FORUM

Demography and Population Projection of *Aphis fabae* (Hemiptera: Aphididae): with Additional Comments on Life Table Research Criteria

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J. Econ. Entomol. 108(4): 1466–1478 (2015); DOI: 10.1093/jee/tov187

ABSTRACT We collected developmental, survival, and reproduction data for *Aphis fabae* Scopoli (Hemiptera: Aphididae) reared on faba bean, *Vicia faba* L. 'Sevilla' at four constant temperatures (15, 20, 25, and 30°C), 70% relative humidity, and a photoperiod of 16:8 (L:D) h. The highest intrinsic rate of increase ($r = 0.4347\ d^{-1}$) and finite rate ($\lambda = 1.5445\ d^{-1}$) were observed at 25°C. The population projection based on the age-stage, two-sex life table quantitatively revealed the growth potential and stage structure of the aphid. We have included the following suggestions to aid researchers in life table studies: 1) The bootstrap method should be used to estimate the variance and SEs of developmental time, survival rate, fecundity, and population parameters. 2) The required number of bootstraps is dependent on the life table data—the higher the variation among individuals, the higher the number of bootstraps should be. In most cases, we suggest that 100,000 bootstraps should be used to obtain a stable estimate of variance and SEs. 3) Computer projection based on the age-stage, two-sex life table should be used to reveal the stage structure during population growth. 4) We used a simple equation based on the total fecundity, survival rate to adult stage, and first reproductive age to detect possible errors in life table parameters. 5) To assist readers in comprehending results, life table studies should include the cohort size, preadult survival rate, number of emerged female adults, mean fecundity, survival and fecundity curves, and population parameters.

KEY WORDS *Aphis fabae*, life table, temperature, bootstrap, population projection

Aphids are global pests of numerous agricultural crops and are characterized by their rapid development coupled with a high reproductive rate. They not only cause direct damage to their host plants but also serve as major vectors of many plant pathogens. The black bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae), is one of the most important pests of many cultivated crops, e.g., beans, tomatoes, potatoes, and tobacco, as well as numerous wild and ornamental plant species; its wide host range includes >200 host plant species throughout the world (Völkl and Stechmann 1998, Barnea et al. 2005). The black bean aphid is one of the most important pests attacking faba bean, *Vicia faba* L., wherever it is cultivated (Basedow et al. 2006). Although faba bean (also known as fava or broad bean) is an important staple food crop in many developing countries, fava beans have received considerably less scientific and control attention than most other comparable crops (Bardner and Fletcher 1974, Saruhan et al. 2014).

Insects are ectothermic organisms, and temperature plays a critical role in their developmental rate, survival, and reproduction. There are many papers reporting the developmental rate of insects at different temperatures based solely on a variety of temperature–developmental rate models (Stinner et al. 1974, Logan et al. 1976, Sharpe and DeMichele 1977, Schoolfield et al. 1981). While important, these papers are restricted to a single variable in insect development. Life table studies, on the other hand, are far more inclusive, and capable not only of predicting development but also survival and reproduction rates and are, thus, far more informative than studying temperature-dependent development alone. In the application of traditional female age-specific life tables (e.g., Lewis 1942, Leslie 1945, Birch 1948, Carey 1993), researchers have had to exclude data from male individuals in their studies, have ignored stage differentiation, and used sex ratio to calculate the "female" offspring. Excluding male individuals and ignoring stage differentiation, however, will inevitably result in errors in life table analysis and interpretation (Huang and Chi 2012a). To take the variable developmental rate and male population into account, Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table. To detect the effect of temperature on the development, survival, and reproduction of *A. fabae*, we collected the life history raw data of

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A. fabae at four constant temperatures and analyzed them using the age-stage, two-sex life table. Although only females from the asexual phase of *A. fabae* were present, we used the age-stage, two-sex life table to correctly describe the stage differentiation. We then used the life tables to project the population growth at different temperatures. Because of the common errors found in many life table reports, we have listed the main parameters that we think should be included in demographic studies.

Materials and Methods

Insect Culture. Apterous adults and nymphs of *A. fabae* were collected from a faba bean, *Vicia faba* (Sevilla), field at the experimental field of the Faculty of Agriculture, University of Ondokuz Mayis, Samsun, Turkey. Insects were reared on *V. faba* plants and kept in a growth chamber at 25 ± 1°C, 70 ± 5% relative humidity (RH), and a photoperiod of 16:8 (L:D) h.

Life Table Study. For the life table study, >30 adults of *A. fabae* were transferred to faba bean leaves. After 24 h, newborn nymphs of *A. fabae* were transferred individually to the undersurface of an apical leaf in plastic Petri dishes (9 cm in diameter). A wetted cotton pad (0.5 cm thick) was placed under the leaf to keep the leaf from drying. To maintain a larger space for the leaf, we rolled a cardboard paper (3 by 10 cm^2) to surround the Petri dish, punctured holes on the cardboard paper with multiple pinholes for ventilation, and then covered with the Petri dish lid. Petri dishes were placed in a climatic cupboard under constant temperatures of 15, 20, 25, and 30°C. Each life table was begun with 50 newborn nymphs produced under the respective temperature. Leaves were replaced with fresh ones as necessary (every 2–3 d). Nymphal development was recorded every 24 h until the adult stage. After adults emerged, survival and number of nymph produced by females were recorded daily until the death of all adults.

Data Analysis. To take the variable developmental rate among individuals into consideration, the life history raw data of *A. fabae* were analyzed based on the theory of the age-stage, two-sex life table developed by Chi and Liu (1985) and Chi (1988). The age-stage specific survival rate (s_{xj}, the probability that a newborn aphid will survive to age x and stage j), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time) were calculated as specified by the following equations. According to Chi and Liu (1985), the age-specific survival rate for the two-sex life table is calculated as follows:

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

where k is the number of stages. The age-specific fecundity is calculated as:

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \tag{2}$$

The intrinsic rate of increase can then be estimated with the iterative bisection method from the Euler-Lotka equation as follows:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{3}$$

with age indexed from 0 (Goodman 1982). The net reproductive rate is calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{4}$$

Although equations 3 and 4 appear similar to those used in a traditional female age-specific life table, they differ because equations 1 and 2 take the whole cohort (both sexes and those that died in the preadult stages) and stage differentiation into account, the l_x and m_x values calculated using equations 3 and 4 in the age-stage, two-sex life table are actually different from those in the traditional female age-specific life table. The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its original size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) as the stable rate of increase (the intrinsic rate r and the finite rate λ) is reached. The mean generation time is calculated as $T = \ln R_0 / r$.

