Research Article

Population and damage projection of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table

Shu-Jen Tuan, Chung-Chieh Lee and Hsin Chi*

Abstract

BACKGROUND: The common cutworm, *Spodoptera litura* (Fabricus), is the most serious pest of peanuts in Taiwan. In order to devise an ecology-based and cost-effective control program, we collected life table data and consumption rates from larvae reared indoors at a constant temperature of 25°C, or outdoors at ambient temperatures during the spring and fall of 2010. A computer simulation was then used to project the population growth and damage potential of *S. litura* on peanuts.

RESULTS: Laboratory-reared *S. litura* individuals produced 3548 eggs/female, whereas those reared outdoors produced 3452 and 3072 eggs/female in the spring and fall, respectively. The intrinsic rate of increase was 0.1828, 0.1308 and 0.1545 day^{-1}, and the net consumption rate was 194.0, 132.2 and 166.6 cm^2 larva^{-1} at 25°C, in spring and fall, respectively. Population projection showed a faster growth and higher damage potential of *S. litura* in the fall.

CONCLUSION: Population projections based on life tables and stage-specific consumption rates can reveal the stage structure and damage potential of the pest population. Our results showed that monitoring data obtained by using pheromone traps were not in concordance with the damage potential of the pest population. This approach offers a promising tool for pest management.
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Keywords: *Spodoptera litura*; *Arachis hypogaea*; life table; consumption rate; population projection

1 INTRODUCTION

Spodoptera litura (Fabricius) is a polyphagous defoliator of over 300 species of plants belonging to more than 100 plant families and often causes heavy damage to economic crops and green manure plants throughout Asia, Africa, North America and many Oceania islands.[1,2] It has been the most serious defoliating pest of peanuts (*Arachis hypogaea*) in Taiwan for several decades.[3] Because its population dynamics and damage vary with climate, crop and agro-practice, its management has always been a difficult task. Among abiotic factors, temperature and photoperiods are of major importance.[4−8] The effect of abiotic factors on the growth rate of a population can be appropriately assessed using life table data collected under different conditions. Traditional female, age-specific life tables, however, ignore both the male component of a population and stage differentiation, thereby limiting their practical application.[9,10] Moreover, because of the difficulties inherent in conducting field experiments, most life table studies have traditionally been carried out in the laboratory under constant or controlled conditions. In order to comprehensively understand and to devise a practical application of the demography of *S. litura*, it is necessary to collect demographic data based on the age-stage, two-sex life tables under both laboratory and field conditions.

In this study, we collected life table data for *S. litura* individuals reared indoors on peanut leaves at 25°C, and outdoors under unregulated conditions during the spring and fall of 2010. We compared the demographic characteristics and consumption rate of *S. litura* using the age-stage, two-sex life table theory. Finally, we integrated the life table data with the consumption rate and, using a computer simulation, we projected the population growth and damage potential under various conditions.

2 MATERIALS AND METHODS

2.1 *Spodoptera litura* colony

The original population of *S. litura* was collected in Wufeng County, Taiwan. Larvae were reared on modified artificial diets and kept in a walk-in growth chamber set to 25°C, a photoperiod of 12L:12D,

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and relative humidity (RH) of $65 \pm 10\%$.[11] Newly hatched neonates were reared en masse on artificial diet in plastic cups (9.5 cm in diameter, 5.5 cm in height) until they reached the late fourth instar. Healthy fourth instars were collected and reared individually in a 30-well plastic plate until pupation. Between 10 and 15 pairs of newly emerged adults were transferred to each mating cylinder (13.5 cm in diameter × 18.5 cm in height, lined with a plain paper towel) and provided with a cotton-wool ball soaked with 18% honey as adult diet.

2.2　*Arachis hypogaea* seedlings

Peanut seeds (Tainan 14 cultivar) were sown in a field that had been pretreated with a single application of the herbicide (Pendimethalin 34% EC). Weeds were removed by hand afterwards. The fertilizer Fer 43 (Taiwan Agricultural Biotechnology Co., Ltd, Taipei, ROC) was applied once per month during the vegetative growth stage. No pesticides were applied throughout the study. Fresh and fully expanded peanut leaves were collected from the field and provided as food for larvae.

2.3　Life table study

Five egg masses laid on paper towels within one 24-h period were randomly selected from the colony and pinned to peanut leaves and kept in a glass cylinder (7 cm diameter × 15 cm height, with fine mesh covering each end). The petiole of leaf was inserted into a small tube filled with water to avoid dehydration. In the preliminary test, we noticed that the egg hatch rate varied with the female age. In order to detect the actual reproductive potential, we used hatched eggs at the beginning of life table study; we then used the hatched eggs produced by females as the age-specific fecundity. Twenty newly hatched first instar larvae were randomly picked from each egg mass. First and second instars were reared in groups. The third instar larvae were transferred to a glass cylinder and reared individually. Fresh leaves were supplied as needed until pupation occurred. Clean soil was supplied to sixth

instar individuals for pupation. Newly emerged male and female adults were paired and kept in individual rearing containers for oviposition. If there were more individuals of one sex, then they were paired with young adults of the opposite sex recruited from the mass-reared colony for mating. Data from those recruited individuals were excluded from the life table analysis. Newly laid egg masses were transferred to a new container and observed daily. The total number of eggs was recorded, but only the hatched eggs were subsequently used in the life table analysis. Experiments were conducted under three different conditions: (1) a walk-in growth chamber set at $25 \pm 1°C$, $65 \pm 10\%$ RH and a photoperiod of 14 L:10 D; (2) outdoors in spring (19 March to 28 May 2010); and (3) outdoors in fall (17 August to 26 October 2010). During the outdoor studies, the ambient temperature and humidity were recorded using a Sigma-II Hygro-Thermograph (NSII-Q, SATO, Japan) throughout the study.

