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## LIFE TABLE ANALYSIS OF *CULEX PIFIENS* UNDER SIMULATED WEATHER CONDITIONS IN EGYPT

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**ABSTRACT.** The effect of fluctuating ambient air and water temperatures and relative humidity (RH) on the population parameters of *Culex pipiens* was studied using life table data during the winter–spring and summer–autumn seasons in Giza Province, Egypt. In winter–spring ( $20.46 \pm 1.8^\circ\text{C}$  and  $51.68 \pm 3.63\%$  RH), the preadult survival rate for *Cx. pipiens* was 80.65%, which was higher than the 50.00% observed in the summer–autumn ( $30.19 \pm 0.67^\circ\text{C}$  and  $52.68 \pm 8.04\%$  RH). During the winter–spring period, the developmental time of egg, larvae, and pupae of *Cx. pipiens* was 3.52, 12.69, and 5.92 days, respectively. There was a significantly shorter developmental period for summer–autumn (1.0, 8.59, and 2.04 days, respectively). Both female and male adults survived longer during winter–spring (61.83 days for female and 42.62 days for male adults) than during summer–autumn (24.38 days for female and 20.83 days for male adults). The fecundity ( $F$ ) of female *Cx. pipiens* (524.7 eggs/female) and the net reproductive rate ( $R_0$ ) (245.4 offspring) were significantly higher during winter–spring seasons than in the summer–autumn (163.3 eggs/female and 38.10 offspring). Despite the higher  $F$  and  $R_0$  values in winter–spring, the intrinsic rate of increase ( $r_m = 0.1181/\text{day}$ ) and the finite rate of increase ( $\lambda = 1.1253/\text{day}$ ) of the *Cx. pipiens* population were significantly lower compared to summer–autumn ( $r_m = 0.1648/\text{day}$ ;  $\lambda = 1.1792/\text{day}$ ). Consequently, the mean generation time during winter–spring was significantly longer (46.6 days) than during summer–autumn (22.09 days). The data suggest that *Cx. pipiens* is an r-strategist.

**KEY WORDS** *Culex pipiens*, fecundity, life table, longevity, weather

### INTRODUCTION

*Culex pipiens* L. (Culicidae: Diptera) is a cosmopolitan mosquito species distributed worldwide, with the exception of Australia and Antarctica (Mattingly et al. 1951, Barr 1957, Belkin 1962, Tanaka et al. 1979, Dahl 1988, Lee et al. 1989, Farajollahi et al. 2011). *Culex pipiens* is an important vector for periodic lymphatic filariasis (Farid et al. 2001), St. Louis encephalitis (Tsai and Mitchell 1989), West Nile virus in the USA (Turell et al. 2001), western equine encephalitis, Japanese encephalitis, and Rift Valley fever (Calisher 1994, Kramer and Ebel 2003, Farajollahi et al. 2011).

Water temperature is one of the most important abiotic factors affecting the biology of immature culicids (Clements 1992). Because mosquitoes are poikilothermic, their development is affected by water temperatures. At lower water temperatures, larval development is slower, and maturation is delayed (Ray 1960, Atkinson 1994). Grech et al. (2015) reported that the mean duration of the larval stage of *Cx. quinquefasciatus* Say decreased from 20.4 days at  $16.6^\circ\text{C}$  to 7.4 days at  $25.2^\circ\text{C}$ , and mean pupal period decreased from 3.2 days at  $16.6^\circ\text{C}$  to 1.6 days at  $18.7^\circ\text{C}$ . Madder et al. (1983) indicated that water temperature was the most important parameter affecting the rate of larval development of *Cx. pipiens*; they also found that larval and pupal development of both *Cx. pipiens* and *Cx. restuans* Theobald was positively correlated with the water temperature. However, in the case of *Cx. eduardoi*

Casal and Garcia and *Cx. hepperi* Casal and Garcia, the developmental time of immature stages was inversely related to water temperature within the ranges of  $7\text{--}25^\circ\text{C}$  and  $15\text{--}25^\circ\text{C}$ , respectively (Loetti et al. 2008). In the case of the immature stages of *Cx. eduardoi*, the high-temperature and optimum-temperature developmental thresholds were  $30^\circ\text{C}$  and  $28^\circ\text{C}$ , respectively. In the case of *Aedes aegypti* L., Couret et al. (2014) found that the development time of the larval stage decreased as the water temperature increased from 21 to 24, to 27, to  $30^\circ\text{C}$ , across different diet concentrations and density treatments. Fontanarrosa et al. (2000) reported the development time of the immature stages of *Aedes albifasciatus* (Macquart) under ambient conditions as 6 days at  $24^\circ\text{C}$  and 32 days at  $13^\circ\text{C}$ . Fava et al. (2001) reported that in seminatural conditions, as the temperature increased, the time required for the development of the 3 larval instars and the pupal stage of *Ae. albifasciatus* decreased.