To facilitate statistical analysis of raw data and calculation of life table parameters, we used the computer program TWOSEX-MSChart (Chi 2015; available at http://140.120.197.173/ecology/, last accessed 25 June 2015). The SEs of the development time, fecundity, and life table parameters were estimated by using the bootstrap technique (Efron and Tibshirani 1993; Huang and Chi 2012a, b; Polat Akköprü et al. 2015) using 100,000 bootstrap replicates ($B = 100{,}000$). In the bootstrap procedure, we randomly selected the life history raw data of 50 individuals with replacement from the original cohort ($n = 50$) and calculate the parameter. The mean of all 100,000 bootstraps is calculated as:

$$s(\cdot) = \frac{\sum_{b=1}^{B} s\left(x^{*b}\right)}{B} \tag{5}$$

where $s(x^{*b})$ is the parameter estimated from the b-th bootstrap sample. The SE of the parameter is then calculated as:

$$SE_{boot} = \sqrt{\frac{\sum_{b=1}^{B} \left[s\left(x^{*b}\right) - s(\cdot)\right]^2}{B-1}} \tag{6}$$

As Efron and Tibshirani (1993) wrote: "the bootstrap estimate of SE is the standard deviation of the

bootstrap replications;" the calculation of SE_{boot} is different from the general statistics. Differences among treatments were compared by using paired bootstrap tests based on the confidence interval of difference.

Population Projection

To demonstrate the advantage of using an age-stage, two-sex life table in revealing the dynamic change of stage structure of a population, we projected the population growth based on the theory of age-stage, two-sex life table (Chi and Liu 1985, Chi 1990) using the computer program TIMING-MSChart (Chi 2014) to predict the population growth of *A. fabae* at different temperatures. For comparative purpose, the same initial population of 10 newborn nymphs were used for the simulation at each temperature. The program TIMING-MSChart is also available at http://140.120.197.173/ecology (last accessed 25 June 2015). To circumvent the tedious process of preparing data file for TIMING-MSChart and also to avoid possible errors in data transcription, the data file for TIMING-MSChart was generated by TWOSEX-MSChart. Because the age-stage, two-sex life table is able to describe the stage differentiation during population growth, we calculated the increase rate of stage j from time t to $t+1$ using common logarithm as:

This equation is corrected as

$$\phi_{j,t} = \log\left(\frac{n_{t+1}+1}{n_t+1}\right) \approx \log\left(\frac{n_{t+1}}{n_t}\right) = \log\lambda \qquad \phi_{j,t} = \frac{\log(n_{j,t+1}+1)}{\log(n_{j,t}+1)} \tag{7}$$

where $n_{j,t}$ is the number of individuals in stage j at time t. We also used the natural logarithm to calculate the increase rate of stage j from time t to $t+1$ as:

$$r_{j,t} = \ln\left(\frac{n_{j,t+1}+1}{n_{j,t}+1}\right) = \ln(n_{j,t+1}+1) - \ln(n_{j,t}+1) \tag{8}$$

When the individual number of a stage is 0 ($n_{j,t}=0$ or $n_{j,t+1}=0$), logarithmic transformation is impossible. Therefore, we used $n_{j,t}+1$ and $n_{j,t+1}+1$ in the calculation of $\phi_{j,t}$ and $r_{j,t}$.

Results

Development Time and Fecundity. In this study, we used the bootstrap method to estimate the SEs of developmental time, longevity, and fecundity. We used the longevity and fecundity data at 15°C to demonstrate the difference between using general statistics and using the bootstrap technique. In general statistics, all individuals in a cohort ($n=50$) were used to calculate the mean; then the variance, SD, and SE were calculated in sequence. In bootstrap, random resampling with replacement from the original cohort was used to detect a possible recombination of individuals in samples; then, the SE is estimated by using the means of all samplings (in this study, $B=100{,}000$). As shown in Figure 1, 100,000 means obtained by using the bootstrap method generated a normal frequency distribution; which is consistent with the important premise of normal distribution for further statistical analysis and comparison. Because the variance estimated by using the bootstrap technique represents the real variance of population, using this technique will result in a correct analysis of variance and comparison between difference treatments.

The mean duration of each stage of *A. fabae* at four constant temperatures is summarized in Table 1. The total duration of the immature stage ranged from the shortest, 5.28 d at 25°C, to the longest, 11.54 d at 15°C. Adult *A. fabae* lived on average 35.6 d at 15°C; decreasing to 11.06 d at 30°C. Consequently, the total longevity of *A. fabae* was highly affected by temperatures as well; the longest longevity, 47.14 d, was observed at 15°C and the shortest, 14.18 d, occurred at 30°C.

The variability of developmental rate among individuals can be clearly observed in the overlaps of the age-stage survival rate (s_{xj}; Fig. 2). At 15 and 20°C, all individuals were able to survive to the adult stage, while at 30°C, the survival rate to adult was only 66%. The width of the s_{xj} curve of the fourth nymph stage showed the cumulative variation in developmental time in the later stage. At 15°C, the adult stage began on age 11 d and ended at 59 d, entailing a range of 49 d. At 25°C, the adult stage began on age 4 d and ended at 32 d, considerably shorter than that at 15°C. The narrowest adult life span, however, was only 20 d at 30°C.

At 15°C, *A. fabae* began to produce offspring at age 12.14 d (TPOP) when the age was counted from birth, which was much later than those reared at 25°C (TPOP = 5.91 d). However, at 30°C, the TPOP was 8.68 d, which was significantly longer than that at 25°C. The shortest reproductive period was 3.2 d at 30°C. The highest mean fecundity ($F=90.44$ offspring) was observed at 15°C, while the lowest F value, 3.61 offspring, was at 30°C (Table 2).

Life Table and Population Parameters. The age-specific survival rate and fecundity of *A. fabae* are plotted in Figure 3. The age-specific survival rate (l_x) is the sum of s_{xj} at each age x and is thus the simplified version of s_{xj} in Figure 2. At 25°C, adults began to produce offspring at age 5 d, which is close to the mean of TPOP (5.91 d) in Table 2. The fecundity curve, m_x, ended at age 27 d and the range of the m_x curve enclosed within the age range of the adult stage of Figure 2 (4–32 d). The shortest range of m_x was 9 d (age 6–14 d) at 30°C. The postreproductive period ranged from 4 d at 25°C to 10 d at 30°C (Fig. 3). The highest age-specific fecundities (m_x) were 5.06, 6.32, 8.19, and 0.73 offspring at 15, 20, 25, and 30°C, respectively.

