplified version of the s_{xj} curves shown in Fig. 2. The product of l_x and m_x is the age-specific maternity ($l_x m_x$) of *H. armigera* on hybrid sweet corn and artificial diet. Higher peaks of f_{x9}, m_x, and $l_x m_x$ were observed in *H. armigera* reared on artificial diet.

The age-stage life expectancy (e_{xj}) shows the total time that an individual of age x and stage j is expected to live (Fig. 4). The age-stage life expectancy of the cohort of *H. armigera* reared on hybrid corn was shorter than that reared on artificial diet. The life expectancy decreased gradually with age because there were no adverse effects in the laboratory similar to those occurring in the field. The reproductive value (v_{xj}) (Fig. 5) is defined as the contribution of an individual of age x and stage j to the future population (Fisher 1930).

The means and standard errors of r, λ, R_0, GRR, and T are listed in Table 2. The intrinsic rate of increase (r) and the finite rate (λ) for *H. armigera* were 0.1015 d^{-1} and 1.1068 d^{-1}, respectively, on artificial diet, significantly higher than those on hybrid sweet corn ($r = 0.0853$ d^{-1}, $\lambda = 1.0890$ d^{-1}). On artificial diet, R_0, T and GRR for *H. armigera* were 104.45 offspring, 46.3 d, and 207.35 offspring, respectively. On hybrid sweet corn, R_0, T and GRR were 50.09 offspring, 46.56 d, and 125.08 offspring, respectively. No differences were found in R_0 or in GRR for *H. armigera* reared on these larval diets. However, significant differences were found in r, λ, and T.

Discussion

The results of this study fully illustrate the concept of the age-stage, two-sex life table. The study also demonstrates the advantages of the age-stage, two-sex life table over the traditional age-specific life table for describing demography (Lewis 1942, Leslie 1945, Birch 1948, Caswell 1989, Carey 1993). For example, the overlap in the developmental stages of *H. armigera* resulting from the variation among individuals in developmental rates is represented by the overlapping s_{xj} curves in Fig. 2. These results show the potential of the age-stage, two-sex life table for revealing the actual scenario of stage differentiation of *H. armigera*. Similar overlapping also can be observed in the e_{xj} and v_{xj} curves (Figs. 4 and 5). However, the age-specific sur-
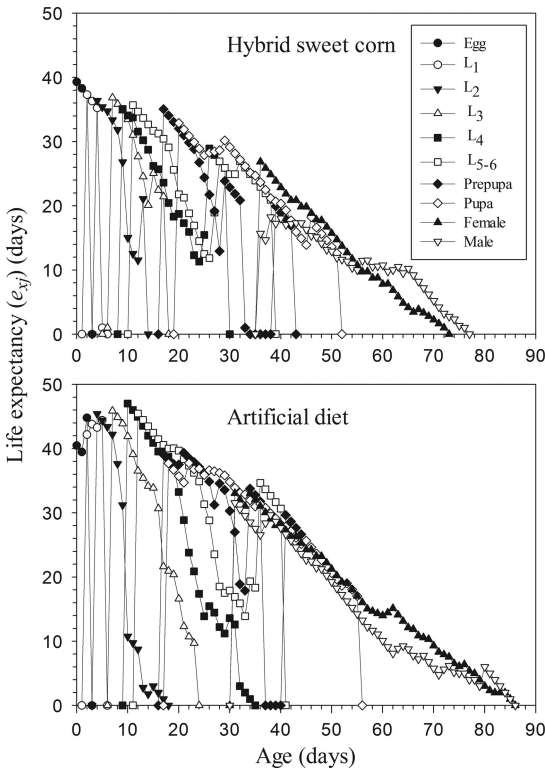
Fig. 4. Age-stage specific life expectancies (e_{xj}) of *H. armigera* reared on artificial diet and hybrid sweet corn.

