Comparative Developmental Times and Laboratory Life Tables for Drosophlia suzukii and Drosophila melanogaster (Diptera: Drosophilidae)

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COMPARATIVE DEVELOPMENTAL TIMES AND LABORATORY LIFE TABLES FOR *DROSOPHLIA SUZUKII* AND *DROSOPHILA MELANOGASTER* (DIPTERA: DROSOPHILIDAE)

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ABSTRACT

Drosophila suzukii (Matsumura) *(Diptera: Drosophilidae)* and *Drosophila melanogaster* Meigen were studied in a laboratory at 25 °C, 60% RH and 16:8 h L:D. Stage-specific developmental times, reproduction, stage-specific survival rates, and adult sex ratios were recorded and organized in separate life tables for each species. The intrinsic rate of increase (r), the finite rate of increase (λ), the net reproduction rate (R0) and the mean generation time (T) were 0.12 day^{-1}, 1.13 day^{-1}, 27.57 offspring, and 28.04 days, respectively, for *D. suzukii* and 0.17 day^{-1}, 1.19 day^{-1}, 38.17 offspring, and 21.27 days, respectively, for *D. melanogaster*. The use of the age-stage, two-sex life table method to study *D. suzukii* and *D. melanogaster* yielded considerably more accurate and useful data than would have been obtained by using the female-only age-specific life table. These life tables can be used for population growth projections, designing mass-rearing programs, and for pest management.

Key Words: intrinsic rate of increase, finite rate of increase, net reproduction rate, mean generation time

RESUMEN

Drosophila suzukii (Matsumura) y *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) fueron estudiados en un laboratorio a 25 ° C, con 60% de humedad relativa y 16: 8 h L: O (Luz: Oscuridad). El tiempo de desarrollo, la reproducción, la tasa de sobrevivencia de cada estadio específico, y la proporción de sexos para los adultos fueron registrados y organizados en tablas de vida independientes para cada especie. La tasa intrínseca de crecimiento (r), la tasa finita de crecimiento (λ), la tasa neta de reproducción (R_0) y el tiempo medio de generación (T) fueron 0.12 dias^{-1}, 1.13 dias^{-1}, 27.57 progenie y 28.04 días para *D. suzukii*, respectivamente, y 0.17 dias^{-1}, 1.19 dias^{-1}, 38.17 progenie, y 21.27 días, respectivamente, para *D. melanogaster*. El uso del método de hacer una tabla de vida segun la edad del estadio y los dos sexos para estudiar *D. suzukii* y *D. melanogaster* resultó en datos considerablemente más precisos y útiles de los que se habría obtenido mediante el uso de la tabla de vida de las edades específicas basada sólo en hembras. Estas tablas de vida pueden ser utilizadas para las proyecciones de crecimiento de la población, para el diseño de programas de criar en masa, y para el manejo de plagas.

Palabras Clave: tasa intrínseca de crecimiento, tasa finita de crecimiento, tasa neta de reproducción, tiempo medio de generación

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) and *Drosophila melanogaster* Meigen are both key pests of fruits. *Drosophila suzukii* damages cherries (Van der Linde et al. 2006) and a variety of small fruits (Dreves et al. 2009). Oviposition in fruits produces little visible damage on the fruit surface. Upon hatching, larvae feed on the fruit, causing it to soften, turn

brown and rot. Many fruits are damaged by *D. suzukii*, including blueberry, blackberry, cherry, strawberry, plums, peaches, grapes, figs, kiwi fruit, and pears (Dreves et al. 2009). In the United States, losses in strawberry, blueberry and raspberry caused by *D. suzukii* have reached 80, 40 and 70%, respectively (Bolda 2010).

Drosophila melanogaster has caused increasing damage to Chinese bayberries and cherries in China. In Tianshui, Gansu Province, some late-maturing varieties of cherries proved especially susceptible to damage by *D. melanogaster* with loss rates generally above 35%, reaching 80% for some cultivars (Guo 2007). In the Aba region of Sichuan Province fruit damage to cherries due to *D. melanogaster* has been as great as 60% (Guo et al. 2007), and in Guiyang, Guizhou Province red bayberry losses have been 38%~57% (Li et al. 2005). Commonly, red bayberry damage is about 60% if control measures are not promptly undertaken to suppress fruit flies (Yang et al. 1998).

Life tables are helpful tools for quantifying and analyzing mortality, development, reproduction, and intrinsic rates of increase of insect populations (Chi & Su 2006) and can be used to make population projections based on computer simulations (Chi 1990). Life tables have been used in diverse types of studies related to population ecology, such as the population biology of invasive species (Sakai et al. 2001), conservation strategies (Wilcox & Murphy 1985), demographic ecotoxicology (Stark & Banks 2003), harvesting theory (Chi & Getz 1988, Chi 1994), and timing of pest control measures (Chi 1990).

