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Postprint: Establishment of a Life Table for Offspring Populations of Western Flower Thrips (Frankliniella occidentalis) Reproduced via Arrhenotoky

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Abstract

Parthenogenesis represents an important reproductive strategy in the western flower thrips, Frankliniella occidentalis. Previous studies have demonstrated that under elevated temperature conditions, female survival rates substantially exceed those of males. To investigate the potential for offspring to establish populations when only female western flower thrips produce males via parthenogenesis following high-temperature treatment, two experimental protocols were established: (1) individual female thrips were subjected to high temperature (45 ℃, 2 h) and subsequently produced male progeny (F1 generation) through arrhenotokous parthenogenesis, which were then backcrossed with their maternal parent to generate the F2 generation; (2) multiple female thrips were subjected to high temperature (45 ℃, 2 h) and produced male progeny (F1 generation) through arrhenotokous parthenogenesis, which subsequently mated with multiple parental females under coexistence conditions to produce the F2 generation. Life tables for the F2 experimental populations were constructed for both treatment regimes. The results indicated that offspring production was successful through mating between maternal females and male progeny under both treatment modes. The female-to-male sex ratio in the F2 generation derived from backcrossing male F1 individuals with their maternal line was 1.05:1, whereas the sex ratio of the F2 generation produced through mating under coexistence with multiple parental females was 1.55:1. The mean fecundity per female (F) and intrinsic rate of increase (rm) in the F2 generation from the maternal backcross treatment were significantly lower than those from the multiple parental female coexistence treatment (P<0.05). The mean developmental duration of each instar, the mean preoviposition period and mean total preoviposition period (two reproductive parameters), and the net reproductive rate (R0) and mean generation time (T) (two population parameters) were significantly prolonged in the former compared to the latter ($P<0.05$); additionally, no significant difference was observed in the finite rate of increase (λ) between the two treatments. These findings demonstrate that western flower thrips can establish populations within a short timeframe under arrhenotokous conditions, exhibiting robust heat resistance and reproductive capacity, thereby providing an ecological basis for its successful invasion.

Full Text

Preamble

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Establishment of Life Tables for Offspring Populations of *Frankliniella occidentalis* Reared Through Arrhenotokous Parthenogenesis*

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Abstract

Parthenogenesis represents a critical reproductive mode for the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). Previous studies have demonstrated that female thrips exhibit significantly higher survival rates than males under high-temperature conditions. To investigate the potential for population establishment when only female individuals survive extreme heat and reproduce via arrhenotokous parthenogenesis (producing male offspring), we conducted two experimental treatments: (1) single female adults were heat-shocked at 45°C for 2 h, then allowed to reproduce parthenogenetically, and their male offspring (F1 generation) were backcrossed with their maternal parent to produce an F2 generation; and (2) multiple female adults were heat-shocked at 45°C for 2 h, reproduced parthenogenetically, and their male F1 offspring were allowed to mate with multiple surviving parental females to produce an F2 generation. Life tables were constructed for both F2 experimental populations. The results revealed that both treatment groups successfully produced fertile offspring. The F2 generation from backcrossing male F1 offspring with their mothers exhibited a female-to-male sex ratio of 1.05:1, whereas the F2 generation from mating male F1 offspring with multiple parental females showed a sex ratio of 1.55:1. The average fecundity per female (F) and intrinsic rate of increase (r) of the F2 generation from the backcross treatment were significantly lower than those from the multiple parental female treatment ($P < 0.05$). Conversely, the mean developmental duration of each instar, adult pre-oviposition period (APOP), and total pre-oviposition period (TPOP) were significantly longer in the backcross group ($P < 0.05$), as were the net reproductive rate (R_0) and mean generation time (T). No significant difference was observed in the finite rate of increase (λ) between the two groups. These findings demonstrate that *F. occidentalis* can rapidly establish populations through arrhenotokous parthenogenesis, exhibiting strong resistance to high temperatures and robust reproductive capacity—ecological traits that likely facilitate its successful invasion. However, the altered sex ratios and reduced fitness parameters observed in the backcross treatment suggest that relying solely on high-temperature control methods may be insufficient for managing this pest.

