How Different Populations and Host Plant Cultivars Affect Two-Sex Life Table Parameters of the Date Palm Hopper, *Ommatissus lybicus* (Hemiptera: Tropiduchidae)

A. Bagheri[1], Y. Fathipour[1*], M. Askari-Seyahooei[2], and M. Zeinolabedini[3]

ABSTRACT

Worldwide distribution of the Date Palm Hopper (DPH), *Ommatissus lybicus* de Bergevin along with intensive regional chemical and cultural practices to control this pest provide a basis for development of high genetic divergence. This genetic divergence can result in demographically distinct populations. In this study, the demographic parameters of three genetically diverged Iranian populations of DPH (Bam, Jiroft, and Tezerj) were determined on two date palm cultivars (Berhi and Khunizi). The age-stage, two-sex life table theory was used to unveil biological differences among these populations. All experiments were carried out in a laboratory at 27±2°C, 65±5% RH, and a photoperiod of 14:10 (L: D) hour. The results revealed significant differences in life history traits and growth parameters of different populations. The shortest development time was observed in the Bam population (75.86 and 85.03 days on Berhi and Khunizi, respectively). The highest values of the intrinsic rate of increase (*r*) and finite rate of increase (*λ*) were detected in Bam population (0.0377 and 1.0433 per day on Berhi as well as 0.0284 and 1.0288 per day on Khunizi, respectively). Based on these results, we can consider Bam as an aggressive population with higher infestation rate compared with the other populations due to its higher *r* and *λ* values as well as shorter mean generation time on both host cultivars. The significant differences in life history traits and variation in population growth parameters may suggest the presence of cryptic species among these populations. It can stem from the high genetic divergence among DPH populations which may be orchestrated by mismanagement of the pest.

Keywords: Berhi date, Demographic parameters, Dubas bug, Khunizi date, Insect population growth.

INTRODUCTION

Ecological isolation and adaptation to local conditions can result in development of geographically isolated populations of an insect or evolution of new species (Suman *et al.,* 2011; Yamaguchi and Iwasa, 2013). These populations can differ in various biological traits such as fecundity and survivorship, which give rise to variation in a range of population parameters (Suman *et al.*, 2011). In intraspecific investigations, significant genetic variability frequently has been documented by molecular markers or phenotypic traits (Benvenuto *et al.*, 2012). These intraspecific variations can also affect biological traits (Lemos-Espinal *et al.,* 2003). Intraspecific variations may be occurring when an insect has a wide geographic distribution (Liu *et al.,* 2001). As a consequence, inability to uncover different

[1] Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, P. O. Box: 14115-336, Tehran, Islamic Republic of Iran.
[*]Corresponding author; e-mail: fathi@modares.ac.ir
[2] Department of Plant Protection, Hormozgan Agricultural and Natural Resources Research Center, Bandar-Abbas, Islamic Republic of Iran.
[3] Department of Genomics, Agricultural Biotechnology Research Institute of Iran (ABRII), Karaj, Islamic Republic of Iran.

populations of insect pests or cryptic species may lead to inappropriate management efforts that could prove quite costly (Hoy, 2003; Cifuentes *et al.,* 2011; Mezghani *et al.,* 2012).

Date Palm Hopper (DPH) or dubas bug, *Ommatissus lybicus* de Bergevin (Hemiptera: Tropiduchidae), is one of the most important pests of date palm. It is distributed from Asia to Africa, where it causes severe damage to date palm trees by sucking the phloem sap and through excretion of honeydew. Both the nymphs and adults of DPH suck the sap from leaflets and midrib of fronds, which can result in direct and indirect damage. DPH is a bivoltine pest, with two distinct generations per year. It comprises many allopatric populations with specific ecological niches. A recent report has shown genetic variation within and among DPH populations (Bagheri and Fathipour, unpublished data). Moreover, an inter-cross trial of DPH populations has shown significant differences in both fecundity and egg hatchability (Bagheri and Fathipour, unpublished data).

For an economically sound integrated pest management program, a thorough knowledge of the pest is essential. An integrated and comprehensive description of development, survival, fecundity, and life expectancy of a population can be generated by life table studies (Taghizadeh *et al.*, 2008; Golizadeh *et al.*, 2009a, b). These data can often be used as a means of projecting the growth of population (Huang and Chi, 2012). Traditional female age-specific life tables only address the survivorship and fecundity of the female individuals as the indicators of population growth parameters. Therefore, they ignore stage differentiation and male effects (Chi and Su, 2006; Khanamani *et al.*, 2013). Moreover, age-stage, two-sex life table theory and corresponding methods for estimating life history parameters were developed (Chi, 1988) to include these realistic biological considerations, e.g., the differentiation of stages and the responsibility of both sexes

(female and male) in population rate (Nikooei *et al.*, 2015).

Demography of DPH has been investigated using female age-specific life tables and age-stage, two-sex life tables (Mokhtar and Al Nabhani, 2010; Payandeh *et al.*, 2010; Mahmoudi *et al.*, 2015). These studies were made using only populations of DPH from one area. Therefore, the span of life table parameters from different populations of DPH is not available. Because of the intra and inter genetic variation among DPH populations, we hypothesized that these populations could differ in their life table parameters. Therefore, the life table parameters of three diverged populations of DPH (Bagheri and Fathipour, unpublished data) were determined on two date palm cultivars.