2.4　Life table data analysis

The life history raw data of individual *S. litura* were analyzed by using the TWO-SEX-MSChart program,[12] based on the age-stage, two-sex life table theory[13] and the method described by Chi.[14] The survival rate (s_{xj}) (x = age, j = stage), which is the probability that a newly laid egg will survive to age x and stage j, and fecundity f_{xj}, which is the number of hatched eggs produced by female adult at age x were calculated. Age-specific survival rate (l_x) was then calculated as

$$l_x = \sum_{j=1}^{m} s_{xj}$$

where m is the number of stages. Age-specific fecundity (m_x) was calculated as

$$m_x = \frac{\sum_{j=1}^{m} s_{xj} f_{xj}}{\sum_{j=1}^{m} s_{xj}}$$

Table 1.　Developmental time, longevity and mean fecundity ($\pm$ SE) of *Spodoptera litura* under different conditions

Stage	25°C n	Developmental time (d)	Spring n	Developmental time (d)	Fall n	Developmental time (d)
Egg	104	$3.0 \pm 0.0a$	148	$3.0 \pm 0.0a$	135	$2.8 \pm 0.0b$
L1+L2	96	$7.5 \pm 0.2b$	120	$11.4 \pm 0.1a$	117	$8.0 \pm 0.2b$
L3	96	$2.9 \pm 0.1b$	116	$4.3 \pm 0.2a$	115	$3.0 \pm 0.1b$
L4	95	$2.3 \pm 0.1b$	103	$3.9 \pm 0.2a$	114	$2.4 \pm 0.1b$
L5	92	$3.0 \pm 0.1b$	100	$4.0 \pm 0.2a$	114	$2.7 \pm 0.1b$
L6	90	$3.9 \pm 0.2b$	93	$4.8 \pm 0.1a$	111	$3.1 \pm 0.1c$
Prepupa	90	$2.0 \pm 0.0a$	92	$2.0 \pm 0.1a$	107	$2.0 \pm 0.0a$
Pupa	88	$10.3 \pm 0.1b$	59	$12.1 \pm 0.2a$	72	$8.5 \pm 0.1c$
Pre-adult	88	$34.6 \pm 0.3b$	59	$45.2 \pm 0.4a$	72	$31.7 \pm 0.2c$
Adult longevity						
Female	44	$12.6 \pm 0.5a$	30	$12.1 \pm 0.7a$	36	$9.3 \pm 0.6b$
Male	44	$17.1 \pm 0.9a$	29	$11.8 \pm 0.6b$	36	$9.6 \pm 0.7b$
APOP	39	0.8 ± 0.2	23	0.9 ± 0.3	23	1.4 ± 0.3
TPOP	39	35.1 ± 0.4	23	45.8 ± 0.8	23	32.8 ± 0.4
Mean fecundity						
Female	44	$2277 \pm 295a$	30	$2494 \pm 338a$	36	$797 \pm 180b$

Means in the same row followed by different letters are significantly different ($P < 0.05$) using the Tukey–Kramer procedure.
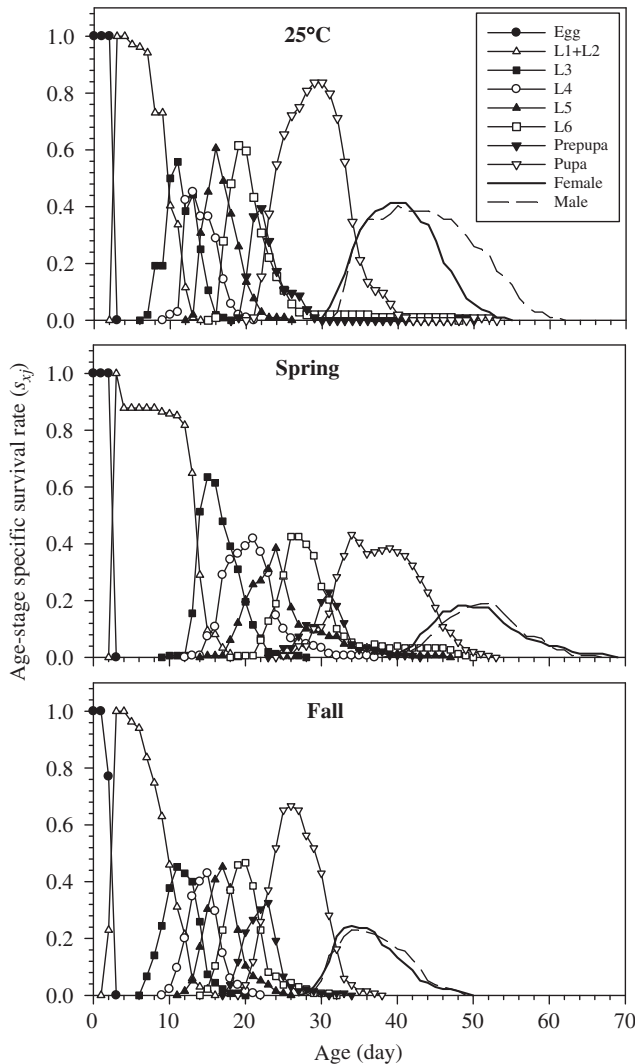
Figure 1. Age-stage-specific survival rate (s_{xj}) of *S. litura* under different conditions.

The net reproductive rate is defined as the total number of offspring that an individual can produce during its lifetime and is calculated as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x.$$

The intrinsic rate of increase was calculated using the Lotka–Euler equation with age indexed from zero, as

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

The mean generation time represents the period that a population requires to increase to R_0-fold of its size as time approaches infinity and the population settles down to a stable age-stage distribution. Mean generation time is calculated as

$$T = \frac{\ln R_0}{r}$$

Age-stage-specific life expectancy (e_{xy}), i.e. the time that an individual of age x and stage y is expected to live, was calculated
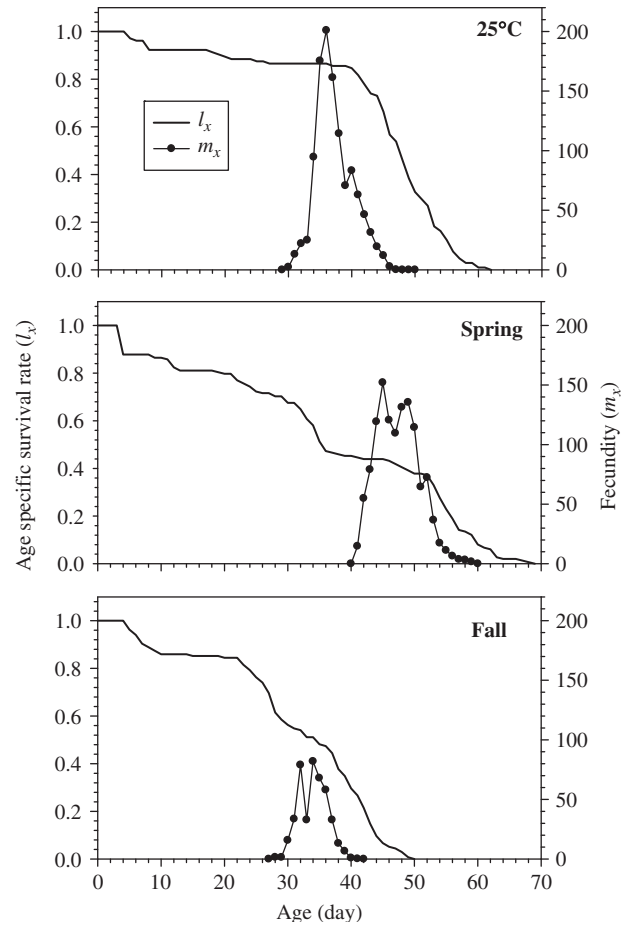