Keywords
Frankliniella occidentalis; arrhenotokous reproduction; population parameters; life table; F1 generation; F2 generation

Introduction

In recent decades, economic globalization has accelerated the introduction of invasive insects into China through various pathways, causing significant impacts on agriculture, forestry, ecological balance, and human health [1-2]. The successful establishment of invasive insect populations depends on a complex interplay of biotic and abiotic factors, including local climate, resource availability, and interactions with native species [3]. However, an insect' s intrinsic adaptive capacity and reproductive potential often play decisive roles in its invasion success. Notably, many invasive insects exhibit distinctive reproductive strategies post-invasion. Some facultatively parthenogenetic pests, such as the common wasp (*Vespula vulgaris*) and aphids (Aphidoidea), can produce both sexual and parthenogenetic lineages to cope with environmental pressures [4]. The rice water weevil (*Lissorhoptrus oryzophilus*), originally bisexual in its native Mississippi River Basin, has shifted to geographical parthenogenesis in China and other invaded regions [5-6]. Parthenogenesis, which includes both arrhenotoky (male-producing) and thelytoky (female-producing) modes, represents a common reproductive strategy in nature. For instance, many hymenopteran insects such as honeybees (*Apis* spp.) and paper wasps exhibit arrhenotoky, whereas the thrips *Thrips tabaci* (Thysanoptera) reproduces through thelytoky [7]. Thus, the capacity and mode of parthenogenesis significantly influence offspring population establishment.

The western flower thrips, *Frankliniella occidentalis*, employs both arrhenotokous parthenogenesis and sexual reproduction, with sexual reproduction being predominant under normal conditions [8]. Previous research has shown that under identical high-temperature conditions, females from parthenogenetic lines exhibit significantly longer lifespans than those from sexual lines, though oviposition rates remain comparable [9]. Moreover, high temperatures affect males and females differentially; exposure to 33-43°C for 2 h results in significantly higher female survival [10], and our laboratory has previously observed that after treatment at 45°C for 2 h, surviving adults are predominantly female [11]. This raises a critical question: if extreme heat eliminates most males from a population, can the remaining females establish a viable population through parthenogenesis? Furthermore, how would the resulting offspring population differ when these parthenogenetically produced males mate with either their maternal parent or with other surviving females?

To address these questions, we constructed age-stage, two-sex life tables to evaluate the F2 generation produced under two scenarios: (1) male F1 offspring from heat-treated single females backcrossed with their mothers, and (2) male F1 offspring from heat-treated multiple females allowed to mate with multiple surviving parental females. Our objectives were to determine whether *F. occidentalis* can successfully establish populations from single or multiple surviving females and to elucidate the biological mechanisms underlying its invasion success, thereby providing a scientific basis for developing effective management strategies.

Materials and Methods

1.1 Experimental Insects

The *F. occidentalis* colony used in this study was maintained on purple cabbage (*Brassica oleracea*) for multiple generations in the Ecology Laboratory at Qingdao Agricultural University. Rearing conditions were constant at 25°C, 55-60% relative humidity, and a 16:8 h light:dark photoperiod. Newly emerged ($ $24 h) female adults were selected for all experiments.

1.2 Experimental Treatments

High-temperature treatment: Newly emerged female adults were placed in an illuminated incubator at 25°C, which was then heated to 45°C for a 2-h exposure period. Surviving females (designated as the parental generation) were subsequently maintained at 25°C, 55-60% RH, and 16L:8D for further experiments.

Treatment 1 (Mating with multiple parental females): More than 60 heat-treated surviving females were placed in 5 mL centrifuge tubes containing five cabbage discs (1.5 cm diameter) for oviposition. After 24 h, the cabbage discs were transferred to Petri dishes for incubation. Upon hatching, 60 first-instar nymphs were individually transferred to new 5 mL tubes containing fresh cabbage discs. When F1 nymphs developed into male adults, they were paired with surviving heat-treated parental females at a 1:1 ratio. After 24 h of oviposition, the cabbage discs were removed, and newly hatched nymphs were again isolated individually (60 individuals) in 5 mL tubes to establish the F2 generation. Developmental duration and fecundity of the F2 generation were recorded.