The net reproductive rate (R_0), intrinsic rate of increase (r), finite rate (λ), and mean generation time (T) are listed in Table 2. The highest R_0 (90.44 offspring) was observed at 15°C, while the lowest was at 30°C (2.38 offspring). The order of R_0 was similar to the mean fecundity (F). In all treatments, the relationship between the mean fecundity (F) and net reproductive rate (R_0) were consistent with the proof published by Chi (1988) as $R_0 = F \times N_f / N$. The

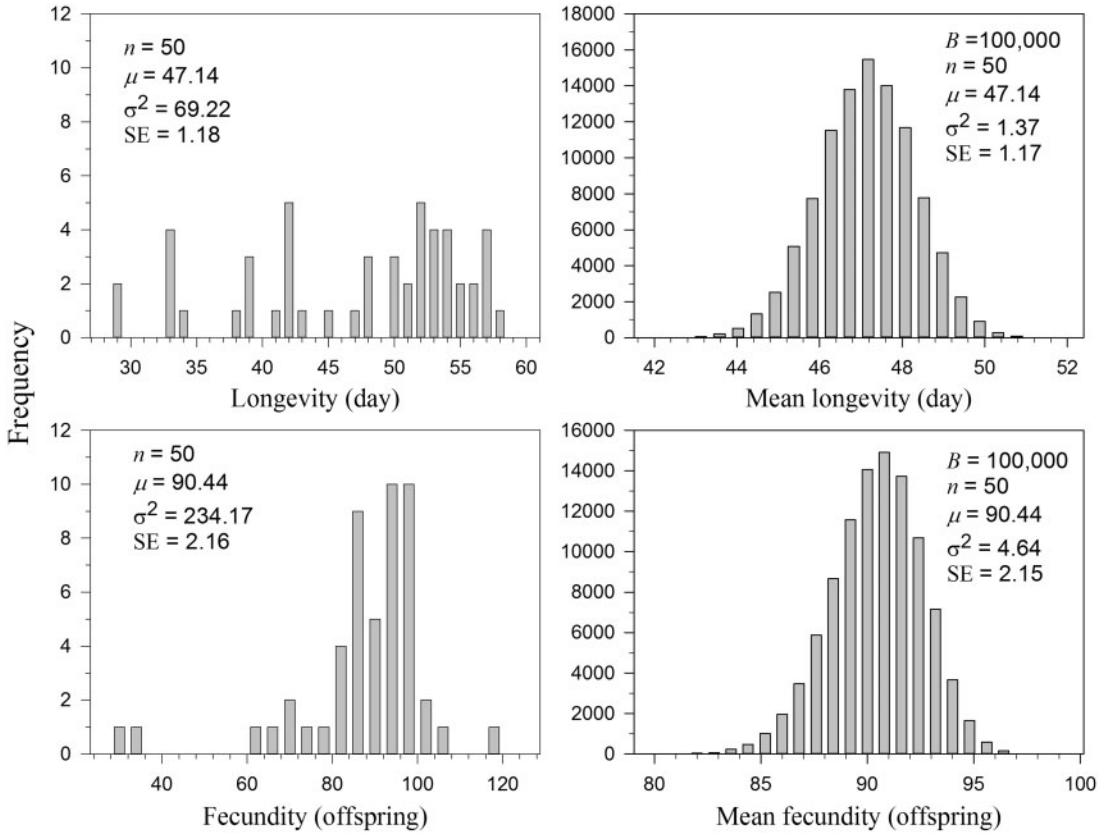

Fig. 1. Frequency distribution of longevity, mean longevity, fecundity, and mean fecundity at 15°C. The frequency distribution of mean longevity and mean fecundity were estimated by using 100,000 bootstraps.

Table 1. Developmental time (mean ± SE) of life stages of *A. fabae* at four constant temperatures, 70 ± 2% RH, and a photoperiod of 16:8 (L:D) h

Duration	15°C	20°C	25°C	30°C
N1	2.74 ± 0.09a	2.14 ± 0.08b	1.49 ± 0.09c	1.60 ± 0.13c
N2	2.90 ± 0.06a	1.82 ± 0.09b	1.23 ± 0.06c	1.98 ± 0.17b
N3	2.52 ± 0.08a	1.8 ± 0.06b	1.21 ± 0.06d	1.51 ± 0.09c
N4	3.38 ± 0.08aA	1.94 ± 0.07cB	1.34 ± 0.07dC	2.33 ± 0.15bB
Total immature	11.54 ± 0.10a	7.70 ± 0.16b	5.28 ± 0.11c	7.18 ± 0.26b
APOP	0.60 ± 0.07bc	0.42 ± 0.08c	0.64 ± 0.071b	1.92 ± 0.27a
TPOP	12.14 ± 0.11a	8.12 ± 0.17b	5.91 ± 0.14c	8.68 ± 0.36b
Reproductive period	23.44 ± 0.61a	16.54 ± 0.49b	14.06 ± 0.35c	3.2 ± 0.31d
Adult longevity	35.60 ± 1.21a	21.76 ± 0.74b	19.43 ± 0.62c	11.06 ± 0.52d
Total longevity	47.14 ± 1.17a	29.46 ± 0.71b	23.44 ± 0.90c	14.18 ± 0.90d

APOP: adult prereproductive period, TPOP: total prereproductive period. The SEs were estimated by using 100,000 bootstraps and compared by using paired bootstrap test based on CI of differences.

shortest mean generation time ($T = 10.01$ d) was observed at 25°C, which was about half the T value at 15°C. However, the highest intrinsic rate of increase ($r = 0.4347\ d^{-1}$) and finite rate ($\lambda = 1.5445\ d^{-1}$) for *A. fabae* were observed at 25°C; they were significantly higher than the other three temperatures (Table 2). Therefore, the optimum temperature for the growth of *A. fabae* population among the four temperatures tested was 25°C. When the temperature increased to 30°C, both the intrinsic rate and finite rate dropped drastically to 0.0831 and $1.0867\ d^{-1}$. The mean generation time decreased when temperature were raised from 15 to 25°C; however, it extended slightly again at 30°C (Table 2).

The life expectancy of different age and stage (e_{xj}) aphids is plotted in Figure 4. Because no other mortality factors existed under the laboratory conditions except aging, the curves of e_{xj}, in general, decreased with age. Slight fluctuation was observed at 30°C. The age-stage reproductive values (v_{xj}) of *A. fabae* are plotted in Figure 5. At different temperatures, the v_{xj} increased significantly when adults emerged and it rose once again when females began to produce offspring.

