Temperature-dependent age-specific demography of grapevine moth (*Lobesia botrana*) (Lepidoptera: Tortricidae): jackknife vs. bootstrap techniques

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Grapevine moth, *Lobesia botrana* (Lep. Tortricidae) is a key pest of grape in Iran and other vineyards of the world. In this study, eight constant rearing temperatures (5, 10, 15, 20, 25, 30, 32 and 35 ± 1 °C) along with 60 ± 10% RH and a 16:8 (L:D) h photoperiod were chosen for demographic studies of the grapevine moth. Immature stages were unable to develop when reared at 5 and 35 °C, and the progeny moths were unable to successfully mate at 10, 15 and 32 °C. The overall developmental time of juveniles decreased at 30 °C (from 320.7 ± 3.4 d at 10 °C to 34.2 ± 0.2 d) followed by an increase to 42.5 ± 0.6 d at 32 °C. Based on values of the stable population growth parameters, the temperature of 25 °C was found to be optimal for propagation of grapevine moth. The highest values of the intrinsic rate of increase, gross and net reproductive rates were 0.0719 d\(^{-1}\), 55.5 and 23 females per generation, respectively, at 25 °C. Since jackknife and bootstrap estimates of mean and standard error were mainly similar, both methods may equally be used for uncertainty estimates. Our data suggest that cold storage of grapes will help to control grapevine moth infestations and damage. In many grape growing regions of Iran, the first generation is expected to cause damage. It is expected since our reproductive life table analysis suggests that the hot summer temperatures may restrict pest development during subsequent generations.

**Keywords:** life table parameters; fecundity; fertility; reproduction; survivorship

**Introduction**

Grapevine moth (GVM), *Lobesia botrana* (Lep.: Tortricidae) is a significant pest of berries in Europe, Mediterranean countries, Southern Russia, Japan, Middle East, Near East, Northern and Western Africa and North America (Fowler & Lakin 2002; Frolov & Saulich 2005; Ifoulis & Savopoulou-Soultani 2006; Varela et al. 2010; Thiery et al. 2014a, 2014b). In Iran, it is a key pest of vineyards (Gharib 1961; Saber 1997; Saeedy 2007) responsible for direct and indirect losses by allowing access to the grey mould, *Botrytis cinerea* Pers (1794) (Helotiales, Sclerotiniaceae) specially in the third generation (Ifoulis & Savopoulou-Soultani 2006; Dalla Monta et al. 2007; Sciarretta et al. 2008). The number of annual generations of *L. botrana* varies depending on the climatic conditions of geographical regions (Roehrich & Boller 1991; Fowler & Lakin 2002; Pavan et al. 2006; Sciarretta et al. 2008; Thiery et al. 2014a, 2014b).
Environmental temperature strongly affects physiology, performance and fitness of ectothermous organisms (Frazier et al. 2006). Adaptation to temperature inevitably influences population dynamics of insects (Huey & Berrigan 2001; Frazier et al. 2006; Iranipour et al. 2010). Local temperature and its fluctuation determine geographical distribution or theoretical niche of an insect. This may be realised via population level effects. It is known that population growth rate ceases beyond borders of distribution range in which temperature exceeds tolerable levels (Pavan et al. 2006; Damos 2012). Therefore, it is often used to predict performance of species under given environmental conditions (Smith 1991; Southwood & Henderson 2000; Huey & Berrigan 2001; Fouly et al. 2011; Damos 2012; Jha et al. 2014). Among life table parameters, intrinsic rate of increase \( r_m \) is a crucial parameter representing the demographic fitness of a species.

No information is available on demographic characteristics of \( L. \) botrana in Asian vineyards which is necessary to predict pest outbreaks and develop pest management strategies. Knowledge on the factors governing development such as temperature, and forecasting models may increase efficacy and success of control measures (Kuhrt et al. 2006). So, the current study aimed to estimate demographic characteristics of an Iranian population of GVM exposed to different constant temperatures by highlighting jackknife and bootstrap techniques for uncertainty estimates of the mean.

Materials and methods

Insect rearing

Fifth instar larvae of GVM were collected from Malekan vineyards (46° 6' longitude E, 37° 9' latitude N, 1290 m ASL), East Azarbaijan province of Iran and maintained in Insect Ecology Laboratory, Department of Plant Protection, the University of Tabriz in Iran. The larvae were placed in plastic containers (10 cm in diameter, 13 cm in height) with a small bunch of ripe grape to feed and a piece of fluted cardboard to provide a substrate for pupation. Four pairs of newly emerged adults were transferred to mating chambers. The mating chambers were made of PVC piping, 9 cm in diameter and 15 cm in height. The two ends of the chambers were covered with transparent polyethylene (PE) sheets to provide oviposition sites. Two holes (12 mm in diameter) were made on two sides of the chamber wall covered by fine mesh cloth to provide ventilation. Another hole (7 mm in diameter) was made in the middle of the chamber wall to fit a glass tube (7 mm in diameter and 50 mm in height) containing a piece of cotton wool saturated with sucrose solution (10%). The cotton wool and the oviposition substrate were replaced daily. The larvae were reared on a modified artificial diet described by Becher and Guerin (2009) at 25 ± 1 °C, 60 ± 10% RH, and 16:8 (L:D) h photoperiod in a growth chamber (model IKH. RH Iran Khodsaz Company, Iran). The transparent PE sheets bearing the GVM eggs were placed in the clear plastic bags (15 × 10 cm) to allow the eggs to hatch. Newly hatched larvae were introduced on artificial diet pieces placed in rectangular cube plastic containers (4 cm in height × 17 cm in length × 11 cm in width) using a fine brush. \( F_2 \) generation of the field collected larvae of \( L. \) botrana was used in the current study.

