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Survival and Reproductive Strategies in Two-Spotted Spider Mites: Demographic Analysis of Arrhenotokous Parthenogenesis of *Tetranychus urticae* (Acari: Tetranychidae)

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Abstract

Tetranychus urticae Koch is a cosmopolitan pest whose rapid developmental rate enables it to produce colonies of thousands of individuals within a short time period. When a solitary virgin female colonizes a new host plant, it is capable of producing male offspring through the arrhenotokous parthenogenesis; once her sons mature, oedipal mating occurs and the female will produce bisexual offspring. To analyze the effect of arrhenotokous reproduction on population growth, we devised and compared separate life tables for arrhenotokous and bisexual populations of *T. urticae* using the age-stage, two-sex life table theory. For the cohort with bisexual reproduction, the intrinsic rate of increase (r), finite rate (λ), net reproductive rate (R_0), and mean generation time (T) were 0.2736 d^{-1}, 1.3146 d^{-1}, 44.66 offspring, and 13.89 d, respectively. Because only male eggs were produced during the first 8 d of the oviposition period and the cohort would soon begin bisexual reproduction, it would be theoretically wrong to calculate the population parameters using the survival rate and fecundity of an arrhenotokous cohort. We demonstrated that the effect of arrhenotokous reproduction could be accurately described and evaluated using the age-stage, two-sex life table. We also used population projection based on life table data, quantitatively showing the effect that arrhenotokous reproduction has on the growth potential and management of *T. urticae*.

Key words: age-stage, two-sex life table, *Tetranychus urticae*, zoogamy, arrhenotoky, oepidal mating

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is a worldwide pest, causing economic damage to many species of crop plants (Helle and Sabelis 1985). So far, >11,745 host plants in 5,380 different geographical localities have been recorded (Migeon et al. 2010). Direct feeding injury caused by *T. urticae* causes a loss of leaf chlorophyll reducing the net photosynthetic rate, resulting in a decrease in crop production, and, ultimately, decline and death of the host plants (Sances et al. 1981, De Angelis et al. 1982, Tomczyk and Kropczynska 1985, Campbell et al. 1990, Park and Lee 2002, Meck et al. 2012). Due to their rapid developmental rate and high fecundity, *T. urticae* is capable of generating high population densities within a very short period of time (Danks 2006, Kavousi et al. 2009). In addition, *T. urticae* has the capacity to produce offspring not only through normal sexual reproduction (zoogamy), but, when necessary, through arrhenotoky. Arrhenotokous reproduction enables a single virgin female mite to initiate a normal bisexual population that can potentially lead to significant economic loss (Toyoshima and Amano 1999). When food resources become scarce, spider mites possess a unique dispersal mechanism of ballooning and crawling, enabling them to exploit new host plants, to disperse over large areas, and to colonize widely separated plants (Hussey and Parr 1963, Jeppson 1975, Bell et al. 2005). The ballooning mites often aggregate to form a "silk ball," which is mainly composed of immature females (Clotuche et al. 2011, 2013). The virgin females establish a new bisexual population by mating with their male offspring, i.e., oedipal mating (Adamson and Ludwig 1993). Another factor favoring the mites' establishment is their ability to survive and develop over a broad temperature range from 10 to 40°C (Liu 1987, Bounfour and Tanigoshi 2001, Praslicka and Huszar 2004). A number of life tables and population parameters of *T. urticae* have been studied using the traditional female age-specific life table theory (Liu 1987, Bounfour and Tanigoshi 2001, Kasap

2004, El-Wahed and El-Halawany 2012, Osman et al. 2012, Riahi et al. 2013). Because female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) ignore the male population and cannot describe the stage differentiation, their applications are limited and will often result in errors (Huang and Chi 2013). To take into account of the contribution of male individuals and the stage differentiation, Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table. To quantitatively analyze the effect of different reproduction strategies, we constructed separate life tables of *T. urticae* cohorts with bisexual and arrhenotokous reproduction using the age-stage, two-sex life table. The data were then used in population projection to determine the potential differences in population growth and management due to the two strategies.

Materials and Methods

Mite Culture and Host Plant Culture
Adults of *T. urticae* were collected from *Hedera helix* L. in Taichung, Taiwan. The runner bean plant, *Phaseolus coccineus* (L.) var. *albonanus* (Bailey), was planted in plastic containers (28 by 19 by 6 cm^3) filled with wet vermiculite, and used as host plants for rearing *T. urticae* in a growth chamber set at $25 \pm 1°C$, $60 \pm 10\%$ relative humidity (RH), and a photoperiod of 12:12 (L:D) h.