Figure 2. Age-specific survival rate (l_x) and fecundity (m_x) of *S. litura* under different conditions.

according to the method described by Chi and Su[9] as

$$e_{xy} = \sum_{i=x}^{n} \sum_{j=y}^{m} s'_{ij}$$

where s'_{ij} is the probability that an individual of age x and stage y will survive to age i and stage j. Fisher[15] defined the reproductive value as the contribution of individuals of age x and stage y to the future population. In the age-stage, two-sex life table, it is calculated as

$$v_{xy} = \frac{e^{-r(x+1)}}{s_{xy}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=y}^{m} s'_{ij} f_{ij}$$ See Erratum in last page.

The means and standard errors of population parameters were calculated by using the bootstrap method.[16,17] Differences among treatments were compared by using the Tukey–Kramer procedure.

2.5 Leaf consumption rate study and analysis

Leaf consumption of individual *S. litura* larvae was recorded daily during the life table study. From the first to the fourth instar, the consumption rate was measured by using graph paper (0.25 mm² per lattice). During the fifth instar, the larvae consumed considerably more leaves. To avoid the time-consuming and tedious process of measuring precise leaf areas, we used the
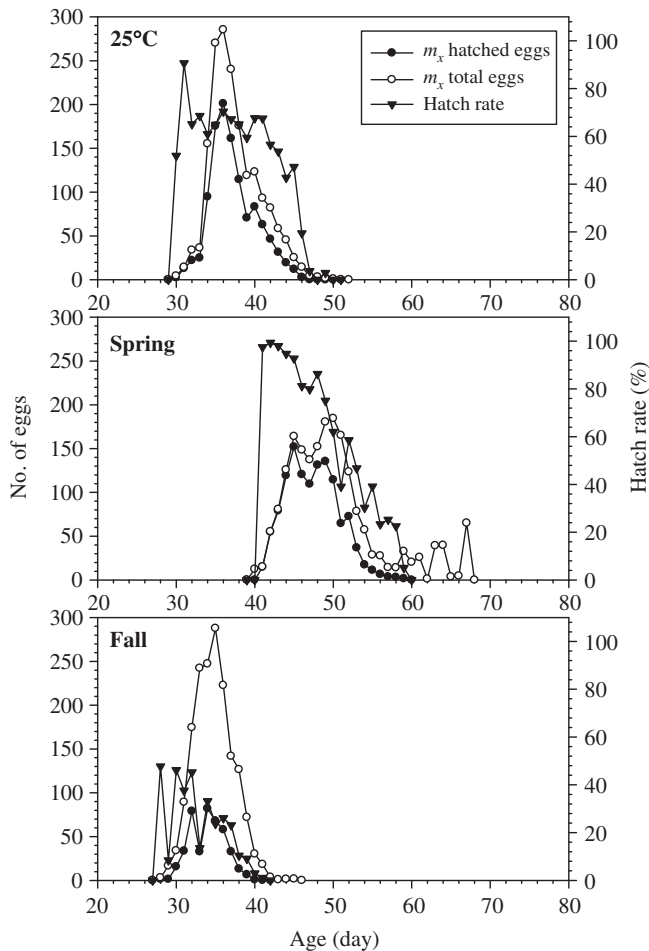
Figure 3. Mean number of eggs laid and hatched and hatch rate of *S. litura* under different conditions.

Figure 4. Age-stage-specific life expectancy (e_{xj}) of *S. litura* fed on peanut leaves at 25°C, in spring and fall 2010.

mean leaf area of 30 randomly selected leaves as the standard leaf area before being fed to the insects. Between 10 and 15 leaves were supplied daily to each larva, and the total leaf area consumed after 24 h was measured using a leaf area meter (Li-Cor, Li-3100A, USA). The differences between before- and post-feeding were recorded as the leaf consumption rate. Raw data of daily consumption rates of each individual were analyzed using the CONSUME-MSChart.[18] The age-stage consumption rate (c_{xj}) (x = age, j = stage) represents the mean consumption rate of an individual of age x and stage j. The age-specific consumption rate (k_x) is calculated as

$$k_x = \frac{\sum_{j=1}^{m} s_{xj} c_{xj}}{\sum_{j=1}^{m} s_{xj}}$$

The age-specific consumption rate represents the mean areas of peanut leaves consumed by *S. litura* at age x when differences among stages are ignored. When the survival rate is taken into consideration, the age-specific net consumption rate (q_x) gives the weighted consumption rate of the cohort at age x and can be calculated as
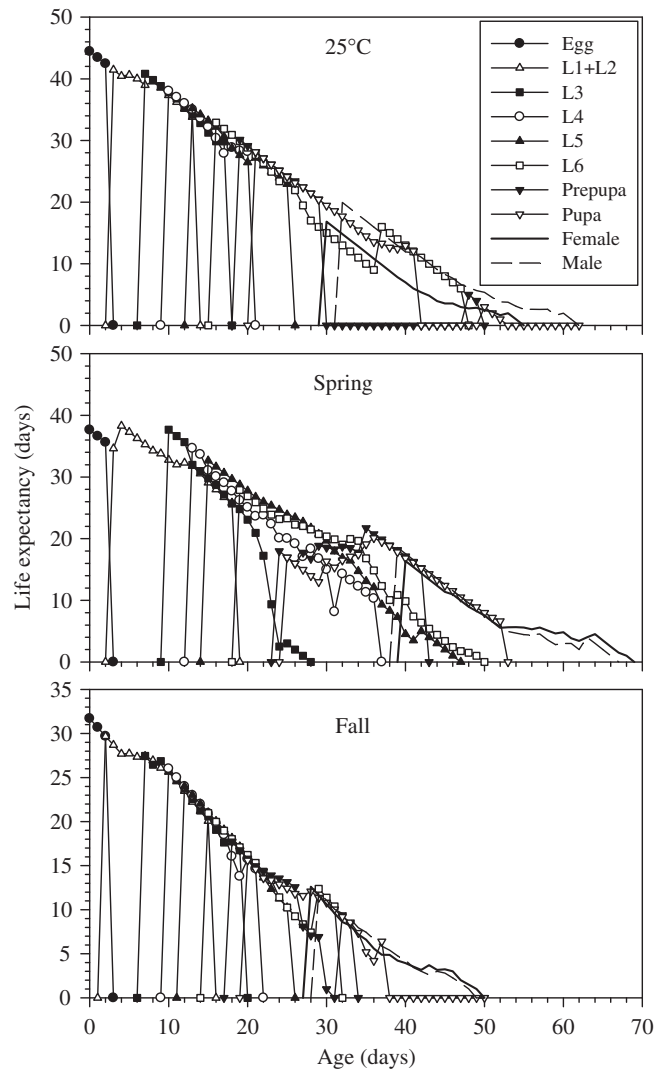
$$q_x = k_x l_x.$$

