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# Linking life table and predation rate for evaluating temperature effects on *Orius strigicollis* for the biological control of *Frankliniella occidentalis*

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**Introduction:** *Orius* spp. are generalist predators released in horticultural and agricultural systems to control thrips. Understanding the effects of temperature on the development, predation rate, and population dynamics of *Orius* is essential for identifying the optimal timing of *Orius* release for establishing an adequate population to facilitate synchrony with thrips population growth and to prevent thrips outbreaks. The biological control efficiency of natural enemies as well as predator–prey relationships can be precisely described by integrating life table parameters and the predation rate.

**Methods:** In this study, the demographic features of *Orius strigicollis* fed on 2nd instar nymphs of western flower thrips (WFT), *Frankliniella occidentalis*, were compared at 18.5, 23.5, 27, and 33°C using the TWOSEX-MSChart program. The CONSUME-MSChart program was used to examine predation rates under different temperatures (18.5, 23.5, and 27°C).

**Results:** The results showed no significant difference in fecundity among those reared at 18.5, 23.5, and 27°C, but fecundity at these temperatures was significantly higher than that at 33°C. The intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), and net reproduction rate ( $R_0$ ) were the highest at 27°C. The net predation rate ( $C_0$ ) and transformation rate ( $Q_p$ ) were significantly higher at 18.5°C ( $C_0 = 168.39$  prey/predator,  $Q_p = 8.22$ ) and 23.5°C ( $C_0 = 140.49$  prey/predator,  $Q_p = 6.03$ ) than at 27°C ( $C_0 = 138.39$  prey/predator,  $Q_p = 3.81$ ); however, the finite predation rate ( $\omega$ ) showed the opposite trend. In addition to temperature, the stage of *O. strigicollis* at release can affect population dynamics.

**Discussion:** Our study showed that temperature influenced the demographic traits and predation rates of *O. strigicollis*. When planning a release, the stage of *O. strigicollis* and temperature should be taken into account to establish an adequate population for the control of WFT.

## KEYWORDS

predator, temperature, release, augmentative biological control, thrips

## Introduction

The western flower thrips (WFT), *Frankliniella occidentalis* Pergrande, is a notorious agricultural and horticultural insect pest worldwide; this species harms plants directly through feeding and oviposition and indirectly through the transmission of plant viruses (Reitz et al., 2011, 2020; Gao et al., 2012; Mouden et al., 2017; He et al., 2020; Wu et al., 2021). Damage by WFT may reduce crop quantity and quality, resulting in severe economic losses for farmers (He et al., 2020; Reitz et al., 2020; Avellaneda et al., 2021). The WFT is a typical *r*-strategist insect pest with a small size, cryptic behavior, and a rapid reproduction rate, and these characteristics make WFT develop resistance to chemical pesticides (Reitz et al., 2011, 2020; Gao et al., 2012; Wu et al., 2021). Moreover, long-term and inappropriate use of chemical pesticides often results in food safety problems, pesticide resistance, and negative impacts on non-target species (Bielza, 2008; Gao et al., 2012; Mouden et al., 2017). Ecology-based methods to reduce insect pest injury in agricultural systems are essential to achieve integrated pest management (Lewis et al., 1997; Demirozer et al., 2012; Mouden et al., 2017). Hence, alternative measures to reduce reliance on chemical insecticides, such as the release of biological control agents, have become important (Mouden et al., 2017; Reitz et al., 2020; Wu et al., 2021).

As biological control agents of key pests that infest cultivated crops, insect predators and parasitoids provide valuable ecosystem services (Landis et al., 2000; Lu et al., 2012; Zhao et al., 2017). The periodic release of natural enemies, also known as augmentative biological control (ABC), is commonly used in greenhouse biological control programs (Messelink et al., 2014; van Lenteren et al., 2018). Minute pirate bugs, *Orius* spp., are useful natural enemies that prey on small and soft-bodied insect pests of agricultural and horticultural crops (De Clercq et al., 2014; Bonte et al., 2017; Zhao et al., 2017; Peterson et al., 2018). Feeding on non-prey food, such as pollen, allows *Orius* to survive when prey are scarce or absent, promoting sustainable insect pest control (Hinds and Barbercheck, 2020; Mendoza et al., 2021, 2022). Accordingly, these generalist predators are preferred in ABC programs and are now mass-reared for pest control purposes, particularly thrips control (Mouden et al., 2017; van Lenteren et al., 2018; Hinds and Barbercheck, 2020; Reitz et al., 2020; Mendoza et al., 2021). Indeed, releasing *O. insidiosus* at a 1:40 WFT ratio can nearly eliminate a WFT population within days (Funderburk et al., 2000). Thus, a comprehensive understanding of the characteristics of *Orius* is crucial for the development and promotion of this natural enemy as a method of thrips control.

Temperature is an important environmental factor that influences both the biological and ecological characteristics

of natural enemies (Wallner, 1987; Sørensen et al., 2013; Helgadóttir et al., 2017) as well as the effectiveness of biological control (Montserrat et al., 2013; Boukal et al., 2019; Bai et al., 2022). In mass-rearing programs, natural enemies are reared indoors at an optimum and constant temperature to ensure rapid and efficient production, but these conditions considerably differ from those of crop systems in the field or greenhouse (Montserrat et al., 2013; Sørensen et al., 2013; Helgadóttir et al., 2017), in which temperatures change with seasonal oscillations and diel activity rhythms. As the temperature has a direct effect on the survival, development, and reproduction of natural enemies (Helgadóttir et al., 2017), population dynamics will be affected by temperature fluctuations (Barton and Schmitz, 2009; Montserrat et al., 2013). Thus, the development, predatory ability, and population dynamics of natural enemies in response to various temperatures must be systematically assessed; these results will facilitate predictions of the ecological effects of climate change on predator-prey interactions (Boukal et al., 2019).

Numerous studies have assessed the influence of temperature on the development, fecundity, and functional response of *Orius* species (Nagai and Yano, 1999; Ohta, 2001; Baniameri et al., 2005; Ballal et al., 2017). Experimental studies on the integrated life table traits and predatory rates of *Orius* species in response to temperature can precisely elucidate the biological control efficiency of *Orius* and predator-prey relationships (Ding et al., 2021). *Orius strigicollis* is a major natural enemy of pests among agroecosystems in southern China, Korea, and Japan (Musolin et al., 2004; Cho et al., 2005; Musolin and Ito, 2008; Ding et al., 2021) that has been mass-reared for thrips control (van Lenteren, 2012; Tuan et al., 2016; van Lenteren et al., 2018). Releasing this biological control agent and establishing an adequate population promotes synchronization with thrips population growth and prevents thrips outbreaks. In this study, to fully understand the effect of temperature on the population dynamics and development of *O. strigicollis*, the demographic characteristics (including development, reproduction, survival, and longevity) of *O. strigicollis* reared at constant temperatures of 18.5–33°C and fed 2nd instar WFT nymphs were quantitatively described using the life table analysis program (TWOSEX-MSChart, Chi, 2022a), which can precisely describe stage differentiation and correctly evaluate the fitness of populations (Chi et al., 2020). The predation rates of *O. strigicollis* fed WFT under different temperature conditions (18.5–27°C) were also evaluated with the CONSUME-MSChart computer program (Chi, 2022b). Additionally, the population growth of *O. strigicollis* under different temperature conditions was projected using the TIMING-MSChart program (Chi, 2022c).

## Materials and methods

### Insects

Western flower thrips were collected from *Cucumis melo* L. grown in the greenhouse at the Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences (39.53 °N, 116.70 °E) in Beijing, China, in 2007 and reared on bean pods (*Phaseolus vulgaris* L.) under laboratory conditions at 26±1°C, with relative humidity (RH) of 60 ± 10% and an L14:D10 photoperiod. *Orius strigicollis* were collected from thrips-damaged pepper (*Capsicum annuum* L.) plants grown in the greenhouse at the Yangdu Experiment Station of Zhejiang Academy of Agricultural Sciences (30.53 °N, 120.68 °E) in Jiaying, Zhejiang Province, China, in 2016 and reared on WFT and bean pods, which were used as a water source and oviposition substrate for *O. strigicollis*. To avoid the negative effects of inbreeding, both WFT and *O. strigicollis* were collected every year from the field to propagate with the laboratory colony.