vival rate (l_x) constructed based on a female age-specific life table (Fig. 1 of Mironidis and Savopoulou-Soultani 2008) or stage-structured life table (e.g., Fig. 1 of Liu et al. 2004) ignores the differences in developmental rates among individuals and assumes that all individuals have the same developmental periods in the preadult stages. Errors in the survival rate curves can be observed in papers using the age-specific female life table (e.g., Sandhu et al. 2010. Figure 1h and 1i). Moreover, calculating fecundity (m_x) based on adult age (Fig. 3 of Mironidis and Savopoulou-Soultani 2008) results in the miscalculation of the fecundity curve. Yu et al. (2005), Chi and Su (2006), and Kavousi et al. (2009) provide detailed discussions or mathematical proofs to indicate the problems that inevitably result from embedding in female age-specific life tables and the problems associated with the calculation of l_x and m_x based on adult age.

As shown by Chi (1988), for a two-sex population, the correct relationship between the net reproductive rate (R_0) and the mean female fecundity (F) is:

$$R_0 = F \cdot \left(\frac{N_f}{N}\right) \qquad [4]$$

where N is the total number of individuals used for life table study and N_f is the number of female adults emerged from N. In this study, the cohort sizes (N) for hybrid sweet corn and artificial diet are 98 and 106, whereas the emerged females (N_f) are 22 and 29,

respectively. All of this study's data for R_0 and F are consistent with the relationship of equation 4. Our results also are consistent with the relationship between R_0 and GRR: $R_0 < l_a \times GRR < GRR$ (Yu et al. 2005), where l_a is the preadult survivorship.

For the female age-specific life table theory applied to a two-sex population, Chi and Su (2006) showed that the relationship between F and R_0 is

$$R_0 = w \cdot \left(\frac{f_a}{f_0}\right) \cdot F = w \cdot s_a \cdot F \qquad [5]$$

where w is the proportion of female offspring ($0 \le w \le 1$), f_a is the number of females surviving to the adult stage, f_0 is the total number of females at the beginning of the life table, and s_a ($= f_a/f_0$) is the preadult survival rate of females in a two-sex population. We applied this formula to a few published life tables of two-sex populations, as listed in Table 3. We identified the preadult mortality s_a, F, w, and the reported net reproductive rate (R_{0_given}) in each paper. We then calculated R_0 (R_{0_cal}) by using equation 5 (Table 3). Theoretically, if the authors had correctly applied the age-specific female life table theory to the respective two-sex population, the calculated R_{0_cal} should be identical to the reported values (R_{0_given}). However, erroneous relationships between F and R_0 appear in Table 3. These errors result from the problems associated with the application of a female age-specific life table to a two-sex population (Chi and Su 2006).

The preadult mortality on hybrid sweet corn was 53.1%, higher than that on artificial diet (43.4%). These findings are similar to those reported by Jallow et al. (2001). However, the detailed survival (s_{xj}) with overlapping among stages could only be described by using age-stage, two-sex life table analysis.