Materials and Methods

Experimental Insects

Drosophila suzukii and *D. melanogaster* populations used in this study were from colonies started with larvae from cherry orchards in Tai'an, Shandong Province in May 2012. Flies were raised in an insectary for about 9 generations at 25 ± 1 °C, 70 ± 5% RH, 16:8 h L:D and 10,000 lux before use in experiments reported here. Both flies were reared on table grapes grapes ('Kyoho' grape cultivar, *Vitis vinifera* L.; Vitales: Vitaceae) purchased from the local market. Grapes were rinsed three times in distilled water and dried before being provided to adult flies for oviposition and subsequent larvae development.

Life Table Construction

To create cohorts for life table analysis of development and survival, grapes were cut into halves and placed in a 2000-mL flat drum bottle with the cut surface upward to provide food for adult fruit flies. About 60 pairs each of mated *D. suzukii* and *D. melanogaster* females were selected and placed in the bottles to lay eggs for 4 h. They were kept in the same conditions as the insectary above. Then, 106 *D. suzukii* eggs and 103 *D. melanogaster* eggs were collected and placed in 209 Petri dishes (1.5 cm diam) with fresh grape halves. All experimental insects were observed daily with a dissecting microscope at 10:00 am until all eggs had either become adults or died at some earlier life stage. Adult flies were sexed, and pairs of one male and one female were placed in 2,000-L flat drum bottles, where they were provided with one grape cut into halves to provide food and an oviposition substrate. Grapes were replaced daily and eggs counted until the adults died.

Data Analysis

The data were analyzed using age-stage, two-sex life tables as described by Chi & Liu (1985) and Chi (1988). The mean development period for each developmental stage, the longevities of adult males and females, the adult pre-oviposition periods (APOP), the total pre-oviposition periods (TPOP), and the fecundities of *D. suzukii* and *D. melanogaster* were calculated. The average APOP was calculated based on meaurements of the pre-ovipositional periods of the adult females, whereas the average TPOP included the developmental times of the pre-adult stages plus the pre-ovipositional period of the adult females. The age-stage specific survival rate (s_{xj}) (where x is the age and j is the stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), and the age-specific fecundity (m_x) were calculated from the daily records of the survival and fecundity of all individuals in the cohort. The population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and T, the mean generation time) were also calculated. The intrinsic rate of increase was estimated by using the iterative bisection method from the equation:

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

with age indexed from 0 (Goodman 1982). In the age-stage, two-sex life table, the l_x and m_x are calculated as:

$$l_x = \sum_{x=0}^{k} s_{xj}$$

$$m_x = \frac{\sum_{x=1}^{k} s_{xj} f_{xj}}{\sum_{x=1}^{k} s_{xj}}$$

where k is the number of stages (Chi & Liu, 1985). The life expectancy (e_{xj}) was calculated according

to Chi & Su (2006). The mean generation time is defined as the period of time needed by a population to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution and is calculated as $T = (\ln R_0)/r$, where $R_0 = \Sigma l_x m_x$, $\lambda = e^r$. The gross reproductive rate (GRR) = Σm_x. For the tedious and complicated calculations involved in the analyses of raw data and of the life table, a computer program (TWOSEX-MSChart) was used in this analysis (Chi 2012). This program is written in Visual BASIC for the Windows operating system and is available at http://140.120.197.173/Ecology.

Results

There were significant differences between *D. suzukii* and *D. melanogaster* in the duration of the egg, L_1 and pupal stages ($P = 0.003$, $P = 0.001$, $P = 0.000$, respectively). The pupation rates of *D. suzukii* and *D. melanogaster* were 70.5 and 75.7%, respectively, and every pupa reached adulthood. The emerged *D. suzukii* males and females had a sex ratio of 1:1.4, while the sex ratio of *D. melanogaster* was 1:2.1. The adult pre-oviposition periods (APOP) of *D. suzukii* and *D. melanogaster* were 3.02 ± 0.16 days and 2.87 ± 0.25 days ($P > 0.05$), and the total pre-oviposition period (TPOP) of *D. suzukii* (19.95 ± 0.65 days) and was significantly longer than that of *D. melanogaster* (15.62 ± 0.39 days) ($P = 0.000$), largely because *D. suzukii* had a longer pupal stage (Table 1).