The net consumption rate (C_0) is defined as the total leaf area that an individual can consume during its life span and is calculated as

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} c_{xj}$$

Means and standard errors were calculated using the bootstrap method.[16,17] Differences in net consumption rate among treatments were analyzed using the Tukey–Kramer procedure.

2.6 Population and damage projection

The computer program TIMING-MSChart[19] was used to project the population growth of *S. litura* and its predicted damage. To take into consideration the variable damage potential among instars, we calculated the stage-specific weighting coefficients (w_j) according to the daily consumption rate of each instar as

$$w_j = \frac{C_j}{C_6}$$

where C_6 is the mean daily consumption of sixth instar and C_j is the mean daily consumption of jth instar. The weighted population
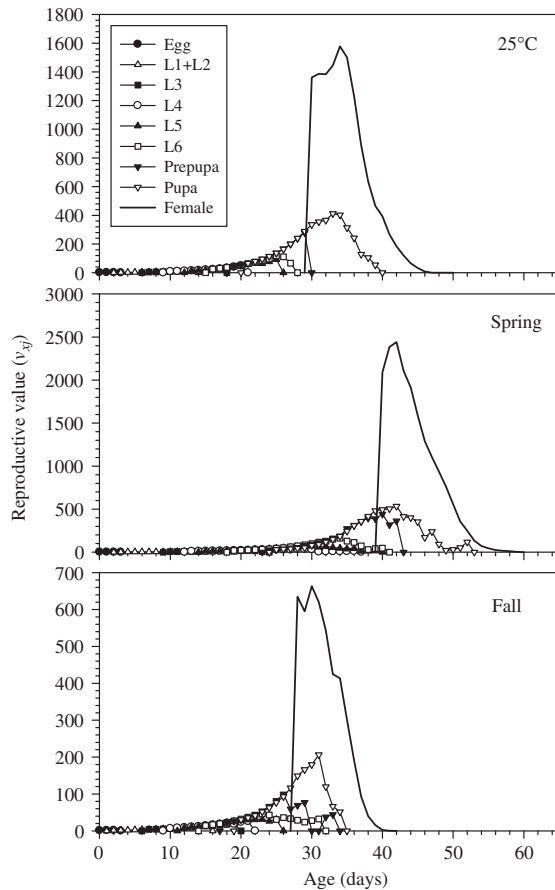
Figure 5. Age-stage-specific reproductive value (v_{xj}) of *S. litura* fed on peanut leaves at 25°C, in spring and fall 2010.

size at time t, i.e. $n_w(t)$, is calculated as

$$n_w(t) = \sum_{j=1}^{8} \left(w_j \cdot \sum_{x=0}^{\infty} n_{xj}(t) \right)$$

where $n_{xj}(t)$ is the number of individuals in age x and stage j at time t.

3 RESULTS

3.1 Life tables

The longest pre-adult duration, 45.2 days, was observed in spring, when the average of daily mean temperature during the experimental period (19 March to 28 May 2010) was 23.6°C, and the daily minimum and maximum temperatures were 14.3 and 29.1°C, respectively. At 25°C, the pre-adult duration decreased to 34.6 days. The shortest pre-adult developmental time was 31.7 days in fall, when the average of daily mean temperature during the experimental period (17 August to 26 October 2010) was 28.3°C, and the daily minimum and maximum temperatures were 25.1 and 30.7°C, respectively. When the adult preoviposition periods (APOP) was used to describe the beginning of reproduction, there were no differences in APOP among the three life tables. In contrast with APOP, the total preoviposition period (TPOP, which is counted from the beginning of the life table study to the first egg production) in spring (45.8 days) was significantly longer than that found under the two other
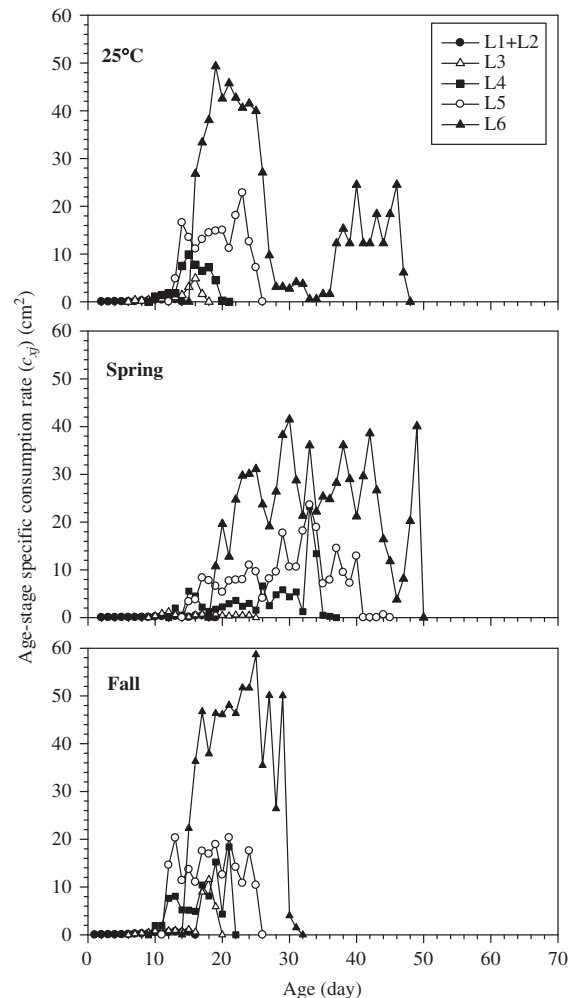

Figure 6. Age-stage, two-sex consumption rate (c_{xj}) of *S. litura* under different conditions.

conditions. Female adults lived shorter in fall and produced fewer eggs than those in spring and those reared at 25°C. The adult sex ratios for all three conditions were ∼1:1 (Table 1).