Neither the adult preoviposition period (APOP) nor the total preoviposition period (TPOP) differed significantly between *H. armigera* reared on hybrid sweet corn and those reared on artificial diet. However, the intrinsic rate of increase of *H. armigera* reared on artificial diet was significantly higher than those reared on hybrid sweet corn. This finding seems contradictory to the concept of Lewontin (1965) that the age at first reproduction plays an important role in the intrinsic rate of increase. Because both APOP and TPOP are the means of preoviposition periods and do not represent the actual beginning of the reproduction of the cohort, their effects on the intrinsic rate of increase should not be overemphasized. The shorter TPOP on artificial diet is, however, consistent with the higher intrinsic rate. In contrast, the shorter APOP on hybrid sweet corn is inconsistent with its lower intrinsic rate. This difference shows that the TPOP is the true preoviposition period. It encompasses the entire length of the preadult stages, and it accurately defines the time interval from birth to the beginning of reproduction. To show the effect of the first egg-producing age on the intrinsic rate of increase and the reproductive value, the age at first reproduction should be used (Lewontin 1965).
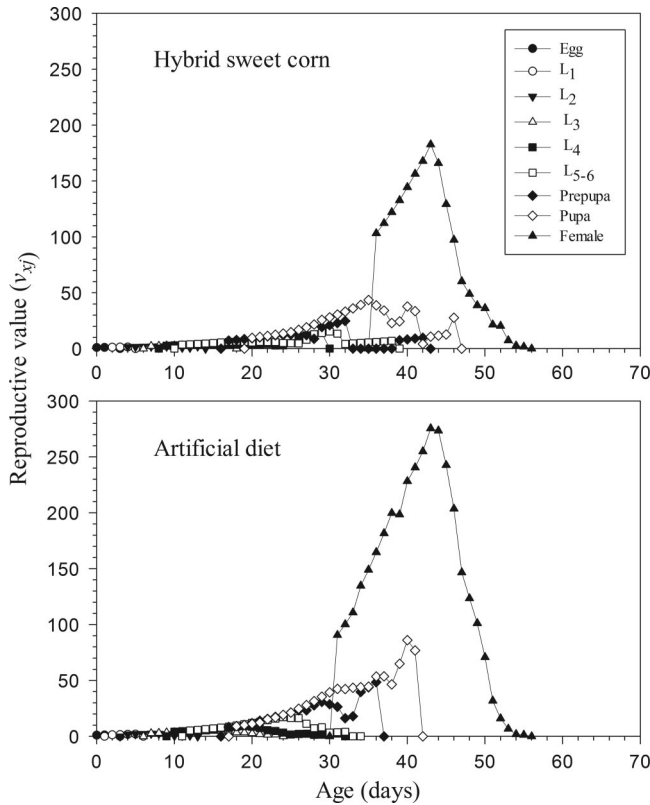
Fig. 5.   Age-stage specific reproductive values (v_{xj}) of *H. armigera* reared on artificial diet and hybrid sweet corn.

In many studies, e.g., Pilkington and Hoddle (2006), Mironidis and Savopoulou-Soultani (2008), and Sandhu et al. (2010), the mean generation time *T* is first estimated by using $T = \Sigma x l_x m_x / \Sigma l_x m_x$. It is then used to estimate *r* (= $\ln R_0/T$). This approximation method was suggested by Birch (1948) and reflects the difficulties of calculation in the 1940s. In this paper, we used the Euler–Lotka equation to calculate the intrinsic rate of increase. We did not use this approximation method. Thus, the differences between our results and those of earlier studies (Liu et al. 2004; Mironidis and Savopoulou-Soultani 2008; Yin et al. 2009, 2010) may result from different diets, rearing conditions, analytical methods, life table theories, or both.

For mass rearing of *B. cucurbitae*, Huang and Chi (2011) demonstrated that the intrinsic rate of increase

of population reared on artificial diet is significantly lower than those reared on cucumber (*Cucumis sativus* L.) and sponge gourd (*Luffa cylindrica* Roem). Our results showed that *H. armigera* reared on artificial diet had a shorter preadult duration, a heavier pupal weight (Table 1) and a higher reproductive performance of female adults compared with those individuals fed on hybrid sweet corn (Fig. 1 and 3). These differences primarily resulted from the higher preadult mortality and the delay in reproduction (Fig. 1 and 3) in *H. armigera* reared on hybrid sweet corn. These differences are consequently expressed in the significant differences in *r* and λ between hybrid sweet corn and artificial diet (Table 2). All these findings would support using an artificial diet when attempting to mass rear *H. armigera*. An improved diet

Table 2.   Mean ± SE of population parameters for *Helicoverpa armigera* fed on artificial diet and hybrid sweet corn estimated with the Jackknife method

Population parameters	Larval diet				*P*
	Hybrid sweet corn		Artificial diet		
	n	Mean ± SE	*n*	Mean ± SE	
Intrinsic rate (*r*) (d^{-1})	98	0.0853 ± 0.0078	106	0.1015 ± 0.0073	0.0010
Finite rate (λ) (d^{-1})	98	1.0890 ± 0.0085	106	1.1068 ± 0.0081	0.0001
Net reproductive rate (*R*$_0$) (offspring per individual)	98	50.1 ± 16.8	106	104.5 ± 32.8	0.3446
Mean generation time (*T*) (d)	98	46.6 ± 0.4	106	46.3 ± 0.9	0.0001
Gross reproductive rate (*GRR*) (offspring per individual)	98	125.2 ± 39.3	106	207.4 ± 62.6	0.1291

All *P* values are calculated from the *U* test.

