Demography and Randomized Life Table Statistics for Peach Twig Borer *Anarsia lineatella* (Lepidoptera: Gelechiidae)

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**ABSTRACT** This work studies for the first time the effect of constant temperatures (15, 20, 25, 30 and 35°C) on the demography of *Anarsia lineatella* Zeller (Lepidoptera: Gelechiidae) based on jackknife and bootstrap randomization methods. Male and female longevity was substantially reduced at the higher temperatures in contrast to intermediate and lower temperatures. According to a second order polynomial regression function, high correlations were observed between temperatures and the age of first reproduction as well as temperature and oviposition times. Net reproductive rate was highest at 25°C and 74.172, while the intrinsic rate of increase displayed its highest values at 30°C and was estimated to be 0.238. Birth rate and finite capacity of increase were higher at 30°C and estimated to be 0.235 and 1.268, respectively. Mean generation time and doubling time varied significantly with temperature and the shortest mean generation and doubling time was obtained at 30°C (25.566 and 2.909 d respectively). Life expectancy had its lowest value 10.3 d at 25°C, whereas cohorts that were maintained at 20 and 15°C increased their life expectation approximately three to sixfold.

**KEY WORDS** *Anarsia lineatella*, life table, demographic parameter, intrinsic rate of increase, actuarial mathematics

The peach twig borer is the most important pest threat of stone fruits worldwide. The economic significance of *Anarsia lineatella* Zeller (Lepidoptera: Gelechiidae) extends to several peach, *Prunus persica*, growing areas of Northern Europe including Italy, France and Spain. The species is also considered as a regular pest in North America after its introduction in the early twentieth century (Bailey 1948, Balachowsky et Mesnil 1935, Brunner and Rice 1984, Jones 1935, Summers 1955). In northern Greece, *A. lineatella* has three to four generations per year and overwinters in bark crevices as second or third instar forming hibernacula (Summers et al. 1959; Damos and Savopoulou-Soultani 2009a,b). The damage potential of the peach twig borer is very high and during recent years, much time and effort has been spent on controlling *A. lineatella* (Aguedelo-Silva et al. 1993, Damos et al. 2011a, Sciarretta and Trematerra 2006). Moreover, because of its intensive presence, *A. lineatella* is considered a key pest in integrated pest management programs and integrated fruit production (Damos and Savopoulou-Soultani, 2010, 2011b).

Although previous studies on *A. lineatella* have demonstrated the effect of temperature on its development (Damos and Savopoulou-Soultani 2008, Damos et al. 2011b), they do not provide information about the species demography and the related life table statistics. There are no other specific works in literature that provide statistical estimates for the demographic parameters of this species.

This work focuses on the effect of temperature on the demography of the peach twig borer. Because life table analysis has not been performed before, the main objective was the determination of the relationship between the various demographic parameters and different constant temperatures. Additionally, based on statistical randomization methods to provide estimates of the parameters, efforts were made to evaluate which of the temperature regimes most favored demography of *A. lineatella*. This knowledge about the different biological characteristics of *A. lienatella* and how they are affected under variable environmental conditions, is required to predict regional and seasonal periodic oscillation and population stability of this important pest threat.

**Materials and Methods**

**Insect Rearing.** A colony of *A. lineatella* was established in the Laboratory of Applied Zoology and Parasitology at Aristotle University of Thessaloniki, from field collected larvae present on infested twigs and peaches, in northern Greece. The colony was maintained at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h, as described by Damos and Savopoulou-Soultani (2008); Damos et al. (2009, 2011).
Age Structured Actuarial Data. Newly hatched larvae were reared on natural nutritional medium (i.e., peach shoots) in insect rearing chambers until pupation. Pupae were removed from the diet and placed individually in small plastic cups (1.5 by 1.5 cm). A piece of cotton moistened with distilled water was placed in each cup to maintain humidity. The pupae were inspected daily until adult eclosion. Adults were sexed by examination of genitalia and then placed in truncated plastic conical caps one male and one female were placed. Adult males were removed after coupling. Cohorts with the respective life tables for each of the five temperature regimes were compared using one way analysis of variance. Tukey (1953) multiple comparison tests were used to compare and separate means, whereas a Games-Howell comparison test was also applied for confirmation (Sokal and Rohlf, 1995, SPSS 1997). In all cases, α was 5% with respect to hypothesis testing.