The age-stage-specific survival rate (s_{xj}) represents the probability that an egg of *S. litura* will survive to age x and stage j (Fig. 1). Owing to the variable developmental rates among individuals, significant overlaps between stages were observed under all conditions. The highest larval survival rate was observed at 25°C; ∼85% of eggs normally survive to the adult stage. In contrast to the high survival rate occurring at 25°C, a significantly lower survival rate (53%) was observed in the fall, while the lowest survival rate (40%) was observed in spring.

When all stages are pooled, the age-specific survival rate (l_x) gives a simplified overview of the survival history of the whole cohort (Fig. 2). Among the three conditions, the life table at 25°C showed the highest age-specific survival rate with a maximal mean longevity of 44.4 days; the single highest age-specific fecundity peak (201.0 offspring, i.e. hatched eggs) occurred at age 36 days (Fig. 2). Because of the lower immature survival rate in spring and fall, the mean longevity for these periods was 37.6 and 31.7 days, respectively. In spring, the reproductive peaks occurred between age 42 and 50 days with the highest fecundity 152.1 hatched eggs. In fall, reproductive peaks occurred between age 32 and 36 days with the highest fecundity 82.0 hatched eggs.
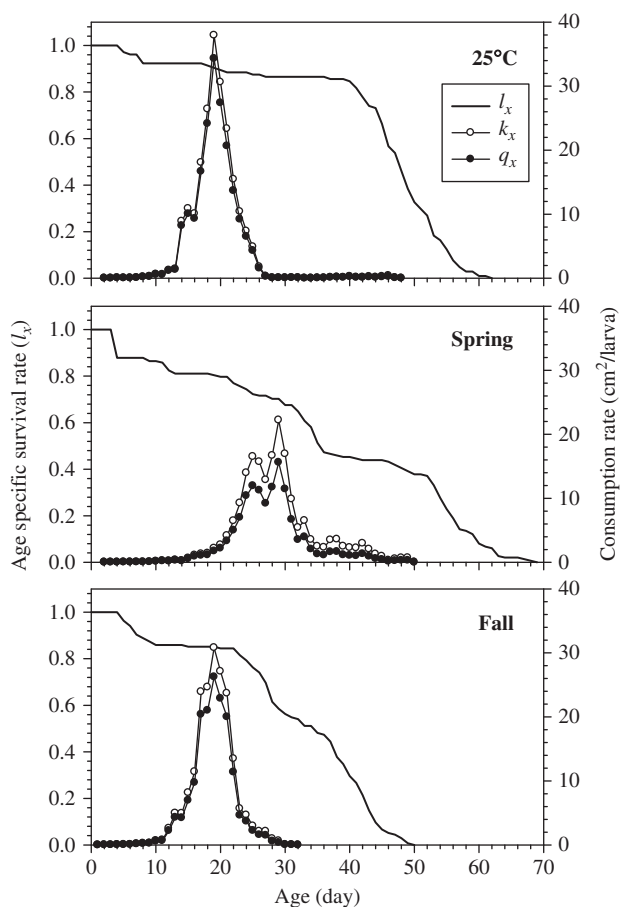
Figure 7. Age-specific survival rate (l_x), consumption rate (k_x), and net consumption rate (q_x) of *S. litura* under different conditions.

The age-specific fecundity and the age-specific hatch rate varied with the age of the female and with the conditions (Fig. 3). Generally, eggs laid by older females showed a lower hatch rate than those laid by younger females. At 25°C, eggs laid by young females during the first 10 days following adult emergence had an average hatch rate of 66%. In spring, the average hatch rate of the first 10 days was as high as 86%. The lowest average hatch rate (30%) was observed in fall. At the end of the reproduction period, the hatch rate was generally low under all three conditions. The mean fecundities at 25°C, in spring, and fall, were 2277, 2494 and 797 hatched eggs, respectively (Table 1).

The intrinsic rate of increase ($r = 0.1830$ day^{-1}) and the finite rate of increase ($\lambda = 1.2009$ day^{-1}) at 25°C were significantly higher than those in spring ($r = 0.1307$ day^{-1} and $\lambda = 1.1397$ day^{-1}) and fall ($r = 0.1544$ day^{-1} and $\lambda = 1.1670$ day^{-1}) (Table 2). The net reproductive rate (R_0) was the highest at 25°C (970.1 hatched eggs). Because of the low fecundity and low hatch rate in fall, the R_0 value of 212.9 offspring was significantly lower than that at 25°C and in spring (506.7 offspring). The mean generation times in the 25°C, spring, and fall groups were 37.5, 47.5 and 34.5 days, respectively.

The life expectancy (e_{xj}) is the length of time that an individual of age x and stage j is expected to live after age x (Fig. 4). The life expectancy in fall was shorter than in spring and at 25°C. The age-stage-specific reproductive values (v_{xj}) of *S. litura* represented the contribution of an individual at age x and stage j to the future population. The reproductive value increased significantly when

S. litura began to produce hatchable eggs. At 25°C, the increase in reproductive value occurred at age 30 days and remained at high reproduction for a few days (Fig. 5). In spring, the reproductive value increased at a later age (41 days) and reached a peak of 2450. Despite the low fecundity and hatch rate in fall, the peak reproductive value occurred much earlier at age 27 days and was as high as 700.