The aims of the study were to: (1) Investigate the life table parameters of three diverged DPH populations on two date palm cultivars; (2) Determine how/when one can apply the life table results of a local population for a pest like DPH that is widely distributed, (3) Address the probability of occurrence of cryptic species among DPH populations.

MATERIALS AND METHODS

Host Plants

Two commercial date palm cultivars, Berhi (tissue culture cultivar, from Hormozgan Agricultural Organization) and Khunizi (obtained as offshoots from Hormozgan Research Center for Agriculture and Natural Resources) were used in this study. Berhi cultivar was as one year old date palms that were planted in nylon pots (Height: 23 cm; Diameter: 8 cm). Khunizi offshoots also were planted in plastic pots (Height: 33 cm; Top diameter: 28 cm; Bottom diameter: 20 cm). All the potted plants were maintained under laboratory conditions at 27±2°C, 60±5% RH, and 14:10 (L: D) photoperiod. No fertilizer and pesticide were applied.

Insect Rearing

Three populations of *O. lybicus* were obtained from the Tezerj (longitude 55°, 40' E; latitude 28°, 16' N), Jiroft (longitude 58°, 00' E; latitude 28°, 22' N), and Bam (longitude 58°, 21' E, latitude 29°, 6' N) districts of Hormozgan and Kerman provinces. Nymphs and adults of three populations were collected from infested date palm orchards by aspirator. The DPH individuals were colonized on the two potted date palm cultivars for one generation before the study commenced.

Leaflet Cages

All biological characteristics of DPH populations were measured on individuals in leaflet cages. The cage consisted of a transparent plastic cylinder (8 cm in diameter and 23 cm in height) which enclosed a single leaflet of the potted date palms. Opposing sides of each cage were covered with fine mesh gauze to allow for ventilation.

Life Table Study

Experiments were done in a laboratory at 27±2°C, 60±5% RH, and 14:10 (L: D) photoperiod. At the beginning of the studies, to obtain age-synchronized eggs of *O. lybicus*, ten to fifteen pairs of virgin DPH adults that had attained reproductive age were released in the leaflet cages for 24 hours. In total, 40 to 50 eggs were used as cohorts for the life table experiments. The eggs were checked daily and the incubation period was recorded. The emerged nymphs were transferred individually to new leaflet cages using a fine brush. Survival rate and developmental time were recorded daily for all immature stages. The presence of a black ovipositor was used to determine the sex of emerged adults (females). After emergence of adults, females were paired with males and kept together to the end of the study.

During the adult stage, daily observations were made to determine longevity, fecundity, and mortality of females and males until the death of all individuals.

Age-Stage, Two-sex Life Table

The raw life history data of all individuals (i.e., males, females and those dead before the adult stage) were analyzed according to Chi (1988). The age-stage specific survival rate (s_{xj}) (where x= Age in days and j= Stage); the age-stage specific fecundity (f_{xj}) (daily number of eggs produced per female of age x); the age-specific survival rate (l_x); the age-specific fecundity (m_x) (daily number of eggs produced per individual – i.e., the number of eggs divided by all individuals (males and females) of age x), and the population growth parameters (the intrinsic rate of increase (r); the finite rate of increase (λ) that $\lambda= e^r$; the net Reproductive rate (R_0) and the mean generation Time (T) were calculated (Khanamani *et al.*, 2013, 2015; Safuraie-Parizi *et al.*, 2014; Goodarzi *et al.,* 2015; Nikooei *et al.*, 2015). The age-specific survival rate included both males and females, and was calculated as follow:

$$l_x = \sum_{j=1}^{k} s_{xj} \qquad (1)$$

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

Where, k is the number of the stages.

The intrinsic rate of increase was estimated by using iterative bisection method from the following equation:

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

With age indexed from 0 to ω (maximum age). The net reproductive rate (R_0) was estimated as (Goodman, 1982):

$$R_0 = \sum_{x=0}^{\omega} \sum_{j=1}^{k} s_{xj} f_{xj} \qquad (4)$$

The mean generation time is the time length that a population needs to increase to R_0-folds of its size as the population reaches the stable age-stage distribution and is calculated as $T= ln\ R_0/r$.

Data analyses and population parameters (r, λ, R_0 and T) were calculated by using the

TWOSEX-MSChart program (Chi, 2015). The variance and standard errors of the population parameters were estimated by using the Bootstrap procedure (Efron and Tibshirani, 1993; Huang and Chi, 2013). Accordingly, a sample of *n* individuals was randomly taken from the cohort with replacement and the $r_{\text{i-boot}}$ for this bootstrap sample was calculated as:

$$\sum_{x=0}^{\omega} e^{-r_{i-boot}(x+1)} l_x m_x = 1 \quad (5)$$

Where, the subscript *i-boot* represents the *i*th bootstrap and l_x and m_x are calculated from the *n* individuals selected randomly with replacement. This procedure was repeated *m* times (m=10,000) and the mean of these m bootstraps was computed as:

$$r_B = \frac{\sum_{i=1}^{m} r_{i-boot}}{m} \quad (6)$$

The Variance ($VAR\ r_B$) and Standard Errors (SE r_B) of these *m* bootstraps were calculated as:

$$VAR\ r_B = \frac{\sum_{i=1}^{m}(r_{i-boot} - r_B)^2}{m-1} \quad (7)$$

$$SEr_B = \sqrt{VAR\ r_B} \quad (8)$$

The same methods were used for the corresponding estimates of the finite rate of increase (λ), net Reproductive rate (R_0), and mean generation Time (*T*). To compare the means of the life table parameters, paired-bootstrap test TWOSEX-MSChart program (Chi, 2015) was applied. One-way ANOVA was used to analyze fecundity and durations of different life stages of DPH populations. In the case of significant differences, mean comparisons were made using the Tukey-Kramer procedure (P< 0.05).

