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Life table parameters and development of *Aphis nerri* (Hem.: Aphididae) at five different temperatures under laboratory conditions

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Abstract

An investigation was carried out to study the life history of *Aphis nerri* Boyer de Fonscolombe on oleander, *Nerium oleander* L., under laboratory conditions (RH of 70 ± 5% and a 16: 8 (L: D) h photoperiod) based on the age-stage, two-sex life table at 10, 15, 20, 25 and 30 ºC. Duration of total pre-adult stages was 35.61 ± 0.833, 19.6 ± 0.343, 12.02 ± 0.243, 9.12 ± 0.182 and 7.42 ± 0.115 days at 10, 15, 20, 25 and 30 ºC, respectively. As temperature increased, the developmental time and longevity of the *A. nerri* shortened. The shortest developmental time (17.72 ± 0.244 days) and longevity (10.3 ± 0.234 days) were obtained at 30 ºC. With decreasing temperature, age-stage survivorship (l_x) extended. Maximum fecundity of females was observed at 25 ºC with 25.54 ± 0.76 nymphs per female. The intrinsic rates of increase (r) at these temperatures were 0.012 ± 0.0014, 0.075 ± 0.0016, 0.13 ± 0.001, 0.23 ± 0.003 and 0.24 ± 0.003 d^{-1}, respectively. The highest net reproductive rate (R_0) was at 25 ºC (25.56 ± 0.73) and the lowest value was at 10 ºC (2.58 ± 0.28). According to our results, 25-30 ºC were the optimum temperature range for *A. nerri* population growth.
Key words: life table, *Aphis nerri*, temperature, oleander, development

چکیده

پارامترهای جدول زندگی و رشد و نمو شته *Aphis nerri* (Hem.: Aphididae) در پنج دمای مختلف در شرایط آزمایشگاهی

مریم آل عصفور و لیدا فکرت

پارامترهای جدول زندگی شته خرزهره، *Aphis nerii* Boyer de Fonscolombe، روی گیاه خرزهره، *Nerium oleander* L.، در پنج دمای ۱۰، ۱۵، ۲۰، ۲۵ و ۳۰ درجه سلسیوس در شرایط آزمایشگاهی (دوره نوری ۸ :۱۶ روشنایی: تاریکی و رطوبت نسبی ۵±۷۰ درصد) مورد بررسی قرار گرفت. مدت زمان نشو و نمای مراحل نابالغ در دمای ۱۰، ۱۵، ۲۰، ۲۵ و ۳۰ درجه سلسیوس، به‌ترتیب ۰/۸۳۳ ± ۳۵/۶۱، ۰/۳۴۳ ± ۱۹/۶، ۰/۲۴۳ ± ۱۲/۰۲، ۰/۱۸۲ ± ۹/۱۲ و ۰/۱۱۵ ± ۷/۴۲ روز به‌دست آمد. با افزایش دما، طول دوره رشدی و طول عمر شته خرزهره کاهش یافت. کوتاه‌ترین طول دوره رشد (۰/۲۴۴ ± ۱۷/۷۲ روز) و طول عمر حشره (۰/۲۳۴ ± ۱۰/۳ روز) در دمای ۳۰ درجه سلسیوس مشاهده شد. با کاهش دما، نرخ زنده‌مانی ویژه سن- مرحله (l_x) افزایش یافت. بیش‌ترین میزان باروری ماده‌ها (۰/۷۶ ± ۲۵/۵۴ پوره/ماده) در دمای ۲۵ درجه سلسیوس مشاهده شد. نرخ رشد ذاتی جمعیت (r) در این دماها به‌ترتیب ۰/۰۰۱۴ ± ۰/۰۱۲، ۰/۰۰۱۶ ± ۰/۰۷۵، ۰/۰۰۱ ± ۰/۱۳، ۰/۰۰۳ ± ۰/۲۳ و ۰/۰۰۳ ± ۰/۲۴ بر روز به‌دست آمد. بیش‌ترین نرخ خالص تولید مثل (R_0) در دمای ۲۵ (۰/۷۳ ± ۲۵/۵۶) و کم‌ترین میزان آن در دمای ۱۰ درجه سلسیوس (۰/۲۸ ± ۲/۵۸) به‌دست آمد. براساس نتایج این پژوهش، دمای بهینه برای رشد جمعیت *A. nerii*، ۳۰-۲۵ درجه سلسیوس می‌باشد.

واژگان کلیدی: جدول زندگی، *Aphis nerri*، دما، خرزهره، نمو

Introduction

Understanding the ecology of a pest by estimating its growth parameters and reproduction potential, is a fundamental step in designing a successful pest management program to combat it (Soroushmehr *et al.*, 2008). Comprehensive and valuable information about developmental time, survival rate, fecundity and life expectancy of a population can be obtained from life table studies. Furthermore, using this method gives us the opportunity for projecting the growth of population and predicting the size of it (Chi, 1990; Southwood & Henderson, 2000).