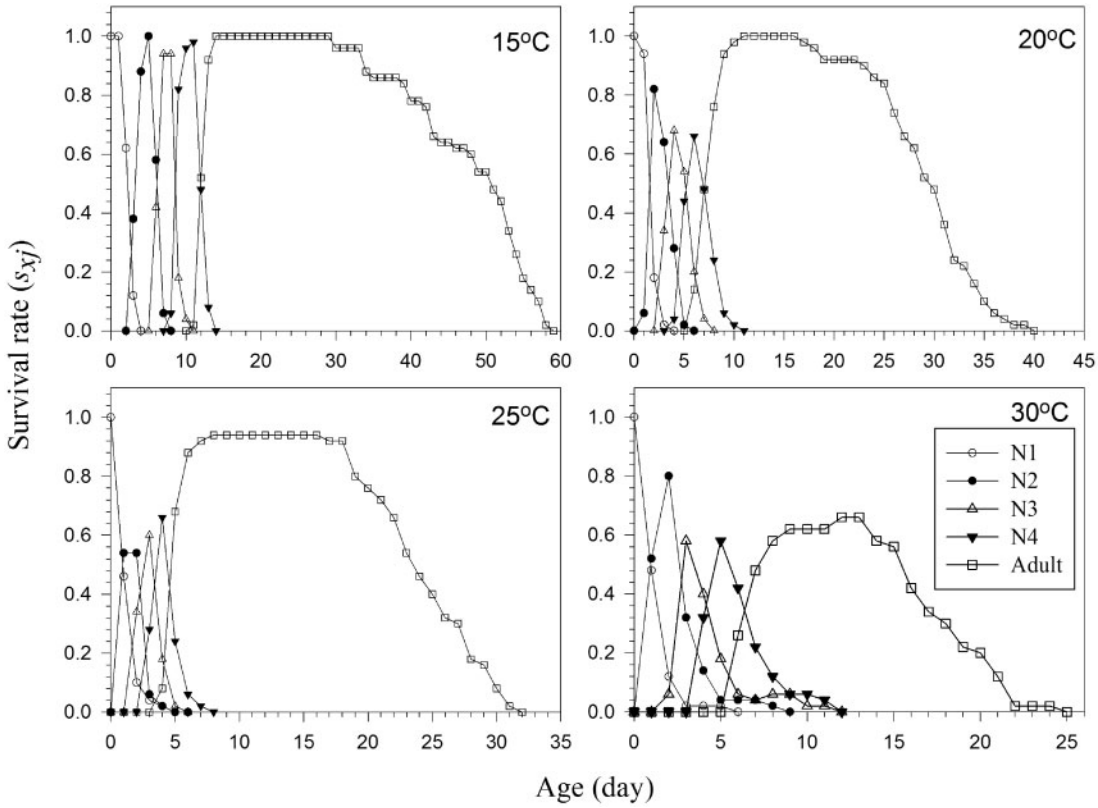

Fig. 2. Age-stage survival rate (s_{xj}) of *A. fabae* reared on faba bean leaves at different constant temperatures.

Table 2. Life table parameters (mean ± SE) of *A. fabae on* faba bean at different temperatures, 70 ± 2% RH, and a photoperiod of 16:8 (L:D) h

Parameters	15°C	20°C	25°C	30°C
Cohort size (N)	50	50	50	50
Female adults (N_f)	50	50	47	33
Fecundity (F)	90.44 ± 2.15a	79.20 ± 2.67b	82.40 ± 2.79b	3.61 ± 0.57c
Generation time (T)	19.52 ± 0.14a	13.35 ± 0.22b	10.01 ± 0.16d	10.43 ± 0.28c
Net reproductive rate (R_0)	90.44 ± 2.154a	79.20 ± 2.67b	77.46 ± 3.82b	2.38 ± 0.45c
Intrinsic rate of increase (r)	0.2307 ± 0.0020c	0.3275 ± 0.0087b	0.4347 ± 0.0100a	0.0831 ± 0.0191d
Finite rate of increase (λ)	1.2595 ± 0.0025c	1.3875 ± 0.0087b	1.5445 ± 0.0154 a	1.0867 ± 0.0206d

The SEs were estimated by using 100,000 bootstraps and compared by using paired bootstrap test based on the CI of difference.

To detect the effect of the bootstrap number (B) on the variability of frequency distribution of an estimated population parameter, we plotted the frequency distribution of net reproductive rate estimated by using four bootstrap runs (two runs with $B = 1{,}000$ and two runs with $B = 100{,}000$ replicates) for data collected at 25°C (Fig. 6). The two frequency distributions of 1,000 bootstrap replicates are different (Fig. 6A and B), while the frequency distributions obtained by using 100,000 replicates generated a similar normal distribution.

Population Projection. The population growth at different temperatures is plotted in Figure 7. The detailed stage composition and population size at different times could be observed. At 20 and 25°C, the populations increased significantly faster than those at 15 and 30°C. At 25°C, the curves of different stages tended to be straight lines, which showed that the population was approaching a stable stage distribution after 20 d. This can also be observed in the stage growth rate curves (Fig. 8) where all stages approached the intrinsic rate 0.4347 at 25°C.

Discussion

Development Time and Fecundity. Because insects are ectothermic organisms, temperature is one of the most important factors that regulates the development, reproduction, mortality, survival, and seasonal occurrence of insect populations (Dixon 1987; Logan et al. 1976; Bayhan et al. 2005, 2006; Satar et al. 2008; Auad et al. 2009; Özder and Sağlam 2013). Our results clearly demonstrated that life table studies at different

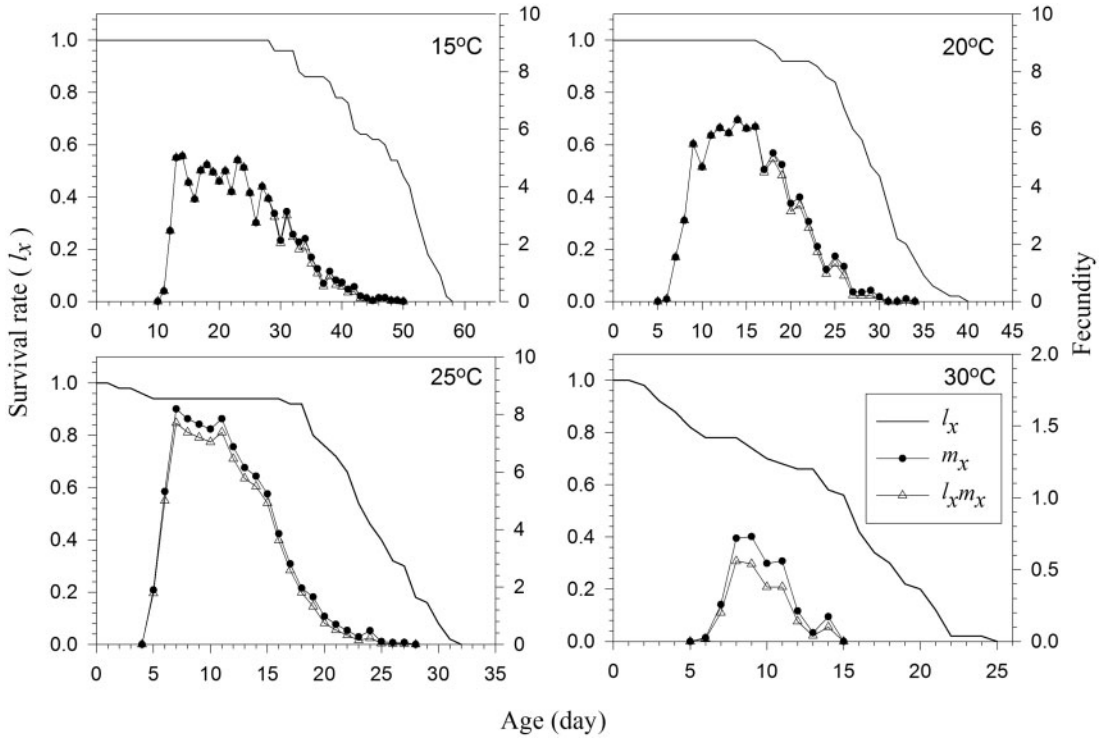

Fig. 3. Age-specific survival rate (l_x), fecundity (m_x), and maternity ($l_x m_x$) of *A. fabae* reared on faba bean leaves at different constant temperatures.

temperature could comprehensively demonstrate the effect of temperature on the survival, development, and fecundity of *A. fabae* (Tables 1 and 2). The duration of immature stages decreased significantly when the temperature increased from 15 to 25°C, but the developmental duration extended again when the temperature increased from 25 to 30°C. Similar results were reported for *Nasonovia ribisnigri* (Mosley) (Diaz and Fereres 2005), *Aphis rumicis* L. (Bayhan et al. 2006), *Rhopalosiphum padi* (L.) (Auad et al. 2009), and *Schizaphis graminum* (Rondani) (Tofangsazi et al. 2012). The adult duration and total longevity dramatically declined as temperatures increased from 15 to 30°C. At higher temperatures, the age-specific survival curves dropped at an earlier age and more sharply when temperatures increased from 20 to 30°C. The deleterious effect of higher temperatures on survivorship is a common phenomenon in various aphids (Asin and Pons 2001, Morgan et al. 2001, Wang and Tsai 2001).