### Life table and predation rate of *O. strigicollis* under various temperature conditions

*Orius strigicollis* eggs oviposited for 24 h on bean pods were selected and randomly separated into four groups, with 82, 98, 78, and 104 eggs per group. The egg groups were maintained at 18.5, 23.5, 27, and 33°C, respectively, with 60 ± 10% RH and an L16:D8 photoperiod. Every 24 h, the eggs were checked, and for viable eggs, the demographic traits were accurately determined (Mou et al., 2015; Ding et al., 2021). In total, 74 (18.5°C), 88 (23.5°C), 71 (27°C), and 89 (33°C) eggs were used as the initial samples. Newly hatched nymphs were individually transferred to Petri dishes (6 cm in diameter) with a fine brush. Two holes (1 cm in diameter) covered with a fine-mesh screen in the lid of the Petri dish allowed for ventilation. A piece of fresh bean pod (2–3 cm in length) was provided as a water source, and different numbers of 2nd instar WFT were provided as food for *O. strigicollis* nymphs (Ding et al., 2021). To prevent the escape of the WFT from the Petri dish, each dish was sealed with Parafilm. Every 24 h, the developmental stage of the nymphs was observed, and fresh bean pods and WFT were replaced in the Petri dish. Since predatory ability varies with developmental stage in *O. strigicollis*, different numbers of WFT were provided daily: 10 WFT for 1st (N1) and 2nd instar (N2), 15 WFT for 3rd (N3) and 4th instar (N4), and 20 WFT for 5th instar (N5) *O. strigicollis* every day (Ding et al., 2021). The number of WFT provided for *O. strigicollis* every day under various temperature conditions was sufficient. The numbers of WFT consumed by *O. strigicollis* reared at 18.5–27°C were recorded every 24 h.

When the adults emerged, sex was determined. Females and males were paired, and each adult pair was moved into a Petri dish (9 cm in diameter) with a 3 cm-diameter hole on the lid covered with a fine-mesh screen. A fresh bean pod (~6 cm in length) was used as the oviposition substrate, and a sufficient number of thrips (30 WFT) were provided as prey. Fecundity, longevity, and survival were recorded every 24 h, and fresh bean pods and WFT were provided daily. If the number of females exceeded that of males or a paired male died, additional males of the same age from the laboratory colony were paired with the females, but the longevity and the number of consumed WFT were not recorded. If the number of males exceeded that of females or a paired female died, additional females of the same age from the laboratory colony were paired with the males, but female fecundity, longevity, and the number of consumed WFT were not recorded (Ding et al., 2021). The numbers of WFT consumed by adult *O. strigicollis* reared at 18.5–27°C were recorded, and a male-to-female ratio of 1:2 was used to determine the consumption rate of paired adults (Ding et al., 2021).

### Data analysis

#### Life table analysis

The demographic characteristics of *O. strigicollis* fed on WFT in response to temperature were analyzed using the computer program TWSEX-MSChart (Chi, 2022a) based on the age-stage, two-sex life table theory (Chi and Liu, 1985; Chi, 1988; Chi et al., 2020). The age-stage-specific survival rate ( $s_{xj}$ ) (where  $x$  indicates age and  $j$  indicates stage), age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), net maternity ( $l_x m_x$ ), age-stage-specific fecundity ( $f_{xj}$ ), intrinsic rate of increase ( $r$ ), net reproduction rate ( $R_0$ ), finite rate of increase ( $\lambda$ ), and mean generation time ( $T$ ) were calculated according to Chi and Liu (1985). The age-stage life expectancy ( $e_{xj}$ ) was calculated according to Chi and Su (2006), and the age-stage reproductive value ( $v_{xj}$ ) was calculated according to Tuan et al. (2014a,b).  $R_0$  was calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (1)$$

The interactive bisection method and the Euler-Lotka equation (Goodman, 1982) were used to estimate  $r$ :

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (2)$$

$\lambda$  and  $T$  were calculated as follows:

$$\lambda = e^r \quad (3)$$

$$T = \frac{\ln(R_0)}{r} \quad (4)$$

The variances and standard errors of all of the parameters were estimated with 100,000 resamplings in the TWOSEX-MSChart program. Significant differences in the parameters under different temperature conditions were determined using the paired bootstrap test based on the 95% confidence intervals.

### Predation rate analysis

The predation rates of *O. strigicollis* at different temperatures (18.5, 23.5, and 27°C) were calculated according to Chi and Yang (2003) using the CONSUME-MSChart computer program (Chi, 2022b). The age-specific predation rate ( $k_x$ , the number of prey consumed by the surviving *O. strigicollis* at age  $x$ ) was calculated as follows:

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \quad (5)$$

where  $c_{xj}$  is the number of 2nd instar nymphs of WFT consumed by *O. strigicollis* at age  $x$  and stage  $j$ , which was calculated as follows:

$$c_{xj} = \frac{\sum_{i=1}^{n_{xj}} d_{xj,i}}{n_{xj}} \quad (6)$$

where  $d_{xj,i}$  is the number of WFT consumed by the  $i$ th *O. strigicollis* at age  $x$  and stage  $j$ , and  $n_{xj}$  is the number of *O. strigicollis* surviving to age  $x$  and stage  $j$ . The age-specific net predation rate ( $q_x$ ) was calculated as follows:

$$q_x = l_x k_x = \sum_{j=1}^{\beta} s_{xj} c_{xj} \quad (7)$$

The cumulative net predation rate ( $C_x$ ) (the number of prey consumed per predator from birth to age  $x$ ) and the net predation rate ( $C_0$ ) (the total number of prey consumed per predator over its lifetime) were calculated as follows:

$$C_x = \sum_{i=0}^x q_i = \sum_{i=0}^x l_i k_i \quad (8)$$

$$C_0 = \sum_{i=0}^{\infty} l_x k_x \quad (9)$$

The transformation rate ( $Q_p$ ) indicates the number of prey consumed to produce one offspring and was calculated as follows:

$$Q_p = \frac{C_0}{R_0} \quad (10)$$

Following Ding et al. (2021), the predation rate of each predator in stage  $j$  ( $P_j$ ) was calculated as follows:

$$P_j = \frac{\sum_{i=1}^{n_j} p_{ij}}{n_j} \quad (11)$$

where  $p_{ij}$  is the number of prey killed by predator  $i$  in stage  $j$  and  $n_j$  is the number of predators that survived in stage  $j$ .

The daily predation rate per predator in stage  $j$  ( $D_j$ ) (Ding et al., 2021) was calculated as follows:

$$D_j = \frac{\sum_{x=a}^b c_{xj} s_{xj}}{\sum_{x=a}^b s_{xj}} \quad (12)$$

where  $a$  and  $b$  indicate the first and last ages of stage  $j$ , respectively. The finite predation rate ( $\omega$ ) (Yu J. K., et al., 2013) was calculated as follows:

$$\omega = \lambda \sum_{i=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj} \quad (13)$$

where  $a_{xj}$  indicates the proportion of individuals at age  $x$  and stage  $j$ .

Significant differences in the parameters under different temperature conditions were determined using the paired bootstrap test in the TWOSEX-MSChart program (Chi, 2022a).

### Population projection

The population growth of *O. strigicollis* under different temperature conditions was projected using the computer program TIMING-MSChart (Chi, 2022c). All of the figures were drawn with GraphPad Prism software (8.0 version).

## Results

### Life table of *O. strigicollis* under different temperatures

The temperature had a strong effect on the developmental duration of *O. strigicollis*, as the developmental duration shortened with an increase in temperature (Table 1). At 18.5°C, the developmental durations of both *O. strigicollis* eggs and nymphs were the longest, followed by those at 23.5°C and 27°C. At 33°C, the developmental durations of *O. strigicollis* eggs and nymphs were the shortest, indicating a fast development rate (Supplementary Table 1). The adult longevity of *O. strigicollis* was not significantly different between the 23.5 and 27°C treatments; both were significantly lower than that at 18.5°C but longer than that at 33°C.