RESULTS

Life Table Parameters of DPH Populations on Berhi

Developmental time of immature stages, adult longevity, mean Adult Pre-Oviposition Period (APOP), mean Total Pre-Oviposition Period (TPOP), total lifespan and fecundity of the three populations of *O. lybicus* feeding on Berhi cultivar are shown in Tables 1 and 2. As it is shown, there were significant differences in duration of different life stages of DPH populations on Berhi. The longest and shortest egg incubation periods were observed in population isolates originating in Tezerj and Bam, respectively (F= 163.622; df= 2, 126; P< 0.0001). The longest periods of individual instars and total nymphal development were observed in the Jiroft population isolate, followed by Tezerj; the shortest nymphal periods were observed in the Bam population isolate (Table 1). Furthermore, the longest total developmental time was found in the Jiroft population, followed by the Tezerj population. The shortest developmental time was observed in the Bam population (F= 206.047; df= 2, 105; P< 0.0001) (Table 1).

No significant differences in the male adult longevities were observed in the three DPH populations, whereas the female adult longevities were significantly different (F= 6.629; df= 2, 46; P< 0.05). The longest female adult longevity occurred in the Bam population and no significant difference in female adult longevity was observed between the Tezerj and Jiroft populations (Table 2). There was no significant difference in total between the Tezerj and Jiroft populations. The total in Bam population was significantly less than Jiroft and Tezerj ones (F= 6.823; df= 2, 105; P< 0.05) (Table 2). Fecundity was significantly different among the different populations of DPH. The highest and lowest fecundity were observed in the Bam and Jiroft populations, respectively (F= 6.211; df= 2, 46; P< 0.05) (Table 2).

The detailed age-stage survival rates (s_{xj}) of the three populations of *O. lybicus* feeding on Berhi are depicted in Figure 1. The curves of age-stage survival rate (s_{xj}) show the probability that a newborn individual survives to age *x* and stage *j*. The curves depict the detailed survival and stage differentiation process of the cohort. In addition, the overlap of stages during the developmental time can be observed in Figure 1. In general, the probability that a

Table 1. Mean (±SE) duration of pre-adult stages (days) of *Ommatissus lybicus* populations on the Berhi cultivar.[a]

Population	Egg	Nymph 1	Nymph 2	Nymph 3	Nymph 4	Nymph 5	Nymphs	Pre-adult
Bam	44.04±1.29b	3.08± 0.05 c	6.08±0.06 c	6.46± 0.09 c	7.68± 0.08 c	8.93± 0.13 c	32.40± 0.27 c	75.86± 1.38 b
Jiroft	66.64±0.98a	4.56± 0.07 a	8.40± 0.12 a	7.97± 0.13 a	10.55± 0.16 a	12.02± 0.13 a	43.62± 0.43 a	109.03± 1.28 a
Tezerj	68.29±0.74a	3.55±0.10b	6.88± 0.10 b	7.34± 0.13 b	9.00± 0.16 b	10.71± 0.28 b	37.71± 0.56 b	105.54± 1.10 a

[a] The means followed by the same letter in each column are not significantly different (P< 0.05, Tukey's test).

Table 2. Mean (±SE) duration of adults, total lifespan, APOP, TPOP (days) and fecundity (eggs) of *Ommatissus lybicus* populations on the Berhi cultivar.[a]

Population	Female longevity	Male longevity	Total lifespan	APOP	TPOP	Fecundity
Bam	52.16± 4.15 a	36.81± 5.48 a	118.82± 4.20 b	9.27± 0.17 b	86.22± 2.52 c	131.66± 9.93 a
Jiroft	25.40± 5.99 b	35.65± 6.94 a	136.09± 3.54 a	9.66± 0.18 b	122.25± 1.06 a	54.40± 20.93 c
Tezerj	33.37± 6.16 b	37.33± 10.84 a	137.04± 4.19 a	11.00± 0.42 a	115.90± 0.948 b	71.43± 18.68 b

[a] The means followed by the same letter in each column are not significantly different (P< 0.05, Tukey's test).
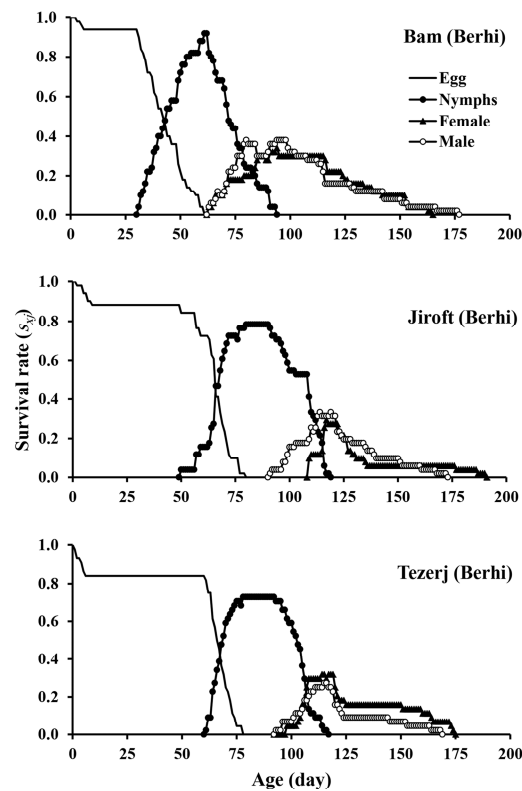APOP: Adult Pre-Ovipositional Period, TPOP: Total Pre-Ovipositional Period (from egg to first oviposition).