At lower temperature, aphids, in general, need longer developmental time before they can produce offspring. This can also be observed in the total preoviposition period (Table 1). The extended APOP and TPOP at 30°C, however, showed the deleterious effect at higher temperatures.

Application of the Bootstrap Method to General Statistics. With the advent of computer technology, computation-intensive statistical methods became accessible to biologists and ecologists (Crowley 1992). Among those new methods, the bootstrap technique is one of the widely applied techniques (Chernick 2008). Hesterberg (2008) even suggested that "The old rule of using z or t tests or confidence intervals if $n \geq 30$ is a relic of the pre-computer era, and should be discarded in favor of bootstrap-based diagnostics." Polat Akköprü et al. (2015) pointed out the advantages of the bootstrap technique and showed the results of using the technique were consistent with the definition of the central limit theorem. In this study, we used the longevity and fecundity data to demonstrate the difference between using general statistics and bootstrapping (Fig. 1). Although the SEs estimated by using general statistics are similar to those estimated by using the bootstrap method, the huge differences in variances are critical to the analysis of variance and significance test. Because most ecological studies are time- and labor-intensive, most scientists traditionally used only a limited number of insects ($n < 100$) in their studies. With the advance of computing speed and memory size, we suggest that the bootstrap method should be used to obtain representative variances and SEs of the population means.

Is There an Optimal Bootstrap Number? Meyer et al. (1986) recommended 500–1,000 bootstrap replicates. In Figure 6, we show the differences in frequency distributions obtained using 1,000 and 100,000 bootstrap replicates. It is clear that 1,000 bootstrap replicates did not generate an acceptable normal distribution of the estimates and there will always be differences between any two runs (Fig. 6A and B). In the 1980s, the application of the bootstrap methods

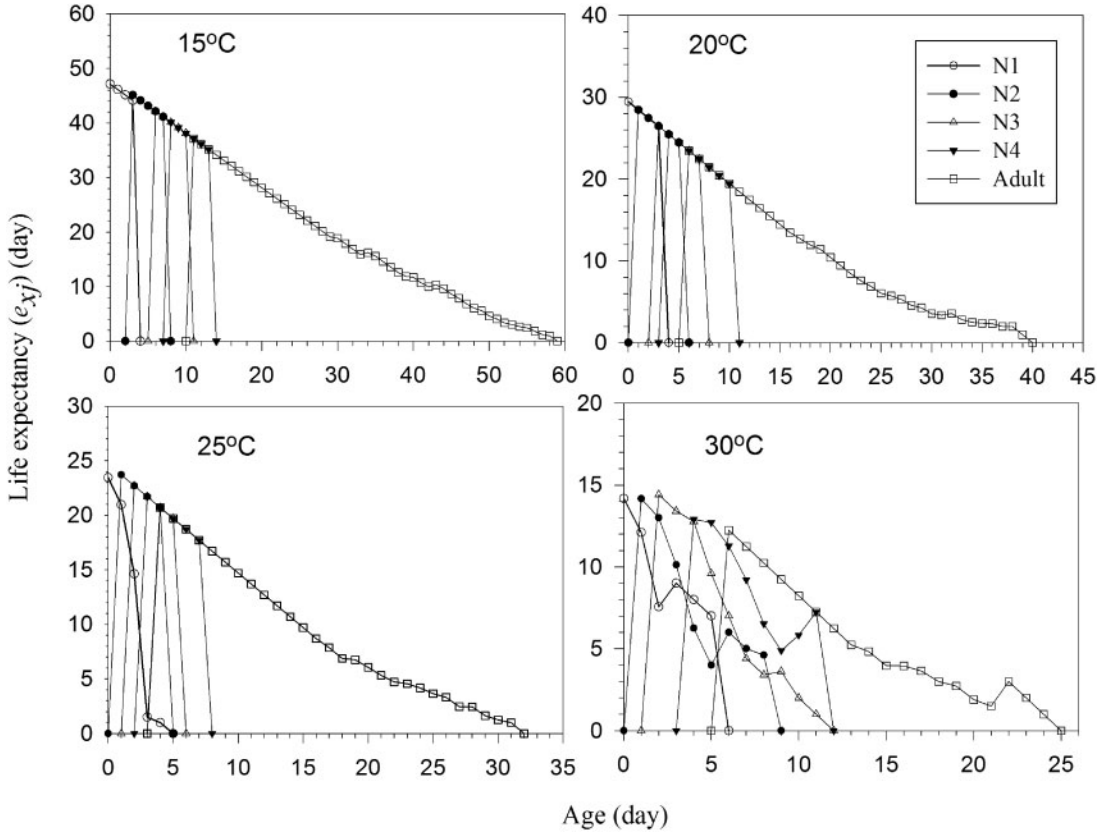

Fig. 4. Age-stage life expectancy (e_{xj}) of *A. fabae* on faba bean leaves at different constant temperatures.

was limited by the computer CPU and memory size. Hesterberg (2008) pointed out that a bootstrap simulation would have taken ~20,000 h in 1981. For a life table study using only 100 individuals, an exact bootstrap method will result in 48×10^{58} combinations—a number that is still impossible for modern-day personal computers. In this paper, 100,000 bootstraps of the Monte Carlo method generated an acceptable normal distribution (Fig. 6C and D), and is consistent with the Hesterberg (2008) statement claiming that "The bootstrap also offers pedagogical benefits" and "offering actual distributions that can be viewed using histograms." Because bootstrapping is a procedure of resampling with replacement, every bootstrap will generate different result as well as the mean, variance, and SEs of 1,000 replicates. Therefore, there is no "optimal number" for bootstrapping. The required number of bootstraps is dependent on the life table data—the higher the variation among individuals, the higher the number of bootstraps should be. In our study, we found that 100,000 bootstraps will generate stable estimates of variance and SEs.