Chuang et al. (2012) reported that higher temperatures ( $>30^\circ\text{C}$ ) had negative effects on the longevity and survival rates of mosquitoes at minimum air temperatures; there was a positive effect on the abundance of adult *Cx. pipiens* during May and June. Similar results were obtained for male and female *Cx. p. pallens* Coquillett mosquitoes by Oda et al. (2002) and for *Cx. p. molestus* Forskal adults by Oda et al. (1999). However, in the case of adult *Cx. quinquefasciatus*, the mean longevity was higher at  $30^\circ\text{C}$  than at  $25^\circ\text{C}$  (Oda et al. 2002); the survival from eclosion to

adult emergence was the highest (85–90%) at a temperature range of 20–30°C, which decreased to 38% at 15°C and 42% at 34°C (Rueda et al. 1990). Horsfall (1955) and Martens et al. (1995) reported that the daily mosquito survival rate decreased from 0.82–0.90 (at 9–20°C) to 0.04 (at 40°C). However, the highest survival rate for immature *Cx. hepperi* was in the range of 20–27.1°C (Loetti et al. 2008), and survival of *Cx. p. molestus* was markedly lower at 25°C (Oda et al. 1999). Grech et al. (2015) found that the total survival rate of the immature stages of *Cx. quinquefasciatus* was positively affected by the water temperature, increasing from 32% at 16.6°C to 88% at 25.5°C. Chuang et al. (2012) suggested that the longevity of adults and larvae of 3 different species of mosquitoes might be affected by temperatures higher than 30°C. However, during July and August, the maximum temperature had a negative influence on the abundance of adult *Cx. pipiens*. Several researchers have shown that air temperature can influence the length of the gonotrophic cycle (Madder et al. 1983, Rueda et al. 1990, Reisen 1995, Vinogradova 2000). Lebl et al. (2013) reported a negative correlation between adult mosquito abundance and humidity, whereas Chuang et al. (2012) showed that relative humidity (RH) had a minor influence on the abundance of *Cx. pipiens* adults.

For a comprehensive understanding of the effects of temperature and RH on population ecology, a life table is the most important tool, because it includes the entire life span and contains detailed information on development, survival, stage differentiation, and reproduction (Huang and Chi 2011). The objective of this study was to assess the responses of laboratory colonies of *Cx. pipiens* to different rearing water and ambient air temperatures and record the response of adults to the differences in RH under controlled laboratory conditions.

## MATERIALS AND METHODS

### Field collection of the larvae

Larvae of *Cx. pipiens* were collected from exposed sewage ponds located in Kerdasa (30°1'55.28"N, 31°6'37.61"E), Giza Province, Egypt. Using a dip net with a 3–5-m metal handle, larvae were sieved into large plastic containers. Containers were filled with water from the sewage ponds. Larvae were transported to the insectary of the Zoology Department, Fayoum University, for identification and mass rearing. Larvae were reared in the laboratory to adults. During the week that adults emerged, blood meals were offered twice (Gerberg 1970). The golden speckled quail (*Coturnix japonica* Temminck and Schlegel) was used as the source of the fresh blood meal. The Committee on Animal Research and Ethics (FU-CARE) of the Zoology Department, Faculty of Science, Fayoum University, permitted and approved the use of the quail (permission #I25-014). The FU-CARE follows the CITES (Convention

on International Trade in Endangered Species of Wild Fauna and Flora) no. 123 of March 18, 1986, the 2005 revision of the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes (<http://conventions.coe.int/Treaty/EN/Reports/HTML/123.htm>), and the Commission Recommendation of June 18, 2007, on guidelines for the accommodation and care of animals used for experimental and other scientific purposes (notified under document number C [2007] 2525: <http://ec.europa.eu/transparency/regdoc/rep/3/2007/EN/3-2007-2525-EN-1-0.Pdf>).

The feeding duration for adult female mosquitoes was 4–6 h. Twenty-four hours after female feeding, a white plastic cup (250 ml) filled with dechlorinated water was offered for oviposition. A single egg raft was used as the origin of all laboratory colonies used in the study.

### Identification of 5th-generation larvae of *Cx. pipiens*

Selected 3rd instars were removed from rearing cups using glass Pasteur pipettes, killed in boiling water, preserved in 75% alcohol, and mounted in Euparal (Bio Quip Products, Rancho Dominguez, CA). Larvae were examined using a stereomicroscope and morphologically identified according to Kirkpatrick (1952) and Harbach (1988).