The age-stage specific survival rate (s_{xj}) (Fig. 1) shows the probability that a newly laid egg will survive to age x and develop to stage j. The curves also shows stage differentiation due to variable developmental rates among individuals. Considering the variable developmental rates among individuals, the stage survival curves can describe generational overlapping. In the *D. suzukii* cohort, pupae were present up to day 39, but all *D. melanogaster* pupae molted to adults by day 19. The horizontal survival curve of *D. suzukii* male adults showed almost no mortality during the age interval 22-39 days, and by the 53rd day all adults of both *D. suzukii* and *D. melanogaster* had died.

Ignoring stage differentiation, a single age-specific survival rate (l_x) (Fig. 2) was calculated that expresses the probability that an egg will survive to age x. The curve of age-specific fecundity (m_x) showed that reproduction began at day 13 for *D. suzukii* and lasted for 37 days, while *D. melanogaster* reproduction began at day 9 and lasted for 36 days. The age-specific reproduction ($l_x m_x$) is the population rate of reproduction at age x, incorporating both fecundity for that age of female and the probability of a fly living to that age.

Based on the age-stage, two-sex life table, the age-stage-specific life expectancy (e_{xj}) gives the expected life span of an individual of age x and stage j (Fig. 3). For example, the *D. suzukii* life expectancy of an egg was 33 days and a 34-day-old female will likely live another month. Because this study was conducted in the laboratory without the adverse effects of field conditions, life expectancy decreased gradually with age.

The reproductive value (v_{xj}) is the contribution of individuals of age x and stage j to the future population (Fig. 4). The reproductive value for a new egg (v_{01}) is the finite rate of increase (λ); the reproductive value gradually increased with age (x) and stage (j), then drops to zero. The peak reproductive value occurred for females 23 and 18 days old for *D. suzukii* and *D. melanogaster*, respectively, implying that in comparison to other ages, these females make the highest contribution to the population.

If all individuals are included, the intrinsic rate of increase (r), the finite rate of increase (λ), the gross reproduction rate (GRR), the net reproduction rate (R_0) and the mean generation

Table 1. Developmental times, longevities and fecundities of *Drosophila suzukii* and *Drosophila melanogaster*.

		D. suzukii		D. melanogaster		
Statistics	Stage or Sex	*n*	Mean ± SE	*n*	Mean ± SE	P
Preadult duration (days)	Egg	106	1.7 ± 0.09	103	1.38 ± 0.07	0.003
Adult longevity (days)	L1	102	2.07 ± 0.06	97	2.29 ± 0.07	0.001
APOP (days)	L2	99	1.92 ± 0.21	90	2.03 ± 0.07	0.364
TPOP (days)	L3	82	2.41 ± 0.12	85	2.25 ± 0.12	0.054
Fecundity (eggs/female)	Pupa	74	8.86 ± 0.21	78	4.87 ± 0.11	0.000
	Male	31	25.84 ± 1.15	25	16.68 ± 1.28	0.000
	Female	43	26.21 ± 0.78	53	20.09 ± 0.91	0.000
	Female	43	3.02 ± 0.16	53	2.87 ± 0.25	0.620
	Female	43	19.95 ± 0.65	53	15.62 ± 0.39	0.000
	Female	43	67.95 ± 3.02	53	74.17 ± 3.81	0.220

APOP, adult pre-oviposition period; TPOP, total pre-oviposition period (from egg to first oviposition).