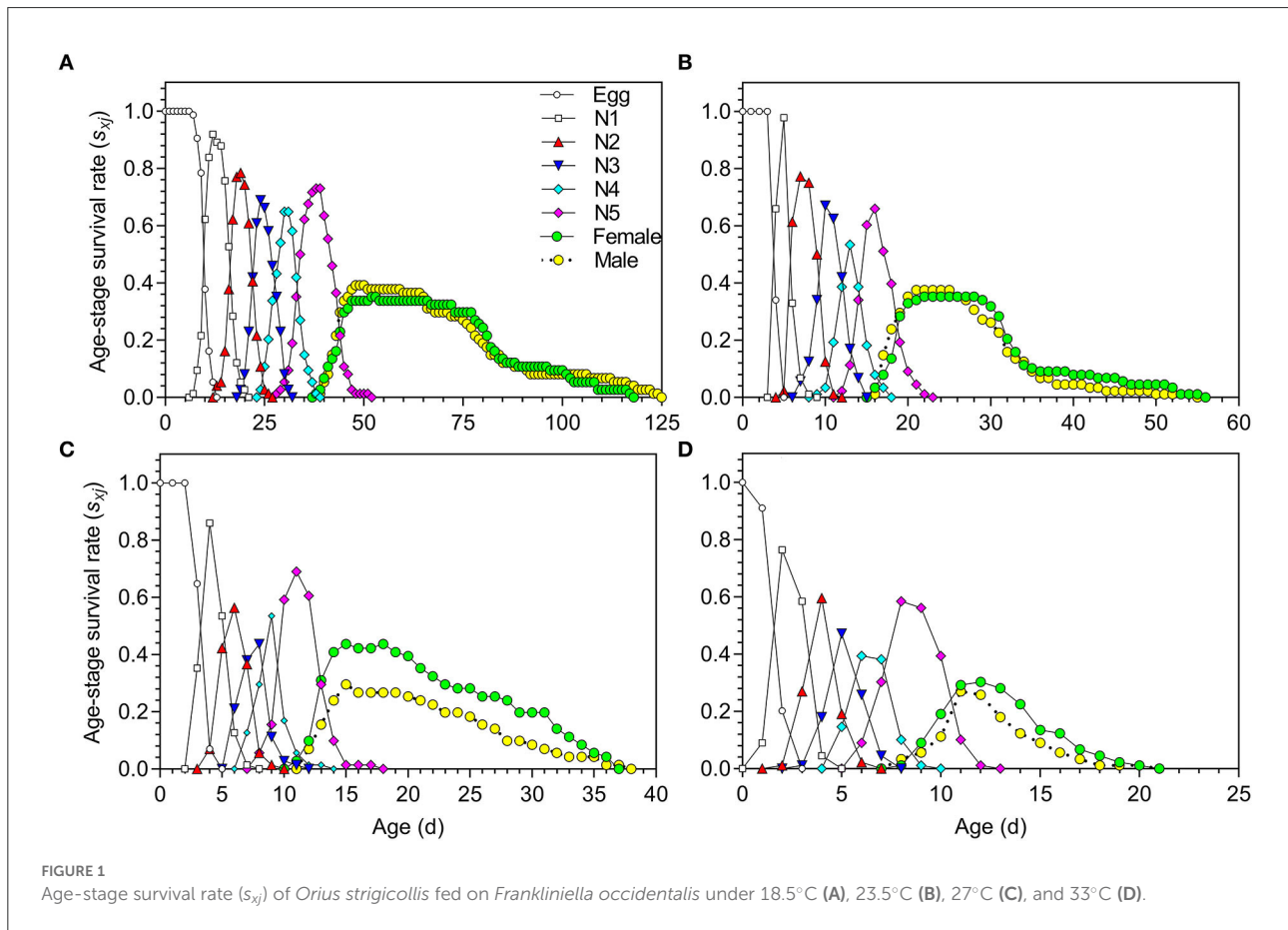
The age-stage survival rate ( $s_{xj}$ ) of *O. strigicollis* under the different temperature conditions is shown in Figure 1; obvious overlaps existed among the stages at all of the tested temperatures. The survival rates of both eggs and nymphs varied with temperature; the survival rates were higher at 18.5, 23.5, and 27°C (Figures 1A–C) and lower at 33°C (Figure 1D).

The adult preoviposition period (APOP), total preoviposition period (TPOP), and oviposition days ( $O_d$ ) were significantly longer at 18.5°C than those at 23.5, 27,

TABLE 1 Developmental times (d) and adult longevities (d) of *Orius strigicollis* fed on *Frankliniella occidentalis* at different temperatures.

Stage	18.5°C		23.5°C		27°C		33°C	
	n	Mean ± (SE)	n	Mean ± (SE)	n	Mean ± (SE)	n	Mean ± (SE)
Developmental time								
Egg	74	10.27 ± 0.15 a	88	4.34 ± 0.05 b	71	3.72 ± 0.07 c	89	2.11 ± 0.06 d
N1	66	6.52 ± 0.11 a	81	2.06 ± 0.04 b	65	1.91 ± 0.08 b	75	1.56 ± 0.06 c
N2	60	5.79 ± 0.12 a	73	3.16 ± 0.11 b	60	1.65 ± 0.06 c	68	1.26 ± 0.05 d
N3	58	5.40 ± 0.14 a	73	2.99 ± 0.11 b	58	1.40 ± 0.07 c	66	1.26 ± 0.06 c
N4	57	5.84 ± 0.20 a	69	2.25 ± 0.10 b	56	1.46 ± 0.08 c	64	1.38 ± 0.06 c
N5	55	9.49 ± 0.21 a	66	3.77 ± 0.10 b	54	3.24 ± 0.09 c	57	2.79 ± 0.07 d
Pre-adult	55	43.25 ± 0.36 a	66	18.48 ± 0.18 b	54	13.31 ± 0.16 c	57	10.32 ± 0.14 d
Adult longevity								
All adult	55	42.55 ± 2.40 a	66	16.17 ± 0.95 b	54	14.02 ± 0.87 b	57	4.75 ± 0.32 c
Female adult	26	44.04 ± 3.14 a	32	17.47 ± 1.49 b	33	14.36 ± 1.13 b	30	5.33 ± 0.42 c
Male adult	29	41.21 ± 3.62 a	34	14.94 ± 1.18 b	21	13.48 ± 1.39 b	27	4.11 ± 0.45 c

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).



and 33°C (Table 2). The parameters of APOP and  $O_d$  did not significantly differ between the 23.5°C (APOP = 4.73 days,  $O_d$  = 10.67 days) and 27°C (APOP = 3.60 days,  $O_d$  = 9.23 days) treatments, but both were significantly longer than those at

33°C (APOP = 1.78 days,  $O_d$  = 3.04 days). The mean fecundity ( $F$ ) of *O. strigicollis* showed no significant difference among the 18.5°C (58.31 eggs/female), 23.5°C (64.03 eggs/female), and 27°C (78.09 eggs/female) treatments but was obviously higher



TABLE 2 Preoviposition period, oviposition period, and fecundity of *Orius strigicollis* preying on *Frankliniella occidentalis* at different temperatures.

Parameters	18.5°C		23.5°C		27°C		33°C	
	n	Mean ± (SE)	n	Mean ± (SE)	n	Mean ± (SE)	n	Mean ± (SE)
Adult preoviposition period, APOP (d)	24	11.79 ± 1.40 a	30	4.73 ± 0.70 b	30	3.60 ± 0.57 b	23	1.78 ± 0.20 c
Total preoviposition period, TPOP (d)	24	55.12 ± 1.45 a	30	23.40 ± 0.68 b	30	16.83 ± 0.63 c	23	11.78 ± 0.30 d
Oviposition days ( $O_d$ , d)	24	24.96 ± 2.13 a	30	10.67 ± 1.25 b	30	9.23 ± 0.91 b	23	3.04 ± 0.41 c
Fecundity ( $F$ , all eggs/female)	26	58.31 ± 6.48 a	32	64.03 ± 8.00 a	33	78.09 ± 9.82 a	30	17.87 ± 3.70 b
Fecundity ( $f$ , eggs/female/d)	26	1.32 ± 0.14 c	32	3.57 ± 0.35 b	33	5.28 ± 0.50 a	30	2.93 ± 0.52 bc

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).