Figure 1. Age-stage survival rate (s_{xj}) of *Ommatissus lybicus* populations reared on the Berhi cultivar.

newly hatched DPH instar would survive to the adult stage was 0.9, 0.68 and 0.63 for Bam, Jiroft, and Tezerj populations, respectively. The survival rates of males in the Bam and Jiroft population isolates were more than that of respective females, whereas in the Tezerj isolate the survival rate of females was more than their respective males. The maximum lifespan (191 days) was observed in Jiroft population.

The APOP of the three DPH populations was significantly different on the cultivar Berhi (F= 11.554; df= 2, 38; P< 0.0001). The longest APOP was observed in the isolate from the Tezerj population. The APOP difference was not significant between the Bam and Jiroft populations (Table 2). The TPOP was significantly different in the populations (F= 96.745; df= 2, 38; P< 0.0001). The longest TPOP was observed in the Jiroft population isolates followed by individuals from the Tezerj population. The shortest TPOP was observed in individuals from the Bam population (Table 2).

The age-stage specific fecundity (f_{xj}) presents the mean number of offspring produced by the adult females at age x and stage j and, because only females produced eggs, there was only a single curve f_{xj} (x, female) (Figure 2). The start of oviposition of the first female derived from the Bam, Jiroft and Tezerj populations was observed at the age of 70, 117, and 108 days, respectively. The highest daily fecundity (peak of f (i, female)) from the Bam, Jiroft and Tezerj populations was 4.6, 9.2, and 8.8 eggs, which occurred at the age of 138, 146, and 168 days, respectively.

The curves of l_x (the age-specific survival rate of all individuals) and m_x (the age-specific fecundity of the total population) are shown in Figure 2. As seen, all *O. lybicus* populations successfully survived and reproduced on the Berhi cultivar under laboratory conditions.
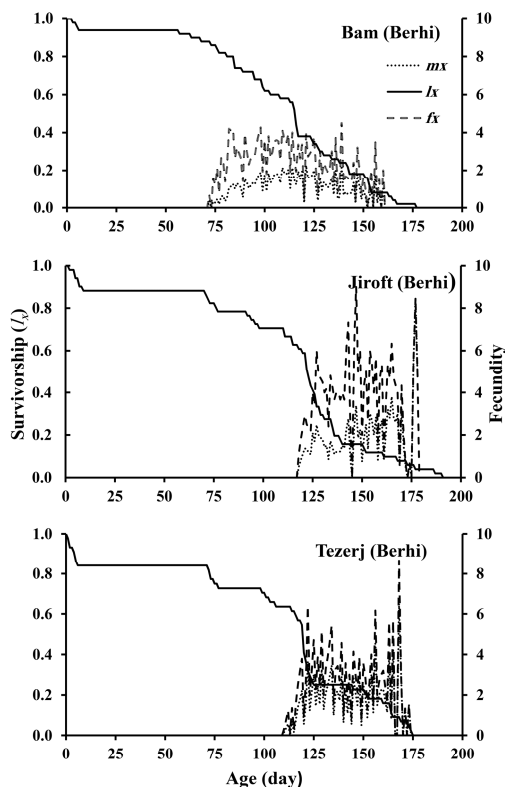
Figure 2. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Ommatissus lybicus* populations reared on the Berhi cultivar.

The population parameters of the three DPH populations are shown in Table 3. In terms of net Reproductive rate (R_0), no significant differences were observed between the Bam and Tezerj populations, as well as the Tezerj and Jiroft populations. The net reproductive rate in the Jiroft population was significantly less than the Bam population. The r and λ parameters showed differences among three DPH populations. The highest values of r and λ

were observed in Bam population (0.0377 and 1.433 per day, respectively). However, no significant difference in both these parameters was observed between the Tezerj and Jiroft populations. There was significant difference in the T parameter among these populations. Long mean generation times were found in the Jiroft and Tezerj populations. The mean generation time in the Bam population was significantly less than the Jiroft and Tezerj values.

Life Table Parameters of DPH Populations on Khunizi Cultivar

Development time of immatures, adult longevity, APOP, TPOP and fecundity of the three populations of *O. lybicus* on the Khunizi cultivar are shown in Tables 4 and 5. Life stages of the DPH populations were significantly different (F= 50.263; df= 2, 136; P< 0.0001). The longest and shortest egg incubation period were observed in the Jiroft and Bam populations, respectively (Table 4). The longest instar stages period were found in the Tezerj population, except for the second instar stage period. There was significant difference in the total instars period among three DPH populations (F= 276.037; df= 2, 109; P< 0.0001). The longest and shortest total instars periods were observed in the Tezerj and Jiroft populations, respectively (Table 4). The total developmental time for all pre-adult stages was also longest in Tezerj population followed by Jiroft population. The shortest developmental time for all pre-adult stages was observed in the Bam population (85.03 days) (F= 46.150; df= 2, 109; P< 0.0001)

Table 3. Age-stage, two-sex life table parameters of *Ommatissus lybicus* populations on Berhi cultivar.[a]

Population	R_0 (Offspring/Individual)	r (1/Day)	λ (1/Day)	T (Day)
Bam	47.36±9.60a	0.0377±0.0025a	1.0433±0.4896a	101.86±3.02b
Jiroft	16.02±6.93b	0.0187±0.0032b	1.0239±0.4998b	141.58±5.16a
Tezerj	25.93±8.31ab	0.0236±0.0026b	1.0282±0.4297b	135.55±2.75a

[a] Means in each column followed by different letters are significantly different (P< 0.05; Paired bootstrap).