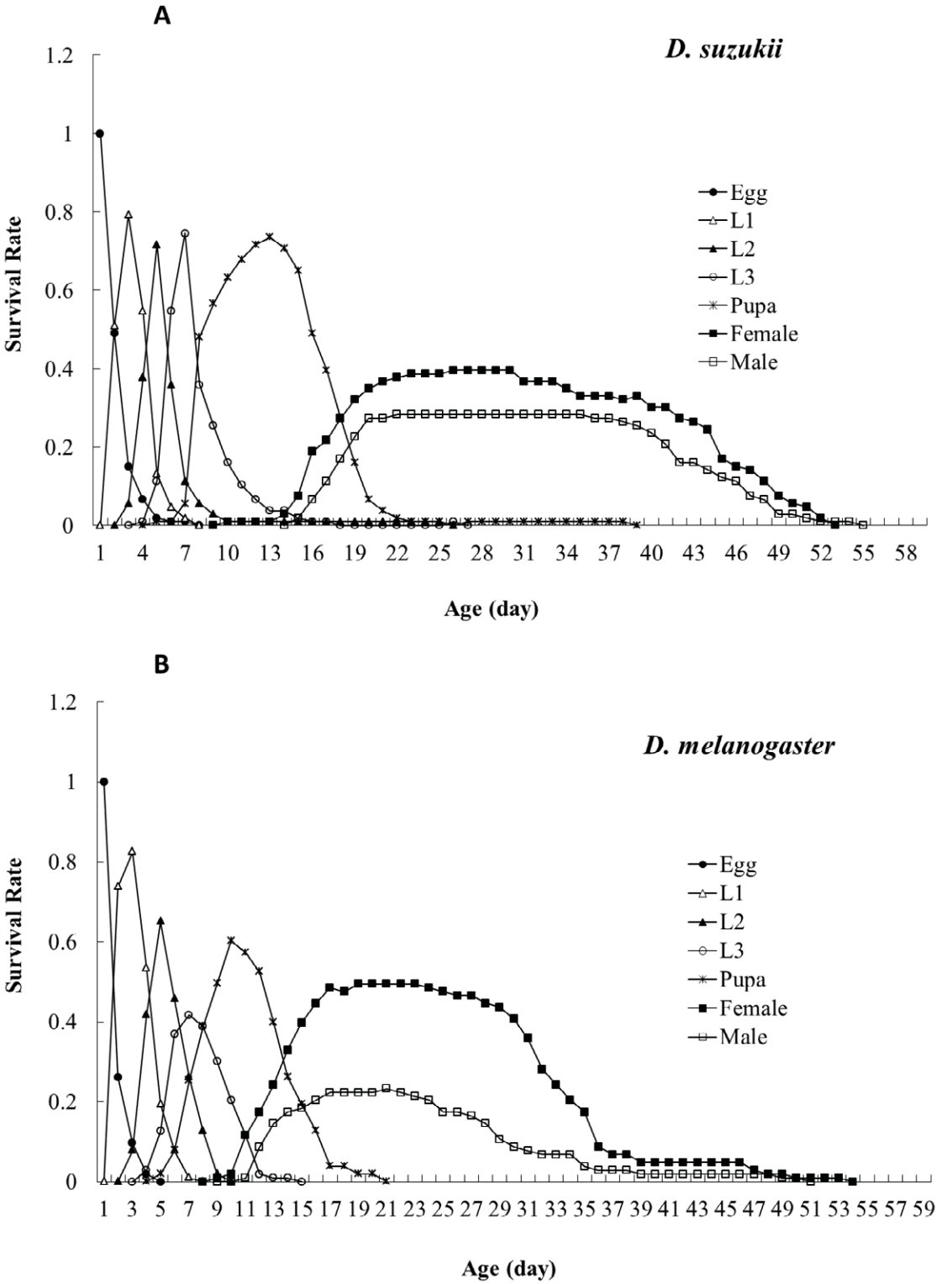

Fig. 1. Age-stage specific survival rate of *Drosophila suzukii* and *Drosophila melanogaster*.