Investigating the influence of temperature on the reproduction, fertility and longevity of *Aphis nerii* Boyer de Fonscolombe improves our knowledge about population dynamics of this aphid and helps us in planning more effective control strategies for its management. So, in order to comprehend assessment of the development and reproduction of *A. nerri* on oleander, life history data at five different temperatures were analyzed based on the age-stage, two-sex life table theory (Chi & Liu 1985; Chi, 1988).

Material and methods

Insect culture

Leaves bearing adults and different instars of *A. nerri* were collected from oleander shrubs at the

College of Agriculture, Shiraz University and kept in a growth chamber at 25 ± 1 ºC, 70 ± 5% relative humidity (RH) and a photoperiod of 16: 8h (L: D). Before aphids were used in the experiments, they had been reared for 2-3 generations in the laboratory (Kindlmann & Dixon, 1989).

Developmental time and mortality

In order to calculate life table parameters, some apterous females were randomly selected from the stock culture and transferred onto excised oleander leaf disks placed upside down in Petri dishes (8 cm diameter). After 24 hr, in order to establish one nymph per each oleander leaf disk, leaf disks were examined and the new-born oleander aphid nymphs were transferred gently with a fine brush on new oleander leaf disks in Petri dishes over a wet filter paper. Those replications in which nymphs died within 24 h after transfer or were lost during the experiment were removed. One opening (2 cm in diameter) had already been made on the lid of each Petri dish that was covered by nylon mesh for ventilation and to prevent possible escapes. The Petri dishes were secured using parafilm. The filter papers in the Petri dishes were dampened daily, and aphid nymphs were transferred to fresh oleander leaf disks every two days.

Experiments were conducted at five constant temperatures ranging from 15 to 30 ± 1 ºC in 70 ± 5 % RH and 16 h of artificial light in temperature cabinets. With daily observation of immature stages at all temperature regimes, nymphal development and survivorship was recorded. To determine molting time, the presence of discarded exuviae was used. When immature nymphs became adults, their survival and reproduction were observed daily and all new-born nymphs were removed from each leaf disk after counting. For each adult aphid, survival, mortality and number of produced nymphs were recorded daily. These observations were continued until the death of all mature aphids in all treatments. Each experiment was replicated 60 times for each temperature. Data of developmental time at different temperature were analyzed based on the concept of linear thermal summation (Arnold, 1959).

Life table parameters

Raw data on developmental time, survivorship, longevity and female fecundity were analyzed based on the age-stage, two-sex life table theory (Chi & Liu, 1985; Chi, 1988; Yu *et al.*, 2013) using TWOSEX-MSChart computer program (Chi, 2013). The age-stage specific survival rate (s_{xj}) (x = age and j = stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the life table parameters (the intrinsic rate of increase (r); the finite rate of increase (λ);the net reproductive rate (R_0); the mean generation time (T); the adult pre-oviposition period (APOP); and the total pre-oviposition period (TPOP) were calculated accordingly.

The intrinsic rate of increase (r) was determined by iteratively solving the Euler-Lotka equation with age indexed from 0 (Goodman, 1982):

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

The finite rate of increase (λ) and R_0 were calculated as follows:

$$\lambda = e^r$$

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

The mean generation time (T) is then calculated using the following equation:

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

Statistical analysis

Data on nymphal development times, adult life span, fecundity and daily reproduction at five constant temperatures were analyzed using ANOVA (SPSS Inc., 2012) and treatment differences were determined by Tukey's studentized Range Test. The bootstrap technique was used to estimate the means, variances,

and standard errors of the population parameters (Efron & Tibshirani, 1993). As bootstrapping uses random resampling, a small number of replications will generate variable means and standard errors. To generate less variable results, 10,000 replications were used in this study (Huang & Chi, 2013). Differences among populations reared on different temperatures were compared by Kruskal-Wallis procedure in R software (R Development Core Team, 2011). Multiple comparison tests among treatments followed by Kruskalmc program in that software. Drawings were done using SigmaPlot software (SigmaPlot, 2011).

Results

In this study, the oleander aphid completed development and produced offspring at all tested temperatures on oleander plants. The mean developmental times decreased with increase in temperature (table 1). The mean and standard errors of the developmental periods for each immature, pre-adult and adult stage, and the total longevities are given in table 1. The developments of pre-adults and adult developmental times were significantly faster at 30 ºC. The longest pre-adult developmental period was 35.61 days at 10 ºC, while the shortest was 7.42 days at 30 ºC (F = 817, df = 4, *P* = 00001) (table 1); in other words, the average time required to develop from first instar nymph (N_1) to adult stage at 30 ºC was less than a quarter of the time required at 20 ºC and almost two days shorter than that of 25 ºC. There were significant differences among total longevities at different temperatures (F = 35385, df = 4, *P* = 00001), and longevity decreased with increasing temperatures at the range of 10 (77.86) to 30 ºC (17.72).