Life table study

Cohorts of 120–130 eggs < 24 h old were chosen randomly from the mating chambers and those were held at eight constant temperatures (5, 10, 15, 20, 25, 30, 32 and 35 ± 1 °C), 60 ± 10% RH and 16:8 (L:D) h photoperiod in different growth chambers.
Newly hatched larvae (20/dish) were transferred to containers (described above) with a fine brush to be reared on modified artificial diet. The larvae were reared individually in transparent plastic Petri dishes (6 cm in diameter) beyond second instar. The larval/pupal mortality, moulting of the larvae and eclosion of the pupae were daily recorded. Sex ratio (SR) was calculated as: \( SR = F/(F + M) \) where F and M are the number of female and male pupae, respectively (Each pupa was sexed just before adult emergence). The difference in sex ratios was compared by a chi-square test between the two genders and among five temperatures using a \( 2 \times 5 \) contingency table.

The newly emerged adults of each cohort were transferred to oviposition containers (described above) in four pair groups in their preoviposition period (24, 48 and 144 h at 25, 30 and 20 °C, respectively, determined based on a pretest). The mated females were separated and transferred individually to a new container of the same kind. All experiments were carried out at growth chambers. The female lifespan was divided into preoviposition, oviposition and postoviposition periods. All data including the number of eggs/female and mortality were recorded daily up to death. One-way ANOVA was done to determine the effect of temperature on all above-mentioned variables except for developmental time. The developmental time was analysed by two-way ANOVA (temperature in three levels and life stages in seven levels including eggs, 1–5 instar larvae and pupae). Interaction between the two factors may imply an anisomorphy in development. To achieve a stronger conclusion, percentage of time spent in each stage also was calculated and discussed by a descriptive manner. Comparisons of means in all analyses were done based on Turkey’s HSD test (\( \alpha = 0.05 \)) using SPSS version 13.0 (SPSS 2004).

Age-specific fecundity-life table parameters including life expectancy (\( e_x \)), gross reproductive rate (GRR), net reproductive rate (\( R_0 \)), intrinsic rate of increase (\( r_m \)), finite rate of increase (\( \lambda \)), mean generation time (\( T \)), doubling time (DT), instantaneous birth rate (b) and death rate (d) were calculated according to Carey (1993).

**Life table analysis**

Because uncertainty of the fecundity-life table parameters including GRR, \( R_0 \), \( r_m \), \( \lambda \), \( T \), DT, b and d could not be estimated using traditional formulae, the jackknife and bootstrap techniques were used instead (Meyer et al. 1986; Sokal & Rohlf 1995; Maia et al. 2000; Jha et al. 2014). Sample size of GVM (\( n \)) was 120–130 individuals for original and jackknife estimations and 1000 individuals for bootstrap estimation.

The jackknife pseudo-values of the parameters were estimated using the following procedure:

Initially, \( r_m \) value (or any other parameter) was estimated for all individuals (\( n = 120 \)) delineated here by \( [r_m(\text{all})] \). The procedure was repeated for any combination of \( n-1 \) individuals, by excluding a different female to estimate \( r_m(\text{i}) \). Finally, pseudo-values for \( r_m(\text{PSV } r_m(\text{i})) \) were calculated using the following equation:

\[
\text{Psv } r_m(i) = n \times r_m(\text{all}) - (n - 1) r_m(i)
\]

In bootstrap technique, population parameters (PP) were estimated by resampling from original cohort by a random manner for 1000 times using a programme written in Microsoft Excel environment (Iranipour 2015).

Mean, variance and standard error of \( n \) jackknife pseudo-values as well as 1000 bootstrap estimates were calculated for each temperature using traditional equations (Meyer et al. 1986).
Differences among the temperatures were determined using one-way ANOVA and the means were compared using Tukey’s HSD test ($\alpha = 0.05$) of SPSS version 13.0 (SPSS 2004). 

The entropy ($H$), a measurement of the heterogeneity in survival pattern was calculated for each temperature using following equation (Carey 1993):

\[
H = \left( \sum_{x=0}^{\omega} \frac{(e_x d_x)}{e_0} \right)
\]

where $e_x$ is life expectancy at age $x$; $d_x$ is the fraction of initial individuals that died between the ages $x$ and $x + 1$; $e_0$ is the life expectancy at birth ($x = 0$) and $\omega$ is the maximum age reached by the last surviving individual. Values of $H < 0.5$, $H = 0.5$ and $H > 0.5$ correspond to Slobodkin’s type I, II and III survivorship curves, respectively (Schowalter 2006; Damos 2012).