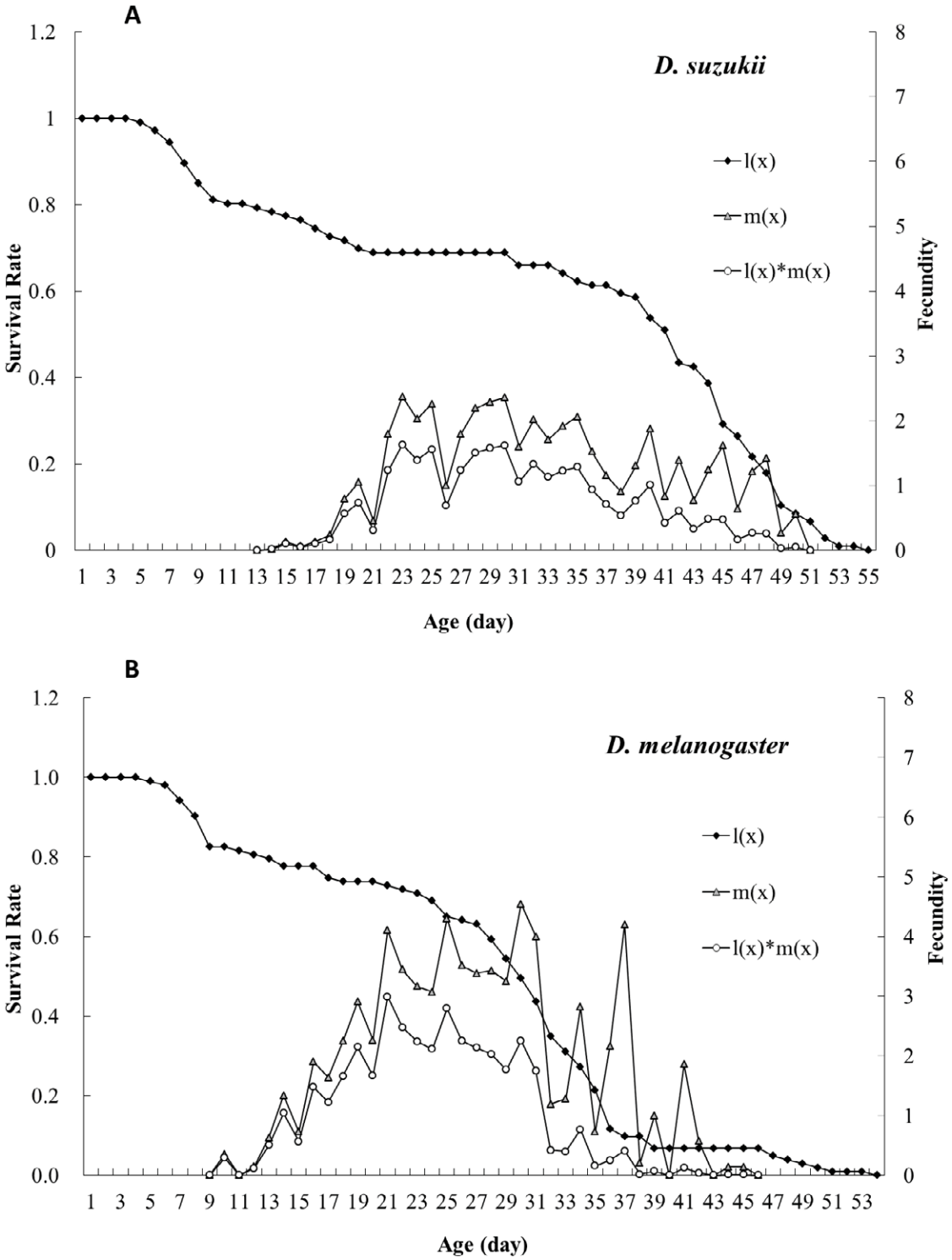

Fig. 2. Age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Drosophila suzukii* and *Drosophila melanogaster*.