Bias, standard errors, and sampling distributions of the demographic parameters, were estimated using jackknifing and bootstrapping estimations. These methods are widely applied to estimate the variance of the original data set and the per capita rate of increase (rm) as well as most of related ‘synthetic’ demographic parameters (Damos 2012, Damos and Savopoulou-Soultani 2011a, Efron 1982, Eliopoulos 2006, McPeek and Kalisz 1993, Meyer et al. 1986.

In the jackknife procedure one of the n, female adults (i = 1, 2, . . . , n) was sequentially omitted from the original data set and the per capita rate of increase r̂, from the remaining individuals (n − 1) was recomputed. For life table parameters, jackknife pseudovalues (r̂, i) were then calculated for the subset of the original values as follows:

\[ r̂_i = n \cdot r − (n − 1) \cdot \hat{r}_i. \]

The mean value of r and the standard error of the n values were calculated as described by Meyer et al. (1986):

\[ \bar{r}_f = \frac{1}{n} \sum_{i=1}^{n} r̂_i, \]

and

\[ SE(\bar{r}_f) = \sqrt{\frac{s^2_f}{n}}, \]

where \( s^2_f \) = variance of the n jackknife pseudovalues (\( \hat{r}_1, \hat{r}_2, \ldots, \hat{r}_n \)) and

\[ s^2_f = \frac{1}{n-1} \sum_{i=1}^{n} (r_o - \hat{r}_i)^2. \]
In the bootstrap method, bootstrap replicates were constructed from the data pool of the original female cluster after random selection and replacement of data. Then a per capita rate of increase ($r_i^*$) was estimated for the $m$ random recombinations and a final bootstrap calculation was computed for the respective mean value as follows:

$$\bar{r}_B = \frac{1}{m} \sum_{i=1}^{m} r_i^*, \quad [12]$$

and

$$SE(\bar{r}_B) = \sqrt{\frac{s^2_{r_i^*}}{m}}, \quad [13]$$

where ($s^2_{r_i^*}$) = variance of the $m$ bootstrap values; ($r_1^*, r_2^*, \ldots, r_m^*$) (Meyer et al. 1986). The given statistical dispersion measures were based on the jackknife randomization procedure, whereas bootstrapping values were estimated only for confirmative reasons.

Results

Adult Longevity and Age Specific Mortality. In general, as expected, temperature had a significant effect on mean male ($F_{4,110} = 25.129, P = 0.000$) and female ($F_{4,121} = 41.882, P = 0.000$) adult longevity. In particular, adults that maintained at 15 and 20°C, expressed prolonged lifespan (20–65 d) when compared with adults that were maintained at the higher temperatures (5–25 d) of 25, 30 and 35°C, regardless of sex. The age specific mortality patterns ($l_x$) are generated in the surface plot (Fig. 1) and describe the relationship between age specific survivorship and temperature. In general, temperature had a significant effect on the probability of surviving of female adults of $A.\ lineatella$. Survivorship curves were similar to those of a typical of poikilothermic organisms that die at constant rate for male and female adults. However, although survivorship gradually declined, showing a fairly age specific schedule of mortality, higher temperatures were associated with steeper declines survivorship curves and this pattern was quite similar in both sexes. In particular, survivorship of adults reared at lower temperatures was higher compared with those reared at higher temperatures. The longest survival was registered at 15 and 20°C, whereas highest mortality rates were observed at 35°C, in which ≈85–90% of the adults died within the first week. Additionally, for population cohorts that were maintained at 15 and 20°C, the adult survivorship for the first week remained static but was followed by an abrupt drop until the third week. After this point a very gentle decrease was observed. At 15 and 20°C, survival showed an abrupt drop, and then was followed by a very gentle decrease.