The APOP (adult pre-reproductive period), TPOP (total pre-reproductive period), female longevity and fecundity are listed in table 2. There was a similar trend between temperature and different reproductive parameters, i.e. adult pre-reproductive period (F = 1316.55, *P* = 0.0001), total pre-reproductive period (F = 1691.95, *P* = 0.0001) and female longevity (F = 138.46, *P* = 0.0001) (table 2); shorter durations observed at higher temperatures. As presented in table 2, the lowest values for total pre-reproductive period were observed at 30 (7.78 ± 0.14) and 25 ºC (9.44 ± 0.194).

There were significant differences in developmental times and in general the developmental rate increases with the temperature (table 3). To complete the development, all nymphal stages needed similar thermal summation, ranged from 43.8 to 48.9 degree-days. An extraordinary linear relationship, as high as 0.9974, was observed between the TPOP and the coefficient of determination (R^2). On the contrary, the APOP showed a much weaker relationship to temperature.

The temperature had tremendous and significant effects on female fecundity (F = 142.39, *P* = 0.0001); with increasing temperature, fecundity reached the highest value (25.56 ± 0.76) at 25 ºC, and then decreased at 30 ºC (18.46 ± 0.88). Age-stage survival rates of *A. nerri* at different temperatures are plotted in fig. 1. The age-stage survival curve depict the survival probability of an individual to get to age *x* and stage *j*. The first nymphal instar mortality can also be seen in fig. 1, where the survival rate to age *x* is approximately 83%. These curves also show the survivorship and stage differentiation, as well as the variable developmental rates. For example, the probability that a new-born nymph survives to the adult stage at 10 ºC is 0.88. Variation in developmental rates among individuals cause some overlap between different stages (fig. 1). Construction of survival curve based on means of each stage or adult stage (Marcic, 2003; Legaspi, 2004; Tsoukanas *et al*., 2006) results in no stage overlap and causes errors in both survival and fecundity curves (Huang & Chi, 2012).

At lower temperatures, individuals survived longer in comparison with higher temperatures. It is also evident from developmental time of pre-adults and longevity of adults (table 1).

The age-specific survival rate (l_x), the age-specific fecundity (m_x), and the age-specific maternity ($l_x m_x$) are depicted in fig. 2. The probability that a new-

born will survive to age *x* is depicted with age-specific survival rate curve. Variable developmental rates among individuals of *A. nerri* stages result in curves with significant overlaps between stages. These overlaps suggest that all individuals do not complete their development simultaneously at the same day. The curve of l_x is a simplified version of the curves in fig. 1. It seems that at five constant temperatures, the adult survival pattern belong to survival cure Type I. The first oviposition at 10, 15, 20, 25 and 30 ºC occurred on day 35, 7, 7, 7, 7, respectively. For these temperatures, the maximum value of m_x was observed on day 43 (28 nymphs), 31 (59 nymphs), 20 (74 nymphs), 11 (211 nymphs), and 10 (175 nymphs), respectively. The first death of adults started on day 24, 28, 21, 14 and 13, for the above mentioned temperatures, respectively.

The fig. 3 shows the age-stage life expectancy (*exj*) curve. This curve reports the life span that an individual (age *x* and stage *j*) is expected to live after age *x* at different temperatures. The life expectancy of the first nymphal instar at 10, 15, 20, 25 and 30 ºC was 77.86, 56.68, 32.60, 22.74 and 17.72, respectively. The maximum life expectancy of *A. nerii* was 77.86 days at 10 ºC (fig. 3). Because our study was conducted in laboratory conditions, with aging at all temperatures, a monotonous decrease trend was observed in life expectancy of *A. nerii* (fig. 3). In other words, increasing the temperature decreases the age-stage specific life expectancy. The life expectancy based on age-stage, two-sex life table distinguishes the difference among individuals of the same age but of different stages.

The contribution of an individual of age *x* and stage *j* to the future population is described with the age-stage reproductive value (v_{xj}) (fig. 4). If the pre-reproduction period is counted as time from birth to first reproduction in females (TPOP), the mean TPOP for *A. nerii* females at 10, 15, 20, 25 and 30 ºC was 66.95 + 1.257, 22.82 + 0.539, 13.78 + 0.310, 9.44 + 0.194 and 7.78 + 0.140, respectively (table 2). These values are close to the age of peak reproductive value (fig. 4).

The finite rate of increase equals to the reproductive value of a new-born (v_{01}) (Huang & Chi, 2012). Once adult female emergence starts, the reproductive value increases dramatically (fig. 4). The major peaks in reproductive values of females were at the age of 60 days (v = 2.4), 25 days (v = 5), 16 days (v = 7)10 days (v = 11) and 9 days (v = 9) at 10, 15, 20, 25 and 30 ºC, respectively.