**Results**

**Developmental time of immature stages**

The mean developmental times of all immature stages at six constant temperatures are presented in Table 1. Two-way ANOVA showed significant differences among the mean developmental times of all life stages, temperatures and interactions between them ($p < 0.0001$). The shortest and the longest developmental time of overall immature stages were found at 30 and 10 °C, respectively. The mean incubation period of eggs varied from 37.06 days at 10 °C to 2.45 days at 30 °C ($F_{5,452} = 26876.05, p < 0.0001$). The eggs’ incubation period decreased as the temperature increased from 10 to 30 °C and followed by an increase at 32 °C. The mean developmental time of the GVM larvae was significantly different at the examined temperatures and decreased from 169 days at 10 °C to 21.20 days at 30 °C ($F_{5,212} = 18054.3, p < 0.0001$) and followed by an increase to 29.47 days at 32 °C. A similar trend was found in different instar larvae (Table 1). The mean developmental time of pupae was significantly different at the examined temperatures from 114 days at 10 °C to 8.18 days at 32 °C ($F_{5,196} = 4390.9, p < 0.0001$). Comparison of the mean developmental time of different stages showed that the egg and larval development times had the shortest and the longest durations of immature life, respectively. Development of the first and fifth instar larvae were the fastest and slowest, respectively. The percentage of time spent by the *L. botrana* at different stages changed by temperature (Table 2). In this regard, a decreasing trend in pupal development by temperature and an opposite trend in larval stages are obvious. At temperatures less than 20 °C, development of the pupae took longer time. In contrast, the larval development was prolonged at higher temperatures. The fifth instar larvae were the most variable stage in terms of percentage of developmental time. Consequently, percentage of the time period that the GVM stays at fifth instar plus pupa was approximately constant in all temperatures (53--57% of overall developmental time) except for 32 °C.

**Adult longevity**

The means’ adult longevity at six constant temperatures are shown in Table 3. No adults emerged at 5, and 35 °C. One-way ANOVA showed significant difference among the
Table 1. The mean developmental times (days) in immature stages of *L. botrana* at different temperatures.

| Stage               | Temperature | 10 ± 1 °C | 15 ± 1 °C | 20 ± 1 °C | 25 ± 1 °C | 30 ± 1 °C | 32 ± 1 °C |
|---------------------|-------------|-----------|-----------|-----------|-----------|-----------|-----------|
|                     | *n* | Mean ± SE | *n* | Mean ± SE | *n* | Mean ± SE | *n* | Mean ± SE | *n* | Mean ± SE | *n* | Mean ± SE |
| Eggs                | 130 | 37.06 ± 0.15E,d | 120 | 17.2 ± 0.11D,e | 120 | 8.81 ± 0.06C,c | 120 | 3.46 ± 0.05B,b | 120 | 2.45 ± 0.05A,b | 130 | 3.47 ± 0.07B,a |
| 1<sup>st</sup> instar larvae | 50  | 14.97 ± 0.13E,a | 71  | 6.52 ± 0.07D,a | 95  | 6.54 ± 0.06D,a | 95  | 2.51 ± 0.60B,a | 95  | 1.95 ± 0.09A,a | 51  | 4.64 ± 0.17C,abc |
| 2<sup>nd</sup> instar larvae | 33  | 19.17 ± 0.34E,b | 48  | 8.27 ± 0.14D,b | 67  | 7.89 ± 0.12D,b | 70  | 3.56 ± 0.06B,b | 67  | 2.35 ± 0.06b,a | 31  | 5.09 ± 0.17C,bc |
| 3<sup>rd</sup> instar larvae | 18  | 28.27 ± 0.54E,c | 41  | 11.3 ± 0.24C,c | 55  | 10.4 ± 0.14C,d | 63  | 3.85 ± 0.09A,b | 55  | 3.53 ± 0.07A,c | 22  | 4.95 ± 0.16b,e |
| 4<sup>th</sup> instar larvae | 11  | 39.22 ± 1.27D,d | 39  | 12.6 ± 0.23C,d | 52  | 10.76 ± 0.16B,d | 61  | 4.70 ± 0.1A,c | 52  | 4.51 ± 0.07A,d | 19  | 3.88 ± 0.17A,abc |
| 5<sup>th</sup> instar larvae | 9   | 68.67 ± 1.76E,e | 38  | 21.2 ± 0.25D,f | 51  | 19.16 ± 0.11C,e | 61  | 9.83 ± 0.16AB,d | 51  | 8.91 ± 0.11A,e | 17  | 10.87 ± 0.19B,f |
| Pupae               | 6   | 114 ± 1.73E,f | 36  | 43.2 ± 0.44D,g | 49  | 37.26 ± 0.28C,f | 59  | 11.05 ± 0.21B,e | 49  | 8.46 ± 0.15A,f | 15  | 8.18 ± 0.35A,c |
| Larvae              | 9   | 169 ± 1.51F | 38  | 59.8 ± 0.28E | 51  | 54.84 ± 0.16D | 61  | 24.41 ± 0.14B | 51  | 21.20 ± 0.15A | 17  | 29.47 ± 0.27C |
| Egg-pupaes          | 6   | 320.7 ± 3.38E | 36  | 120 ± 0.40D | 49  | 102.77 ± 0.24C | 59  | 40.95 ± 0.18B | 49  | 34.19 ± 0.21A | 15  | 42.45 ± 0.56B |