Age Specific Fertility. Figure 2a, is a surface plot of the average age specific fertility ($m_x$), expressed as number of eggs per female per d and Fig. 2b is the respective age specific cumulative egg production of $A.\ lineatella$ at the five constant temperatures that were tested.

In most cases a left-skewed bell-shaped unimodal pattern is observed, although at the extreme temperatures (15 and 35°C) less irregular curves were also observed (Fig. 2). On any temperature, oviposition started with high values and kept them for 1–2 wk, then dropped to a lower level with small rises until females stopped laying eggs some 4 wk before the death of the last adults. At higher temperatures, 30 and 35°C, a more abruptly reproduction pattern was observed when compared with all other temperature regimes.

Reproductive peak was registered during the first and second wk at 25 and 30°C and in concrete was 26.6 eggs at day 5 and 10.1 eggs at day 8, respectively. At 20°C the reproductive peak occurred a few days later corresponding to the second wk and was 15 eggs at day 9, whereas at the extremes temperatures of 15 and 35°C, 6.2 eggs were laid at day 12 and 3.8 eggs at day 8, respectively (Fig. 2a).

The effect of extreme temperatures (i.e., 15 and 35°C) on the cumulative number of eggs laid caused a delay, which was expressed by a prolonged oviposition period of ≈1 wk (Fig. 2b) and eggs laid at a lower
rate compared with the other temperature regimes. The ovipositional period was probably longer because of longer duration times at this temperature. According to Fig. 2b, oviposition rates at 25 and 30°C are similar over the first wk period, but they were sustained at higher rates at 25°C. The cumulative number of eggs laid per female ranged from ≈30–130 eggs at the temperatures that were tested.

Reproductive Characteristics. Temperature had a significant effect on the preovipositional period of *A. lineatella* (*F*$_{4,131}$ = 8.637, *P* = 0.000), as well as on the mean ovipositional period (*F*$_{4,131}$ = 24.598, *P* = 0.000) (Fig. 3). On average, the females started to lay their first eggs on the third day at 25 and 30°C, on the fifth and sixth day at 20 and 15°C respectively, and on the seventh day at 35°C. The average oviposition time was significantly shorter at 25 and 35°C and was estimated to be ≈9 and 10 d, respectively (Fig. 3). In the intermediate temperatures, of 20 and 30°C, the females laid their eggs during a period of 2 wk and the last eggs were laid approximately on the 14th d. The longest ovipositional time was observed at the lower temperature of 15°C and extended till the 19th d in which the females laid the last eggs.

According to second order regression model, high correlations were also observed between temperatures and the age of first reproduction, \[ y(x) = 0.0257(0.0072)x^2 - 1.2657(0.3639)x + 18.485(4.3021), R^2 = 0.9904, \] as well as between temperature and average ovipositional period \[ y(x) = 0.0372(0.0121)x^2 - 1.853(0.608)x + 26.188(7.186), R^2 = 0.9953 \] (Fig. 4).

Demographic Parameters and Life Table Statistics. The age specific mortality schedule of *A. lineatella* provided the necessary data for the estimation of the demographic parameters. Patterns of life table statistics, as affected by temperature, are summarized in Figs. 5, 6, 7 and 8. In particular, the net reproductive rate (*R*$_0$) had highest values at 25°C and was 74.172 per female. Moreover, *R*$_0$ showed an enormous reduction at 35 and 15°C and was estimated to be 1.640 and 12.457 per female, respectively, whereas at 20 and 30°C it was 48.499 and 63.761, respectively (Fig. 5). However, the intrinsic rate of increase (*r*$_m$) had highest values at 30°C and was 0.238, while at 25 and 20°C it was estimated to be 0.144 and 0.093, respectively. In contrast, rearing at the extreme temperatures of 15 and 35°C had strong negative effect on the intrinsic rate of