Life Table and Population Parameters. Although both F and R_0 showed a similar trend at different temperatures, the trends of r and λ are different. The estimated R_0 values were different at all tested temperatures, and were significantly lowest at 30°C. Because the intrinsic rate of natural increase (r) is calculated by including x, l_x, and m_x (equation 2), it reflects the effects of the first reproductive age, the peak of reproduction, the length of reproductive period, and the survival rate on the population growth rate; thus, it is a good parameter to represent the growth potential of a population under different conditions (Birch 1948, Andrewartha and Birch 1954). On the other hand, the R_0 is calculated using only l_x and m_x, and is the total offspring that an individual can produce during its lifetime. In this study, r increased as temperature increased from 15 to 25°C and was consistent with the trend of developmental rate. At 30°C, fecundity significantly decreased and the value of r dropped to $0.0831\ d^{-1}$. Consequently, in our study, the optimum temperature for the highest population growth potential of *A. fabae* among treatments occurred at 25°C ($r = 0.435\ d^{-1}$). In addition to temperature, host plant selection also plays an important role in aphid biology. For example; Fernandez-Quintanilla et al. (2002) reported a range of intrinsic rate of *A. fabae* on winter and summer weed species as 0.14 to $0.36\ d^{-1}$, Razmjou and Fallahi (2009) report the range of r values on sugar beet varieties as 0.1336 to $0.2202\ d^{-1}$ (the unit used in their article was nymphs per female per day).

Population Projection. Huang and Chi (2012a) discussed that there are two types of information that can be obtained through life table study: the basic data (s_{xj}, f_{xj}, etc.) and the derived parameters (r, λ, T, etc.).

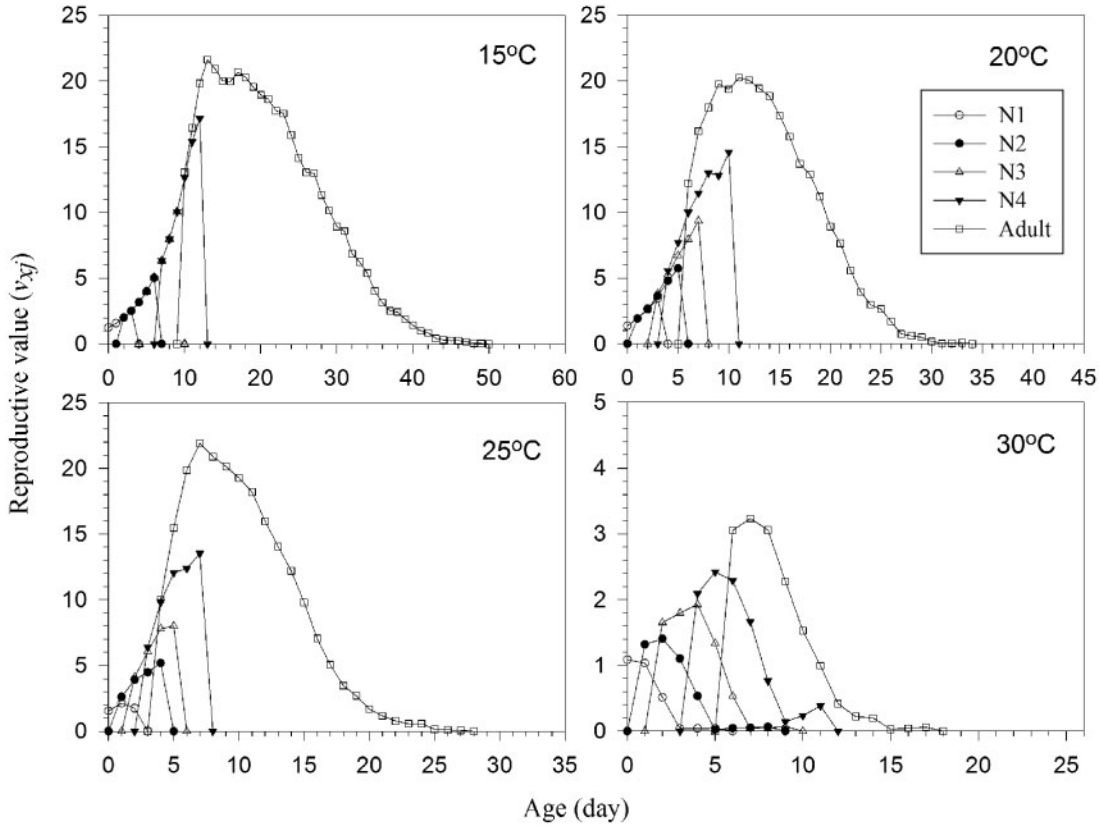

Fig. 5. Age-stage reproductive value (v_{xj}) of *A. fabae* on faba bean leaves at different constant temperatures.

Both intrinsic rate (r) and finite rate (λ) are the derived parameters and are calculated by assuming the population settles down to a stable age-stage distribution as the time approaches infinity. As shown in Figure 7, it is clear that the *A. fabae* populations did not reach the "stable age" or "stable age-stage" distribution by 30 d; therefore, it was impossible to predict the population size and stage structure by only using the intrinsic rate or finite rate. The population projection based on the basic data (s_{xj} and f_{xj}) of a life table offers a comprehensive understanding of the age and stage composition of a population during its growth. Similarly, Yu et al. (2013) and Tuan et al. (2014) demonstrated the advantage of population projection based on using life tables in biological control and pest damage prediction. On the contrary, if the traditional female age-specific life table had been used in the population projection instead, the stage structure would not have been observed.

Stage Growth Rate. Because of the rapid population increase potential of *A. fabae*, and the possibility that the population size can theoretically increase to 1,000-fold of the initial 10 nymphs within 30 d, we used logarithmic transformation to show the population size over time. To describe the dynamics of stage structure, we used equations 7 and 8 to describe the growth and fluctuation of each. If the population approaches the stable age-stage distribution, the population will increase at the intrinsic rate and finite rate as:

$$n_{j,t+1} = n_{j,t}e^{r} = n_{j,t}\lambda \tag{9}$$

With the larger n, it gives $n_{j,t}+1 \approx n_{j,t}$ and $n_{j,t+1}+1 \approx n_{j,t+1}$. When the population approaches the stable age-stage distribution, the increase rates of the total population and all stages will approach λ and all stages will increase exponentially. Consequently, it gives

$$r_{j,t} = \frac{\log(n_{j,t+1}+1)}{\log(n_{j,t}+1)} \approx \frac{\log(n_{j,t+1})}{\log(n_{j,t})} = \log\lambda \tag{10}$$

The curves of all stages will be linear ones when plotted in logarithmic scale (e.g., Fig. 7, 25°C). The slope of the curves of all stages after 20 days will approach $\log(\lambda)$. If equation 8 is used, the increased rates of different stages will all approach the intrinsic rate r at stable age-stage distribution as:

$$r_{j,t} = \ln\left(\frac{n_{j,t+1}+1}{n_{j,t}+1}\right) = \ln(n_{j,t+1}+1) - \ln(n_{j,t}+1) \approx \ln(e^{r}) = r \tag{11}$$

Thus, by using equation 8, the fluctuation of growth rates of different stages can be depicted. A negative rate represents a decrease of stage size from time t to $t+1$,

This equation is corrected as Huang et al. 2017. JEE.

$$\phi_{j,t} = \log\left(\frac{n_{t+1}+1}{n_t+1}\right) \approx \log\left(\frac{n_{t+1}}{n_t}\right) = \log\lambda$$