Life Table Study
In the life table studies, *T. urticae* were reared on leaf discs (2 cm in diameter) of runner bean. The leaf disc was placed upside down on a water-saturated cotton wool pad in a plastic cup (9 cm in top diameter, 8 cm in bottom diameter, and 5.5 cm in height). A filter paper with a hole (2 cm in diameter in the center) was placed on the leaf disc to form a water-fence and to prevent mites from escaping. All studies were carried out in a growth chamber set at $25 \pm 1°C$, $60 \pm 10\%$ RH, and a photoperiod of 12:12 (L:D) h.

Life Table of Bisexual *T. urticae*
Sixty pairs of *T. urticae* were randomly selected from the mite culture and placed on separate leaf discs. After 24 h, adults were removed, and their eggs placed individually on new leaf discs. In total, 88 eggs were used at the beginning of the life table study. The development stage and survival data were recorded daily, and the leaf discs were replaced with new ones. When adults emerged, virgin male and female mites were paired. The longevity of adults and their daily fecundity were recorded until the death of all individuals. If an individual died during the experiment, another individual of the same sex was obtained from the mass-rearing colony and substituted for mating purposes. Data for drowned or escaped individuals and mites recruited from the mass-rearing colony were excluded from the life table analysis. Eggs laid by the female mites at different ages were kept until all neonates reached the adult stage to determine the sex of the offspring.

Life Table of Arrhenotokous *T. urticae*
Eggs were collected as in the zoogamy life table study. After the emergence of adults, the virgin females were isolated in individual rearing containers, and the fecundity and survival were recorded daily. The development time, survival, and fecundity of a total of 124 females were used for life table analysis. Each new egg laid by the virgin females were transferred to a separate new leaf disc and observed daily until mites reached the adult stage. The first male offspring to reach the adult stage was reintroduced into the box containing its mother and allowed to mate with her. The survival and daily fecundity were recorded until the death of the mother. If a

male died, a new male adult from the offspring of the same female was substituted. Data for individuals that drowned or escaped were excluded from the life table analysis. Eggs produced by females after mating with her son were kept separately and reared to the adult stage to determine the sex of the offspring. According to the procedure suggested by Huang and Chi (2011) and Mou et al. (2015), we used only data from those eggs that successfully developed to the adult stage for the following analysis.

Life Table Analysis
The life history raw data were analyzed according to the age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988, Huang and Chi 2011). The age-stage-specific survival rate (s_{xj}, where x = age, and j = stage), the age-specific survival rate (l_x), the female age-stage-specific fecundity (f_{x5}), the age-specific fecundity (m_x), and the population parameters (R_0, the net reproduction rate; r, the intrinsic rate of increase; λ, the finite rate of increase; T, the mean generation time) were calculated accordingly. The adult preoviposition period (APOP) is considered to be the time duration from the emergence of the adult female to its initial oviposition, while the total preoviposition period (TPOP) was the total time duration from the beginning of the life table study to the female's initial oviposition. To take both sexes into consideration, the age-specific survival rate (l_x) in the age-stage, two-sex life table was calculated as:

$$l_x = \sum_{j=1}^{k} s_{xj} \tag{1}$$

where k is the number of stages. The age-specific fecundity (m_x) was calculated as:

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

The net reproduction rate (R_0) is defined as the mean number of offspring that an individual can produce during its life span. It was calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

The intrinsic rate of increase (r) was estimated using the Euler–Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

with the age indexed from day 0 (Goodman 1982). The finite rate (λ) was calculated as $\lambda = e^r$. The mean generation time (T) is defined as the length of time that is required by a population to increase to R_0-fold of its size at the stable age-stage distribution, and was calculated as:

$$T = \frac{\ln R_0}{r} \tag{5}$$

The age-stage life expectancy (e_{xj}) is the time length that an individual of age x and stage j is expected to survive and it was calculated as:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} s'_{iy} \tag{6}$$

where s'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y and was calculated by assuming

$s'_{xj} = 1$, following the procedures described in Chi (1988) and Chi and Su (2006).According to Fisher (1993), the age-stage reproductive value (v_{xj}) is defined as the contribution of an individual of age x and stage j to the future population. According to Huang and Chi (2011) and Tuan et al. (2014a, b), the reproductive value (v_{xj}) in the age-stage, two-sex life table is calculated as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{k} s'_{iy} f_{iy} \qquad (7)$$

The computer program TWOSEX-MSChart (Chi 2015b) was used for the raw data analysis and calculation of population parameters. The program is available for free download at http://140.120.197.173/ecology. The standard errors of the developmental time, longevity, fecundity, and population parameters were estimated by using the bootstrap method (Efron and Tibshirani 1993, Huang and Chi 2012, Polat Akköprü et al. 2015), with 100,000 bootstraps to obtain stable estimates of standard errors (Akca et al. 2015). The paired bootstrap test was used to compare differences (Efron and Tibshirani 1993).