Notes: Means followed by different capital letters within a row show significant difference between temperatures (Tukey’s HSD test, *p* < 0.05). Means followed by different lowercase letters within a column show significant difference between life stages (Tukey’s HSD test, *p* < 0.05).
examined temperatures in terms of mean adult longevity both in females and males ($F_{5,77} = 832.5$ and $F_{5,98} = 956.72$ for females and males, respectively; $p < 0.0001$). Comparison of the mean longevity between females and males by t test showed no significant difference at 15 and 32 °C ($t_{32} = 0.14$, $p = 0.88$ at 15 °C and $t_{10} = 0.29$, $p = 0.77$ at 32 °C), while it was different at 20, 25 and 30 °C ($t_{45} = 2.47$, $p = 0.017$ at 20 °C, $t_{49} = 3.17$, $p = 0.003$ at 25 °C and $t_{43} = 2.53$, $p = 0.015$ at 30 °C). In the latter temperatures, female longevity was higher than that of the males. Adult longevity decreased along with temperature elevation from 10 to 32 °C in both sexes (Table 3). Due to the lower number of observations at 10 °C, comparison of the female and male longevity was not possible.

Reproduction events

Because no development occurred at 5 and 35 °C and the moths inability to mate at 10, 15 and 32 °C, the reproduction events including mean preoviposition, ovipoision and postoviposition periods, total number of eggs and hatched eggs laid by females were analysed only for 20, 25 and 30 °C. One-way ANOVA showed a significant effect of temperature on both preoviposition ($F_{2,61} = 519.4$, $p < 0.0001$) and oviposition periods ($F_{2,60} = 205.5$, $p < 0.0001$). Postoviposition period was not affected by temperature ($F_{2,60} = 1.23$, $p = 0.30$). Comparison of means by Tukey’s HSD test ($\alpha = 0.05$) revealed that the mean preoviposition period significantly decreased as the temperature increased from 20 to 25 °C followed by an increase at 30 °C. The mean oviposition period, on the other hand, significantly decreased in the higher temperatures (from 20 to 30 °C) (Table 3). The mean number of eggs and the number of eggs hatched were significantly different at the examined temperatures ($F_{2,60} = 245.5$, $p < 0.0001$). Comparison of means showed that the mean number of eggs per female reached the maximum as the temperature increased from 20 to 25 °C, and further declined to minimum at 30 °C (Table 3). Although egg hatch was similar at all temperatures, comparison of means revealed significant differences between 30 °C and the other temperatures (Table 3).

Although the emerged moths were unable to mate successfully at 10, 15 and 32 °C, the inseminated eggs incubated at those temperatures were able to hatch successfully. The percentage of eggs hatched at 10, 15, 20, 25, 30 and 32 °C, were 38.47, 59.17, 79.17, 79.17, 80 and 39.23%, respectively. These percentages were drawn from the two first rows of n column for each temperature in Table 1.

Table 2. The percentage of developmental time of immature stages of *L. botrana* at different temperatures.

| Stage                 | Temperature          | 10 ± 1 °C | 15 ± 1 °C | 20 ± 1 °C | 25 ± 1 °C | 30 ± 1 °C | 32 ± 1 °C |
|-----------------------|----------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Eggs                  |                      | 11.56     | 14.33     | 8.57      | 8.45      | 7.62      | 8.71      |
| First instar larvae   |                      | 4.56      | 5.433     | 6.36      | 6.44      | 6.06      | 10.93     |
| Second instar larvae  |                      | 5.97      | 6.87      | 7.68      | 9.14      | 7.31      | 11.99     |
| Third instar larvae   |                      | 8.74      | 9.42      | 10.38     | 9.88      | 10.98     | 11.77     |
| Fourth instar larvae  |                      | 12.23     | 10.51     | 10.49     | 12.06     | 14.32     | 9.96      |
| Fifth instar larvae   |                      | 21.41     | 17.61     | 19.64     | 24.95     | 27.71     | 26.46     |
| Pupae                 |                      | 35.55     | 36        | 36.87     | 28.98     | 25.91     | 19.98     |
| Larvae                |                      | 52.91     | 49.83     | 54.55     | 62.47     | 66.38     | 71.12     |
Table 3. The effect of different temperatures on reproductive periods, adult longevity and the number of eggs laid by each female of *L. botrana*.