Table 4. Mean (±SE) duration of pre-adult stages (days) of *Ommatissus lybicus* populations on the Khunizi cultivar.[a]

Population	Egg	Nymph 1	Nymph 2	Nymph 3	Nymph 4	Nymph 5	Nymphs	Pre-adult
Bam	41.97±1.1c	3.06±0.036b	7.91±0.042a	9.17±0.098b	10.61±0.23b	12.0±0.11b	42.81±0.35 b	85.03±1.45c
Jiroft	58.87±0.95a	3.04±0.029b	6.2±0.06c	8.77±0.12c	10.0±0.13c	11.48±0.19b	39.44±0.44 c	98.4±1.17b
Tezerj	51.06±1.47b	3.97±0.079a	7.11±0.13b	12.70±0.12a	13.47±0.12a	14.79±0.16a	51.88±0.27 a	102.88±1.31a

[a] The means followed by the same letter in each column are not significantly different ($P < 0.05$, Tukey's test).
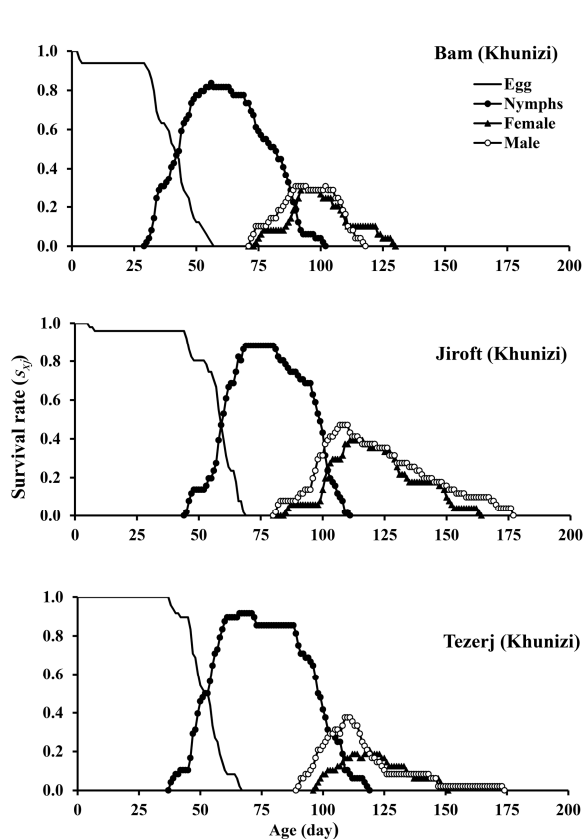
(Table 4).

The male adult longevity was significantly different in the three DPH populations ($F = 7.313$; $df = 2, 60$; $P < 0.05$). The longest male adult longevity occurred in the Jiroft population. No significant difference in male adult longevity was observed between the Bam and Tezerj populations (Table 5). The female adult longevity of the populations was significantly different ($F = 5.201$; $df = 2, 46$; $P < 0.05$). The female adult longevity in the Tezerj population was significantly less than the Jiroft population. No significant difference of female adult longevity was observed between the Jiroft and Bam populations (Table 5). The total lifespan was significantly different among the various DPH populations ($F = 33.605$; $df = 2, 109$; $P < 0.0001$). The longest and shortest total lifespan periods were observed in Jiroft and Bam populations, respectively (Table 5). No significant difference in the total fecundity occurred among the *O. lybicus* populations ($F = 1.506$; $df = 2, 46$; $P > 0.05$) (Table 5).

The detailed age-stage survival rates (s_{xj}) of the three populations of DPH on the Khunizi cultivar are presented in Figure 3. An overlap of stages during the development time can be observed. In general, the probability that a newly hatched DPH instar would survive to the adult stage on the Khunizi cultivar was 0.67, 0.88, and 0.7 for the Bam, Jiroft, and Tezerj populations, respectively. In all DPH populations, adult males had higher survival than their respective females. The maximum lifespan (179 days) occurred in the Jiroft population. The APOP was significantly different in the DPH populations on the Khunizi cultivar ($F = 7.774$; $df = 2, 43$; $P < 0.05$). The shortest APOP was observed in the Tezerj population. The APOP was not significantly different in the Bam and Jiroft populations (Table 5). The TPOP was significantly different in the populations ($F = 28.927$; $df = 2, 43$; $P < 0.0001$). The longest TPOP was observed in the Tezerj and Jiroft populations (116.33 and 111.2 days, respectively). The TPOP in the Bam population was 95.57 days, which was significantly less than the