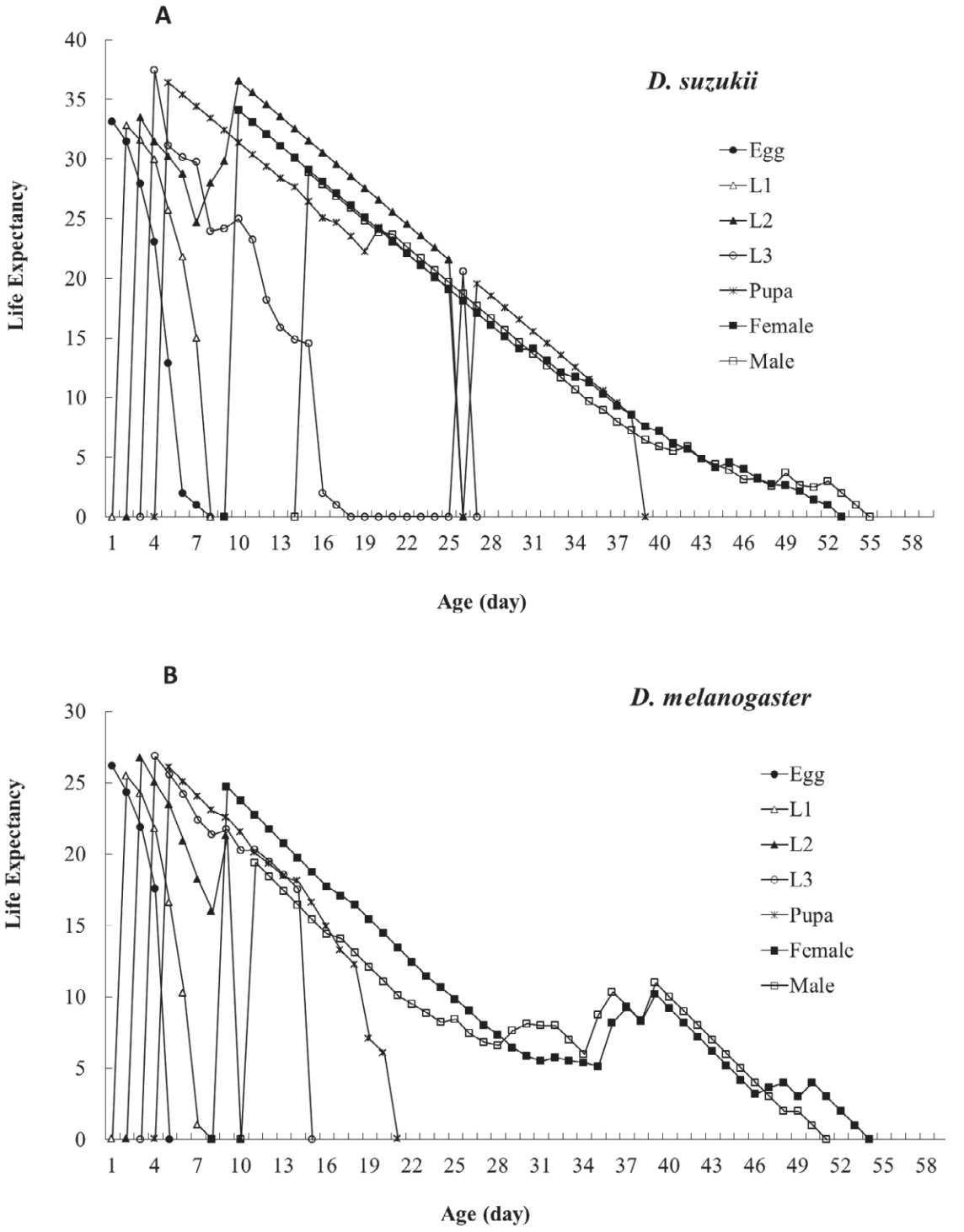

Fig. 3. Age-stage-specific life expectancies of *Drosophila suzukii* and *Drosophila melanogaster*.