Table 3. Consistency in published relationships between F and R_0 in the life table literature

Ref.	Source	Subject species	Life table theory	N	N_f	N	w	s_a	F	R_{0_cal}[a]	R_{0_given}[b]	Reference treatment	Remark
1	Hoddle et al. 2001	*Franklinothrips orizabensis*	Female age-specific	30	NA		0.500	0.9000	114.40	51.48	60.80	Diet no. 5	Inconsistent
2	Mo and Liu 2006	*Feltiella acarisuga*	Age-stage, two sex	48	22		0.564	0.8125	33.27	15.25	15.25	–	Consistent
3	Wang et al. 2008	*Helicoverpa assulta*	Female age-specific	300	NA		0.625	0.7380	613.60	283.02	291.40	Artificial diet	Inconsistent
4	Nielsen et al. 2008	*Halyomorpha halys*	Female age-specific	NA	22		0.500	0.6100	159.90	48.77	60.02	25°C	Inconsistent
5	Wang et al. 2009	*Liposcelis paeta*	Female age-specific	NA	50		0.500	0.4514	72.70	16.41	11.41	25°C	Inconsistent
6	Yang and Liu 2009	*Bactericera cockerelli*	Not specified	NA	20		0.459	0.5020	338.10	77.90	84.51	Egg plant	Inconsistent
7	Mironidis and Savopoulou-Soultani 2008	*Helicoverpa armigera*	Female age-specific	108	NA		0.500	0.4537	1007.69	228.59	203.14	25°C	Inconsistent
8	Chen and Parajulee 2010	*Lygus hesperus*	Female age-specific	NA	33		0.500	0.7000	75.00	26.25	12.45	Artificial diet	Inconsistent
9	Soufbaf et al. 2010	*Plutella xylostella*	Female age-specific	NA	17		0.500	0.5600	184.20	51.58	55.20	Hayula 420	Inconsistent
10	Golizadeh and Razmjou 2010	*Phthorimaea operculella*	Female age-specific	NA	19		0.527	0.7844	122.74	50.74	50.74	Buren	Consistent
11	Atlihan and Chi 2008	*Scymnus subvillosus*	Age-stage, two sex	40	14		0.560	0.6250	224.80	78.68	78.70	27°C	Consistent
12	Hu et al. 2010	*Nilaparvata lugens*	Age-stage, two sex	89	36		0.570	0.7100	167.67	67.82	67.82	*Oryza rufipogon*	Consistent

[a] R_{0_cal}: The net reproductive rate (R_0) calculated by using equation 2.
[b] R_{0_given}: The net reproductive rate (R_0) given in the respective papers.

will produce healthier insects as well as save labor and rearing costs. The superiority of the artificial diet over natural food also has been observed for *H. asulta* (Zhang et al. 2006; Wang et al. 2008). In this study, the superiority of the artificial diet may be because of the antibiotics which inhibit microbial contamination and the addition of cholesterol, which serves as a precursor for insect molting hormone (Kim and Lan 2010).

Age-stage, two-sex life tables provide comprehensive insights into the stage differentiation of *H. armigera*, compared with the traditional female age-specific life tables. Moreover, calculating the age-stage specific fecundity of *H. armigera* based on the number of eggs hatched produces more realistic estimates of population parameters than calculations by using the number of eggs laid because the hatch rate varies with the mother's age in both cohorts. In conclusion, the age-stage, two-sex life table analysis showed that the artificial diet is better for *H. armigera* than the diet of hybrid sweet corn. These life tables can further be used for population growth projections, for the design of mass-rearing programs, and for pest management.

Acknowledgments

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