![Fig. 2. Response surfaces of temperature and mean number of offspring’s (mx) (a) and temperature and cumulative eggs laid (b) for the peach twig borer *A. lineatella*.](image-url)

![Fig. 3. Effect of five constant temperatures on reproductive characteristics. Preoviposition and oviposition times ± SE of *A. lineatella* (columns followed by different letters are significantly different), Tukey’s multiple comparison tests, *α* = 0.05.](image-url)
increase and was estimated to be 0.028 and 0.059, respectively (Fig. 5).

Fig. 6, depicts the effect of temperature on the birth rate ($b$) and finite capacity of increase ($\lambda$) of *A. lineatella*. Birth rate and finite capacity of increase had their highest values at 30°C and estimated to be 0.235 and 1.268, respectively. This was not surprisingly considering that these parameters are in one or the other way directly related to the intrinsic rate of increase. Consequently, all these parameters displayed similar patterns in relation to temperature reaching their lowest values at the extreme temperature of 15°C, and estimated to be 0.09 and 1.028 for the $b$ and $\lambda$ respectively (Fig. 6).

Furthermore, the mean generation time ($G$) and doubling time (DT) of *A. lineatella* was the shortest at 30°C and was estimated to be 25.566 and 2.909 d respectively (Fig. 7). The mean generation time was also quite short at 35 and 20°C and estimated respectively to be 34.707 and 43.681 d, whereas it decreased to 60.728 and 138.494 at 20 and 15°C, respectively. The DT estimates expressed analogous patterns with that of $T$ and a 5–10-fold increase, to 11.61 and 24.722 d at 35 and 15°C was respectively observed (Fig. 7).

Finally, the life expectancy ($e_x$) were estimated to be 10.3 d at 25°C, which was also the lowest value, whereas estimates at 30 and 35°C were estimated to be 16.1 and 16.5 d, respectively. In contrast, cohorts of *A. lineatella* maintained at 20 and 15°C increased their life expectancy approximately three to six times and were estimated to be 28.3 and 59.8 d, respectively (Fig. 8).

Discussion

This study clearly shows the effects of temperature on adult longevity and age specific mortality of *A. lineatella*. Additionally, it provides realistic information on how the species demographic parameters are affected by a broad range of constant temperatures. Unfortunately, there are very few laboratory data for the peach twig borer with which to compare results of
the current work. Additionally, because there is no other reference concerning demographic parameters of *A. lineatella*, a comparison on the estimated parameters can be made only with other close related Lepidoptera species.

According to the results, adult life span is considerably prolonged at the lower rearing temperatures, while is adversely affected by the higher temperature regimes. Depictions of age specific survivorship patterns, instead of summary statistics as given in prior studies (Damos and Savopoulou-Soultani 2008), has advantages because they show underlying patterns of longevity without making any normality assumptions over its statistical distribution. Furthermore, they indicate outliers and how the degree of data dispersion is modified in relation to temperature. Combined with survivorship curves, they may explain controversial results for *A. lineatella* adult longevity reported from previous investigations. Moreover they are a prerequisite for life table randomization procedures and facilitate further statistical analysis and accurate estimates of demographic parameters.

The first comprehensive works on *A. lineatella* that were carried out by Bailey (1948) and King and Dennen (1960), show adult longevity to be extremely variable (with adults living up to 20 d, and occasionally, as long as 5 wk). Considering that the daily temperature limits during a typical growth season in a Mediterranean like temperate climate, i.e., northern Greece CA, are in the range of 15–35°C, the results of the current work justify these first empirical estimations. Increased replications and sampling, based on randomization statistics, confirmed the summary statistics for adult longevity given by Damos and Savopoulou-Soultani (2008) and therefore are not included in this work. Thus, current detailed demographic results, along with prior summary statistics as given by Damos and Savopoulou-Soultani (2008), provide more evidence for the optimum temperature ranges of *A. lineatella*.