Population Projection

The life table data of the bisexual and arrhenotokous cohorts generated from this study were used to project the population growth by using the program TIMING (Chi 2015a). The program TIMING is also available for download at the above web site. In projecting the bisexual population growth, the two-sex life table was used to simulate the growth beginning with an initial population of 10 eggs. An identical number of eggs (10) obtained from oedipal mating were also used to project the production of arrhenotokous parthenogenetic individuals using data obtained from the two-sex life table to simulate population growth. To demonstrate the effect that arrhenotokous reproduction has on pest management applications, we also simulated a practical population management situation by assuming an economic threshold value of 400 mites per sample of 40 leaves (see: Wyman et al. 1979, English-Loeb and Hesler 2003, Nyoike and Liburd 2013).

Results

In this study, 10 males and 8 females predeceased their mates in the bisexual cohort. To compensate, 10 males and 8 females were recruited from the mass-rearing colony and placed with the surviving individuals to allow mating. There were significant differences in the preadult developmental times between females and males ($P = 0.0064$) of the bisexual cohort, and also between bisexual and arrhenotokous females ($P < 0.0001$) of *T. urticae*. The female adult longevity of the bisexual cohort was significantly longer than that of the arrhenotokous cohort ($P < 0.0001$); no difference was found, however, in the adult longevity between females and males in the bisexual cohort ($P = 0.1044$; Table 1). The length of the APOP required for producing female offspring was significantly shorter ($P = 0$) in bisexual than in arrhenotokous reproduction. Both the APOP and TPOP needed for producing male offspring in arrhenotokous production were significantly shorter than those in bisexual reproduction ($P = 0$). In contrast, both the APOP and TPOP for producing female offspring were much longer in the arrhenotokous group than those with bisexual reproduction ($P = 0$). There was no difference in the TPOP in producing female and male offspring in bisexual individuals ($P = 0.4996$). In the bisexual cohort, the two oviposition periods for producing female offspring were significantly longer than they were for producing

male offspring ($P = 0.0273$). The oviposition periods for producing female and male offspring in the bisexual cohort were significantly longer than those in the arrhenotokous cohort ($P < 0.05$).

There was clear overlapping in the age-stage survival curves (s_{xj}) between successive stages, demonstrating the variable developmental rates occurring among *T. urticae* individuals of both reproductive types (Fig. 1). There were separate curves for the female and male adults in the bisexual cohort (Fig. 1A), but only the single female adult curve in the arrhenotokous cohort (Fig. 1B). The age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of *T. urticae* are plotted in Fig. 2. In bisexual reproduction, females began to produce male and female offspring at age 9 d with the daily fecundity of producing female offspring being significantly higher than that of producing male offspring (Fig. 2A). In arrhenotokous reproduction, the fecundity curve of the male-only offspring began from age 8 to 15 d, while the female offspring began on age 16 d, i.e., 8 d after oedipal mating (Fig. 2B). Although females in the arrhenotokous reproduction group could produce female offspring beginning with age 16 d, the net maternity ($l_x m_x$) value was very low due to the low survival rate ($l_x = 0.23$) from age 15 d onward (Fig. 2B and Table 1). In bisexual reproduction, females produced an average of 46.3 female and 12.4 male eggs during their lifetime, while arrhenotokous females produced only 2.3 female offspring and 40.7 male offspring (Table 1). Although, prior to oedipal mating, virgin female adults produce only male eggs, they were capable of producing more male eggs than bisexual females. After oedipal mating, the proportion of male eggs decreased with the mother's age; the daily mean fecundity of mated females increased and mainly female eggs were produced (Fig. 2B).

The life table parameters of *T. urticae* with bisexual reproduction are detailed in Table 2. Using the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988), the intrinsic rate of increase (r), finite rate (λ), net reproductive rate (R_0), and mean generation time (T) of the bisexual cohort were 0.2736 d^{-1}, 1.3146 d^{-1}, 44.66 offspring, and 13.89 d, respectively. To determine if the sex ratio of offspring is dependent on female age, we also calculated the population parameters using the theory developed by Huang and Chi (2011); the values for r, λ, R_0, and T were 0.2706 d^{-1}, 1.3107 d^{-1}, 46.28 offspring, and 14.17 d, respectively. There were no significant differences between the values ($P > 0.05$).