Table 5. Mean (±SE) duration of adults, total lifespan, APOP, TPOP (days) and fecundity (eggs) of *Ommatissus lybicus* populations on the Khunizi cultivar.[a]
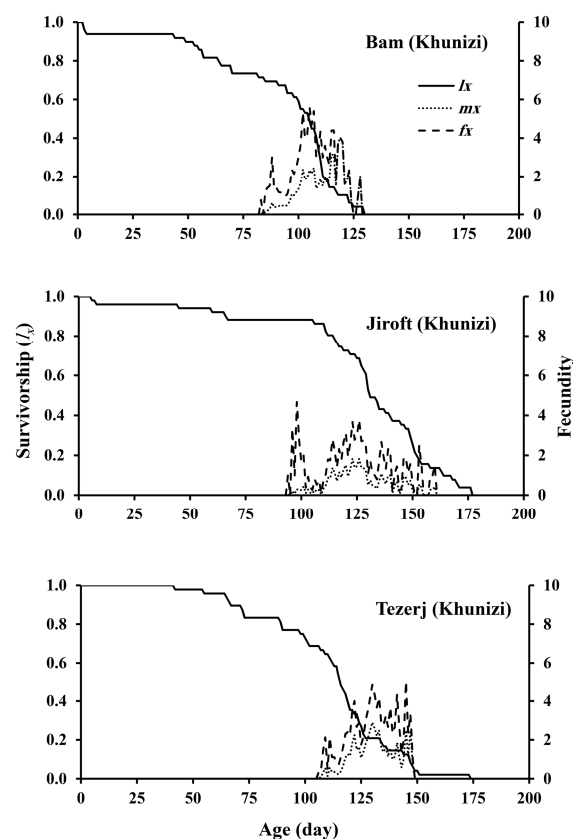
Population	Female longevity	Male longevity	Total lifespan	APOP	TPOP	Fecundity
Bam	26.26± 3.47ab	24.27± 2.89b	110.21± 1.53 c	10.07± 0.26a	95.57± 1.83b	63.26± 8.31a
Jiroft	38.45± 4.04a	42.88± 4.44a	139.31± 2.8 a	10.25± 0.23a	111.2± 1.66a	63.35± 4.81a
Tezerj	21.42± 4.07b	24.3± 4.28b	126.0± 2.69 b	9.0± 0.0b	116.33± 2.33a	44.42± 13.08a

[a] The means followed by the same letter in each column are not significantly different (P< 0.05, Tukey's test). APOP: Adult Pre-Ovipositional Period, TPOP: Total Pre-Ovipositional Period (from egg to first oviposition).

Figure 3. Age-stage survival rate (s_{xj}) of *Ommatissus lybicus* populations reared on the Khunizi cultivar.

Figure 4. Age-specific survivorship (l_x), age-stage specific fecundity (f_{xj}) and age-specific fecundity (m_x) of *Ommatissus lybicus* populations reared on Khunizi cultivar.

Tezerj and Jiroft populations (Table 5).

The start of oviposition of the first female in the Bam, Jiroft, and Tezerj populations was observed at the age of 82, 93, and 105 days, respectively. The highest daily fecundity (peak of *f* (*i*, female)) in the Bam, Jiroft and Tezerj populations was 5.8, 4.8, and 5 eggs, which occurred at the age of 105, 99, and 144 days, respectively.

The curves of l_x (the age-specific survival rate of all individuals) and m_x (the age-specific fecundity of the total population) are shown in Figure 4. All *O. lybicus* populations successfully survived and reproduced on the Khunizi cultivar under laboratory conditions.

The population parameters of the three DPH populations on the Khunizi cultivar are

shown in Table 6. As seen, there was no significant difference in R_0 parameter among the three *O. lybicus* populations. The analysis of r and λ parameters showed significant differences among populations. No significant difference was observed between the Bam and Jiroft populations. In addition, the Tezerj population was not significantly different from Jiroft, whereas it differed significantly from the Bam population in the r and λ parameters. The mean generation time (T) values of the three DPH populations were significantly different. The longest and shortest mean generation times occurred in the Tezerj and Bam populations, respectively.

DISCUSSION

Demographic parameters of the three genetically diverged DPH populations (Bam, Jiroft, and Tezerj populations) were determined on two date palm cultivars (Berhi and Khunizi) to unveil biological differences of DPH populations. Highly significant differences observed in the life table parameters of DPH populations on both cultivars may even suggest the presence of cryptic species among these populations. Considerable discrepancies in life table parameters of two populations of *Brontispa longissima* (Coleoptera: Chrysomelidae), as cryptic species, has been documented by Takano *et al.* (2013). However, according to the population growth parameters on the Berhi cultivar, there were significant differences based on the R_0, λ, r and T parameters among

populations. For instance, the highest level of λ and r was observed in Bam population which was significantly higher than Tezerj population; however, the Tezerj population had longest mean generation time (T). Almost the same pattern was detected for the growth parameters of the populations on the Khunizi cultivar in which Bam population had significantly higher levels of r and λ compared with the Tezerj population. Similar to the Berhi cultivar, the longest mean generation time (T) was observed for Tezerj population; however, no difference was observed among populations according to R_0 parameter. Interesting point in this study is a clear-cut distinction between Bam and Tezerj populations based on life history and population growth parameters; however, the Jiroft population behaved considerably different in intermediate position with some parameters close to Bam and the others close to Tezerj. According to the life table study of these three populations on the Khunizi cultivar, Jiroft population revealed no significant difference with Bam population in r and λ parameters, whereas the results were completely different for Jiroft population when we studied these parameters on the Berhi cultivar. The life table parameters including r and λ showed no significant difference between Jiroft and Tezerj populations on Berhi cultivar. In our study, the relationship between R_0 and F was consistent with the proof of Chi (1988) that $R_0 = F (Nf/N)$, where N is the number of eggs used at the beginning of life table study and Nf is the number of female adults emerged from N. If traditional female age-specific life table were used, this relationship would not