3.2 Consumption rate

The age-stage consumption rates (c_{xj}) of *S. litura* increased with age and stage (Fig. 6). Because larvae stopped feeding before each molt, the consumption rate dropped at the end of each stage. The age-specific consumption (k_x) represents the mean damage potential per individual of age x. When the survival rate was taken into consideration, the age-specific net consumption rate (q_x) revealed the weighted consumption of the entire cohort at age x. Although peaks in consumption rate were observed for individual older larvae at 25°C and in spring (Fig. 6), the respective net consumption rates (q_x) for these times were low because only isolated individuals remained as larvae at these older ages (Fig. 7). The consumption of the last instar accounted for $> 70\%$ of the lifelong consumption under all conditions. By assigning the sixth instar consumption rate as unity, the weighting coefficients (w_j) of other instars under different conditions were calculated. The values of w_5 for the fifth instar were 0.26, 0.27 and 0.30 for 25°C, spring and fall, respectively. The w_j values of the first to fourth instars for all conditions ranged from 0.01 to 0.11 (Table 3). In summary, the amount of damage caused by a sixth instar individual was more than three times that caused by fifth instar larvae, nine times that of fourth instars, 50 times that of third instars and 100 times that of the first and second instars. By taking the survival rate into account, the net consumption (C_0) was 190.2, 133.7 and 165.1 cm^2 larva^{-1} at 25°C, in spring and fall, respectively. The net consumption rate in spring was significant less than that in fall and at 25°C.

3.3 Population and damage projection

By using the life table and consumption rate data collected under different conditions, the growth and damage capacity of *S. litura* were projected to show the increase of the pest population, the stage structure and the weighted population (L6-equivalent, or the damage potential) during the process of population growth at varying conditions (Fig. 8). Because the age-stage, two-sex life table is capable of integrating stage differentiation and includes the effects of both sexes, the derived population projection will accurately characterize details of the stage structure. When different weighting coefficients were assigned to each instar (Table 3), the weighted population (L6-equivalent) precisely revealed the change of the damage potential of the *S. litura* population.

4 DISCUSSION

Because insects are ectothermic organisms, their developmental rates are affected by temperature.[2,5,20–22] Their responses to fluctuating and constant temperature, however, can vary widely. For example, in a laboratory study, Mironidis and Savopoulou-Soultani[23] compared the development rate of *Helicoverpa armigera* at constant and alternating temperatures around the same mean temperature; their results showed that there were no significant difference between constant 25°C and alternating temperatures with the same mean temperature 25°C.

Table 2. Population parameters (mean ± SE) of *S. litura* fed on peanut leaves under different conditions

Parameter	25°C	Spring	Fall
Intrinsic rate of increase, r (day^{-1})	0.1828 ± 0.0051a	0.1308 ± 0.0049c	0.1545 ± 0.0083b
Finite rate of increase, λ (day^{-1})	1.2006 ± 0.0061a	1.1397 ± 0.0056c	1.1671 ± 0.0098b
Net reproductive rate, R_0 (offspring)	962 ± 164a	507 ± 106b	212.9 ± 56.7b
Mean generation time, T (day)	37.5 ± 0.4b	47.5 ± 0.6a	34.5 ± 0.4c
Net consumption rate, C_0 (cm^2)	194.0 ± 8.3a	132.2 ± 8.2c	166.6 ± 7.2b
Finite consumption rate (ω)	1.3834	0.7024	1.7687

Means in the same row followed by different letters are significantly different ($P < 0.05$) using the Tukey–Kramer procedure.

Table 3. Mean consumption rate (cm^2 larva^{-1}) by each larval instar of *S.litura* and conversion to sixth instar larval injury equivalent under different conditions

| | | Consumption rate (cm^2) | | | | | | | | Weighting coefficient (w_j) | | |
| | | 25°C | | | Spring | | | Fall | | | | |
Instar	n	Mean ± SE	%	n	Mean ± SE	%	n	Mean ± SE	%	25°C	Spring	Fall
First to second	96	0.96 ± 0.06a	0.4	120	1.12 ± 0.04ab	0.6	117	1.21 ± 0.08b	0.6	0.003	0.004	0.003
Third	96	2.65 ± 0.26	1.2	116	2.09 ± 0.16	1.1	115	2.60 ± 0.22	1.3	0.022	0.017	0.020
Fourth	95	12.78 ± 1.24	5.8	103	12.57 ± 1.14	6.6	114	15.30 ± 1.12	7.7	0.132	0.114	0.142
Fifth	92	42.35 ± 1.52	19.3	100	37.33 ± 2.77	19.6	114	40.95 ± 1.53	20.6	0.338	0.325	0.335
Sixth	90	160.8 ± 3.9a	73.2	93	137.5 ± 4.1b	72.1	111	138.3 ± 3.6b	69.7	1.000	1.000	1.000

Means in the same row followed by different letters are significantly different ($P < 0.05$) using the Tukey–Kramer procedure. Percentage consumption is the stage-specific consumption rate of each larval stage divided by the net consumption rate.

But, significant differences were observed between constant and alternating temperature at mean temperature 20°C.[23] Miyashita showed that the development of *S. litura* larvae and pupae tended to be faster under alternating temperatures.[24] The main purpose of this study was not to determine the development rate at constant and fluctuating temperature around the same mean temperature. Instead, our intention was to collect the life table data under constant temperature indoors and compare these results with those obtained under realistic field conditions in the spring and fall to determine whether the results could be feasibly used in an effective pest control program. Because of low spring temperatures, field-reared *S. litura* larvae required an extended amount of time to complete their development when compared with those reared at 25°C and in the fall. Female adults also began oviposition later compared with females reared at 25°C and in the fall. Using the age-stage, two-sex life table we were able to accurately and precisely describe the survival rate and the stage structure due to metamorphosis throughout the life history (Fig. 1). The stage differentiation would not have been observed if traditional age-specific female life tables had been used.[25–27] Considering that the susceptibility of insects to numerous environmental factors, natural enemies, pesticides, etc., often varies depending on their developmental stage, information regarding the population stage structure is critical to effective pest management.[28]

In our study, the shortest immature stages were observed in the fall when the average daily mean temperature was 28.3°C; and the longest was in spring when the average daily mean temperature was 23.6°C. Our data demonstrated the effect of fluctuating and changing field conditions on the life table of *S. litura* over a 60-day period of the peanut-growing season. According to Rao *et al*,[29] the upper developmental threshold temperature of *S. litura* was

37°C, and 40°C was lethal. In our study, the highest temperature recorded was 37°C (less than 2 h during a few exceptionally hot days) around noon in the fall. The overall survivorship of all larval stages, however, remained as high as 84%. Thus, under fluctuating conditions, *S. litura* was able to survive and thrive over a wide temperature range, partially explaining the durability of *S. litura* as an important pest. Mironidis and Savopoulou-Soultani[23] also reported that the age-specific survivorship was enhanced under fluctuating temperature conditions.