Life table parameters

The intrinsic rate of increase (r), the finite rate of increase (λ), the gross reproductive rate (*GRR*), the net reproductive rate (R_0) and the mean generation time (T) of *A. nerii* are shown in table 4. There were significant differences for the effect of different temperatures on mentioned parameters (table 4). As the temperature increased, the intrinsic rate of increase (r) and the finite rate of increase (λ) increased, and peaked at 30 ºC. The lowest value for r was observed at 10 ºC. The highest value for r was found at 25 and 30 ºC and resulted in the shortest mean generation time (T). By contrast, with increasing the temperature, the mean generation time (T) decreased from 77.37 days at 10 ºC to 12.03 days at 30 ºC (table 4).

Discussion

Temperature is an important abiotic factor that affects growth, development and reproduction of aphids (Campbell & Mackauer, 1975; Eastop, 1977). In the current study, oleander aphid developed successfully over the temperature range of 10-30 ºC. Conti *et al.* (2010) studied the effect of temperature on reproduction and fertility life table of three aphid species and determined the most favorable temperature for their reproduction. The effect of temperature on biological parameters of rose aphid, *Macrosiphum rosae* (L.), was studied by Mehrparvar & Hatami (2007). They found the shortest developmental time at 25 ºC and the longest at 15 ºC. In both studies, the developmental time depended on the environmental temperature and with increasing the temperature until a threshold (optimal temperature), the developmental

period was decreased. These results are in agreement with the present results. Kuo & Chiang (1999) reported the effect of temperature on developmental time of oleander aphid on blood-flower, *Asclepias curassavica* L., at seven constant temperatures varying from 5 to 35 ºC, and estimated the low developmental threshold as -0.46 ºC for the fourth nymphal stage. We recalculated the low developmental threshold by using their data (Kuo & Chiang, 1999, table 1) and noticed that they included the data of 35 ºC in linear regression analysis. Because their data at 35 ºC was obviously deviated from the concept of linear thermal summation, the low developmental threshold as -0.46 ºC was an incorrect estimate with a low coefficient of determination (R^2 = 0.7494).

The mean pre-reproductive, reproductive and post-reproductive periods and the longevity of oleander aphids decreased with increasing temperature (table 2). The same trend was reported by Mehrparvar & Hatami (2007) for rose aphid. The significant linearity of TPOP at different temperatures showed that TPOP is a much better parameter for the description of the time length from birth to first oviposition as pointed by Gabre *et al*. (2005).

In the present work, the mean number of fecundity reached its highest value at 25 ºC (25.54 ± 0.76). This result suggests that 25 ºC is the optimal temperature for reproduction.

Under a given set of conditions, population growth is indicated well using life cycle parameters. In the present study, the highest values for *r* were 0.23 and 0.24 at 25 ºC and 30 ºC, respectively. Maximum fecundity was observed at 25 ºC and the observed r_m value correlated with it. Furthermore, we obtained maximum values for *GRR* and R_0 at 25 ºC (table 4). According to these results we can conclude that 25 ºC was the optimum temperature for *A. nerri* population growth. Kuo & Chiang (1999) reported the highest value for *r* at 25 ºC (0.1463). This value is slightly lower than that presented in this study. The difference could be due to the traditional use of age-specific life table of Birch's method by Kuo & Chiang (1999) who ignored the variable developmental rate among individuals. In general, significant effects of temperature on the development and survival of *A. nerri* was confirmed again in the present study.

Generally speaking, environmental conditions, as well as host plants, have tremendous effects on life table studies and as a result, life table construction and its application in pest management programs seems to be very tedious and unsatisfactory process; but planning a successful and environmental friendly pest management strategy is impossible without the basic and solid knowledge of life table and therefore, construction of life tables on different target pests, especially economically important ones, and their application in control programs are undoubtedly worth pursuing.

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Table 1. Mean developmental time and standard errors (in parentheses) of each life stage, and total longevity of *Aphis nerii* at different temperatures.

Temperature	Nymph 1	Nymph 2	Nymph 3	Nymph 4	Adult	Pre-adult	Total longevity
10	7 (0.339)	8.44 (0.419)	9.44 (0.316)	10.63 (0.568)	47.24 (2.523)	35.61 (0.833)	82.85 (3.609)
15	3.64 (0.213)	4.28 (0.134)	5.22 (0.181)	6.46 (0.190)	37.08 (1.783)	19.6 (0.343)	56.68 (1.909)
20	3 (0.099)	2.94 (0.129)	3.06 (0.088)	3.02 (0.116)	20.58 (0.403)	12.02 (0.243)	32.6 (0.529)
25	1.9 (0.082)	2.62 (0.140)	2.28 (0.064)	2.32 (0.067)	13.62 (0.379)	9.12 (0.182)	22.74 (0.412)
30	1.86 (0.05)	1.8 (0.057)	1.86 (0.051)	1.9 (0.043)	10.3 (0.234)	7.42 (0.115)	17.72 (0.244)