When all eggs were included in the calculation of population parameters for the arrhenotokous cohort, the values for r, λ, R_0, and T were 0.3403 d^{-1}, 1.4054 d^{-1}, 45.10 offspring, and 11.19 d, respectively. The values of r, λ, and R_0 were significantly higher than those found in the bisexual cohort ($P < 0.05$), while the mean generation time was shorter than that of the bisexual cohort ($P < 0.05$). When only female eggs were included in the calculation, the values of r, λ, and R_0 were 0.0412 d^{-1}, 1.0420 d^{-1}, and 2.27 offspring, respectively. These values were significantly lower than those in the bisexual cohort ($P < 0.05$). The mean generation time (19.87 d) was significantly longer than that of the bisexual cohort as well as the arrhenotokous cohort when calculated using all eggs ($P < 0.05$). Because including total eggs or only female eggs in calculating the population parameters of the arrhenotokous cohort is theoretically wrong, we did not list the above data in Table 2. This will be explained in the Discussion section.

The age-stage life expectancies (e_{xj}) of the bisexual and arrhenotokous cohorts of *T. urticae* are plotted in Fig. 3. The life expectancies at different ages of the bisexual cohort are mostly higher than those in the arrhenotokous cohort. The age-stage reproductive value (v_{xj}) of the bisexual cohort of *T. urticae* is plotted in Fig. 4. Because

Table 1. Mean ($\pm$SE) of preadult and adult developmental time, APOP, TPOP, and oviposition days of zoogamous and arrhenotokous cohorts of *T. urticae* reared on runner beans
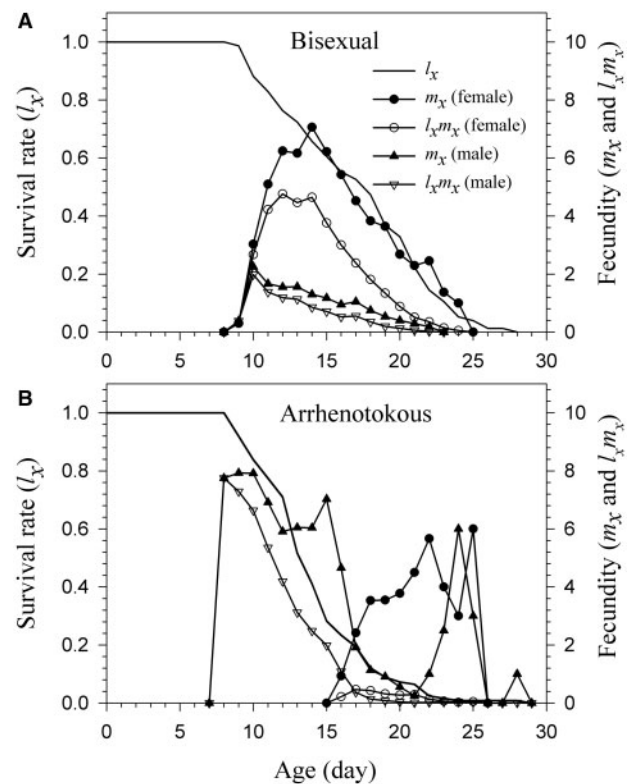
Statistics	Cohort type							
	Bisexual				Arrhenotokous			
	Female		Male		Female		Male	
	n	mean $\pm$ SE	n	mean $\pm$ SE	n	mean $\pm$ SE	n	mean $\pm$ SE
Preadult	58	9.10 ± 0.08Aa	18	8.67 ± 0.14b	124	8.00 ± 0.00B	–	–
Adult	58	8.86 ± 0.59Aa	18	6.44 ± 1.39a	124	6.31 ± 0.33B	–	–
	Production of female offspring		Production of male offspring		Production of female offspring		Production of male offspring	
APOP	51	0.98 ± 0.09aB	51	0.88 ± 0.08aA	17	8.42 ± 0.12aA	114	0.02 ± 0.02bB
TPOP	51	10.12 ± 0.11aB	51	10.02 ± 0.09aA	17	16.41 ± 0.12aA	114	8.02 ± 0.01bB
Total fecundity	58	46.3 ± 4.1AaA	58	12.4 ± 1.3bB	124	2.3 ± 0.8bB	124	40.7 ± 2.4aA
Oviposition days	51	8.25 ± 0.53aA	51	6.71 ± 0.47bA	17	3.00 ± 0.53bB	114	5.31 ± 0.31aB