### Laboratory conditions

In order to simulate the natural weather conditions of the region (excluding rainfall and wind velocity), temperature and RH were not controlled inside the laboratory but were allowed to fluctuate with natural ambient values. Inside the insectary, 2 maximum/minimum thermo-hydrometers (accuracy of  $\pm 1^\circ\text{C}$  and  $\pm 5\%$  RH) were placed opposite to each other at the corners of the laboratory to record the daily changes in the temperature and RH. Water temperature was recorded using a digital water thermometer with waterproof sensor probe dipped inside each rearing white plastic cup (temperature range 50°C to 70°C, accuracy  $\pm 1^\circ\text{C}$ ). The photoperiod was kept constant (light:dark [L:D] = 16:8 h) during both winter–spring and summer–autumn experiments, and white fluorescent lamps were used to simulate the 16:8 day/night photoperiod.

The winter–spring experiment began during the early winter season (December 24, 2013) and continued up to the spring season (April 10, 2014). The temperature during the winter experiment ranged from 19°C to 25°C with an average of  $20.46 \pm 1.8^\circ\text{C}$ , while the mean water temperature was  $18.17 \pm 0.29^\circ\text{C}$ . The RH ranged from 35% to 68% with an average of  $51.68 \pm 3.63\%$ .

The summer–autumn experiment began during the summer (July 14, 2014) and continued to early autumn (September 30, 2014). The temperature ranged from 27°C to 32°C, with an average of

30.19 ± 0.67°C; the RH was 35–65%, with an average of 52.68 ± 8.04%.

**Laboratory rearing of *Cx. pipiens***

Two to 4 h after hatching, larvae were removed under a dissecting stereomicroscope (Leica MS 50) using glass Pasteur pipettes. Ten larvae were placed into each white plastic cup (250 ml) supplied with dechlorinated water. Daily, larvae were offered a few pellets (4–6 pellets) of commercial fish diet as food. The commercial fish diet consisted of crude protein (41%), crude fat (7%), crude fiber (3%), moisture (8%), and phosphorus (1%).

Five cups were prepared in winter, and the 6th cup contained 12 larvae instead of 10 ( $n = 62$ ). Nine cups were used in the summer–autumn experiment ( $n = 90$ ). Each cup was examined daily for mortality and to record the date of development to pupation.

Once pupation occurred, pupae were transferred to a new cup with water and placed into rearing cages (30 × 30 × 30-cm) supplied with sugar crystals and a glass bottle containing a piece of wet cotton as a water source for future emerging adults. Each cage was labeled with the number of pupae and date of pupation. Cages were checked daily for pupal mortality, adult emergence, and daily adult mortality. After emergence, female mosquitoes were supplied with a fresh golden speckled quail blood diet twice per week. Females fed on blood for 4–6 h during each blood meal. Following each blood meal, a 250-ml cup filled with dechlorinated water was placed inside each cage for oviposition. Cups were checked daily for egg rafts. Each egg raft was soaked in 10% sodium hypochlorite, for 4–6 h, to separate the eggs. Eggs were counted under a stereo dissecting microscope to calculate the average daily number of eggs/female.

**Life table analysis**

Raw data were analyzed according to Chi and Liu (1985) and Chi (1988) using the program TWOSEX-MSChart (Chi 2016; <http://140.120.197.173/Ecology/>). The age-stage survival rate ( $s_{xj}$ ), age-specific survival rate ( $l_x$ ), and fecundity ( $m_x$ ) were calculated. The estimated population parameters were the net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r_m$ ), finite rate of increase ( $\lambda$ ), and mean generation time ( $T$ ). The age-stage life expectancy ( $e_{xj}$ ) was calculated according to Chi and Su (2006), while the reproductive value ( $v_{xj}$ ) was calculated according to Huang and Chi (2011). The intrinsic rate of increase ( $r_m$ ) was estimated using the iterative bisection method from the Euler-Lotka formula with age indexed from 0 (Goodman 1982):

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

Furthermore, the standard errors for  $r_m$ ,  $\lambda$ ,  $R_0$ , and  $T$  were calculated by using a bootstrap technique with

200,000 resampling. A paired bootstrap test was used to test the difference between the corresponding parameters of each experiment at 5% significance level (Efron and Tibshirani 1993, Huang and Chi 2013).