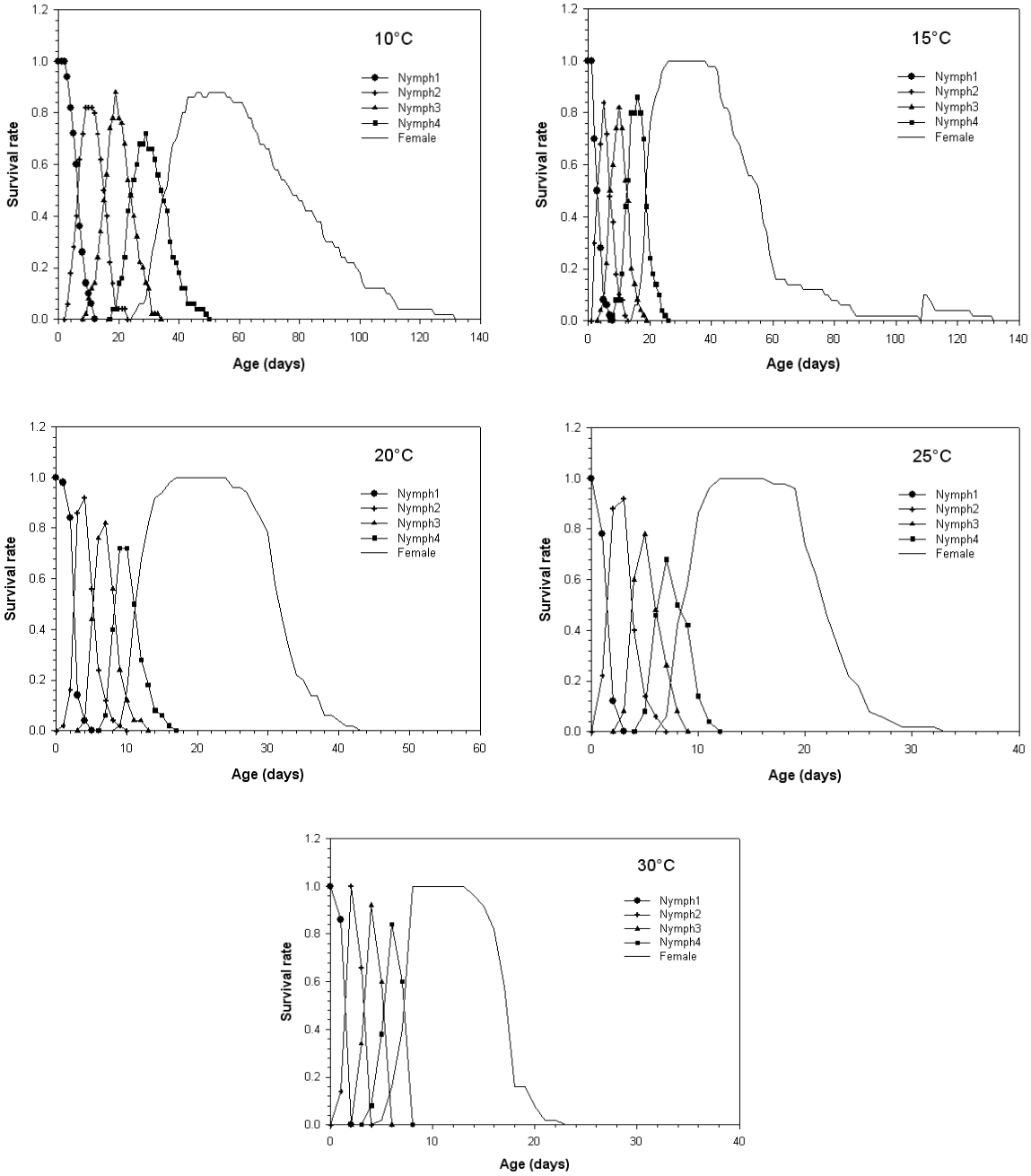

Fig. 1. Age-stage survival rate (s_{xj}) of *Aphis nerii* at different temperatures.

Table 2. Means and standard errors (in parentheses) of adult pre-oviposition period, total pre-oviposition period, female longevity and mean fecundity of *Aphis nerii* at different temperatures.

Temperature	Adult Pre-reproductive period (APOP)	Total pre-reproductive period (TPOP)	Female longevity	Fecundity
10	30.88 (0.671)	66.95 (1.257)	82.85 (3.609)	2.8 (0.301)
15	3.22 (0.393)	22.82 (0.539)	56.68 (1.909)	14.4 (0.920)
20	1.76 (0.218)	13.78 (0.310)	32.6 (0.529)	18.76 (0.580)
25	0.32 (0.066)	9.44 (0.194)	22.74 (0.412)	25.54 (0.760)
30	0.36 (0.074)	7.78 (0.140)	17.72 (0.244)	18.46 (0.880)