These results are in agreement with prior observations published by McElfresh and Millar (1993) and by Molinari and Zanrei (2004), which respectively cite that adults maintained on 27°C lived on average 9.2–20 d, and males and females maintained at 23°C lived 13.5 and 24 d, respectively.

Reproductive characteristics were also most affected by the extreme temperatures. In general, within a lower and upper temperature threshold, oviposition and fecundity usually increases with temperature, up to an optimal point. In this study, a higher number of eggs were laid in the intermediate temperature range of 20–30°C, while females laid significantly lower number of eggs at 15°C. Although there is no previous oviposition threshold defined for *A. lineatella*, based on the results of this study, a lower ovipositional threshold can be assumed to be near 15°C. At this temperature females laid fewer eggs. Moreover, this value is also near to the thresholds that have been estimated for closely related fruit moths such as *Adoxophyes orana*, *Cydia pomonella* and other Lepidoptera (Charmillot et al. 1984, Rodriguez-del-Bosque et al. 1989, Saathre and Hofsvang, 2002). Nevertheless, it is already known that the mean number of eggs is significantly affected by temperature, and that the mean egg hatch has its lowest values at the extremes (Damos and Savopoulou-Soultani 2008).

According to the estimated demographic parameters, optimum temperature for reproduction is close to 30°C, despite the fact that a slightly higher average number of eggs is laid at 25°C (Damos and Savopoulou-Soultani 2008). Furthermore, the result that the highest value of *r*<sub>m</sub> was observed at 30°C, instead of 25°C as in the case of *R*<sub>o</sub>, can be explained by the fact that *r*<sub>m</sub> is a function of both insect fecundity and generation time. This observed paradox may be misleading considering that life table analysis is applied in situations in which the scope is the selection of optimal temperature for laboratory mass rearing and simply maintaining a colony for experimental purposes (Abbas et al. 2010, Legaspi 2004).

The number of cumulative eggs laid up to first reproduction and the average ovipositional times, indicate a more favorable reproductive trend of prolonged egg production over a longer period at 20 and 25°C, which may be more suitable for maintaining a colony of *A. lineatella* than 30°C. This probably explains why previous researchers made efforts to maintain their laboratory colonies at 25 and 26°C, because this temperature may be generally optimal for insect growth and development (Anthon et al. 1971, Damos and Savopoulou-Soultani 2008, Damos et al. 2009, McElfresh and Millar 1993).

Nevertheless, because life table analysis takes into account age dependent mortality and reproduction in the estimation of the demographic parameters, it is more suitable for the description of realized population growth compared with simple reproductive summary statistics. Thus, randomized life table statistics and statistically derived demographic parameters such as those calculated in this work, may provide useful
values for summarizing the reproductive capacities of *A. lineatella* which may be closer to field conditions.

In most peach growing countries (i.e., southern Europe) temperatures close to 30°C are usually registered for several hours during a typical summer day. The estimation of optimum reproduction thresholds for *A. lineatella* (close to 30°C) are important and can be used to predict the reproduction potential of the first emergent generation and may explain the duration and number of the forthcoming generations (i.e., the higher field population pressures observable during the second and third summer generations with no overlapping generations). Clearly, the laboratory trials far exceed the longevity observed in the field (Damos and Savopoulou-Soultani 2010) and can be used to accurately estimate generation times during the growth season, whereas differences compared with field trials (i.e., prolonged third generation or additional fourth flight), may be attributed to several factors including delayed mating that occurs because of environmental conditions or other factors.

When assessing the risk posed by *A. lineatella*, temperature is among the most critical components to determine the reproductive potential of the species in field situations. The above demographic information when coupled with developmental data from prior studies may contribute to the development and improvement of current population models that are used for successful management of *A. lineatella* in peach growing areas.

**References Cited**


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