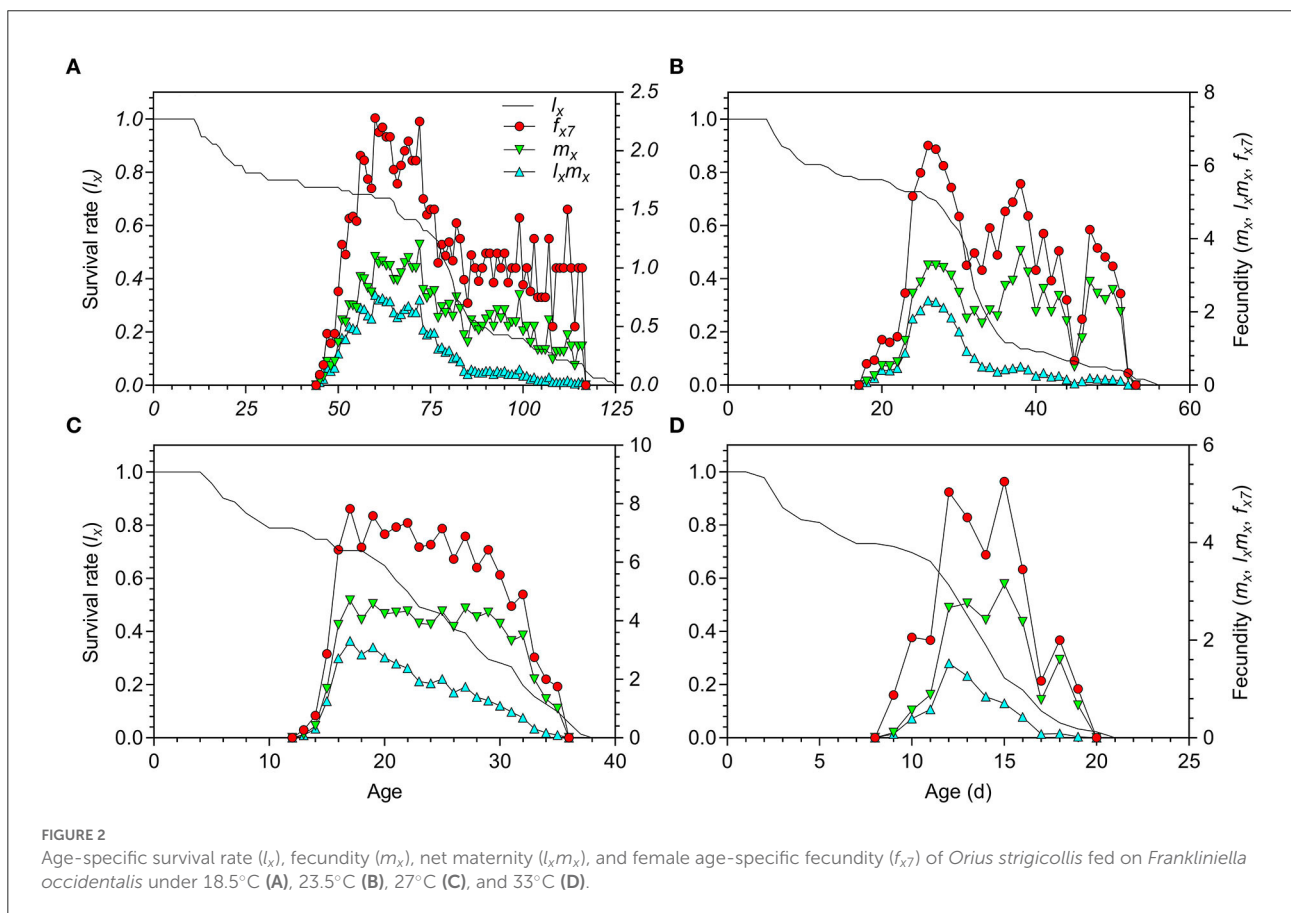


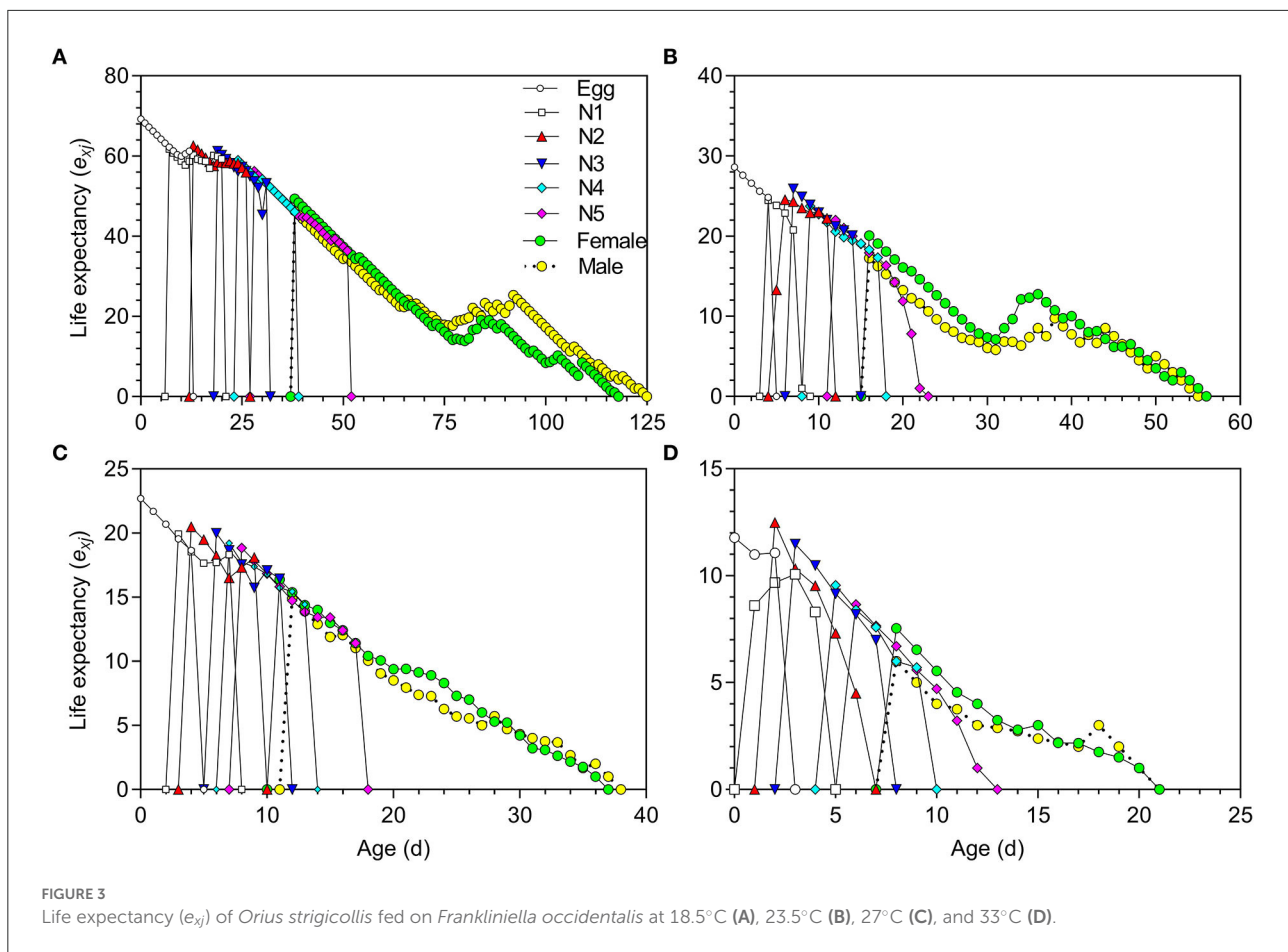
FIGURE 2

Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), net maternity ( $l_x m_x$ ), and female age-specific fecundity ( $f_{x7}$ ) of *Orius strigicollis* fed on *Frankliniella occidentalis* under 18.5°C (A), 23.5°C (B), 27°C (C), and 33°C (D).

than that at 33°C (17.87 eggs/female). However, the number of eggs laid per female per day ( $f$ ) at 27°C (5.28 eggs) was obviously larger than those at 23.5°C (3.57 eggs), 33°C (2.93 eggs), and 18.5°C (1.32 eggs). Among the tested temperatures, the female age-specific fecundity ( $f_{x7}$ ) first increased rapidly, peaked, and then decreased (Figure 2). The peak  $f_{x7}$  of *O. strigicollis* was 7.83 eggs/female at 27°C, which was higher than that at 23.5°C (6.55 eggs/female), 33°C (5.25 eggs/female), and 18.5°C (2.28 eggs/female). Fecundity ( $m_x$ ) and net maternity ( $l_x m_x$ ) are plotted in Figure 2.