Means in the same row followed by the same upper case letter denotes no significant difference between the same sex of bisexual and arrhenotokous cohorts, while means followed by the same lower case letter denotes no significant difference between male and female in the same treatments based on the paired bootstrap test.
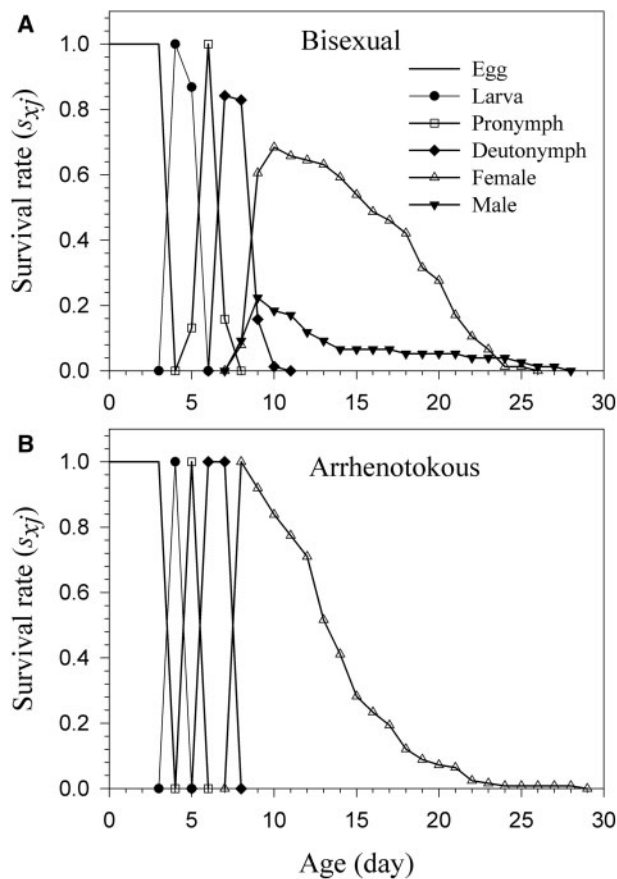
Fig. 1. Age-stage-specific survival rate (s_{xj}) of the parent cohort of bisexual (**A**) and arrhenotokous (**B**) *T. urticae* reared on runner beans.

Fig. 2. Age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of bisexual (**A**) and arrhenotokous (**B**) *T. urticae* reared on runner beans.

calculation of the reproductive value is inapplicable to the arrhenotokous cohort, we did not plot a corresponding v_{xj} curve for it.

The simulated population growths of *T. urticae* with bisexual and arrhenotokous reproduction are plotted in Fig. 5. The bisexual cohort increased much faster than the arrhenotokous cohort—after 50 d, the estimated total population size was almost 2,800,000

individuals, while the total population of the arrhenotokous cohort was ~23,000 individuals. Assuming a control treatment causes 95% mortality to all stages and the economic threshold is 400 mites per sample (40 leaves), the bisexual cohort would require a total of three separate treatments on days 19, 28, and 39 to keep the mites population below the desired economic threshold. However, to maintain the arrhenotokous cohort at the same economic threshold, treatment can be initiated at a much later time period (33 d), and requires only a single additional treatment on day 46 (Fig. 6).

Table 2. Population parameters (mean ± SE) of bisexual cohorts of *T. urticae* reared on runner beans

Parameter	Age-stage model (Chi and Liu 1985)	Age-stage-sex model (Huang and Chi 2011)	*P*
Intrinsic rate of increase (r) (d^{-1})	0.2736 ± 0.0078a	0.2706 ± 0.0059a	0.7728
Finite rate of increase (λ) (d^{-1})	1.3146 ± 0.0102a	1.3107 ± 0.0078a	0.7720
Net reproductive rate (R_0) (offspring)	44.66 ± 4.86a	46.28 ± 4.13a	0.7716
Mean generation time (T) (d)	13.89 ± 0.13a	14.17 ± 0.15a	0.1422

Means in a row followed by the same letter are not significantly different according to paired bootstrap test at 5% significance level.
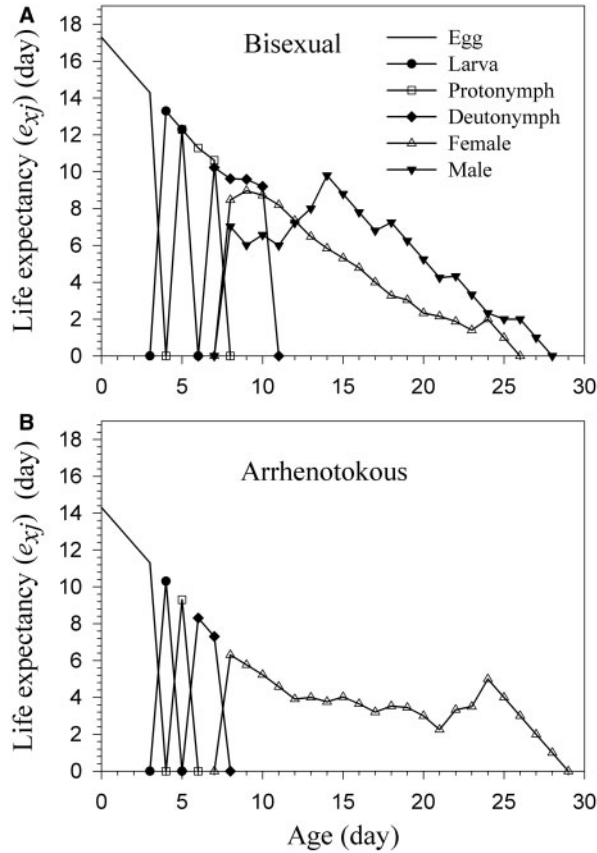