| Temperature | Mean ± SE | Mean ± SE | Mean ± SE | Mean ± SE | Mean ± SE | Mean ± SE |
|-------------|-----------|-----------|-----------|-----------|-----------|-----------|
| 10 ± 1 °C*  | –         | 6.61 ± 0.12c | 1.75 ± 0.09a | 2.47 ± 0.12b | –         | –         |
| 15 ± 1 °C*  | 6.61 ± 0.12c | 15.89 ± 0.21c | 1.28 ± 0.19a | 2.47 ± 0.12b | 5 ± 0.88a | 486 ± 0.26a |
| 20 ± 1 °C   | 6.61 ± 0.12c | 8.98 ± 0.17b | 1.22 ± 0.13a | 2.47 ± 0.12b | 5 ± 0.88a | 486 ± 0.26a |
| 25 ± 1 °C   | 6.61 ± 0.12c | 8.98 ± 0.17b | 3.67 ± 0.11a | 2.47 ± 0.12b | 6.67 ± 0.18ab | 5 ± 0.88a |
| 30 ± 1 °C   | 6.61 ± 0.12c | 8.98 ± 0.17b | 7.33 ± 0.18b | 2.47 ± 0.12b | 6.67 ± 0.18ab | 5 ± 0.88a |
| 32 ± 1 °C*  | 6.61 ± 0.12c | 8.98 ± 0.17b | 11.92 ± 0.14c | 2.47 ± 0.12b | 8.25 ± 0.17b | 5 ± 0.88a |

*Means followed by different letters within each row were significantly different (Tukey's HSD test, p < 0.05).*
Sex ratio

Although sex ratio was not affected significantly by temperature ($\chi^2 = 3.098, p = 0.54$), it revealed tendency towards male progeny except for 25 °C. The values of this ratio were 0.44, 0.46, 0.57, 0.46 and 0.36 at 15, 20, 25, 30 and 32 °C, respectively.

Age-specific survival rate

Age-specific survival rates ($l_x$) of *L. botrana* at three constant temperatures are shown in Figure 1. General patterns of survivorship curves in all temperatures showed a sharp decline at younger stages followed by a plateau and a further decline at senescence. The main differences at various temperatures were the time of these events. The survivorship curve of individuals at 20 °C declined sharply between days 5–17 and beyond 109th day. The survival patterns of the cohorts at 25 and 30 °C were similar to 20 °C and the
first decline occurred in days 3–7 and 2–5 at 25 and 30 °C, respectively followed by
the second one at days 42 and 35. The mortalities of eggs and 1st instar larvae were
20.83 and 29.47% at 20 °C, respectively. The highest mortality occurred at the egg
stage (20.83 and 20%) and first instar larval stage (26.31 and 31.25%) at 25 and 30 °C,
respectively.

The entropy values (\(H\)) found for \(L. \ botrana\) were 0.98, 0.84, 0.71, 0.58, 0.66 and 1
at 10, 15, 20, 25, 30 and 32 °C, respectively. There was a high mortality rate during
early life stages indicating a type III or IV survivorship curve in Slobodkin (1962) scale.
It is obvious that demographic heterogeneity (\(H\)) is lower at intermediate temperatures,
but considerably higher at extremes.

**Life expectancy**

Life expectancy \((e_x)\) of \(L. \ botrana\) at six constant temperatures is shown in Figure 2.
This figure shows the mean duration that individuals at age \(x\) were expected to survive.
The life expectancy at birth was 49.5, 54.07, 54.69, 25.88, 19.69 and 9.28 days at 10,
15, 20, 25, 30 and 32 °C, respectively. The highest \(e_x\) values were 146.77, 105.28,
86.63, 35.09, 27.41 and 22.57 days occurred at 10, 15, 20, 25, 30 and 32 °C, respec-
tively at days 77, 27, 18, 8, 5 and 9. These maximum values were obtained when the
cohort was at the third and fourth instar larval stages at 10 °C and the second and third
instar larval stages at the other temperatures (Figure 2).

**Stable population growth parameters**

Values of population growth parameters of \(L. \ botrana\) using jackknife and bootstrap
estimates for uncertainty are summarised in Table 4. Survivorship curves and temporal
distribution of reproduction are also shown in Figure 1. One-way ANOVA showed sig-
nificant differences in all parameters among the temperatures in both estimations
\((df = 2, 180 \text{ in jackknife estimation, } df = 2, 2997 \text{ in bootstrap estimation, } p < 0.0001)\).
The mean estimates of both jackknife and bootstrap methods were largely similar to
original cohort estimates. The standard errors of both estimates were also largely similar.
Nevertheless, minor differences in Tukey’s classification were obtained mainly due to
smaller degrees of freedom (and as a result larger \(t\)-statistic) of jackknife estimates and
broader confidence intervals leading to higher overlap in those means close to each

![Figure 2. Life expectancy \((e_x)\) of \(L. \ botrana\) at six constant temperatures.](image-url)
Table 4. The effect of three constant temperatures on life table parameters of _L. botrana_ estimated by jackknife and bootstrap techniques.