Treatment 2 (Backcross with maternal parent): Individual heat-treated surviving females were placed in separate 5 mL centrifuge tubes (each containing one cabbage disc) and sequentially labeled. After 24 h of oviposition, each cabbage disc was transferred to a labeled Petri dish while the corresponding parental female continued to be maintained individually. Upon hatching, one first-instar nymph from each of 60 labeled Petri dishes was isolated in a new 5 mL tube. When these F1 individuals developed into male adults, they were backcrossed with their corresponding labeled maternal parent at a 1:1 ratio. After 24 h of oviposition, the cabbage discs were removed, and newly hatched nymphs were isolated individually (60 individuals) to establish the F2 generation. Developmental duration and fecundity were recorded as in Treatment 1.

Data collection for F2 generation:
- **Developmental duration:** F2 nymphs were observed twice daily to record developmental stage and survival. Fresh food was provided every 2–3 days until adult emergence.
- **Fecundity:** Newly emerged F2 females were paired with males from the same F1 parental group at a 1:1 ratio, and daily oviposition was recorded.

To maintain consistent temperature and humidity within centrifuge tubes, lids were perforated and covered with 200-mesh nylon mesh.

1.3 Data Analysis

All data were analyzed using age-stage, two-sex life table software [12–13]. Developmental duration and adult longevity were further analyzed using SPSS 19.0 (IBM, Armonk, NY, USA). Differences in developmental duration, immature stage length, oviposition, and female longevity between treatments were compared using one-way ANOVA and t-tests. Population parameters including mean adult longevity, APOP, TPOP, net reproductive rate (R_0), intrinsic rate of increase (r), mean generation time (T), and finite rate of increase (λ) were calculated from the life table data. SigmaPlot 12.0 was used to generate graphical outputs including age-stage survival rates (s), age-stage-specific fecundity (f), age-specific survival (l), age-specific fecundity (m), life expectancy (e), and reproductive value (v).

Population parameters were calculated as follows:
- Net reproductive rate: $R_0 = \Sigma l\ m$
- Intrinsic rate of increase: r was solved iteratively from Σl m e^(-r (x+1)) = 1
- Mean generation time: $T = (\ln R_0)/r$
- Finite rate of increase: λ = e^(r)

Results

2.1 Development of the F2 Generation from Mating Between Parental Parthenogenetic F1 Males and Females

As shown in Table 1 , when parental female adults were treated at 45°C for 2 h, both mating treatments successfully produced F2 offspring. However, all developmental stages were significantly longer in the backcross treatment compared to the multiple parental female treatment (egg: t = 4.515, df = 118, $P < 0.0001$; first instar: t = 8.737, df = 86, $P < 0.0001$; second instar: t = 3.996, df = 82, $P < 0.0001$; prepupa: t = 3.391, df = 80, P = 0.01; pupa: t = 2.1890, df = 80, $P < 0.05$). The total immature period was also significantly prolonged in the backcross group (t = 9.645, df = 78, $P < 0.0001$). These results indicate that the backcross treatment had a greater impact on development, likely due to incompatibility between F1 males and their maternal parents.

Table 1 Developmental durations of the F2 offspring of *Frankliniella occidentalis* under arrhenotokous reproduction conditions at high temperature (45°C)

Insect stage	Mating with multiple parental females (d)	Backcross with maternal parent (d)
Egg	3.28 ± 0.059	3.67 ± 0.061***
1st instar	2.26 ± 0.059	3.07 ± 0.073***
2nd instar	2.60 ± 0.072	3.16 ± 0.070***
Prepupa	1.18 ± 0.058	1.53 ± 0.069**
Pupa	2.52 ± 0.080	2.82 ± 0.078*
Immature	11.75 ± 0.071	14.12 ± 0.155***

Data were analyzed using t-test. Values are mean ± SE. Asterisks indicate significant differences: $P < 0.05$, **$P < 0.01$,** *$P < 0.001$.*

2.2 Longevity and Fecundity of F2 Female Adults

The pre-oviposition period (APOP) refers to the interval between adult emergence and first oviposition, while the total pre-oviposition period (TPOP) spans from egg hatch through development to first oviposition. As shown in Table 2 , the APOP (3.13 d) and TPOP (17.19 d) of F2 females from the backcross treatment were significantly longer than those from the multiple parental female treatment (APOP: 2.85 d; TPOP: 14.45 d) (APOP: t = 2.845, df = 38, $P < 0.05$; TPOP: t = 7.570, df = 38, $P < 0.0001$). Fecundity was also significantly lower in the backcross group (44.45 eggs per female) compared to the multiple parental female group (62.25 eggs per female) (t = 2.168, df = 30, $P < 0.05$). No significant difference was observed in female longevity between treatments. These reproductive parameters collectively indicate that the backcross treatment exerted greater adverse effects on F2 generation fitness.