Despite having the lowest hatch rate, shortest female longevity and lower net reproductive rate in the fall, the shorter immature developmental time, higher larval survival rate and shorter TPOP resulted in a higher intrinsic increase rate in fall than that in spring. Our results show that predicting insect potential based solely on development or fecundity may be misleading. The overall effect of environmental factors on insects can only be properly described and interpreted by using life table analysis.

Despite the comprehensive amount of information contained in a life table, it describes only the survival, stage differentiation and reproduction of the population being studied. To determine the amount of damage that different ages and stages of *S. litura* were capable of causing to the host plant, we calculated the consumption rate of *S. litura* concurrent with the life table study. *Spodoptera litura* is only damaging during its larval stages, and consumption rate varies depending on the instar.[30] Consumption measurement can be accurately measured using the age-stage-specific consumption (c_{xj}) (Fig. 6). As in most other species,[30,31] maximum leaf-consumption rate occurred during the final (sixth) instar. A few individuals remained in the sixth instar for an extended period, resulting in peaks of c_{xj} at the end of the sixth instar. When the survival rate was calculated, the consumption of these atypical individuals was diminished in the age-specific net consumption
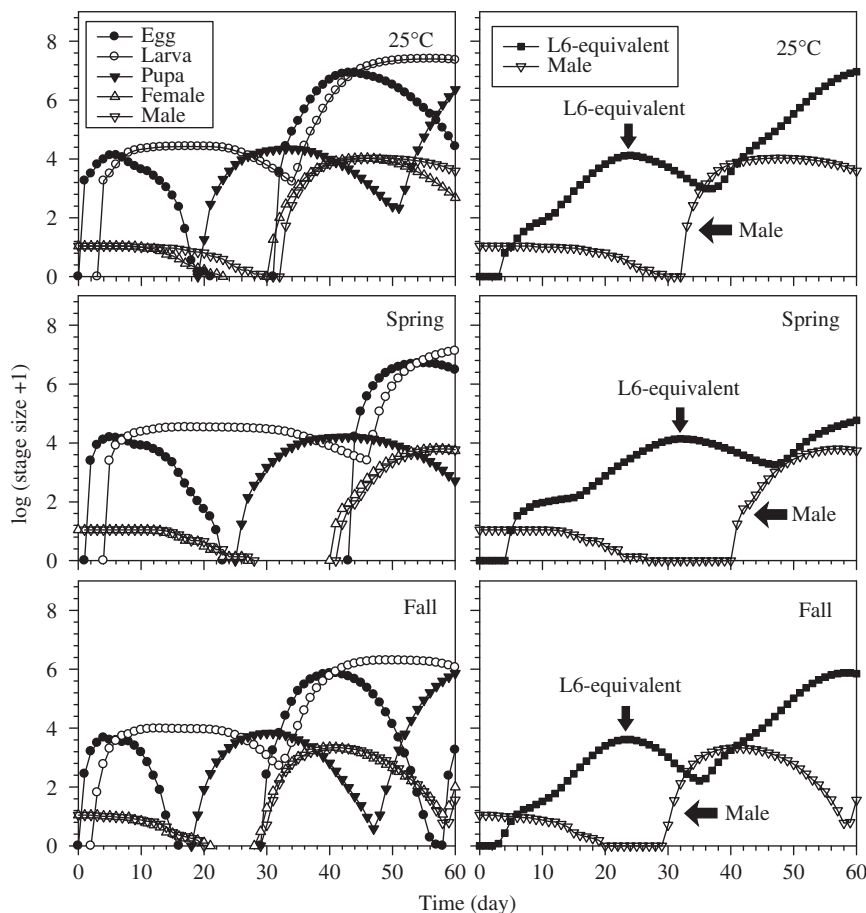
Figure 8. Simulated population growth (left) and damage potential (L6-equivalent) of *S. litura* under different conditions. (Left) All instars are grouped as a single curve, whereas the L6-equivalent (right) is calculated by taking the difference in consumption rates of each instar into consideration.

rate (q_x) (Fig. 7). Generally, the consumption rate increased at higher temperature due to increased metabolism rate.[32] In this study, *S. litura* larvae were reared on leaves collected from the field during different crop seasons; the consumption rates generated are realistic estimates of injury caused by *S. litura* through the entire season.

Predicting the growth of a pest population and anticipating its probable physical and monetary damage are critical in formulating the correct timing schedule in the development of a successful pest management strategy. Timing errors will not only lead to control failure, but, inevitably, also end up wasting money, labor and time.[28,33–36] A computer projection of pest population growth using life table data is, therefore, an indispensable tool in pest management and decision-making.[28] At present, management of *S. litura* in Taiwan is based mainly on monitoring of *S. litura* male adults using pheromone traps. When the mean number of males caught per pheromone trap reaches 256 or more during a 10-day interval within a county, an emergent chemical control (TARI 2012)[37] is recommended. Our projection shows, however, that the dynamics of male adults of *S. litura* is totally different from that of the L6-equivalent (Fig. 8). Therefore, we strongly suggested that the existing pheromone-monitoring program in Taiwan be reassessed and adjusted as soon as possible.

In nature, many biotic and abiotic factors affect the life tables of insect populations. Accordingly, life tables developed from field studies are, in general, more variable than those obtained from a controlled environment.[17] This is certainly understandable because life table data collected in the laboratory are usually collected under constant conditions and the insects receive better care. In this study, we demonstrated once again that the differences between field and laboratory life tables are significant; and that to be of use in an applied pest management program, it is necessary to collect life table data under field conditions and then integrate these results in a computer simulation.

ACKNOWLEDGEMENTS

REFERENCES

1 Chen CN and Hsiao WF, Influence of food and temperature on life history traits and population parameters of *Spodoptera litura* Fabricius. *Plant Prot Bull* **26**:219–229 (1984).
2 Guan BB, Chen QJ, Chen JH, Zhang YZ, Zhang ZH and Zhang JZ, Studies on biology and ecology of *Prodenia litura* (Fabricius). *Entomol J East China* **8**:57–61 (1999).
3 Fei WC, Wang YC, Chen FH, Lin HM and Li YH, *Plant Protection Manual*. TACTRI/COA, Taichung, Taiwan, pp.109–111 (2010).
4 Greenberg SM, Sétamou M, Sappington TW, Liu T-X, Coleman RJ and Armstrong JS, Temperature-dependent development and reproduction of the boll weevil (Coleoptera: Curculionidae). *Insect Sci* **12**:449–459 (2005).