**Specific calculations and abbreviations**

- 1) Age-specific survivorship:  $l_x = y_x/y_0$ , where  $y_x$  = the number of males or females alive on each day,  $x$ .
- 2) Age-specific fecundity ( $m_x$ ) = 1/2 number of offspring born to parent of age  $x$ , where  $m_x$  is usually measured as female offspring per female of age  $x$ .
- 3) Net reproductive rate,  $R_0 = \sum l_x m_x$ . This is average lifetime reproduction, summed across all ages.
- 4) The mean generation time ( $T$ ). This is defined as the length of time that a population needs to increase to  $R_0$ -fold of its population size at the stable age-stage distribution and is calculated as  $T = (\ln R_0)/r$ .
- 5) Intrinsic rate of increase:  $r_m = \log e(R_0/T)$ , where  $\log e$  is the natural logarithm. It is the difference between the rate of births per unit time, and the rate of deaths per unit time (individuals produced per unit time).
- 6) Finite rate of increase:  $\lambda = \text{anti-log } e^{r_m}$ , which is the change in population size from one generation to the next, or it is the number of individuals “replacing” each adult in the previous generation.
- 6) The reproductive value ( $v_{xj}$ ). This is the expected current and future reproductive output for an individual of age  $x$ :

$$v_{xj}^0 = \sum_{t=x}^{\infty} [(l_t/l_x)m_t]$$

The term  $l_t/l_x$  gives the probability of living from age  $x$  to age  $t$ , and  $m_t$  is the number of offspring produced by those that survive to age  $t$ .

**RESULTS**

**Effect of temperature and humidity on the development of *Cx. pipiens***

During the summer–autumn experiment, the air temperature significantly increased ( $df = 100$ ,  $t = 37.4$ ,  $P = 0.0001$ ; 30.19 ± 0.67° C) as compared to the temperature during winter–spring (20.46 ± 1.8°C). The mean water temperature (29.36 ± 0.36°C) during summer–autumn significantly exceeded ( $df = 32$ ,  $t = 22.7$ ,  $P = 0.0001$ ) that recorded during the winter–spring experiment (18.17 ± 0.29°C).

The recorded mean RH inside the laboratory during winter–spring (55.58 ± 1.13%) was not significantly different ( $df = 103$ ,  $t = 1.6$ ,  $P = 0.11$ ) from the average of the RH reported during summer–

Table 1. Developmental durations (days) of *Culex pipiens* during winter–spring and summer–autumn seasons, where *n* refers to the number of individuals used in the experiments. Standard errors (SE) were estimated by using 200,000 bootstrap resampling. Differences between treatments were compared by using paired bootstrap test at 5% significance level.

Stage	Winter–spring		Summer–autumn		<i>P</i>
	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	
Egg	62	3.52 ± 0.06	90	1.0 ± 0.0	<0.0001
Larva	62	12.69 ± 0.19	90	8.59 ± 0.23	<0.0001
Pupa	50	5.92 ± 0.17	45	2.04 ± 0.03	<0.0001
Male adult	21	42.62 ± 6.15	24	20.83 ± 3.07	0.0017
Female adult	29	61.83 ± 2.59	21	24.38 ± 5.47	<0.0001

autumn (52.74 ± 1.29%) experiments. At low water temperature during the winter–spring experiment, the egg rafts of *Cx. pipiens* required a significantly longer time to hatch (3.52 ± 0.06 days, *P* < 0.0001). The eggs hatched within 24 h (1 ± 0.0 days) during the summer–autumn experiment (Table 1).

During the winter–spring experiment, the larval and the pupal periods were significantly of longer duration (*P* < 0.0001; 12.69 ± 0.19 days and 5.92 ± 0.17 days, respectively) as compared to the larval (8.59 ± 0.23 days) and pupal (2.04 ± 0.03 days) durations in the summer–autumn experiment (Table 1).

Males (42.62 ± 6.15 days) and females (61.83 ± 2.59 days) had significant longer life span (*P* = 0.001) during the winter–spring experiment, compared to 20.83 ± 3.07 days for males and 24.38 ± 5.47 days for females during the summer–autumn experiment (Table 1).

**Seasonal differences in mortality and survival rates**

The mortality rate of the larvae during the winter–spring experiments was higher (17.7%) as compared to mortality (1.1%) during the summer–autumn period. However, the pupal mortality was lower (1.6%) during the winter–spring experiment as compared to (49%) during summer–autumn. The mortality rate of males was 33.87% during the winter–spring experiment, which exceeded the mortality rate of males (27%) during summer–autumn. The mortality rate of the females reached 46.77% during winter–spring versus 23% during the summer–autumn experiment.

**Survival (*s<sub>xj</sub>*) and the age-specific survival (*l<sub>x</sub>*) of *Cx. pipiens* population**

During the initial days of the summer–autumn season, the survival (*s<sub>xj</sub>*) of the larvae of *Cx. pipiens* decreased sharply as compared to the winter–spring season (Fig. 1). During the winter–spring season, the survival (*s<sub>xj</sub>*) of the pupal stage was nearly double the survival of the pupal stage during summer–autumn (Fig. 1). The preadult survival (*s<sub>a</sub>*) was significantly higher (0.806 ± 0.050, *P* < 0.0001) during the

winter–spring experiment as compared to 0.5 ± 0.053 during the summer–autumn (Table 2).