Table 2 Reproduction parameters of the F2 offspring of *Frankliniella occidentalis* under arrhenotokous reproduction conditions at high temperature (45°C)

Reproduction parameter	Multiple parental females	Backcross with maternal parent
APOP (d)	2.85 ± 0.82	3.13 ± 0.06*
TPOP (d)	14.45 ± 0.27	17.19 ± 0.20***
Eggs per female	62.25 ± 5.65	44.45 ± 2.69*
Female longevity (d)	18.90 ± 1.21	17.55 ± 0.79

2.3 Population Parameters of the F2 Generation

Age-stage, two-sex life table analysis yielded population parameters including fecundity (F), mean generation time (T), net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ). As shown in Table 3 , both treatments produced R_0 values greater than zero, indicating positive population growth. However, the multiple parental female treatment yielded a lower R_0 (20.70) compared to the backcross treatment (22.97), suggesting that the backcross group could potentially increase 23-fold per generation. The intrinsic rate of increase was higher in the multiple parental female treatment (r = 0.1468) than in the backcross treatment (r = 0.1339), indicating superior population growth potential. The mean generation time was shorter in the multiple parental female treatment, while its finite rate of increase was higher. These results demonstrate that the multiple parental female treatment produced offspring with faster population growth rates.

Table 3 Population parameters of the F2 offspring of *Frankliniella occidentalis* under arrhenotokous reproduction conditions at high temperature (45°C)

Population parameter	Multiple parental females	Backcross with maternal parent
Net reproductive rate (R_0)	20.70 ± 4.24***	22.97 ± 3.18
Intrinsic rate of increase (r)	0.1468 ± 0.0106***	0.1339 ± 0.0061
Mean generation time (T)	20.49 ± 0.55	23.32 ± 0.49***
Finite rate of increase (λ)	1.1582 ± 0.0122	1.1434 ± 0.0069

2.4 Life Table Analysis of the F2 Generation

Age-stage survival rate (s): Figure 1 [Figure 1: see original paper] illustrates the age-stage survival curves for F2 offspring. The s value represents the probability that an individual survives from birth to age x and stage j. Since thrips eggs are difficult to observe visually, egg survival was assumed to be 100%. Survival rates declined progressively through developmental stages in both treatments. However, post-eclosion survival differed markedly between treatments: female survival was 33.3% over 39 days in the multiple parental female treatment, compared to 51.6% over 42 days in the backcross treatment. Male survival did not differ significantly between treatments. The overlapping and stepwise nature of the curves reflects asynchronous development among individuals (Figure 1 [Figure 1: see original paper]).

Age-specific survival and fecundity: Figure 2 [Figure 2: see original paper] presents age-specific survival rate (l), female fecundity (f), age-stage fecundity (m), and age-specific maternity (l m). The l curve represents a simplified summary of survival across all stages. The f value (daily eggs per total individuals) exceeded m (daily eggs per total individuals including immatures) during the period when some individuals had matured while others remained immature; the curves converged once all individuals reached adulthood. Both treatments exhibited normal distributions for f , m , and l m , indicating that daily oviposition rates increased initially then declined. The reproductive period was significantly longer in the multiple parental female treatment, suggesting that backcrossing exerted greater negative impacts on F2 reproductive output.

Life expectancy (e): Figure 3 [Figure 3: see original paper] shows age-stage-specific life expectancy. Newborn eggs had life expectancies of 24 days (multiple parental female treatment) and 29 days (backcross treatment), indicating differential effects on early survival. From the prepupal stage onward, the backcross treatment showed a marked decline in life expectancy relative to the multiple parental female treatment. Male adults exhibited higher e   values than females in both treatments, with the backcross group showing higher values for both sexes.