The life expectancy ( $e_{xj}$ ) of *O. strigicollis* decreased with increasing temperature (Figure 3). The highest reproductive values ( $v_{xj}$ ) of *O. strigicollis* at 18.5, 23.5, 27, and 33°C were 29.43, 34.60, 35.78, and 13.57 day<sup>-1</sup>, respectively (Figure 4).

The intrinsic rate of increase ( $r$ ) and finite rate of increase ( $\lambda$ ) of *O. strigicollis* were highest at 27°C ( $r = 0.1682$  day<sup>-1</sup>,  $\lambda = 1.1833$  day<sup>-1</sup>) but did not differ significantly from those of at 33°C ( $r = 0.1298$  day<sup>-1</sup>,  $\lambda = 1.1387$  day<sup>-1</sup>) (Table 3); those at 23.5°C ( $r = 0.1094$  day<sup>-1</sup>,  $\lambda = 1.1157$  day<sup>-1</sup>) and 18.5°C ( $r = 0.0457$  day<sup>-1</sup>,  $\lambda = 1.0467$  day<sup>-1</sup>) were lower.



The net reproductive rate ( $R_0$ ) of *O. strigicollis* at 27°C (36.29 offspring/individual) was not significantly different from that at 23.5°C (23.28 offspring/individual), but the  $R_0$  values at both of these temperatures were significantly higher than those at 18.5°C (20.48 offspring/individual) and 33°C (6.02 offspring/individual). The mean generation time ( $T$ ) of *O. strigicollis* decreased as the temperature increased. The longest generation time was observed at 18.5°C (66.06 days), while the shortest generation time was observed at 33°C (13.83 days).

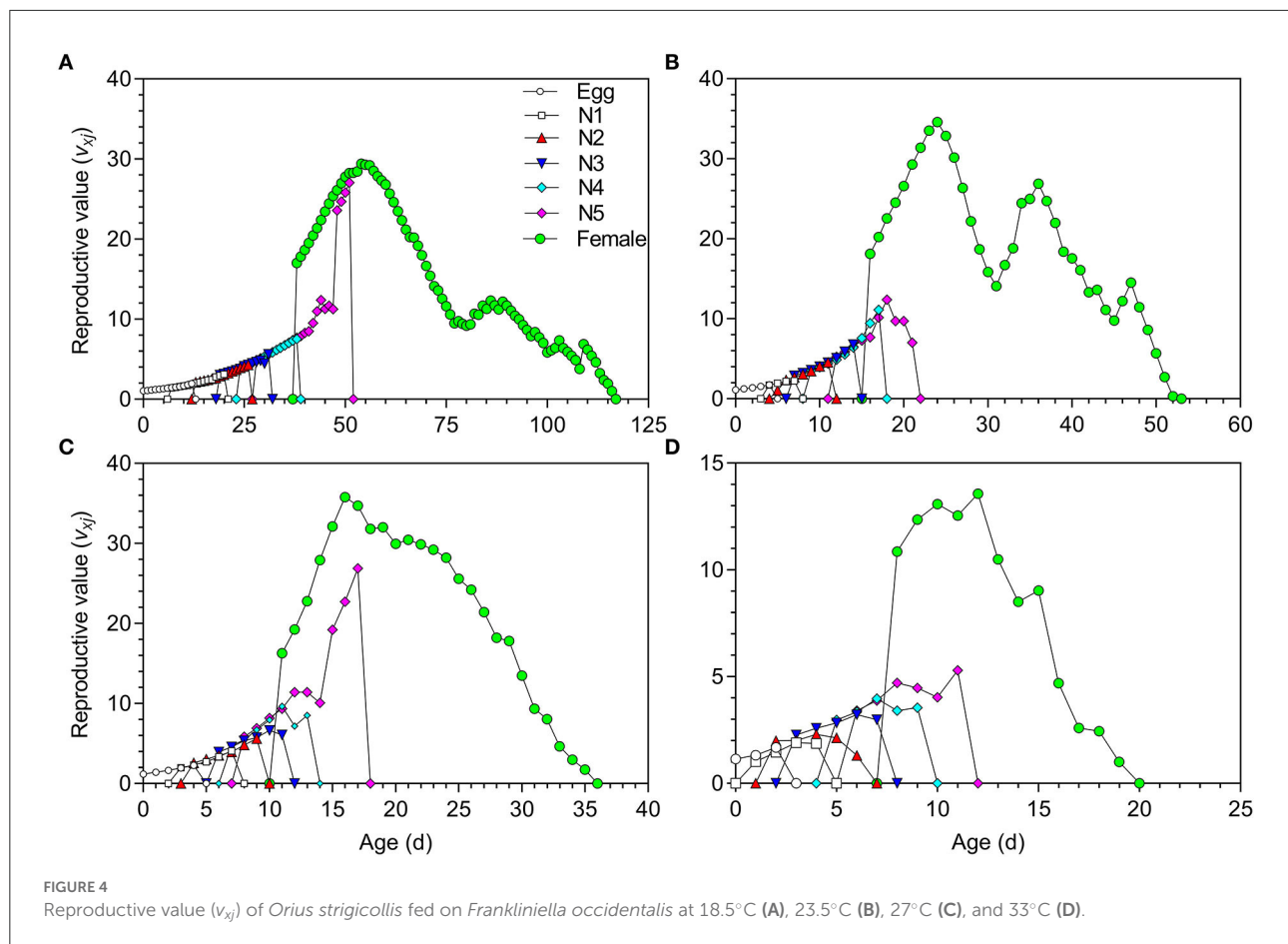
## Predation rate

The daily predation rate ( $D_j$ ) of *O. strigicollis* increased as the temperature increased within the tested temperature range (Table 4), and the  $D_j$  of each stage was the highest at 27°C. For *O. strigicollis* female adults, the  $D_j$  showed no significant difference between 27°C (9.88 prey/predator) and 23.5°C (9.44 prey/predator), but these  $D_j$  values were significantly higher than that at 18.5°C (4.40 prey/predator). The total numbers of WFT consumed ( $P_j$ ) during the preadult stage were 69.96, 63.61, and 60.28 per predator at 18.5, 23.5, and 27°C, respectively

(Table 5). The adult  $P_j$  at 18.5°C was higher than those at 23.5 and 27°C. The  $P_j$  of female adults was the highest at 18.5°C (198.87 prey/predator), followed by 23.5°C (164.92 prey/predator) and 27°C (141.93 prey/predator).

The first peaks of the age-specific predation rate ( $k_x$ ) and age-specific net predation rate ( $q_x$ ) in *O. strigicollis* fed on WFT at 18.5°C occurred at the age of 39.00 days in the N5 stage; these rates then decreased until adult emergence at the age of 44.00 days (Figure 5A). The peaks occurred significantly later than those at 23.5°C (15.00 days) (Figure 5B) and 27°C (10.00 days) (Figure 5C).

The net predation rate ( $C_0$ ) varied significantly among temperature conditions (Table 6). Each *O. strigicollis* consumed an average of 168.39 prey over its lifetime when reared at 18.5°C, which was significantly higher than the numbers of prey consumed at 23.5°C (140.49 prey/predator) and 27°C (138.39 prey/predator). The finite predation rate ( $\omega$ ) increased as the temperature increased. The transformation rate ( $Q_p$ ) indicated that at 18.5°C, *O. strigicollis* needed to consume 8.22 WFTs to produce one egg, which was not significantly different from that at 23.5°C (6.03); however, both were higher than that at 27°C (3.81).

TABLE 3 Population parameters of *Orius strigicollis* preying on *Frankliniella occidentalis* at different temperatures.

Population parameters	18.5°C		23.5°C		27°C		33°C	
	<i>n</i>	Mean ± (SE)	<i>N</i>	Mean ± (SE)	<i>n</i>	Mean ± (SE)	<i>n</i>	Mean ± (SE)
Intrinsic rate of increase, $r$ ( $d^{-1}$ )	74	0.0457 ± 0.0032 c	88	0.1094 ± 0.0065 b	71	0.1676 ± 0.0085 a	89	0.1298 ± 0.0185 ab
Finite rate of increase, $\lambda$ ( $d^{-1}$ )	74	1.0467 ± 0.0034 c	88	1.1157 ± 0.0072 b	71	1.1826 ± 0.0100 a	89	1.1387 ± 0.0209 ab
Net reproductive rate, $R_0$ (offspring/individual)	74	20.48 ± 3.94 b	88	23.28 ± 4.36 a	71	36.29 ± 6.45 a	89	6.02 ± 1.52 c
Mean generation time, $T$ (d)	74	66.06 ± 1.66 a	88	28.76 ± 0.74 b	71	21.33 ± 0.55 c	89	13.83 ± 0.36 d

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).