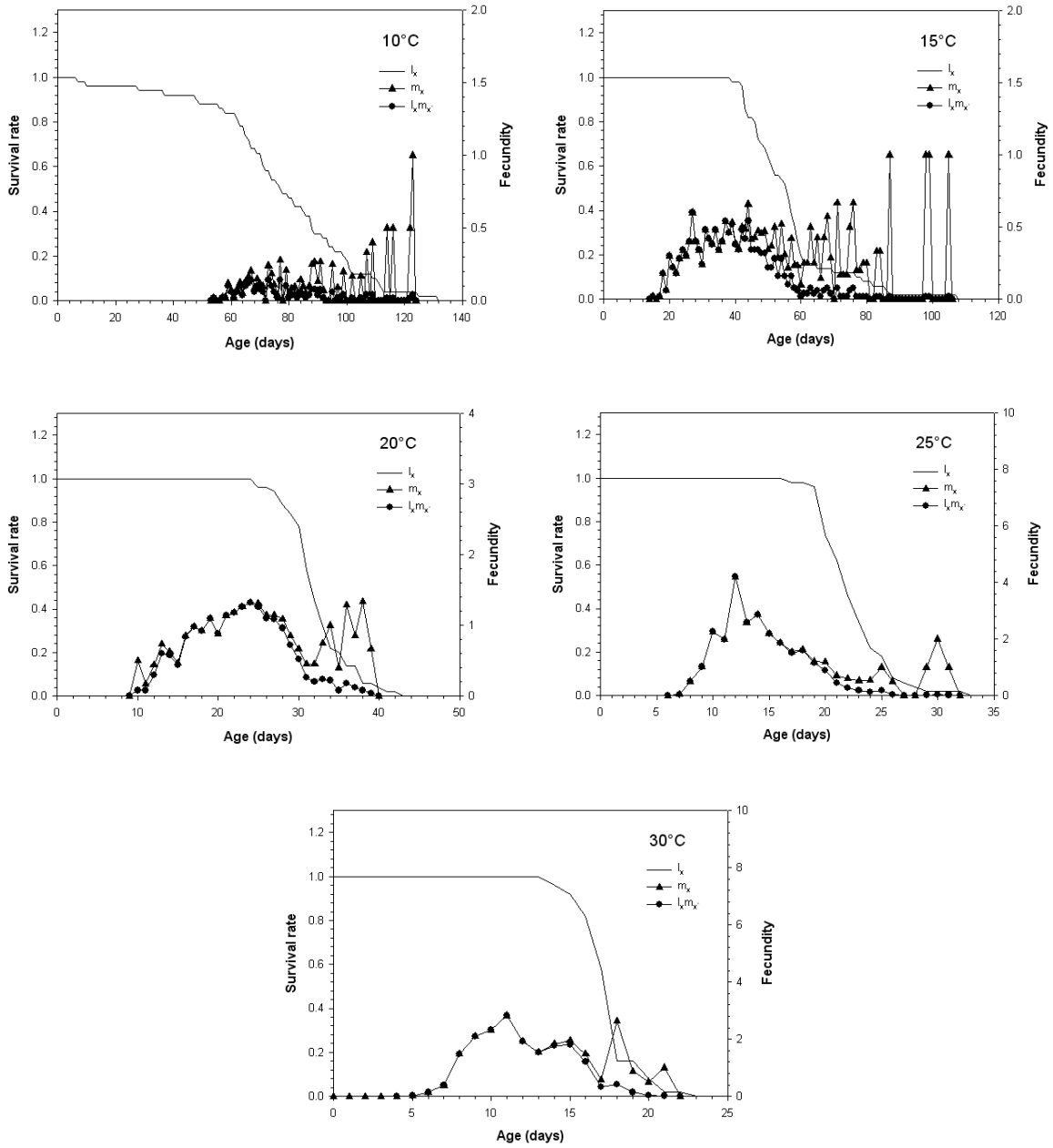

Fig. 2. Age-specific survival rate (l_x), age-specific fecundity (m_x), age-specific maternity (l_xm_x) of *Aphis nerii* at different temperatures.

Table 3. Thermal summation (K) and lower developmental threshold (T_0) of *Aphis nerii* at different temperatures calculated based on the concept of linear thermal summation.

Developmental stage	Regression equation	K (degree-day)	T_0 (ºC)	R^2
First instar nymph (N1)	y = -0.053485 + 0.020823x	48.0	2.57	0.9483
Second instar nymph (N2)	y = -0.082972 + 0.020444x	48.9	4.06	0.9712
Third instar nymph (N3)	y = -0.124066 + 0.022209x	45.0	5.59	0.9960
Fourth instar nymph (N4)	y = -0.148819 + 0.022814x	43.8	6.52	0.9816
Total pre-adult	y = -0.027459 + 0.005440x	183.8	5.04	0.9978
TPOP	y = -0.042564 + 0.005786x	172.8	7.36	0.9974
APOP	y = -1.959311 + 0.166105x	6.02	11.79	0.8006