Reproductive value (v): Figure 4 [Figure 4: see original paper] depicts the reproductive value curves, which quantify an individual' s expected contribution to future population growth. Female v   values peaked then declined in both treatments, with maximum contributions occurring at day 15 (28 eggs) in the multiple parental female treatment and day 19 (23 eggs) in the backcross treatment. The reproductive value declined to zero by day 42 in the multiple parental female treatment versus day 38 in the backcross treatment, further indicating the greater reproductive impact of backcrossing.

2.5 Sex Ratio of the F2 Generation

The sex ratio of F2 offspring was significantly altered by the mating treatment. The multiple parental female treatment produced a nearly equal sex ratio (: = 1:1), while the backcross treatment yielded a female-biased ratio of 1.55:1. This demonstrates that mating with multiple parental females had a more pronounced effect on offspring sex ratio than maternal backcrossing.

Discussion and Conclusion

Reproductive capacity is a fundamental factor regulating insect population dynamics [14], and reproductive mode serves as a primary determinant of this capacity. Numerous insects capable of sexual reproduction can also reproduce parthenogenetically [15-16], including the desert locust (*Schistocerca gregaria*) and the rotifer *Brachionus calyciflorus* [17-18]. Parthenogenesis facilitates colonization because a single female transported to a new region can potentially establish a population. Research has shown that under adverse conditions, rotifers capable of both reproductive modes will switch to parthenogenesis to maintain population stability [18]. Arrhenotoky represents an important parthenogenetic strategy that can stabilize population numbers, though it may cause heritable changes in life history and population characteristics that affect subsequent generations [19].

Under environmental stress, not all females successfully mate, particularly in species where females exhibit higher stress tolerance than males. In such scenarios, female-only populations may persist. How do these populations sustain themselves? Some species establish new colonies through parthenogenesis: in Japan, unpaired female termites (*Reticulitermes speratus*) may either pair with other females or nest alone, subsequently reproducing parthenogenetically to found new colonies [20]; similarly, male honeybees from arrhenotokous lines can backcross with queens to produce viable offspring [21]. However, other species like *Reticulitermes aculabialis* can reproduce through female-female mating only when multiple females are present, as single females cannot produce offspring [22]. These examples illustrate that the capacity to establish populations via parthenogenesis depends heavily on species-specific biology.

The western flower thrips is a major invasive pest in China whose cryptic feeding behavior makes it particularly damaging. Current management relies heavily on physical methods such as high-temperature treatment [23]. While previous studies have examined parthenogenesis and sexual reproduction at 25°C [8-9], our findings reveal limitations of single-application high-temperature control (45°C for 2 h). Surviving females, particularly those that are heat-tolerant, can establish F1 male populations through either single-female or multiple-female arrhenotoky. These females maintain strong fecundity, with oviposition peaks occurring at 15–20 days post-eclosion and continuous egg production beginning 3 days after emergence until death. This enables them to engage in sexual reproduction with F1 males, though this process alters population characteristics, most notably the sex ratio. The F2 sex ratios observed (approximately 1:1) were significantly lower than the natural ratio of 2.69:1 reported previously [24], resembling findings in *Bemisia tabaci* where high temperatures increased male proportions in the F1 generation [25]. Such sex ratio shifts may enhance sexual reproductive potential and could trigger population outbreaks. Therefore, the effectiveness of single-application high-temperature treatments (45°C for 2 h) requires careful reevaluation, and integrated control strategies should be developed.

The capacity for both parthenogenesis and sexual reproduction likely represents an adaptive evolutionary outcome [26]. While parthenogenesis can rapidly produce large numbers of offspring in favorable environments, it suffers from reduced genetic diversity that may limit adaptive potential. Interestingly, parthenogenetic species continue to evolve; for example, recombination rates do not decline in parthenogenetic honeybees [27], though the underlying mechanisms remain unclear. For invasive species like *F. occidentalis* that can switch between reproductive modes, investigating the genetic and physiological differences between parthenogenetic and sexual reproduction may provide crucial insights into how maternal parthenogenesis can still yield viable, adaptable offspring populations.

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