5 Barteková A and Praslička J, The effect of ambient temperature on the development of cotton bollworm (*Helicoverpa armigera* Hübner, 1808). *Plant Prot Sci* **42**:135–138 (2006).

6 Yang TC and Chi H, Life tables and development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at different temperatures. *J Econ Entomol* **99**:691–698 (2006).

7 Atlihan R and Chi H, Temperature-dependent development and demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) reared on *Hyalopterus pruni* (Homoptera: Aphididae). *J Econ Entomol* **101**:325–333 (2008).

8 Wang X-G, Johnson MW, Daane KM and Nadel H, High summer temperatures affect the survival and reproduction of olive fruit fly (Diptera: Tephritidae). *Environ Entomol* **38**:1496–1504 (2009).

9 Chi H and Su HY, Age-stge, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenotera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ Entomol* **35**:10–21 (2006).

10 Jha RK, Chi H and Tang LC, A comparison of artificial diet and hybrid sweetcorn for the rearing of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) based on life table characteristics. *Environ Entomol* **41**:30–39 (2012).

11 Tuan SJ, Kao SS, Chao YC and Hou RF, Investigation of pathogenicity of AcMNPV to nine Lepidopteran pests in Taiwan. *Chin J Entomol* **17**:209–225 (1997).

12 Chi H, *TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis*. http://140.120.197.173/Ecology/. National Chung Hsing University, Taichung Taiwan (2012).

13 Chi H and Liu H, Two new methods for the study of insect population ecology. *Bull Inst Zool* **24**:225–240 (1985).

14 Chi H, Life-table analysis incorporating both sexes and variable development rates among individuals. *Environ Entomol* **17**:26–34 (1988).

15 Fisher RA, *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford (1930).

16 Efron B and Tibshirani RJ, *An Introduction to the Bootstrap*. Chapman & Hall, New York (1993).

17 Huang YB and Chi H, Life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae): with an invalidation of the jackknife technique. *J Appl Entomol* http://onlinelibrary.wiley.com/doi/10.1111/jen.12002 (2012).

18 Chi H, *CONSUME-MSChart: a computer program for the age-stage, two-sex consumption rate analysis*. http://140.120.197.173/Ecology/. National Chung Hsin University, Taichung, Taiwan (2012).

19 Chi H, *TIMING-MSChart: a computer program for timing of control*. http://140.120.197.173/Ecology/. National Chung Hsin University, Taichung, Taiwan (2012).

20 Qin HG, Ye ZX, Ding J, Huang SJ and Luo RH, Effect of temperature on the development, survival and fecundity of *Spodoptera litura* Fabricius. *Chin J Eco-Agric* **10**:76–79 (2002).

21 Chen CN and Su WY, Influence of temperature on development and leaf consumption of three caterpillars on cauliflower. *Plant Prot Bull* **24**:131–141 (1982).

22 Gregg P, A simulation model of the development of *Chortoicetes terminifera* (Orthoptera: Acrididae) under fluctuating temperatures. Proc 3rd Australasian Conf Grassl Invert Ecol, Adelaide (1981).

23 Mironidis GK and Savopoulou-Soultani M, Development, survivorship, and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) under constant and alternating temperatures. *Environ Entomol* **37**:16–28 (2008).

24 Miyashita K, Effects of constant and alternating temperatures on the development of *Spodoptera litura* F. (Lepidoptera: Noctuidae). *Appl Ent Zool* **6**:105 (1971).

25 Lewis EG, On the generation and growth of a population. *Sankhya: Indian J Stat* **6**:93–96 (1942).

26 Leslie PH, On the use of matrices in certain population mathematics. *Biometrika* **33**:183–212 (1945).

27 Birch LC, The intrinsic rate of natural increase of an insect population. *J Ani Ecol* **17**:15–26 (1948).

28 Chi H, Timing of control based on the stage structure of pest populations: a simulation approach. *J Econ Entomol* **83**:1143–1150 (1990).

29 Rao GVR, Wightman JA and Rao DVR, Threshold temperatures and thermal requirements for the development of *Spodoptera litura* (Lepidoptera: Noctuidae). *Environ Entomol* **18**:548–551 (1989).

30 Chen CN and Su WY, Influence of temperature on development and leaf consumption of three caterpillars on cauliflower. *Plant Prot Bull* **24**:131–141 (1982).

31 Yao WH, Biology characteristic of *Prodenia litura*. *Entomol J East China* **14**:122–127 (2005).

32 Hunt TE, Higley LG and Haile FJ, Imported longhorned weevil (Coleoptera: Curculionidae) injury to soybean: physiological response and injury guild-level economic injury levels. *J Econ Entomol* **96**:1168–1173 (2003).

33 Pedigo LP, Hutchins SH and Higley LG, Economic injury levels in theory and practice. *Annu Rev Entomol* **31**:341–368 (1986).

34 Pedigo LP and Higley LG, Introduction to pest management and thresholds, in *Economic Thresholds for Integrated Pest Management*, ed. by Higley LG and Pedigo LP. University of Nebraska Press, Lincoln, pp. 1–8 (1996).

35 Rogers DJ and Brier HB, Pest-damage relationships for *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on vegetative soybean. *Crop Prot* **29**:39–46 (2010).

36 Pedigo LP and Rice ME, Economic decision levels for pest populations, in *Entomology and Pest Management*, ed. by Pedigo LP and Rice ME. Pearson/Prentice Hall, Columbus, OH, pp. 253–284 (2006).

37 TARI, 10-day monitor report of three noctuids in Changhua, Chiayi, and Tainan area. http://www.tari.gov.tw/df_ufiles/g/bulletin_worm_20120603.pdf (2012).

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Population and damage projection of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table

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Following publication of the above article (DOI 10.1002/ps.3618) on Wiley Online Library on 19 August 2014 and in *Pest Manag Science* **70**: 805–813, the following error was found:

In the section 'Materials and Methods' the equation for the reproductive value was shown as:

$$v_{xy} = \frac{e^{-r(x+1)}}{s_{xy}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=y}^{m} s'_{ij} f_{ij}$$

This should read:

$$v_{xy} = \frac{e^{r(x+1)}}{s_{xy}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=y}^{m} s'_{ij} f_{ij}$$