| Population parameter                  | 20 ± 1 °C | 25 ± 1 °C | 30 ± 1 °C | 20 ± 1 °C | 25 ± 1 °C | 30 ± 1 °C | 20 ± 1 °C | 25 ± 1 °C | 30 ± 1 °C |
|--------------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Gross reproductive rate (GRR) (offspring) | 24.47     | 55.47     | 12.40     | 24.44 ± 0.64b | 55.47 ± 2.26a | 12.40 ± 0.73c | 24.50 ± 0.63b | 55.54 ± 2.19a | 12.38 ± 0.69c |
| Net reproductive rate (R_0) (offspring) | 7.87      | 22.99     | 4.09      | 7.87 ± 1.51b | 22.98 ± 3.37a | 4.09 ± 0.77b | 7.83 ± 1.47b | 23 ± 3.35a | 4.06 ± 0.77c |
| Intrinsic rate of increase (r_m) (day⁻¹) | 0.0183    | 0.0719    | 0.0386    | 0.0184 ± 0.0017c | 0.0723 ± 0.0036a | 0.0391 ± 0.0052b | 0.0180 ± 0.0017c | 0.0717 ± 0.0034a | 0.0379 ± 0.0054b |
| Finit rate of increase (λ) (day⁻¹)      | 1.0184    | 1.0746    | 1.0394    | 1.0186 ± 0.0017c | 1.0749 ± 0.0036a | 1.0399 ± 0.0054b | 1.0182 ± 0.0018c | 1.0744 ± 0.0037a | 1.0386 ± 0.0056b |
| Mean generation time (T) (day)          | 113.02    | 43.55     | 36.50     | 113.02 ± 0.20a | 43.55 ± 0.12b | 36.49 ± 0.27c | 113.03 ± 0.19a | 43.55 ± 0.11b | 36.51 ± 0.25c |
| Doubling time (DT) (day)                | 37.96     | 9.63      | 17.94     | 37.29 ± 3.61a | 9.57 ± 0.45b | 17.39 ± 2.46b | 38.81 ± 4.13a | 9.68 ± 0.48c | 18.74 ± 3.23b |
| Instantaneous birth (b)                 | 0.0385    | 0.0894    | 0.0384    | 0.0384 ± 0.0023c | 0.1164 ± 0.0055a | 0.0886 ± 0.0055b | 0.0386 ± 0.0024c | 0.1162 ± 0.0055a | 0.0896 ± 0.0059b |
| Intrinsic death rate (d)                | 0.0202    | 0.044     | 0.0508    | 0.0200 ± 0.0035b | 0.0442 ± 0.0076a | 0.0495 ± 0.0083a | 0.0206 ± 0.0036c | 0.0444 ± 0.0077b | 0.0517 ± 0.0089a |

*Sample size was _n_ = 120 for original and jackknife estimation and _n_ = 1000 for bootstrap estimation. Mean followed by different letters within a row separately for jackknife and bootstrap methods were significantly different at _p_ < 0.05 (Tukey’s HSD test).
other. Consequently, the differences between some pairs of the means were not significant in jackknife estimates (see \( R_0 \), DT and \( d \) in Table 4).

GRRs were 2.4–3.1-times higher than net reproductive rates implying a heavy mortality (60–70%) prior to and during reproductive period. Also, the highest value of both statistics occurred at 25 °C suggesting the temperature to be optimum for reproductive activity of \( L. \ botrana \). Value of GRR at 25 °C was about twice that of the 20 °C. The latter was in turn twice of 30 °C. Inter-treatment variations among \( R_0 \)-values were even stronger. The mean generation time declined non-linearly as was expected. The highest \( r_m \)-value occurred at 25 °C emphasising the optimal thermal condition for \( L. \ botrana \). Instantaneous population growth rate in a stable population at 25 °C was 2–4 times higher than those at 30 and 20 °C, respectively.

The non-parametric Kolmogorov–Smirnov test of normality showed the frequency distribution of jackknife pseudo-values may not come from a normal population (Table 5); however, the sample means of 1000 bootstrap recombinants taken randomly from the original population were well-fitted the normal distributions. Frequency distribution of pseudo-values estimated by the jackknife technique and the sample means estimated by the bootstrap technique regarding four important parameters of population growth including GRR, \( R_0 \), \( r_m \) and \( T \) are shown in Figure 3. Frequency distribution of the other parameters also followed a similar pattern.

**Discussion and conclusions**

Information on the effects of temperature on life cycle and PP of an insect pest is essential to develop effective strategies for integrated pest management (Diaz & Fereres 2005). The main focus of our study was to evaluate the response of \( L. \ botrana \) to different levels of temperatures prevalent in dispersal range of it. Thermal range of \( L. \ botrana \) was above 5 and below 35 °C. It may suggest it is a stenotherm insect with a narrow range of thermal tendencies more adaptive to temperate zones. In our area, the temperatures sometimes exceed 35 °C in warm hours of summer days (Figure 4). On the other hand, \( L. \ botrana \) spends freezing winters in diapause with many days below 5 °C and occasionally the temperature may even fall below −15 °C. Frolov and Saulich (2005) reported a biological heterogeneity within the geographical range of \( L. \ botrana \) in terms of development and other biological parameters. Northern borders of the range substantially determined by winter temperature. Temperatures below −20 °C are lethal