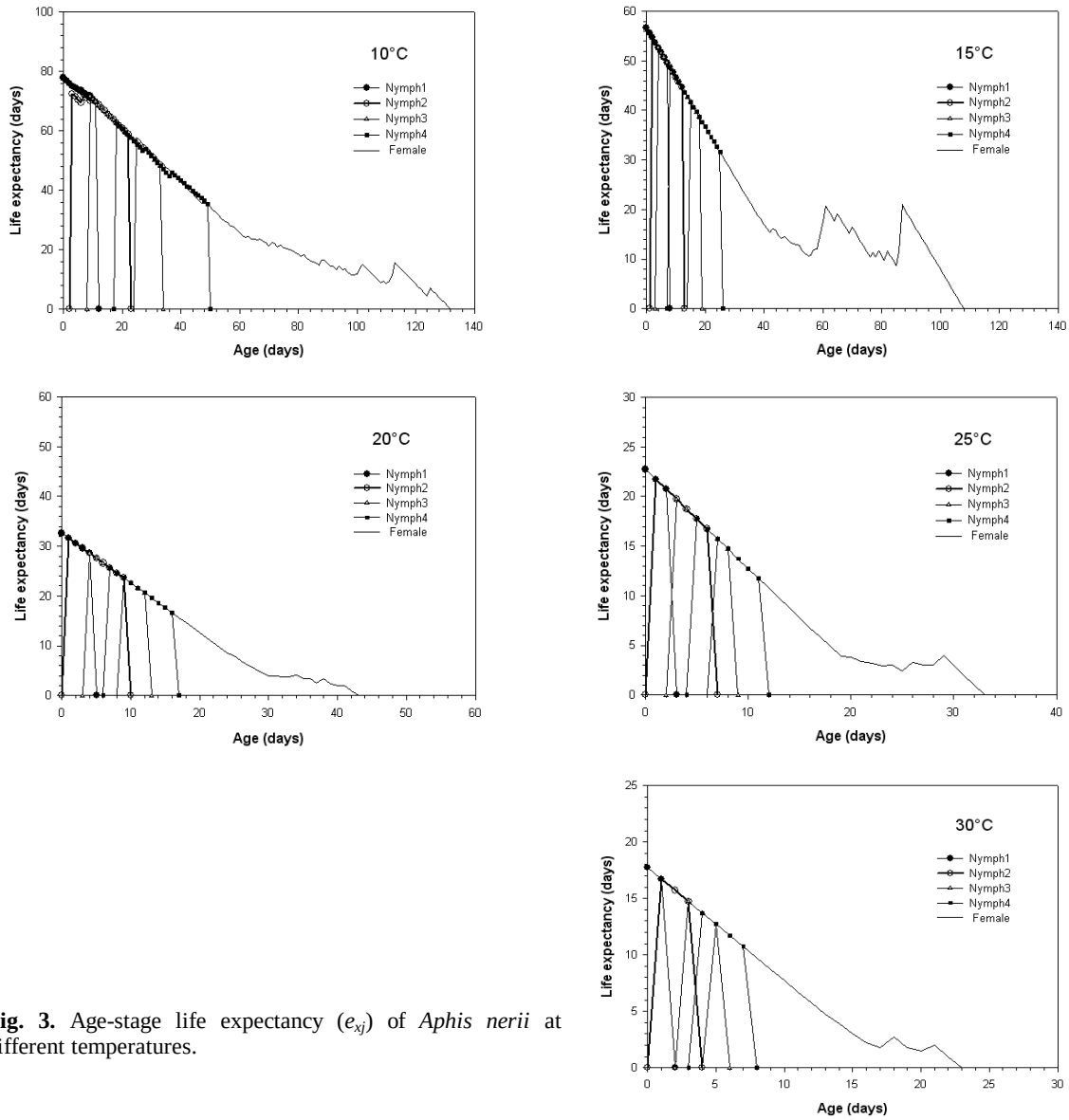

Fig. 3. Age-stage life expectancy (e_{xj}) of *Aphis nerii* at different temperatures.

Table 4. Population parameters of *Aphis nerii* at different temperatures estimated by using all individuals and bootstrap techniques. Standard errors are given in parentheses.

Param.	Temperature										Chi-square	*P*-value
	10 ºC		15 ºC		20 ºC		25 ºC		30 ºC			
	Boot. median	Boot. Mean	Boot. median	Boot. Mean	Boot. median	Boot. Mean	Boot. median	Boot. Mean	Boot. median	Boot. Mean		
R (day^{-1})	0.012 d	0.0123 (0.0014)	0.075 c	0.075 (0.0016)	0.136 b	0.13 (0.001)	0.238 a	0.23 (0.003)	0.242 a	0.24 (0.003)	47773.99	0.0001
λ (day^{-1})	1.012 d	1.012 (0.0014)	1.078 c	1.07 (0.001)	1.145 b	1.14 (0.002)	1.268 a	1.26 (0.004)	1.274 a	1.27 (0.004)	47773.99	0.0001
R_0 (Offsp.)	2.580 e	2.58 (0.28)	14.380 d	14.4 (0.94)	18.740 c	18.76 (0.55)	25.540 a	25.56 (0.73)	18.40 b	18.46 (0.84)	45738.52	0.0001
T (day)	77.250 a	77.33 (1.96)	35.318 b	35.37 (0.78)	21.551 c	21.54 (0.33)	13.983 d	13.98 (0.21)	12.029 e	12.027 (0.15)	47999.04	0.0001
GRR (Offsp.)	8.045 e	8.34 (0.975)	26.199 b	27.06 (2.30)	25.170 c	25.11 (1.40)	32.111 a	32.55 (2.42)	23.244 d	23.58 (1.60)	39948.42	0.0001