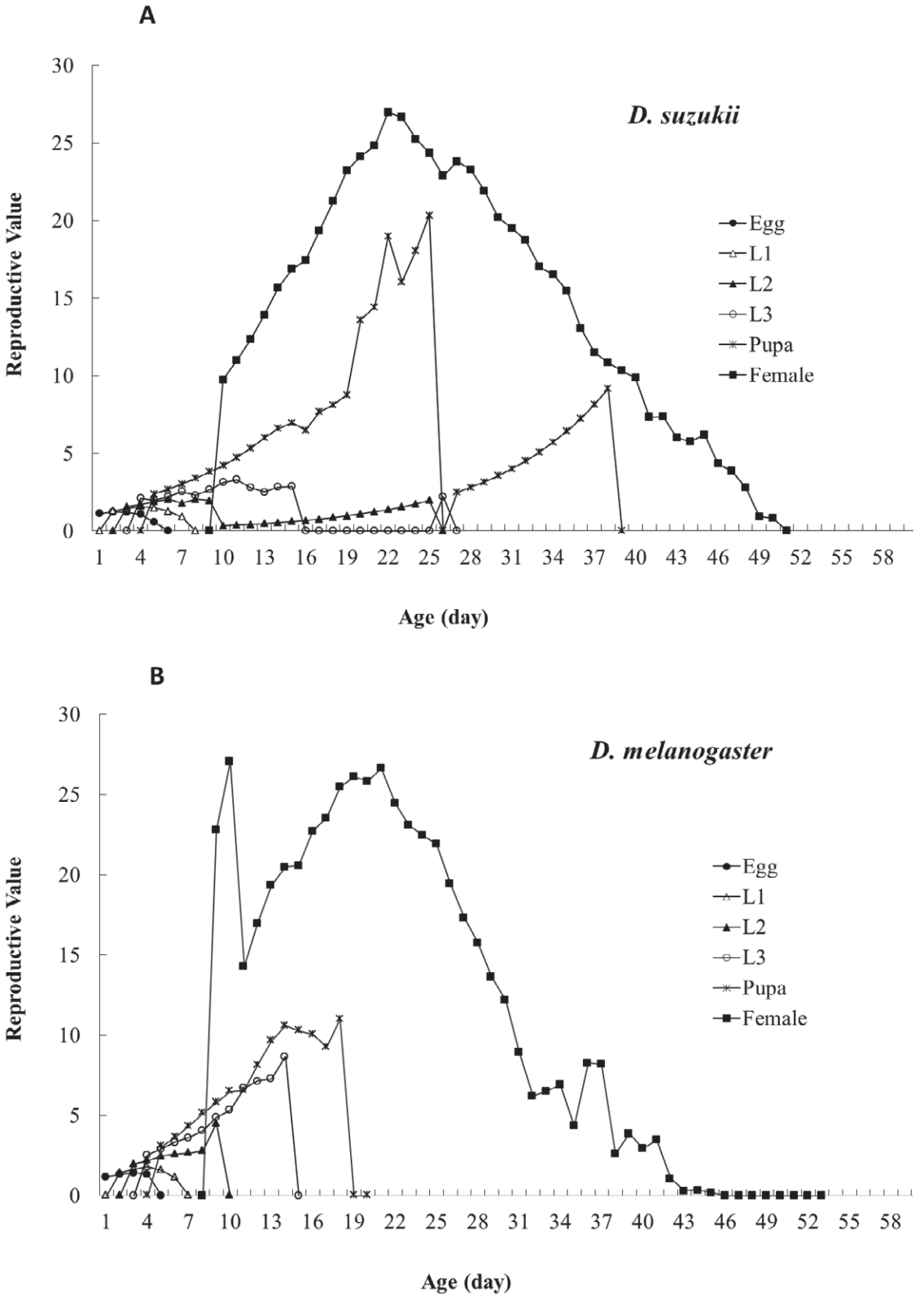

Fig. 4. Age-stage-specific reproductive value of *Drosophila suzukii* and *Drosophila melanogaster*.

time (T) of *D. suzukii* were 0.12 ± 0.0053 day^{-1}, 1.13 ± 0.006 day^{-1}, 47.01 ± 5.14 offspring, 27.57 ± 3.48 offspring, 28.05 ± 0.55 days, and r, λ, GRR, R_0, and T of *D. melanogaster* were 0.17 ± 0.0074 day^{-1}, 1.19 ± 0.0088 day^{-1}, 70.67 ± 8.36 offspring, 38.17 ± 4.16 offspring, 21.29 ± 0.63 days (Table 2). With the exception of the R_0 values, significant differences were found between the r, λ, GRR, and T values for these two fruit fly species.

Discussion

This study found that *D. suzukii* had a longer mean generation time than *D. melanogaster*, while *D. suzukii* adult males and females lived longer than those of *D. melanogaster*. The finite rate of increase (λ) (days^{-1}) indicated that rate of increase of *D. suzukii* from one generation to next was significantly less than that of *D. melanogaster*. In this study, there was no significant difference in fecundity between *D. suzukii* and *D. melanogaster*, so did their net reproduction rates (R_0) (offspring), were less than that when they are reared groups. Thus when the flies live together in groups, the females may lay more eggs than when reared in pairs. This apparent effect of isolated rearing seems more obvious in the case of *D. melanogaster* than that of *D. suzukii*. However this hypothesis requires additional investigation.

Zhang et al. (2010) reported that the developmental periods of *D. melanogaster* stages reared on grape at 25 °C were 1.08 days for the egg stage, 4.39 days for the larval stage, and 3.9 days for the pupal stage; these values are slightly shorter than in our study. A variety of factors, including host plants, temperature, and rearing methods have been reported to cause differences in the developmental times. Guo (2007) reported that the durations of the egg. larval and pupal stages of *D. melanogaster* reared on cherries at 25 °C were 0.95 days, 4.5 days and 4.1 days, respectively; and that the number of days required by *D. melanogaster* reared on cherries to reach the adult stage at various temperatures were 9.5 days at 25 °C, 15.7 days at 20 °C and about 30.9 days at 15 °C. Considering that cherries are greatly influenced by the season, and since grapes are one of the hosts of these two fruit fly species, grapes were used to rear *D. suzukii* and *D. melanogaster*. Also in this study the eggs were reared singly to the adult stage, and this may have influenced the developmental times of the various life stages.

The developmental times analyzed by age-stage, two-sex life tables of *D. suzukii* and *D. melanogaster* in our study are generally consistent with those found by previous studies calculated in traditional way. Kanzawa (1939) reported that the developmental durations of *D. suzukii* were 2-72 h, 3-13 days and 3-15 days for egg, larvae and pupal stages, respectively, and the life-cycle was completed in 21-25 days at a constant temperature of 15°C, and in 9-11 days at 25 °C.

Because the age-stage, two-sex life table incorporates variations among individuals in developmental rates, stage overlaps in the survival rate can be observed in this study. Both *D. suzukii* and *D. melanogaster* can produce over 10 generations in a single year (Kanzawa 1939; Guo 2007; Steck et al. 2009), both species have overlapping stages and generations in nature.

Although insects are rarely subject to constant temperatures in nature, controlled laboratory studies can provide basic and valuable insights into the population dynamics of a particular species (Summers et al. 1984). The results obtained in this study provide information useful for predicting the population potentials of *D. suzukii* and *D. melanogaster* as key targets in biological control programs. The use of the age-stage, two-sex life table method to study *D. suzukii* and *D. melanogaster* yielded considerably more accurate and useful data than would have been obtained using the female-only age-specific life table. These life tables can be used for population growth projections, designing of mass-rearing programs, and for timing interventions in pest management.

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Table 2. Population parameters for *Drosophila suzukii* and *Drosophila melanogaster*.