Adult female *Cx. pipiens* individuals lived for more than 120 days during winter–spring experiment, as compared to 80 days in the summer–autumn. Adult males survived more than 105 days during the winter–spring experiment, compared to 55 days during the summer–autumn experiment. Females lived longer than the males (Fig. 1).

During the winter–spring experiment, the age-specific survival rate curve (*l<sub>x</sub>*) of *Cx. pipiens* was similar to a type I curve as described by Slobodkin (1962). The mortality rates were greater in the adult stage compared to during immature stages of its life history (Fig. 2). The survivorship curve was stable during the first 3 days of the *Cx. pipiens* population. The curve showed a gradual rate of decrease, reaching 0.5 on day 74. On day 86, the survivorship curve dropped from 0.419 to 0.29. The decrease in survivorship continued to day 87, from 0.29 to 0.19. The curve subsequently continued at the expected rate of decline to death of all individuals on day 123 (Fig. 2).

During summer–autumn, the survival curve showed a rapid decrease from 0.988 on day 2 to

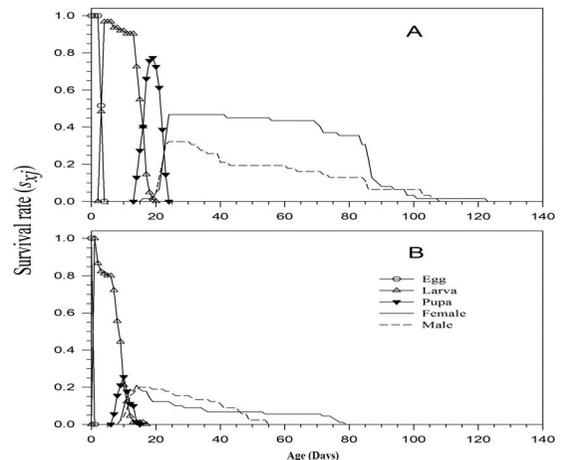


Fig. 1. Survival rate (*s<sub>xj</sub>*) of *Culex pipiens* under simulated winter–spring (A) and summer–autumn (B) conditions.

Table 2. Seasonal variations of the life table parameters of *Culex pipiens* population, where  $n$ , number of individuals used during the experiments;  $r_m$ , intrinsic rate of increase ( $d^{-1}$ );  $\lambda$ , the finite rate of increase ( $day^{-1}$ );  $R_0$ , net reproductive rate;  $T$ , mean generation time;  $F$ , mean fecundity;  $APOP$ , adult preoviposition period (days);  $TPOP$ , total preoviposition period (days);  $s_a$ , preadult survival rate.

Parameters	Winter-spring		Summer-autumn		$P$
	$n$	Mean $\pm$ SE	$n$	Mean $\pm$ SE	
$r_m$ ( $day^{-1}$ )	62	0.1181 $\pm$ 0.0090	90	0.1648 $\pm$ 0.0166	0.0166
$\lambda$ ( $day^{-1}$ )	62	1.1253 $\pm$ 0.0101	90	1.1792 $\pm$ 0.0195	0.0173
$R_0$ (offspring)	62	245.4 $\pm$ 74.7	90	38.10 $\pm$ 11.8	0.0071
$T$ (days)	62	46.6 $\pm$ 1.5	90	22.1 $\pm$ 0.8	<0.0001
$F$ (eggs/female)	62	524.7 $\pm$ 144.3	90	163.3 $\pm$ 40.5	0.0163
Oviposition days	16	5.87 $\pm$ 1.20	16	2.25 $\pm$ 0.51	0.0062
$APOP$	16	20.0 $\pm$ 2.82	16	8.31 $\pm$ 0.62	0.0007
$TPOP$	16	41.75 $\pm$ 2.89	16	19.19 $\pm$ 0.76	<0.0001
Preadult survival rate ( $s_a$ )	62	0.806 $\pm$ 0.050	90	0.500 $\pm$ 0.053	<0.0001

0.866 on day 3. The curve showed a nearly constant logarithmic mortality rate following a type II curve as described by Slobodkin (1962).

**Female fecundity**

The age-stage reproductive value ( $v_{xj}$ ) of female *Cx. pipiens* individuals usually indicated 2 periods of activities, either during the winter-spring or summer-autumn experiment (Fig. 3). During the winter-spring experiment, the reproductive value ( $v_{xj}$ ) of females had higher values during the final days of their life spans (100–120 days). However, during the summer-autumn experiment, the best reproductive values for females were achieved during the early days of the female life span (10–28 days; Fig. 3).