Means within a row followed by the same letter are not significantly different at the 5% confidence level according to Kruskalmc test.
Boot. = Bootstrap, Offsp. = Offspring, Param. = Parameter, *r* = Intrinsic rate of increase, λ = Finite rate of increase, R_0 = Net reproductive rate, *T* = Mean generation time, *GRR* = Gross reproductive rate.

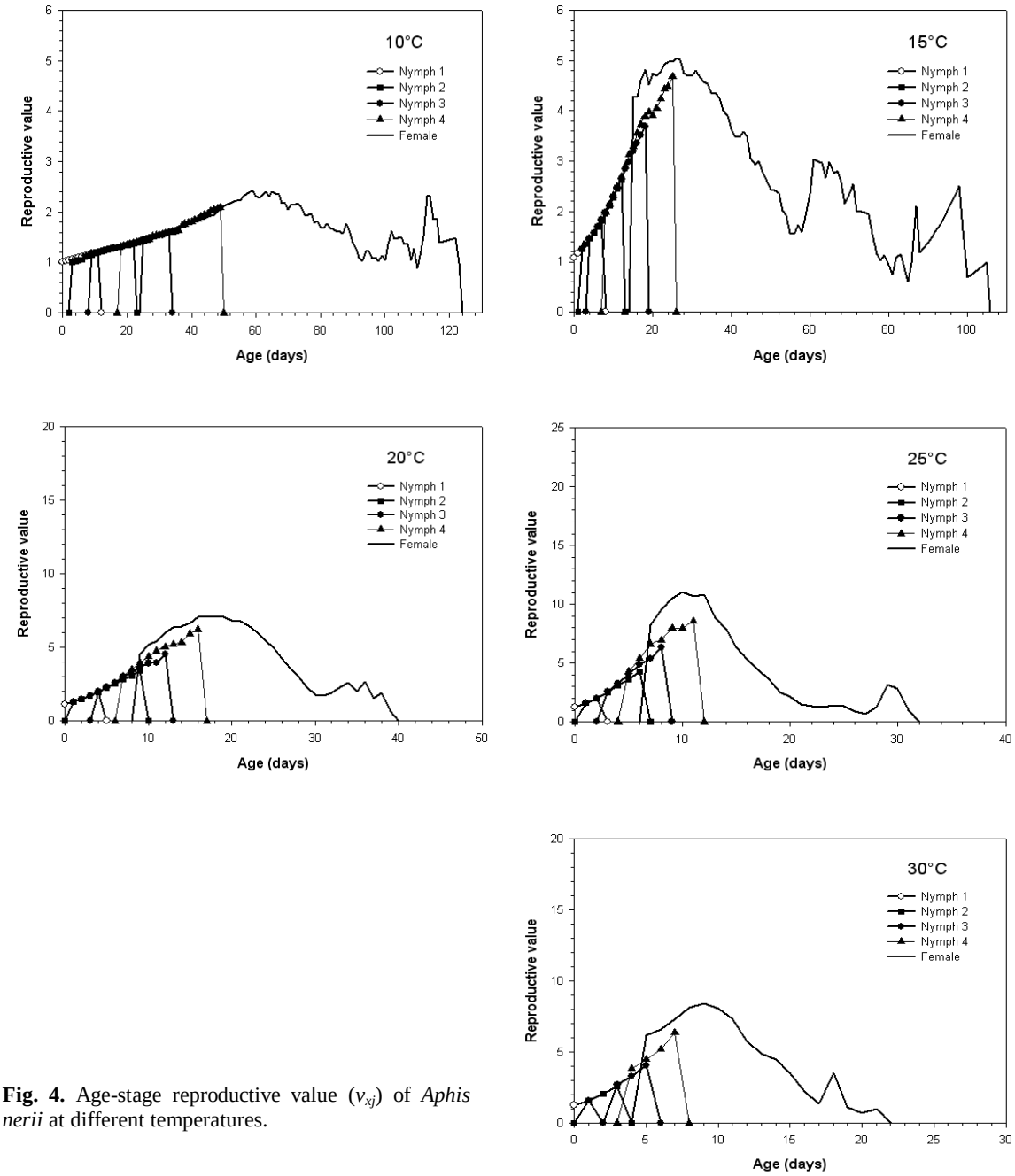

Fig. 4. Age-stage reproductive value (v_{xj}) of *Aphis nerii* at different temperatures.

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