| Population parameter          | Asymptotic significance | Bootstrap | Jackknife |
|-------------------------------|-------------------------|-----------|-----------|
| Gross reproductive rate (GRR) | 0.19                    | 0.000     |           |
| Net reproductive rate (\( R_0 \)) | 0.93                  | 0.000     |           |
| Intrinsic rate of increase (\( r_m \)) | 0.16              | 0.000     |           |
| Finit rate of increase (\( \lambda \)) | 0.17             | 0.000     |           |
| Mean generation time (\( T \)) | 0.36                  | 0.01      |           |
| Doubling time (DT)            | 0.04                  | 0.000     |           |
| Instantaneous birth (b)       | 0.83                  | 0.11      |           |
| Intrinsic death rate (d)      | 0.30                  | 0.000     |           |
for overwintering pupae even for a short period of time. Hence, natural range of distribution is restricted to regions where minimal temperatures are not below \(-15\) °C. On the other hand, southern borders of the insect range are limited both by higher temperatures (over 32 °C) and lower relative humidity (below 30%) during flight and egg development. Moreover, absence of conditions for diapause removal (warm winters with temperature limits of 5–15 °C) are also restrictive.

Although development occurred in the range of 10–32 °C, the thermal range for reproduction was narrower. Successful reproduction was only recorded at temperature range of 20–30 °C. In this case, June is the best time for activity of *L. botrana*.

Figure 3. Frequency distribution of pseudo-values estimated by the jackknife technique and sample means estimated by the bootstrap technique (1000 repetitions) in four population growth parameters of *L. botrana*. The normality was tested by non-parametric test of Kolmogorov–Smirnov (\( \alpha = 0.05 \)).
However, the condition would also be favourable during days in May and summer nights. Nocturnal nature of L. botrana suggests May evenings and summer mornings as the best time for reproduction in the studied area (Figure 4). Frolov and Saulich (2005) reported adult activities in the evening and sunrise when temperatures were in the range of 15–32 °C. The lower threshold of oviposition was reported to be 15 °C. In contrast, no reproduction was recorded at this temperature in our study. Optimal conditions for adult activity and oviposition were reported by Roehrich and Boller (1991) and Frolov and Saulich (2005) to be 20–27 °C and 40–70% RH. These results support our findings on reproduction events. However, Deseo et al. (1981) showed the thermal range of oviposition of 13–34.5 °C with the optimal temperature range of 21–25 °C in central–northern Italy. In addition, they found that the fecundity decreased at temperatures below 15 °C. The differences may be due to inter-population variations. Immature development in colder conditions allows overwintering individuals and their progeny to complete their slow development successfully at early March. Eghtedar (1996) showed that a generation can be completed in 30–32 days under warm temperatures (30–32 °C) and a moderate relative humidity (40–45%). Our results also demonstrated the immature development and generation time less than 1.5 month in the main part of season; so three generations in a year is expected for our geographical zone. This prediction is confirmed by other researchers (Saber 1997; Venette et al. 2003; Sciarretta et al. 2008). Lengthening development by an increase in temperature from 30 to 32 °C suggests negative effects of temperatures higher than 30 °C. Thus, restricted activity of L. botrana and its population decline may be expected in vineyards of the region in mid-June to mid-August. Relatively similar observations were also found in other countries. In central Jordan Valley, the pest activity begins at mid-February and ends by mid-November; a prolonged duration of season with an additional fourth generation (Al-Zyoud & Elmosa 2001). In Central Europe, development of L. botrana begins approximately on 5 March and ends around 11 November, unless temperature threshold for development is not reached (Gabel & Mocko 1984; Venette et al. 2003). So, local variations in climatic factors may explain major differences in life history components.

Figure 4. Temperatures recorded in a vineyard located at Malekan during growth seasons (March–October 2011–2013). The textured grey part represents preferable range of L. botrana. Temperatures fall bellow or exceed this range more frequently both prior to and after June (the highlighted interval).
Expectedly, temperature influenced survival and developmental time of all immature stages. Thermal range for development of all immature stages was 10–32 °C, and no development was recorded at either 5 or 35 °C. Briere and Pracros (1998) reported 12–30 °C as the optimal temperature range for development of all immature stages in *L. botrana*. According to their studies, neither eggs nor pupae developed at 8, 10 and 34 °C. In addition, although eggs developed up to the blackhead stage at 32 °C, no larvae could hatch (Briere & Pracros 1998). These data largely support our findings. Although, developmental time of immature stages was consistent with our data at the range of 12–25 °C, it diverged at 25–32 °C. These differences can be caused by a series of factors such as genetic differences, geographical origin of the populations, feeding status and humidity of the areas. Zalom et al. (2014) reported that the optimal development conditions for *L. botrana* were 26–29 °C and 40–70% relative humidity. They also reported larval mortality at temperatures below 8 °C and above 34 °C similar to our findings. Higher reproductive output and higher survival rate could be expected at optimal temperatures (Savage et al. 2004; Yang & Chi 2006; Goldasteh et al. 2009; Ranjbar- Aghdam et al. 2009). Hence, the temperature of 25 °C was the best among the studied temperatures on the basis of GRR, $R_0$, and $r_m$.