Table 6. Age-stage, two-sex life table parameters of *Ommatissus lybicus* populations on Khunizi cultivar.[a]

Population	R_0 (Offspring/Individual)	r (1/Day)	λ (1/Day)	T (Day)
Bam	19.36±4.86a	0.0284±0.0025a	1.0288±0.00261a	104.06±1.64c
Jiroft	24.84±4.69a	0.0263±0.0017ab	1.0267±0.0017ab	121.78±1.74b
Tezerj	12.95±4.70a	0.0202±0.0031b	1.0204±0.0031b	126.37±1.27a

[a] Means in each column followed by different letters are significantly different (P< 0.05; Paired bootstrap).

be observed.

Significant difference in the life table parameters is in line with the results of cross population experiment, which can be elucidated by genetic differences in these populations according to our previous studies (Bagheri and Fathipour, unpublished data). Cross experiment results showed that the number of eggs produced from the crossing between (Tezerj×Bam) was significantly lower compared with the corresponding parental crossing (Tezerj×Tezerj or Bam×Bam). Moreover, the percentage of the egg hatchability and rate of survival from nymphal into adult stage was very low in Tezerj×Bam cross trial.

Study on genetic diversity of DPH populations indicated that the genetic diversity in Jiroft population was higher than the other populations (Bagheri and Fathipour, unpublished data). For instance, different haplotypes in the Jiroft population resembled either Bam or Tezerj populations. High genetic diversity in Jiroft population may explain the intermediate position of this population and justify the flexible condition of this population in the life table studies. Along with genetic variation, another factor which might affect the life table parameters of DPH is secondary endosymbiont *Wolbachia*. This endosymbiont is capable of altering the developmental time and reproduction of its hosts (Ahantarig and Kittayapong, 2011). This can be taken into account as an additional factor because *Wolbachia*, as a most efficient symbiont, was detected in different populations of DPH in Iran (Bagheri and Fathipour, unpublished data). Another important point regarding secondary endosymbionts is their role in changing the host adaptation which, in turn, could affect feeding behavior of the insect host to utilize resistant plant hosts for feeding. For instance, secondary endosymbionts such as *Asaia* sp. can help its insect host to feed from the resistant cultivars (Tang *et al.*, 2010). As a result of *Wolbachia* detection in several DPH populations (Bagheri and Fathipour,

unpublished data), role of this endosymbiont should be considered in study of the resistant cultivars to date palm hopper.

Current results on life table parameters of Tezerj and Jiroft populations demonstrated considerable differences from previous studies conducted on DPH life table. For instance, egg incubation period in Jiroft and Tezerj populations on Berhi cultivar (66.64 and 68.29 days, respectively) was considerably longer than those reported by Mahmoudi *et al.* (2015) (ranged from 39.1 to 41.7 days in different cultivars), Payandeh *et al.* (2010) (32.41 and 30.89 days for 25 and 30°C, respectively) as well as Mokhtar and Al Nabhani (2010) (47.6 and 50.8 days for 25 and 30°C, respectively). Moreover, in comparison with the previous studies, difference in parameter of total development time was observed for the two populations of Jiroft and Tezerj on Berhi cultivar. For example, total developmental time for Jiroft and Tezerj populations on Berhi cultivar was considerably longer (109.3 and 105.54 days, respectively) compared with those reported by Mahmoudi *et al.* (2015) (ranged from 85.21 to 88.39 days relating to cultivars), Payandeh *et al.* (2010) (82.48 and 75.79 days for 25 and 30°C) as well as Mokhtar and Al Nabhani (2010) (83.9 and 88.4 days for 25 and 30°C, respectively). Almost the same pattern for two other population parameters (r and R_0) was observed for Jiroft and Tezerj populations on Berhi and Khunizi cultivars compared with the previously mentioned studies. However, the values for r and R_0 parameters in Jiroft and Tezerj populations (0.0187 and 0.0236 per day on the Berhi cultivar, respectively; 0.0263 and 0.0202 per day on the Khunizi cultivar, respectively) were considerably lower compared with the previously mentioned results.

Based on the life table of Jiroft and Tezerj populations on the Khunizi cultivar, the results were rather similar to the results obtained by Mokhtar and Al Nabhani (2010). Egg incubation period for Jiroft and Tezerj populations on the Khunizi cultivar was 58.87 and 51.06 days, respectively,

which were close to the results of Mokhtar and Al Nabhani (2010). Similar condition regarding total development time was also observed for the two populations of Jiroft and Tezerj (98.4 and 102.88 days, respectively) in relation to previous study conducted by Mokhtar and Al Nabhani (2010). In Bam population, the obtained results of the mentioned parameters (egg incubation period, total developmental time, r and R_0) were relatively close to the results reported by Mokhtar and Al Nabhani (2010).

Differences in the current results and similar studies conducted on the life table parameters of DPH unveiled the profound effect of the populations on the life table parameters. Considerable genetic variation in populations of DPH can lead to discrepancies in the results of previous studies as well as the differences observed in the current results.