During winter-spring seasons, females had high fecundity values ( $m_x$ ) as compared to the summer-autumn experiment (Fig. 2). Four major fecundity peaks were present during the final 100–120 days of the experiment. The highest peak was at 160 eggs/female. However, in the case of the summer-autumn experiment, the 4 major peaks were recorded during the initial days of the experiment (Fig. 2). The highest peak of fecundity (19 eggs/female) was recorded on day 20 of the summer-autumn experiment.

During the winter-spring experiment, females required a significantly longer time ( $P = 0.0007$ ) to lay the first egg raft,  $20.0 \pm 2.82$  days, as compared to only  $8.31 \pm 0.62$  days during the summer-autumn

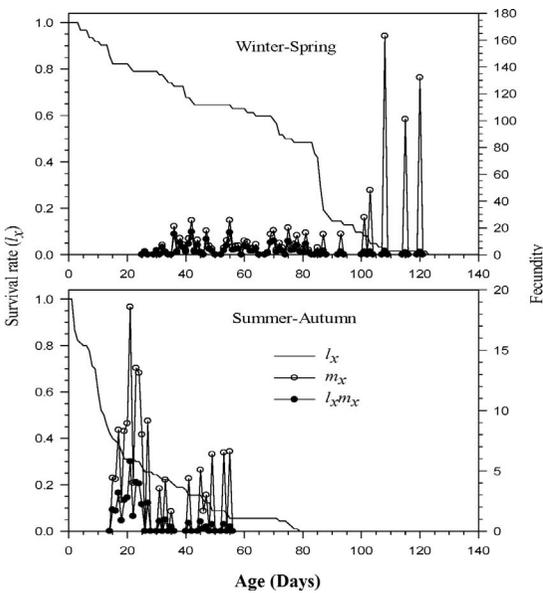


Fig. 2. Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), and maternity ( $l_x m_x$ ) of *Culex pipiens* under simulated winter-spring and summer-autumn conditions.

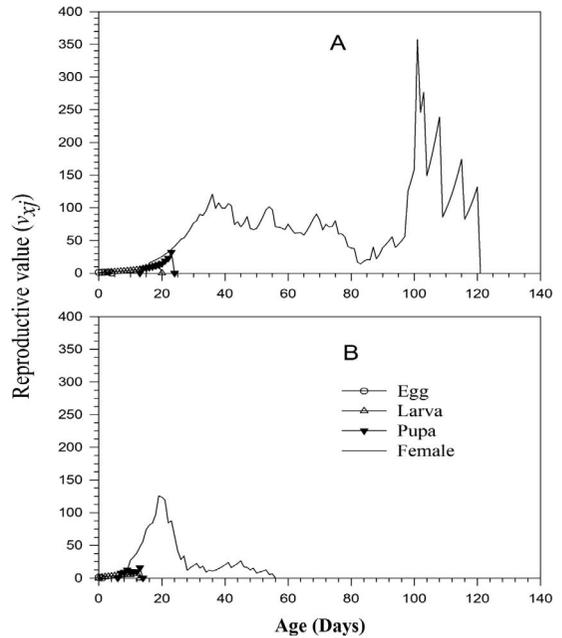


Fig. 3. Age-stage reproductive value ( $v_{xj}$ ) of *Culex pipiens* under simulated winter-spring (A) and summer-autumn (B) conditions.

experiment (Table 2). In addition, during the winter–spring experiment, females produced more eggs ( $F = 524.69 \pm 144.3$  eggs/female,  $P = 0.0163$ ), resulting in a net reproductive rate ( $R_0$ ) of  $245.42 \pm 74.7$  eggs/female/life span. In comparison, females during the summer–autumn experiment (Table 2) produced a very low number of eggs ( $F = 163.3 \pm 40.5$  eggs/female), resulting in a lower net reproductive rate ( $R_0 = 38.10 \pm 11.80$  eggs/female/life span).

### Life table analysis

The experimental populations of *Cx. pipiens* had a significantly lower intrinsic rate of daily increase ( $r_m = 0.1181 \pm 0.0090$  d<sup>-1</sup>,  $P = 0.0166$ ) during the winter–spring experiment as compared to during the summer–autumn experiment ( $r_m = 0.1648 \pm 0.0166$  d<sup>-1</sup>). Similarly, the finite rate of increase ( $\lambda$ ) was significantly lower for the winter–spring period ( $1.1253 \pm 0.0101$ ) than the summer–autumn experiment ( $1.1792 \pm 0.0195$ ,  $P = 0.0173$ ). However, the mean generation time during winter–spring was nearly two times longer ( $46.6 \pm 1.5$  days) than the summer–autumn experiment ( $22.09 \pm 0.8$ ,  $P < 0.0001$ ; Table 2).