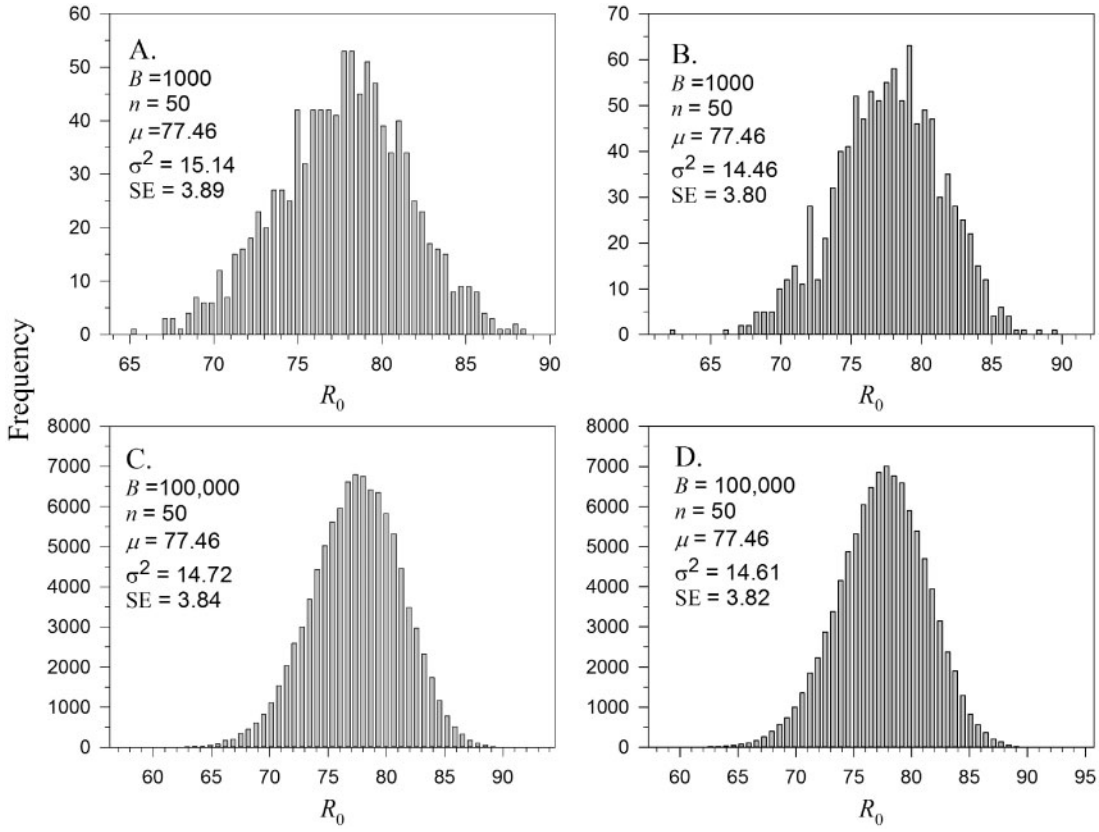

Fig. 6. Effect of bootstrap number on the estimates of net reproductive rate at 25°C. A, B = 1,000, Run 1;B, *B* = 1,000, Run 2; C, B = 100,000, Run 1; D and B = 100,000, Run 2.

while a positive rate represents an increase in stage size. When the population approaches stable age-stage distribution, the growth rate of all stages will approach the intrinsic rate (r), as shown in Fig. 8 (25°C).

Total Fecundity and First Reproductive Age. As Lewontin (1965) pointed out, both the first reproductive age and the age of reproductive peak play a determinative role in the population growth rate. We use the mean fecundity (F), the age of the first offspring (a), and the preadult survival rate (l_a) to critically examine the intrinsic rate as:

$$e^{-r(a+1)}F \cdot l_a = 1 \qquad (12)$$

Equation 12 is actually a simplified version of the Lotka–Euler equation by assuming all eggs were laid at age a. Zou et al. (2015) reported the preadult duration (20.58 d), preoviposition period (5.94 d), mean fecundity (229.16 eggs), and preadult survival rate (0.81) of *Arma chinensis* (Fallou) (Heteroptera: Pentatomidae). By using the female age-specific life table, they reported an intrinsic rate for the treatment prey-fed F6 as 0.5367 d^{-1} in the first version (Advance Access published 13 February 2015), which was later revised as 0.4441 d^{-1} in the April issue. Because they did not report the age of the first offspring or the fecundity curve (m_x), it would be impossible to evaluate their calculation of r. However, by assuming all 229.16 eggs were laid on age 20 d, the r value, using equation 12, should only be 0.261 d^{-1}. This shows that their extraordinary high r value of 0.5357 d^{-1} or 0.4441 d^{-1} was certainly an erroneous estimate. Similar errors can be noticed in other r values in Zou et al. (2015). Other possible problems of applying female age-specific life tables to insect populations were discussed in Huang and Chi (2012a).

In conclusion, temperature significantly affects the developmental rate, survivorship, reproduction, and longevity of *A. fabae*. Based on our comparative life table study, temperatures of 20 and 25°C appear to be most suitable for population growth among those tested (15, 20, 25, and 30°C). The life table data can be used to predict population growth (Chi 1990) and to plan mass rearing of this aphid species for biological control purposes (Chi and Getz 1988). Yu et al. (2005), Chi and Su (2006), Jha et al. (2012), and Huang and Chi (2012a) discussed a number of problems encountered in life table studies of insect populations, their ecology, and the applications of these studies. We would like to make the following suggestions for designing and publishing life table studies: 1) because common statistical methods generally overestimate the variances of