Fig. 3. Age-stage-specific life expectancy (e_{xj}) of bisexual (**A**) and arrhenotokous (**B**) *T. urticae* reared on runner beans.
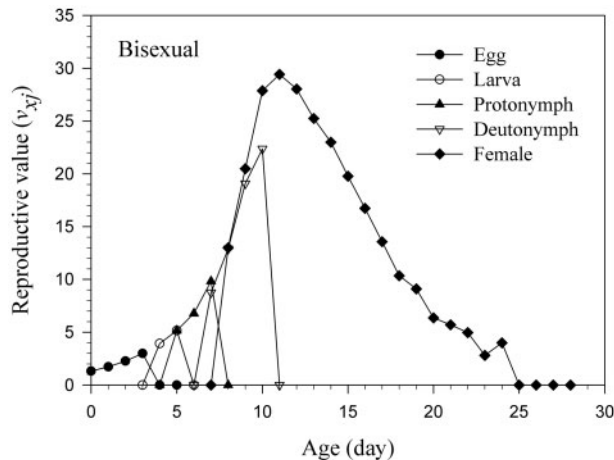

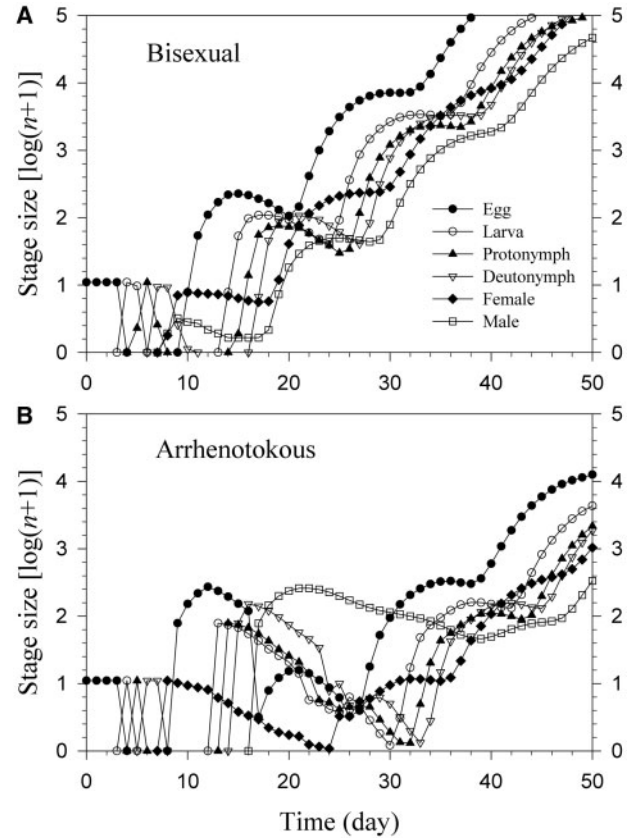**Fig. 4.** Age-stage-specific life expectancy (v_{xj}) of bisexual *T. urticae* reared on runner beans.

Fig. 5. Simulated population growth of *T. urticae* reared on runner beans with an initial population of 10 eggs. (**A**) Bisexual reproduction. (**B**) Arrhenotokous reproduction at the beginning and bisexual reproduction after oedipal mating.