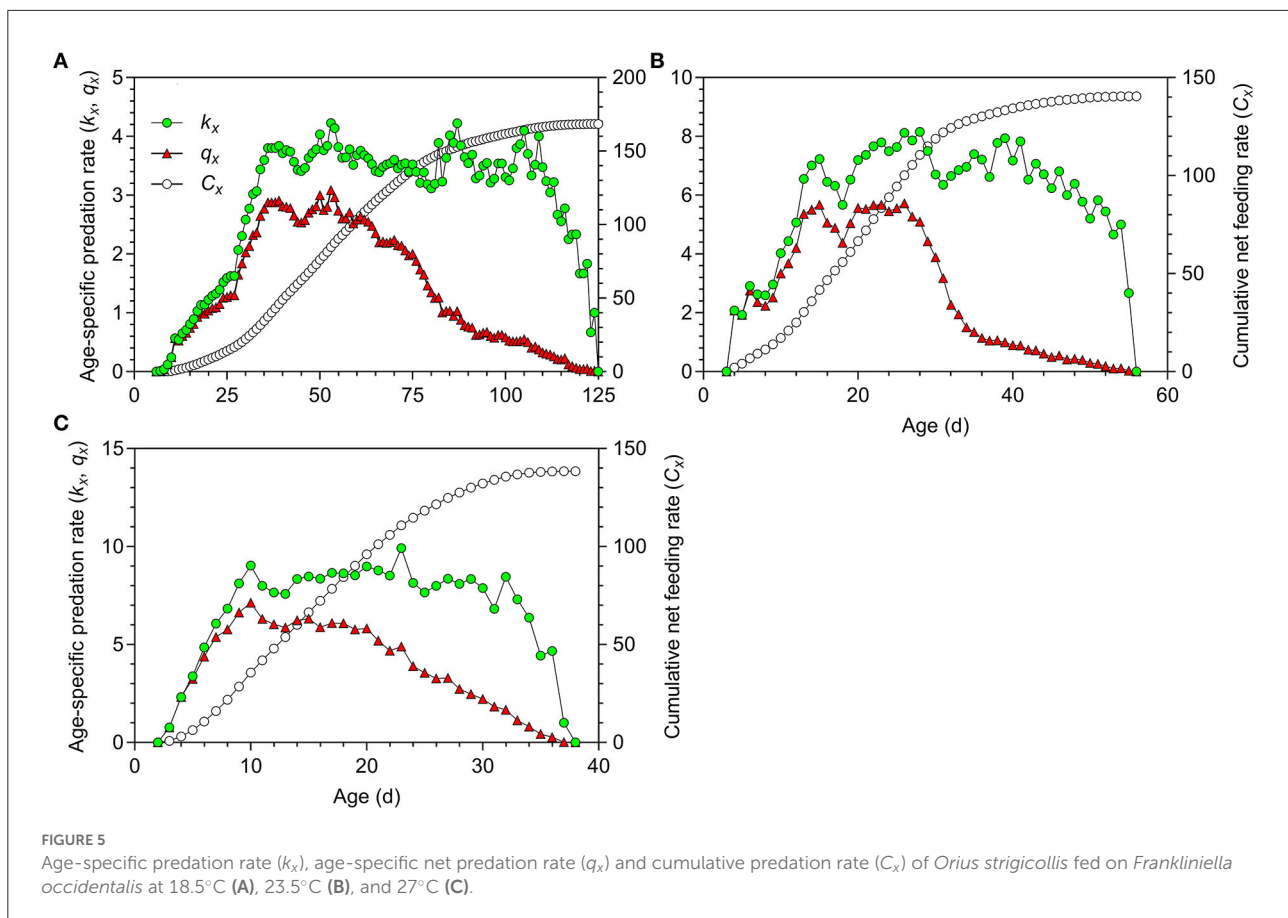
## Population projections of *O. strigicollis* in response to temperature

Data from the life table study were used to project the population growth of *O. strigicollis* with an initial number of 10 viable eggs (Figure 6). The population increased faster at 27°C than at 18.5, 23.5, and 33°C. After 40 days, the total numbers of *O. strigicollis* produced under 18.5, 23.5, 27, and 33°C conditions were 8 (0 eggs, 6 nymphs, 1 female adult, and 1 male adult), 181 (21 eggs, 152 nymphs, 4 female adults and 4 male adults), 3,308 (2,014 eggs, 1,115 nymphs, 109 female adults, and 70 male

adults), and 855 (430 eggs, 299 nymphs, 73 female adults, and 53 male adults), respectively.

With an initial population of five pairs of newly hatched adults, after 40 days, the total numbers of *O. strigicollis* produced at 18.5, 23.5, 27, and 33°C were 223 (79 eggs, 137 nymphs, 4 female adults, and 3 male adults), 2,926 (1,695 eggs, 1,062 nymphs, 87 female adults, and 82 male adults), 12,888 (5,380 eggs, 5,936 nymphs, 986 female adults, and 586 male adults), and 3,085 (564 eggs, 2,195 nymphs, 184 female adults, and 142 male adults), respectively (Figure 7).