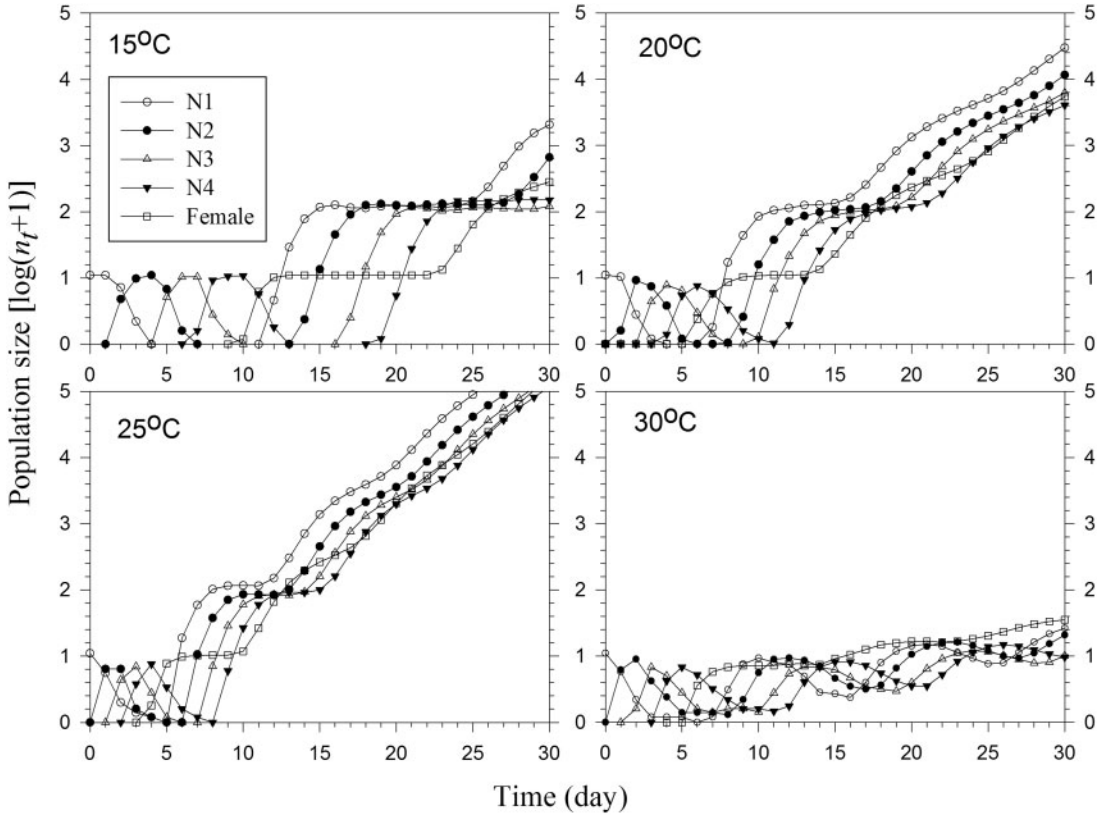

Fig. 7. Population projection of *A. fabae* on faba bean leaves at different constant temperatures with an initial population of ten newborns.

developmental time, fecundity, and longevity, we suggest using the bootstrap method to estimate the variance and SEs of population means. 2) The required number of bootstraps is dependent on the life table data—the higher the variation among individuals, the higher the number of bootstraps should be. To obtain a stable estimate, we suggest 100,000 bootstraps should generally be used. 3) Computer projection based on life tables is a valuable tool for the prediction of the stage structure and growth of pest populations. On the contrary, the traditional female age-specific life table is incapable of doing this. 4) The total fecundity and first reproductive age can be used to detect possible errors in life table parameters. 5) We suggest that life table studies should include the cohort size (N), preadult survival rate (l_a), number of emerged female adults (N_f), mean fecundity per female (F), survival and fecundity curves (s_{xj}, l_x, and m_x), and population parameters (r, λ, R_0, and T). 6) The survival and fecundity curves and equations of population parameters should clearly show the age index (from 0 or 1) because these curves are critical data showing the age of adult emergence and the age at which reproduction begins. The age index is important for the calculation of intrinsic rate and finite rate. All these criteria are essential in allowing readers to critically evaluate the results. On the other hand, using the female age-specific life table will almost always result in problems (Huang and Chi 2012a). For example, were the female age-specific life table to be applied to a female parthenogenetic population, the ratio of emerged female adults (N_f) to the cohort size (N) would represent the immature survival rate as well. However, when the female age-specific life table is applied to a two-sex population, because the sex of individuals dying during the immature stage is unknown, the immature survival rate of the female population cannot be accurately calculated. Consequently, when the female age-specific life table is applied to a two-sex population, not only is the data regarding the male component of that population ignored but also the important effect of sex ratio on population parameters cannot be considered at all. On the contrary, when bootstrap is incorporated into the age-stage, two-sex life table analysis, the effect of sex ratio can be revealed in the procedure involving resampling with replacement. In addition, because female age-specific life tables are incapable of describing population growth while taking into account the stage differentiation and male populations, they are not of any practical use in pest management or biological control programs. To avoid the aforementioned disadvantages inherent in the female age-specific life table and to

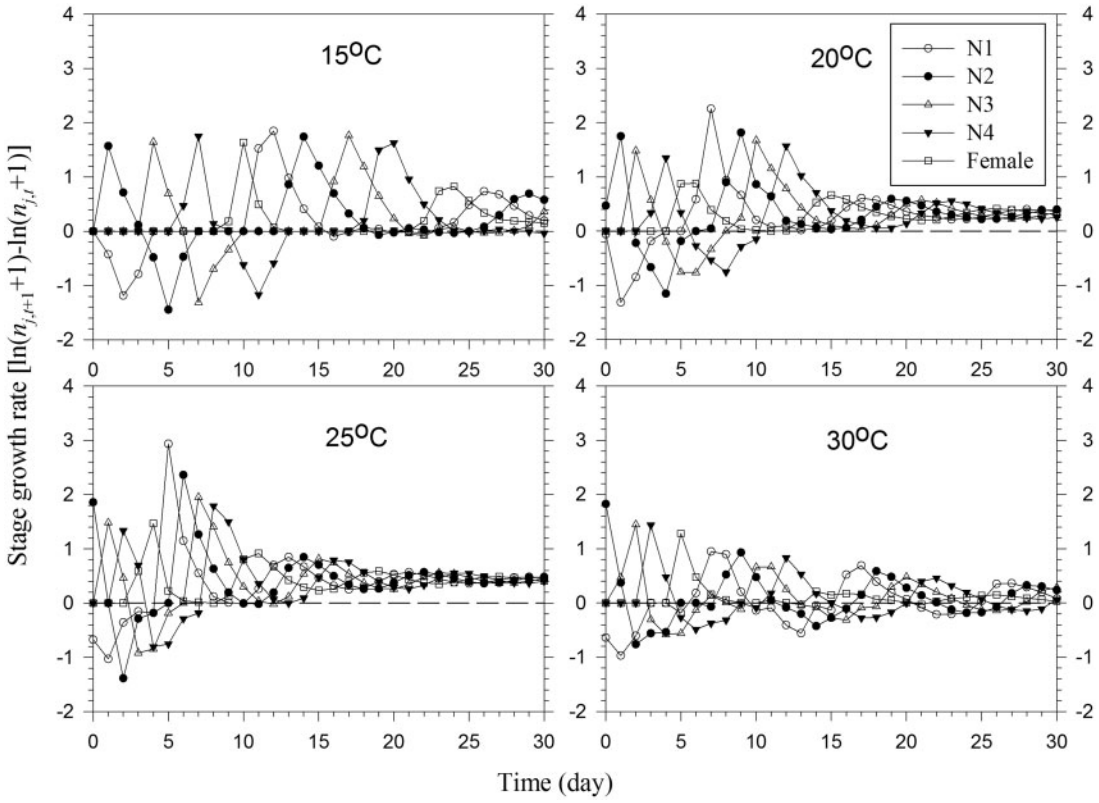

Fig. 8. Stage growth rate of *A. fabae* on faba bean leaves at different constant temperatures with an initial population of 10 newborns.

ensure accurate analyses when studying life tables, we strongly suggest that researchers utilize the age-stage, two-sex life table when working with two-sex populations.

Acknowledgments

We would like to acknowledge the contributions of the reviewers and editor for their valuable comments and suggestions, all of which were instrument in improving this article. This project was partly supported by MEVLANA program of Turkish Government to Prof. Dr. Celal Tuncer (Ondokus Mayis University).

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Received 1 May 2015; accepted 9 June 2015.