Discussion

Arrhenotokous parthenogenesis is a phenomenon that enables a virgin female to initiate and build a bisexual population. This study thoroughly describes and compares the demographic characteristics of separate populations of bisexual and arrhenotokous *T. urticae* by using the age-stage, two-sex life table. The results illustrate the superiority of the age-stage, two-sex life table over traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993); allow for a thorough and detailed description of demographic variables by including male individuals and stage differentiation; and avoid many of the problems inherent to the female age-specific life tables as discussed by Huang and Chi (2012). Because variable developmental rates among individuals are essentially universal to all arthropod species, and the role of male individuals in two-sex populations is often substantial, traditional female age-specific life tables are incapable of producing satisfactory demographic
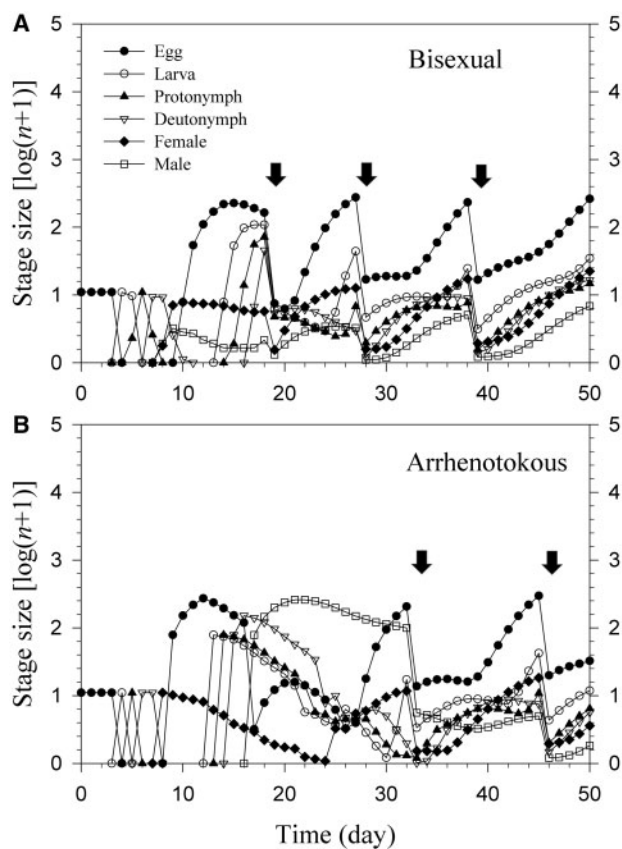
Fig. 6. Simulation of control of *T. urticae* reared on runner beans with an initial population of 10 eggs and economic threshold of 400 mites. (**A**) Three treatments (arrows) are needed to control cohort with bisexual reproduction. (**B**) Two treatments are needed to control a cohort with arrhenotokous reproduction at the beginning and bisexual reproduction after oepidal mating.

predictions (Yu et al. 2005, Kavousi et al. 2009, Huang and Chi 2012).

Population parameters are calculated for a population by assuming it attains a stable age-stage distribution as time approaches infinity, but as only male offspring are present before oedipal mating in arrhenotokous populations, it is invalid to calculate population parameters for these cohorts. Therefore, the values obtained for the estimation of population parameters, r, λ, and R_0 (i.e. 0.3403 d^{-1}, 1.4054 d^{-1}, and 45.10 offspring when all eggs were included; and 0.0412 d^{-1}, 1.042053 d^{-1}, and 2.27 offspring when only female eggs were included) are illegitimate overestimates or underestimates. Using similar reasoning, it would be inappropriate to calculate the reproductive value for the arrhenotokous cohort.

By using the age-stage, two-sex life table, we illustrated the differences in life expectancies between the arrhenotokous and bisexual cohorts (Fig. 3). These differences consequently lead to the differences in population growth as well as in management strategies (Figs. 5 and 6).

The life table is one of a few theories in ecology with a solid mathematical base. Unfortunately, however, mathematical errors in published life tables are not uncommon. According to accepted life table theory, if $R_0 > 1$, then $r > 0$ and $\lambda > 1$; if $R_0 = 1$, then $r = 0$ and $\lambda = 1$; if $R_0 < 1$, then $r < 0$ and $\lambda < 1$ (Lotka 1907, Lewis 1942, Huang and Chi 2012). As an example, in the study of *Bactrocera cucurbitae* Coquillett reported by Vargas et al. (1997), the value for r was −0.0003, and R_0 was 1.5. Such discrepancies are mainly due

to the application of the female life table theory on a bisexual population, and the fecundity being calculated based on the adult age (Huang and Chi 2012). The results of the present study are entirely consistent with above the theoretical relationship (Table 2). Another important consideration to keep in mind is that the age of first reproduction is an important factor in the intrinsic rate (Lewontin 1965). Roy et al. (2011) reported on the life history parameters of the mite *Petrobia harti* (Ewing) (Acari: Tetranychidae). In their report, the preadult duration was ∼10 d (Table 1 and Fig. 2 of Roy et al. (2011)), the preadult survival rate was ca. 21% (Tables 2–4 of Roy et al. (2011)), and the mean fecundity was 6.75 eggs, while the intrinsic rate was unrealistically calculated as high as 0.365 d^{-1} (Table 5 of Roy et al. (2011)). Zou et al. (2015) reported the preadult duration (20.58 d), preoviposition period (5.94 d), mean fecundity (229.16 eggs), and preadult survival rate (0.81) of *Arma chinensis* (Fallou) (Heteroptera: Pentatomidae) (Table 5 of Zou et al. (2015)), with a surprisingly high intrinsic rate of increase of 0.4441 d^{-1}. The extraordinarily high intrinsic rates noted in Roy et al. (2011) and Zou et al. (2015) can be readily disproven by using the equation suggested by Akca et al. (2015).