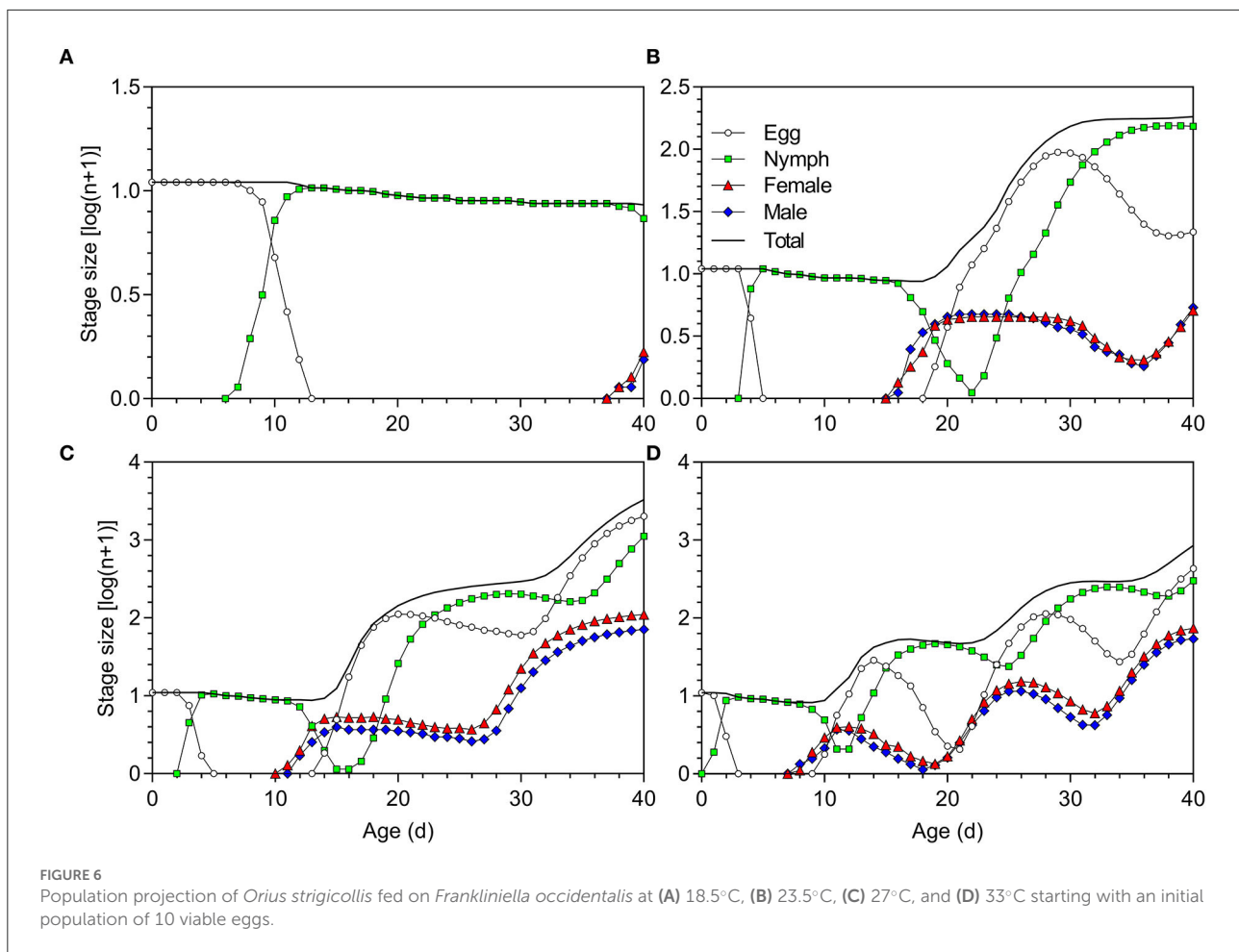


## Discussion

### Effect of temperature on the development and fecundity of *O. strigicollis*

Variability in temperature conditions can directly affect the physiology, survival, fecundity, behavior, and other characteristics of insects (Harrison et al., 2012; González-Tokman et al., 2020), ultimately affecting population dynamics (Bai et al., 2022). The development rate of insects is temperature-dependent (Bai et al., 2022), and the developmental duration of *Orius* can be significantly affected by this abiotic factor. Consistent with these findings, our results showed that temperature had a significant effect on the developmental duration of *O. strigicollis*. The prolongation of developmental duration observed at decreased temperatures may be due to a decrease in insect metabolism at lower temperatures (Howe, 1967; Brown et al., 2004; Garcia et al., 2007; Williams III and Roane, 2007; González-Tokman et al., 2020). Thus, the adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition days ( $O_d$ ), and mean generation time ( $T$ ) exhibited temperature dependence (Table 2).

Low temperatures resulted in fewer eggs laid per day by *O. strigicollis*, similar to *Bicyclus anynana*, which laid fewer eggs per day at lower temperatures than at higher temperatures (Geister et al., 2008). However, the mean number of eggs laid per *O. strigicollis* female over a lifetime revealed no significant difference between 18.5, 23.5, and 27°C when considering the longevity and survival of adults. The fecundity of insects is limited under high-temperature conditions (Harrison et al., 2012). For example, when the temperature was 32–36°C, the fecundity of *Orius tantillus* decreased substantially (Ballal et al., 2017), and the fecundity of both *Orius laevigatus* and *Orius albidipennis* decreased substantially as the temperature was increased to 35°C (Cocuzza et al., 1997; Sanchez and Lacasa, 2002). As a result of physiological trade-offs, insects may need to reduce their fecundity to ensure high-quality egg production (Berger et al., 2008). Fand et al. (2015) also reported reduced adult longevity at high temperatures, as well as a shortening of the reproductive phase with decreased oviposition. In the current study, the high temperature had an obvious effect on the fecundity of *O. strigicollis*, resulting in a significantly low net reproductive rate ( $R_0 = 6.02$  offspring/individual at 33°C).



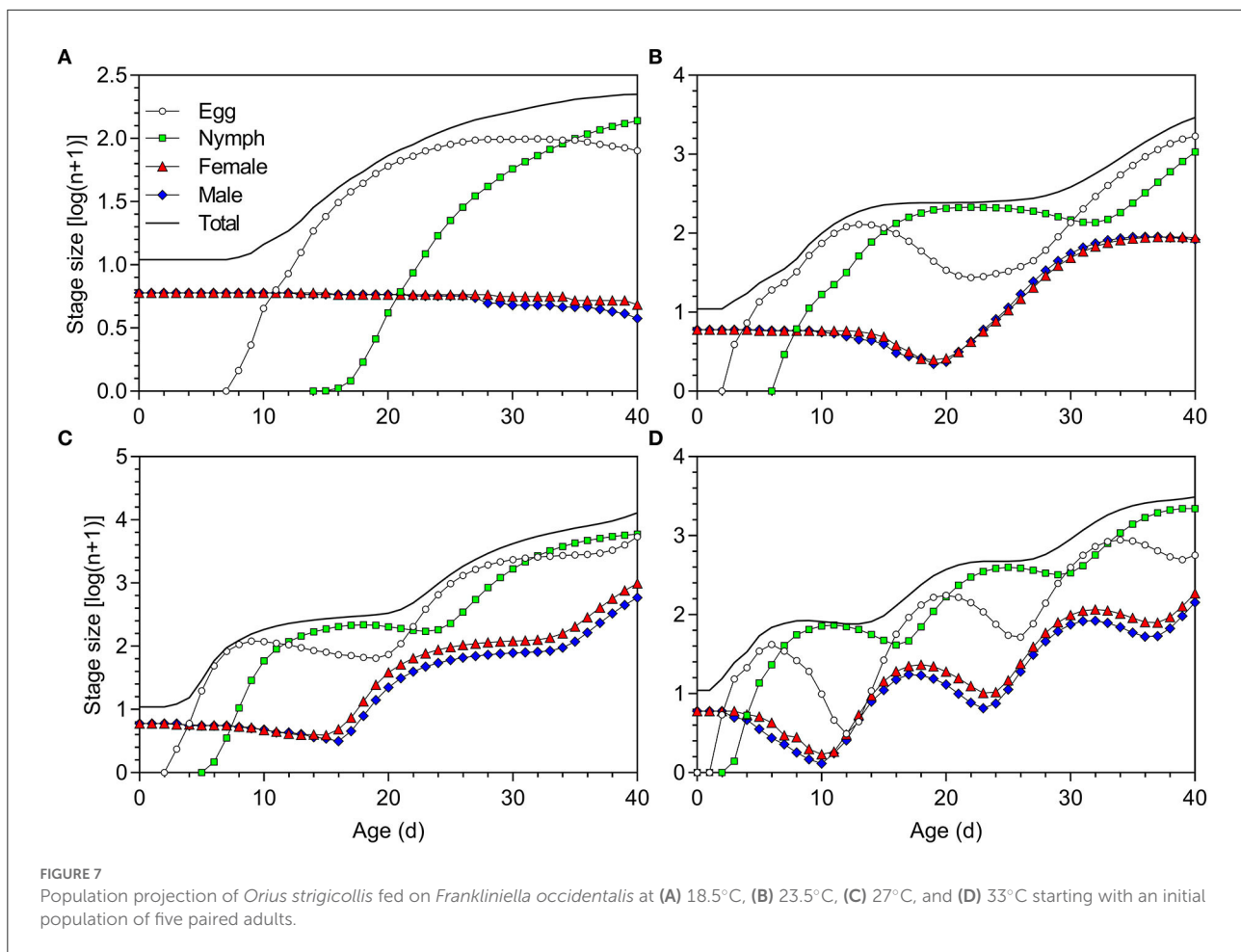
## Effect of temperature on the population parameters of *O. strigicollis*

Previous studies by Tuan et al. (2016) and Ding et al. (2021) showed that the intrinsic rate of increase ( $r$ ) and finite rate of increase ( $\lambda$ ) of *O. strigicollis* fed on *Cadra cautella* ( $r = 0.1677 \text{ day}^{-1}$ ,  $\lambda = 1.1826 \text{ day}^{-1}$ ) and *Frankliniella intonsa* nymphs ( $r = 0.1437 \text{ day}^{-1}$ ,  $\lambda = 1.1546 \text{ day}^{-1}$ ) at 25°C were similar, and these rates were also similar to those of *O. strigicollis* fed on WFT nymphs at 27°C in this study ( $r = 0.1682 \text{ day}^{-1}$ ,  $\lambda = 1.1833 \text{ day}^{-1}$ ). The temperature had obvious effects on developmental duration, longevity, survival, and fecundity; thus, both the population parameters of  $r$  and  $\lambda$  were also temperature dependent (Yu J. K., et al., 2013; Ali et al., 2020). For *O. strigicollis* reared at 18.5°C and 23.5°C, a slow developmental rate (Supplementary Table 1) was the primary factor resulting in the low rate of population increase. However, despite the low fecundity of *O. strigicollis* at 33°C, the short preadult duration and adult longevity enhanced population growth, resulting in large increases in these rates ( $r = 0.1298 \text{ day}^{-1}$ ,  $\lambda = 1.1387 \text{ day}^{-1}$ ). These findings are similar to the results of a previous

study, where the recorded values were  $0.12 \text{ day}^{-1}$  ( $r$ ) and  $1.13 \text{ day}^{-1}$  ( $\lambda$ ) for *O. strigicollis* reared on eggs of *Pectinophora gossypiella* at 31°C (Ali et al., 2020).