In the present study, the value of r for the two populations of Tezerj and Jiroft on both cultivars was lower than the Bam population. This can be explained by the fact that r is a function of both fecundity and developmental time, as a consequence, longer developmental time in Jiroft and Tezerj populations on both Berhi and Khunizi cultivars (due to genetic differences) may impose lower r for these two populations compared with the Bam population. The findings of this study indicate that Bam is an aggressive population with higher potential to cause economic damage on the Berhi cultivar compared with Jiroft and Tezerj populations due to greater r and λ as well as lower mean generation time. Moreover, total developmental time and APOP of Bam is shorter in comparison with the other populations and can start to lay egg earlier. The same condition with minor differences was observed for Bam population on Khunizi cultivar. As expected, the Bam population revealed the lowest total developmental time and highest values of r and λ in comparison with the other two populations, showing that the Bam population is potentially an aggressive population.

These results can be considered as turning points in the way to include the effect of genetic structure of populations and genetic based variation on the life table studies. Because of long history of DPH along with the high variation in host plant and the worldwide distribution of this insect in date palm orchards, it is highly recommended to avoid generalizing results derived from studying a local population of DPH. This issue may even become worse in considering any changes in the population which may ultimately change the effect of cultivar on the biological and reproductive parameters, and because of the high variation in the date palm cultivars all over the world, the consequence becomes more complicated. Hence, in such studies, it will be important to attribute the effect of cultivar to specific population or other populations which are grouped genetically and biologically in the same category. Along with mentioned issues, several points such as lack of convergence between genetic and geographic distances in different populations of a pest should be taken into consideration when the results of life table, thermal models, and bioassay tests are used. In this context, there are various instances of pests *e.g.* DPH (Bagheri and Fathipour, unpublished data; Shabani *et al.,* 2012) with no correlation between genetic and geographical distances despite having geographically close populations. This is also true in the case of biological control, where geographically close populations of a pest's natural enemy do not have the same performance. Presence of cryptic strains has been suggested as a reason for such behavior (Ito *et al.*, 2011).

We can conclude that genetic structure of a pest population can play a key role in providing an insight for better understanding and management of the pest population to avoid mismanagement in the pest control strategy in agro-ecosystems.

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چگونی تاثیر جمعیت و رقم گیاه میزبان بر پارامترهای جدول زندگی دوجنسی زنجره خرما *Ommatissus lybicus* (Hemiptera: Tropiduchidae)

ع. باقری، ی. فتحی پور، م. عسکری سیاهویی، و م. زین العابدینی

چکیده

پراکنش جهانی زنجره‌ی خرما، *Ommatissuslybicus* de Bergevin، در کنار منطقه‌ای بودن عملیات کشاورزی و استفاده‌ی زیاد از آفت‌کش‌ها برای کنترل این آفت، باعث فراهم شدن شرایط لازم برای به وجود آمدن واگرایی ژنتیکی شدید آن شده است. این واگرایی ژنتیکی میان جمعیت‌های یک آفت می‌تواند منجر به ظهور جمعیت‌هایی با پارامترهای دموگرافیک متفاوت شود. در پژوهش حاضر، پارامترهای دموگرافیک سه جمعیت کاملاً واگرای زنجره‌ی خرما در ایران (جمعیت‌های بم، جیرفت و تزرج) روی دو رقم خرمای برحی و خنیزی بررسی شد. روش جدول زندگی دو جنسی با هدف مشخص نمودن تفاوت‌های بیولوژیک میان جمعیت‌های مورد مطالعه استفاده گردید. تمامی آزمایش-های مورد نظر در شرایط آزمایشگاهی در دمای ۲ ± ۲۷ درجه‌ی سلسیوس، رطوبت نسبی ۵± ۶۵ درصد و دوره‌ی نوری ۱۴ ساعت روشنایی و ۱۰ ساعت تاریکی انجام شد. نتایج به دست آمده وجود تفاوت-های معنی‌دار را در پارامترهای زیستی و رشدی جمعیت‌های مورد مطالعه نشان داد. کوتاه‌ترین طول دوره‌ی نمو روی دو رقم برحی و خنیزی در جمعیت بم با ۷۵/۸۶ و ۸۵/۰۳ روز مشاهده شد. همچنین، جمعیت بم دارای بیشترین مقدار نرخ ذاتی و نرخ متناهی افزایش جمعیت (به ترتیب ۰/۰۳۷۷ و ۱/۰۴۳۳ در روز روی رقم برحی و ۰/۰۲۸۴ و ۱/۰۲۸۸ در روز روی رقم خنیزی) بود. با توجه به نتایج موجود می‌توان جمعیت بم را به‌عنوان یک جمعیت مهاجم به دلیل بالاتر بودن مقادیر نرخ ذاتی و نرخ متناهی افزایش جمعیت و کوتاه‌تر بودن طول دوره‌ی زندگی روی رقم‌های مورد مطالعه معرفی نمود. وجود تفاوت‌های فاحش در پارامترهای زیستی و رشدی این جمعیت‌ها احتمالاً نشانه‌ای از وجود گونه‌ی مخفی در این آفت است که می‌تواند در نتیجه‌ی واگرایی ژنتیکی بین جمعیت‌های زنجره‌ی خرما و تشدید آن در نتیجه‌ی مدیریت نامناسب این آفت باشد.