### DISCUSSION

A better understanding of vector population dynamics is a fundamental step towards predicting the transmission of mosquito-borne disease in a temperate climate (Stenseth et al. 2002, Jones et al. 2008). In addition, exogenous (e.g., temperature and RH) and endogenous (e.g., density limitations) parameters are both important regulators of mosquito abundance (Jian et al. 2014).

Under the laboratory conditions of this study, the variation in RH was negligible during winter–spring ( $55.58 \pm 1.13\%$ ) and summer–autumn ( $52.74 \pm 1.29\%$ ). Lebl et al. (2013) reported a negative correlation between mosquito abundance and humidity. Chuang et al. (2012) concluded that RH had a little effect on adults of *Cx. pipiens*. The water temperature was the most important abiotic parameter affecting the experimental populations of *Cx. pipiens*.

Durations of both the larval and the pupal stages of *Cx. pipiens* were longer during the winter–spring experiments as compared to the durations of the larvae and pupae during the summer–autumn experiments. Similar findings were reported by Fontanarrosa et al. (2000) and Fava et al. (2001) for *Ae. albifasciatus* (Macquart); and by Loetti et al. (2008), Loetti et al. (2011), Couret et al. (2014), and Grech et al. (2015) for *Cx. hepperi* Casal and Garcia, *Cx. eduardoi* Casal and Garcia, *Aedes aegypti* L., and *Cx. quinquefasciatus* Say, respectively. Loetti et al. (2011) concluded that the development time of the immature stages of mosquitoes was generally shortened by warm temperatures and lengthened by cooler temperatures. However, Madder et al. (1983)

found that larval and pupal development of both *Cx. pipiens* and *Cx. restuans* was positively correlated with water temperature.

In the present study, male and female adults of *Cx. pipiens* showed prolonged longevity at air temperatures of 20.46°C as compared to 30.19°C. Similar findings were reported by Oda et al. (1999) for *Cx. p. molestus* Forskal and by Oda et al. (2002) for *Cx. p. pallens* Coquillett. However, in the case of adult *Cx. quinquefasciatus*, the mean longevity was higher at 30°C than that recorded at 25°C (Oda et al. 2002). The difference in adult longevity of females at 2 air temperature regimes, 20.46°C and 30.19°C, during the present study may have implications of virus transmission. At lower air temperatures, the females lived longer, possibly having more opportunities to bite and infect hosts. Longevity is one of the key variables in the vectorial capacity equation (Garrett-Jones 1964). Longer-lived females in the population increased the overall risk of pathogen transmission (MacDonald 1957).

In my experiments, the survival rates of the larval and pupal stages and adults of *Cx. pipiens* increased greatly at lower winter–spring temperature and greatly decreased at higher summer–autumn temperature. Similar findings were reported by Martens et al. (1995) and Horsfall (1955). Madder et al. (1983), in the case of both *Cx. pipiens* and *Cx. restuans*, and Oda et al. (1999), in the case of *Cx. p. molestus*, demonstrated a reduction in survival rates of the immature stages at high water temperatures. Shelton and Rohlf (1973) found that the survival of 8 mosquito species was not affected at 12–26°C, but they had 100% mortality at 32–35°C. However, at high temperatures, the survival rate of immature stages increased in *Cx. hepperi* (Loetti et al. 2008) and *Cx. quinquefasciatus* (Rueda et al. 1990, Grech et al. 2015).

At the temperature range of  $18.17 \pm 0.29^\circ\text{C}$  to  $20.46 \pm 1.8^\circ\text{C}$ , the survival curve of the *Cx. pipiens* population resembled a type I curve as described by Slobodkin (1962). At a higher temperature range ( $29.36 \pm 0.36$  up to  $30.19 \pm 0.76^\circ\text{C}$ ), the survival curve of *Cx. pipiens* during this study resembled a type II curve. Ludueña Almeida and Gorla (1995) described the survival curve of *Ae. albifasciatus* as type II (Slobodkin 1962), whereas Ernesto and Elena (2003) described the survival curve of *Ae. albifasciatus* in the field, during spring, summer, and fall as intermediate between type III and type I (Slobodkin 1962).

At  $18.17 \pm 0.29^\circ\text{C}$ , the mortality rate of *Cx. pipiens* larvae was higher than that recorded at  $29.36 \pm 0.36^\circ\text{C}$ , whereas the mortality rate of the pupae was lower at these temperatures. In comparison, at a relatively high temperature of  $27 \pm 1^\circ\text{C}$ , the mortality rates of larvae and pupae of *Cx. quinquefasciatus* were 14.5% and 7.7%, respectively (Suman et al. 2011).