An anisomorphy was observed in development at different temperatures. Lower temperatures benefit the larvae to complete development sooner and spend more time as pupae. On the other hand, the *L. botrana* encountering hot summers stay as larvae longer and have a delayed pupation. This may be due to natural respect of incidence of each developmental stage. It means larvae which experience lower temperatures in spring, favour from cold conditions, whereas pupae that appear later in the season, experience higher temperatures; hence, they are more adapted to warmer conditions.

Our study revealed that the sex ratio of *L. botrana* tends to be male-biased except for optimal temperature. The sex ratio reported by Thiery et al. (2014b) was 0.48 at 24 °C which confirms our results. It may be the case that females are the calling gender and the males need to fly and orient themselves towards female pheromones, so the lower temperatures may prevent successful mating. The males may have to wait longer to get a chance for successful mating and this may decrease survival prior to mating. So, it may act as a selective pressure to select the females to produce a higher number of male offsprings. At optimal temperatures however, such a pressure disappears and the females gain higher fitness by producing more daughters. This hypothesis must be confirmed by further studies in the future.

A similar pattern of combined types I and III survivorship curves in Slobodkin (1962) classification was observed in all temperatures. It means a higher initial mortality in cohort life followed by a higher survival up to senescence and then a gradual increase in deaths (Southwood & Henderson 2000; Schowalter 2006; Damos 2012; Sule et al. 2012). Initially higher mortality may be due to the stress caused by intensive crowding of the larvae that may confuse their movement and host location (Ifoulis & Savopoulou-Soultani 2006; Sciarretta et al. 2008; Thiery et al. 2014b).

In this research, we compared the jackknife and bootstrap resampling techniques. Both techniques are used to estimate mean, variance and standard error of PP (Meyer et al. 1986; Oyeyemi 2008; Ebrahimi et al. 2013; Jha et al. 2014). As mentioned earlier, standard error of both methods were very close. Also the mean estimates were very close to the reference cohort. These findings may imply both methods have the same value in parameter estimations. However, bootstrap technique separates significant minor
differences more distinctly; a result previously obtained by Meyer et al. (1986). The reason is being higher number of replications in bootstrap compared to jackknife technique. It can be expected that the jackknife estimates of life history parameters of a cohort as large as 100 or more individuals has the same results in mean comparisons because when df tends to infinity, the critical $t$-value approaches constant value of 1.96 for $\alpha = 0.05$ and 2.58 for $\alpha = 0.01$. This is the situation observed in the current study ($n = 120$ or 130 for jackknife estimates). In small cohorts, however, such a difference may be considerable. That is why Meyer et al. (1986) and Oyeyemi (2008) preferred jackknife over bootstrap technique. In their opinion, bootstrap underestimates SE values only due to repeated sampling from a small universe many times. As a result, minor differences are shown as significant. Although Meyer et al. (1986) and Oyeyemi (2008) claimed jackknife is more cost-effective in computation time; with the fast advances in computer technology, computation time is no longer a matter of concern. In contrast, other scientists questioned the validity of jackknife estimates (Huang & Chi 2012a, 2012b; Ebrahimi et al. 2013; Jha et al. 2014). Meyer et al. (1986) also consider bootstrap as a superior procedure in circumstances where the data deviate from normality considerably.

Our results support similar efficiency of both methods in uncertainty estimates in large cohorts. However, a definite statement needs handling a large enough data on life history with different sample sizes and different characteristics of survivorship curves. Frequency distribution of the jackknife pseudo-values of most parameters revealed significant discrepancies from a normal population. The bootstrap means however had normal distributions. This is a known principle in statistics that the sample means taken even from non normal populations tend to approach normality. This is known as the central limit theorem (Zar 1984). In this sense, jackknife pseudo-values resembles identities measured for whole members of a small universe. Each bootstrap replication is a random sample taken from this universe. Finally, repeatedly sampling many times gives a population of means with a normal distribution. Because sampling is done with replacement, population of means is an infinite population. In spite of non-normal nature of jackknife pseudo-values, this may imply the means obtained from random samples follow normal distribution and one must not be worried on the results of statistical analysis and comparison of means because means are normal anyway).

As a conclusion, the effect of temperature was studied on demographic parameters of L. botrana. The results were used for prediction of natural events in the regional vineyards of Iran. Results revealed that 25 °C is preferable temperature for L. botrana and reproduction occurs only in the range of 20–30 °C. June is the best time for L. botrana and a three generation population would be expected in our study area. Also cold storage may restrict insect activity in stores, although immature development may continue in a wider range of temperature (10–32 °C). Hot summers also may restrict natural populations. It was shown that jackknife and bootstrap techniques of uncertainty estimates in reproductive-life tables lead to the same results and, no major difference may be found between these estimates. It was found that small sample sizes may be the main source of difference between the two methods and if one takes a sample large enough, difference might be disappears.

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