## Effects of temperature on the predation rates of *O. strigicollis*

Temperature strongly affects the predation ability of predaceous insects, as frequently confirmed by the functional response (Sørensen et al., 2013; Ge et al., 2018; Rehman et al., 2020; Bai et al., 2022). As the temperature increases within a tolerable temperature range, physiological metabolism increases, and predators consume more prey to meet these energetic demands (Schwarz and Frank, 2019; González-Tokman et al., 2020). Similarly, the mean predation rates per day ( $D_j$ ) of both nymphs and adults of *O. strigicollis* on WFT increased as the temperature increased (Table 4). The finite predation rate ( $\omega$ ) can be used to assess the potential predation of natural enemies (Chi et al., 2011; Yu J. K., et al., 2013); this rate showed an increase with increasing temperature in the



current study, similar to trends in previous studies (Sørensen et al., 2013; Helgadóttir et al., 2017; Ge et al., 2018). When considering the survival rate, longevity, and predation rate, higher net predation rates ( $C_0$ ) were observed at 18.5 and 23.5°C than at 27°C, similar to the result reported by Yu J. K., et al. (2013). Additionally, when developing at low temperatures, some insects can physiologically adapt by accumulating energy reserves to improve cold stress tolerance (Denlinger and Lee, 2010). Thus, *O. strigicollis* reared at 18.5°C may need to accumulate more energy reserves for survival by increasing the predation rate. Accordingly, the transformation rate ( $Q_p$ ) was highest at the lowest temperature (18.5°C), allowing individuals to maximize fitness at this temperature.

## Population projections and release

The computer simulation in this study showed the stage structure and population dynamics of *O. strigicollis* in response to different temperatures, providing a reference for the field application of this natural enemy under various

environmental temperature conditions. The optimal predator stage, release time, and release ratio of natural enemies at various temperatures can be determined based on population projections (Yu L. Y., et al., 2013; Mou et al., 2015; Ding et al., 2021) to ensure the establishment of sufficient natural enemy populations for pest population suppression (Janssen and Sabelis, 2015; Mendoza et al., 2021). Obviously, the developmental stage of natural enemies released can affect population dynamics, and the *O. strigicollis* population increased faster when initiated using five pairs of adults than when using 10 viable eggs, similar to the results reported by Ding et al. (2021). As the predation rate was also age-dependent (Table 4), the release of adults or nymphs of *O. strigicollis* with a high predation rate is favorable for achieving immediate pest control (van Lenteren et al., 2018; Ding et al., 2021). In addition, the preventative release of natural enemies (one aspect of ABC) by introducing natural enemies in the greenhouse first and supporting natural enemy establishment before pest arrival has also been proposed (Messelink et al., 2014; van Lenteren et al., 2018; Pijnakker et al., 2020). This method facilitates the establishment of an adequate population of natural enemies,

TABLE 4 Predation rate for daily ( $D_j$ ) of *Orius strigicollis* fed on *Frankliniella occidentalis* at different temperatures.

Development stage	18.5°C		23.5°C		27°C	
	<i>n</i>	Mean ± (SE)	<i>N</i>	Mean ± (SE)	<i>n</i>	Mean ± (SE)
N1	74	0.63 ± 0.02 c	88	2.09 ± 0.06 b	71	2.34 ± 0.09 a
N2	66	1.19 ± 0.03 c	80	2.52 ± 0.06 b	65	4.40 ± 0.17 a
N3	61	1.50 ± 0.04 c	73	3.79 ± 0.09 b	60	6.64 ± 0.03 a
N4	58	2.58 ± 0.08 c	73	5.85 ± 0.18 b	58	8.37 ± 0.27 a
N5	56	3.71 ± 0.08 c	66	6.92 ± 0.14 b	56	8.09 ± 0.19 a
Preadult	74	1.46 ± 0.04 c	88	3.21 ± 0.07 b	71	4.11 ± 0.12 a
All adult	55	3.60 ± 0.13 c	66	7.28 ± 0.32 b	54	8.34 ± 0.33 a
Female adult	26	4.40 ± 0.11 b	32	9.44 ± 0.19 a	33	9.88 ± 0.19 a
Male adult	29	2.72 ± 0.09 c	34	4.91 ± 0.19 b	21	5.75 ± 0.23 a

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).

TABLE 5 Predation rate for the stage of *Orius strigicollis* survived ( $P_j$ ) fed on *Frankliniella occidentalis* at different temperatures.

Development stage	18.5°C		23.5°C		27°C	
	<i>n</i>	Mean ± (SE)	<i>N</i>	Mean ± (SE)	<i>n</i>	Mean ± (SE)
N1	66	4.18 ± 0.15 a	80	4.45 ± 0.10 a	65	4.45 ± 0.18 a
N2	60	6.90 ± 0.19 b	73	8.08 ± 0.27 a	60	7.35 ± 0.26 ab
N3	58	8.16 ± 0.29 c	73	11.33 ± 0.35 a	58	9.55 ± 0.38 b
N4	57	14.93 ± 0.68 a	69	13.09 ± 0.42 b	56	12.63 ± 0.49 b
N5	55	35.36 ± 0.84 a	66	26.62 ± 0.72 b	54	26.20 ± 0.71 b
Preadult	55	69.96 ± 0.98 a	66	63.61 ± 1.01 b	54	60.28 ± 1.17 c
All adult	55	152.96 ± 0.12 a	66	117.76 ± 9.00 b	54	116.90 ± 8.68 b
Female adult	26	198.87 ± 13.21 a	32	164.92 ± 12.77 a	33	141.93 ± 11.28 b
Male adult	29	108.69 ± 11.71 a	34	73.38 ± 6.74 b	21	77.55 ± 8.33 b

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).

allowing predator synchronization with pest population growth. Thus, in the preventative release of this natural enemy, both the effects of environmental temperatures and the release stage of *O. strigicollis* on the population dynamics should be considered to determine the timing of release to prevent thrips outbreaks.

Integrated analysis of the demography and predation rate of the natural enemy in response to temperature can facilitate the biocontrol efficacy of natural enemy release for pest control. This study comprehensively described the demographic characteristics and predation rate of *O. strigicollis* in response to temperature. Increasing temperature promoted the development and shortened the longevity of *O. strigicollis*. At 27°C and 33°C, *O. strigicollis* exhibited rapid population growth; in contrast, relatively low temperatures, especially 18.5°C, led

TABLE 6 Parameters of *Orius strigicollis* preying (Mean ± SE) on *Frankliniella occidentalis* at different temperatures.

Parameter	18.5°C		23.5°C		27°C	
	<i>n</i>	Mean ± (SE)	<i>N</i>	Mean ± (SE)	<i>n</i>	Mean ± (SE)
Net predation rate, $C_0$ (prey/predator)	168.39	± 13.36 a	140.49	± 10.21 a	138.39	± 10.72 b
Finite predation rate, $\omega$ ( $d^{-1}$ )	1.14	± 0.04 c	2.63	± 0.09 b	3.24	± 0.14 a
Transformation rate, $Q_p$	8.22	± 1.42 a	6.03	± 0.98 a	3.81	± 0.58 b

Different letters within the same rows indicate significantly different temperatures determined by the paired bootstrap test with 100,000 resamplings ( $P < 0.05$ ).

to slow population growth. The predation rates of *O. strigicollis* in various developmental stages varied greatly at different temperatures. Consequently, when releasing *O. strigicollis* in the field to control WFT, both environmental temperature and developmental stage should be taken into consideration to establish sufficient populations.

## Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request. Requests to access these datasets should be directed to [luybcn@163.com](mailto:luybcn@163.com).

## Author contributions

XR, LZ, and YL conceived the research, designed experiments, and wrote the manuscript. XL, JH, and ZZ collected and prepared material. XR, JZ, LC, and SZ performed experiments and collected data. XR, XL, and MH analyzed data. All authors read and approved the manuscript.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2022.1026115/full#supplementary-material>

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