The present study indicated that *Cx. pipiens* females produced a higher average number of eggs

at  $20.46 \pm 1.8^\circ\text{C}$  than at  $30.19 \pm 0.76^\circ\text{C}$ . Similarly, Oda et al. (2002) found that female insemination and egg hatchability in *Cx. p. pallens* were significantly higher at  $25^\circ\text{C}$  than at  $30^\circ\text{C}$ . In contrast, Madder et al. (1983) reported that field overwintering females of both *Cx. pipiens* and *Cx. restuans* produced fewer eggs than females of the summer generations.

In my study, *Cx. pipiens* females produced more ( $245 \pm 74.7$  eggs/female/life span) at  $20.46 \pm 1.8^\circ\text{C}$  than at  $30.19 \pm 0.76^\circ\text{C}$  ( $163.3 \pm 40.5$  eggs/female/life span). Suman et al. (2011) reported that *Cx. quinquefasciatus* females produced an average of  $512.4 \pm 6.64$  eggs/female at  $27 \pm 1^\circ\text{C}$ , possibly due to a higher insemination rate. Oda et al. (2002) indicated that dissected *Cx. p. pallens* females showed high insemination rates at  $25^\circ\text{C}$ , with no insemination observed at  $30^\circ\text{C}$ . Unlike *Cx. p. pallens*, the insemination in *Cx. quinquefasciatus* females was high at  $30^\circ\text{C}$ . In southern and central California, during warm winter temperatures, *Culex* females showed early gonotrophic activity during January (Reisen et al. 2010). According to Fox and Czesak (2000), adverse environmental conditions may favor the production of a greater number of offspring to increase the probability of the new progeny reaching the adult stage. High temperature could apparently reduce copulation or insemination, or negatively impact the reproductive system of the female *Cx. pipiens* complex (Oda et al. 2002).

In the present study, the values of both the intrinsic rate of daily increase ( $r_m$ ) and the finite rate of increase ( $\lambda$ ) for *Cx. pipiens* populations were  $0.12 \pm 0.009$  and  $1.13 \pm 0.010$  at  $20.46 \pm 1.8^\circ\text{C}$  and  $0.17 \pm 0.0167$  and  $1.18 \pm 0.0196$ , respectively, at  $30.19 \pm 0.76^\circ\text{C}$ . Similarly, at  $27 \pm 1^\circ\text{C}$ , the intrinsic rate of daily increase of *Cx. quinquefasciatus* was  $0.15 \pm 0.0$ , and the finite rate of increase was  $1.16 \pm 0.0$  (Suman et al. 2011). The authors indicated that warmer climate had a positive effect on increasing the inherent capacity for reproduction.

The mean generation time of the *Cx. pipiens* population used in my study was longer ( $46.6 \pm 1.5$  days) at  $18.17$ – $20.46^\circ\text{C}$  than the mean generation time at  $29.36$ – $30.19^\circ\text{C}$  ( $22.1 \pm 0.8$  days). In contrast, the mean generation time of *Cx. quinquefasciatus* at  $27 \pm 1^\circ\text{C}$  was  $31.6 \pm 0.80$  days (Suman et al. 2011). Gomez et al. (1977) and Suleman and Reisen (1979) recorded higher values for mean generation time of 39.6 days and 44.7 days for *Cx. quinquefasciatus*, respectively. However, the mean generation time for different strains of *Cx. quinquefasciatus* was 32.1 days for the Bangkok strain, 26.8 days for the Vero Beach strain, and 28.5 days for the Houston strain (Walter and Hacker 1974). In contrast to our results, Becker et al. (2003) and Loetti et al. (2011) reported that *Cx. pipiens* exhibited a relatively short generation time, approximately 1 wk, at a water temperature above  $25^\circ\text{C}$  under laboratory conditions.

At low temperatures of  $18.17$ – $20.46^\circ\text{C}$ , our *Cx. pipiens* laboratory colony was able to replicate itself 245.4 times, with 0.118 as an exponential rate of

daily increase, within 46.6 days. However, at temperatures of  $29$ – $30^\circ\text{C}$ , the colony reproduced only 38.1 times, with 0.164 daily rate of increase, within a relatively short time of 22.01 days. This population of *Cx. pipiens* is characterized by high fecundity and short generation time, accompanied by a higher rate of daily increase. There was an inverse relationship between the mean generation time and the number of offspring produced.

The genus *Culex* has been reported as an r-strategist by several authors, e.g., *Cx. quinquefasciatus* (Gomez et al. 1977, Suleman and Reisen 1979) and *Cx. tritaeniorhynchus* Giles (Reisen et al. 1979) from Taiwan and Pakistan. Data from this study suggest that *Cx. pipiens* populations may also be an r-strategist, especially during the winter–spring seasons.

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