Population parameters	*D. suzukii* Mean ± SE	*D. melanogaster* Mean ± SE	*P*
Intrinsic of increase (r) (days^{-1})	0.12 ± 0.01	0.17 ± 0.01	0.000
Finite rate of increase (λ) (days^{-1})	1.13 ± 0.01	1.19 ± 0.01	0.000
Gross reproduction rate (GRR) (offspring)	47.01 ± 5.14	70.67 ± 8.36	0.016
Net reproduction rate (R_0) (offspring)	27.57 ± 3.48	38.17 ± 4.16	0.052
Mean generation time (T) (days)	28.05 ± 0.55	21.29 ± 0.63	0.000

References Cited

Bolda, M., Goodhue, R. E., and Zalom, F. G. 2010. SWD: potential economic impact of a newly established pest. Giannini Foundation Agric. Econ. 13: 5-8.

Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. Environ. Entomol. 17(1): 26-34.

Chi, H. 1990. Timing of control based on the stage structure of pest populations: a simulation approach. J. Econ. Entomol . 83(4): 1143-1150.

Chi, H. 1994. Periodic mass rearing and harvesting based on the theories of both the age-specifc life table and the age-stage, two-sex life table. Environ. Entomol. 23: 535-542.

Chi, H. 2012. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. (http://140.120.197.173/Ecology/Download/359 Twosex-MSChart.zip).

Chi, H., and Getz, W. M. 1988. Mass rearing and harvesting based on an age-stage, two-sex life table: a potato tuberworm (Lepidoptera: Gelechiidae) case study. Environ. Entomol. 17(1): 18-25.

Chi, H., and Liu, H. 1985. Two new methods for the study of insect population ecology. Bull. Inst. Zool. Academia Sinica 24(2): 225-240.

Chi, H., and Su, H. Y. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead)(Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer)(Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. Environ. Entomol. 35(1): 10-21.

Dreves, A. J., Walton, V. M., and Fisher, G. C. 2009. A new pest attacking healthy ripening fruit in Oregon: spotted wing Drosophila: *Drosophila suzukii* (Matsumura). Oregon State Univ., Ext. Serv. EM 8991, Corvallis, OR.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. American Naturalist 119: 803-823.

Guo, D. J., Jiang, H., Zhang, Y. H., Zhang, C. L., and Yang, H. B. 2007. Occurrence of *Drosophila melanogaster* and *Drosophila immigrans* in Aba Prefecture. Plant Protect. 33(1): 134-135. In Chinese.

Guo, J. 2007. Bionomics of fruit flies, *Drosophila melanogaster*, damage cherry in Tianshui. Chinese Bull. Entomol. 44(5): 743-745. In Chinese.

Kanzawa, T. 1939. Studies on *Drosophila suzukii* Mats, Abstract of studies on *Drosophila suzukii* Mats. Kofu, Yamanashi Agr. Export Station. 49 pp.

Li, D. Y., Zuo, R., Yuan, J., Xiong, Y., Chen, C. Q., and Xie, S. W. 2005. Injury of fruit fly and its food source in red bayberry. Guizhou Agric. Sci. 33(2): 77-78. In Chinese.

Stark, J. D., and Banks, J. E. 2003. Population-level effects of pesticides and other toxicants on arthropods. Annu. Rev. Entomol. 48(1): 505-519.

Steck, G., Dixon, W., and Dean, D. 2009. Spotted wing Drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), a fruit pest new to North America. Pest Alerts DACS-P-01674 http://www.freshfromflorida.com/pi/pestalerts/pdf/drosophila-suzukii.pdf.

Summers, C., Coviello, R., and Gutierrez, A. P. 1984. Influence of constant temperatures on the development and reproduction of *Acyrthosiphon kondoi* (Homoptera: Aphididae). Environ. Entomol. 13(1): 236-242.

Van Der Linde, K., Steck, G. J., Hibbard, K., Birdsley, J. S., Alonso, L. M., and Houle, D. 2006. First records of *Zaprionus indianus* (Diptera: Drosophilidae), a pest species on commercial fruits from Panama and the United States of America. Florida Entomol. 89(3): 402-404.

Wilcox, B. A., and Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. American Nat. 125(6): 879-887.

Yang, Y. S., Ren, G. Y., Yao, D. F., Li, Y. Q., and Luo, H. B. 1998. Effect of killing *Drosophila melanogaster* with food bait in red bayberry. Guizhou Agric. Sci. 26(3): 25-29. In Chinese.

Zhang, P. F., Mao, Y. R., Yang, R. H., Meng, L. L., Wang, J. Z., and Wei, Y. M. 2010. Biological characteristics of *Drosophila melanogaster*. J. Beijing Univ. Agric. 25(1): 16-19.