In our results, the intrinsic rate of increase ($r = 0.2736$ d^{-1}) at 25°C was higher than the values reported by Bounfour and Tanigoshi (2001; $r = 0.188$ d^{-1}) and Kavousi et al. (2009; $r = 0.159$ d^{-1}). This difference could be attributable to the choice of host plant, rearing conditions, or both. Mou et al. (2015) showed that if the hatch rate was constant for all eggs laid by females at different age, using hatchable eggs versus using all eggs generated the same estimates of population parameters. They then demonstrated that if the hatch rate varies with the maternal age, using only hatchable eggs can accurately estimate the population parameters. Similarly, if the preadult mortality is constant for all eggs laid by females at different ages, using eggs surviving to the adult stage will not affect the population parameters. However, if the preadult mortality varies with eggs laid by female at different age, using eggs surviving to the adult stage will give accurate estimates. Proof similar to that of Mou et al. (2015) can be easily derived. Accordingly, we only used the eggs that developed to the adult stage for the parent cohort and for determining the daily fecundity in the life table analysis. In other words, we excluded the preadult mortality from both the parent cohort and the daily fecundity calculations. We used the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) to calculate the population parameters of *T. urticae* and determined the population parameters r, λ, R_0, and T of the bisexual cohort to be 0.2736 d^{-1}, 1.3146 d^{-1}, 44.66 offspring, and 13.89 d. To detect any possible effect of variability of the offspring sex ratio on population parameters, we also used the method of Huang and Chi (2011) to calculate the population parameters and obtained the values of r, λ, R_0, and T of the zoogamy cohort as 0.2706 d^{-1}, 1.3107 d^{-1}, 46.28 offspring, and 14.17 d. There were no significant differences in the results obtained using the two procedures described by Chi and Liu (1985) and Huang and Chi (2011), showing that the sex ratio did not vary significantly among eggs produced by females at different ages.

The formation of "silk balls" is important for the dispersal of *T. urticae* mites Clotuche et al. (2011, 2013). The composition of the mite aggregation within the "silk balls" is critical in determining the success or failure in establishing new colonies. In our study, we dissected three of the mite silk balls and found the mean number of mites within a ball was 349.7 immature and 15.7 mature individuals. These numbers were similar to those reported by Clotuche et al. (2011; 418 immature and 6 mature individuals). Rearing the immature individuals to adults and calculating the sex ratio of each

silk ball showed that there were an average of 317.3 females and 1.7 males per silk ball (Lin 2014). It is reasonable to expect that virgin females from these and similar silk balls would initially produce only male eggs, and, later, produce female eggs after oedipal mating. This study demonstrates that arrhenotokous parthenogenesis allows *T. urticae* to find new colonies from a single virgin female, but there is a "time lag" before successful oedipal mating occurs. As a result, a newly established arrhenotokous population of *T. urticae* increases at a much slower rate than a sexually generated population. Consequently, the number of acaricide applications needed to control an arrhenotokous population would be limited to two, compared with a bisexual population, which would need to be controlled much earlier and with more applications.

By using the age-stage, two-sex life table, we could quantitatively simulate the effect of arrhenotokous reproduction on the population size and stage structure of *T. urticae* mites. English-Loeb and Hesler (2003) recommended an economic threshold of five mites per leaf for perennial strawberries. Nyoike and Liburd (2013) recommended an action threshold level of <80 mites per strawberry leaf for temperatures >18°C. Wyman et al. (1979) reported an acaricide application at a density of 50 mites per strawberry leaflet would provide effective control. Because bisexual and arrhenotokous reproduction do significantly affect the life table parameters and potential population growth, this effect should be taken into consideration in strategizing a pest management program. In this study, we demonstrated the importance of properly analyzing the demographics of arrhenotokous reproduction as well as the need for including this data in planning appropriate insect management programs. We also demonstrated the theoretical illegitimacy of calculating population parameters when male eggs are included at the beginning of arrhenotokous parthenogenesis.

Acknowledgments

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