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With 3 figures and 2 tables

Abstract: Climate change generally influences all the living world, including insects, so all organisms cope with these stresses to survive. Temperature rise leads to increased insect pest severity, while cold acclimation helps insects to survive in temperate areas in several complex ways. The Oriental fruit fly, *Bactrocera dorsalis*, is one of the most economically important invasive pests of fruits and vegetables worldwide. In this study, we investigated the effect of low (LT: 3 °C) and high (HT: 38 °C) temperature stress on key biological and population parameters of *B. dorsalis* using an age-stage, two-sex life table approach. The results showed that the mean developmental duration of the larval stage was significantly prolonged in both HT (6.82 d) and LT (7.80 d) compared to the untreated group (6.33 d). The developmental duration of pre-adult stage was substantially increased when treated with LT (19.57 d) and HT (18.03 d) as compared to control insects (17.51 d). Compared to the control, the mean longevity of male and female flies was significantly prolonged in both LT and HT treatments. The adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), and oviposition days of *B. dorsalis* were increased under both temperature stress conditions. The number of eggs per female was also significantly higher in LT (869.70 eggs) and HT treatments (846.90 eggs) compared to control (684.56 eggs). Furthermore, the total population size of *B. dorsalis* was highest in HT treatment followed by LT compared to control after 100 d. This study reveals that temperature stresses at larval stage increased the reproduction, development, and life span of *B. dorsalis*, these altered biological traits during the heatwave and cold conditions could have significant agricultural impacts.

Keywords: Tephritidae, climate change, abiotic stress, heat stress, cold stress, biological traits, life table

1 Introduction

Climate change affects all living organisms, including insects, and only adapting organisms have a better chance of survival. It is among the factors that drive invasions of new ecologies. The invasive species can have far-reaching ecological and economic consequences in invaded areas (Hulme. 2009). Climate change may assist invasive species by improving their probability of establishing if previously unsuitable environments have become more suitable (Hulme. 2009). In particular, this is true for insects, which are cold-blooded organisms that depend on local environmental factors to survive and develop within their temperature ranges. The impact of climate change on the distribution of agricultural insects is a critical component for determining the future risk they pose to agricultural productivity and

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trade. Extremely high summer temperatures are becoming increasingly common due to climate change. Because insects are poikilothermic, high temperatures often cause population fluctuations. Thermal variations impact physiological processes (Feder et al. 1997) and ecological systems of most insect species, including sublethal or lethal extreme high temperatures (Easterling et al. 2000). The thermo regulatory behavior enhances the survival following exposure to extremely high temperatures (Woods et al. 2015). Extremely high temperatures in the initial stages may impact the performance of later stages (Zhang et al. 2015).

Insects have a temperature range optimal for their reproduction and growth and their biological and physiological processes (Wang et al. 2020; Nika et al. 2021; Lumbierres et al. 2021). Heat stress occurs when temperatures rise over their typical range. The Oriental fruit fly, *Bactrocera dorsalis* Hendel (Diptera: Tephritidae), is one of the most economically important Tephritid species that causes severe damage to the production and trade of vegetables and fruits. This polyphagous pest infests more than 300 commercial/edible plants and wild hosts (Vargas et al. 2015). This pest is highly invasive, originated in Asia, and spread to many places throughout the globe (Vargas et al. 2015). Temperature is a critical abiotic environmental factor that influences many biological characteristics of insects (Yao et al. 2020). Under changing climates, organisms, including insects, have been demonstrated to vary their phenology, geographical ranges, trophic interactions, population dynamics, and community structure (Han et al. 2019). Previous studies focused on the impact of temperature on the development, survival rate, and fecundity of *B. dorsalis* under different temperature stress (Danjuma et al. 2014). Fiaboe et al. (2021) predicted temperatures ranging between 20 and 30 °C as favorable for the development and survival of *B. dorsalis*. Moreover, they reported the optimal fecundity of *B. dorsalis* at temperatures between 20 to 25 °C.These studies revealed that the response of *B. dorsalis* to constant temperature in the laboratory varied among different populations, potentially leading to variances in understanding and forecasting *B. dorsalis* distribution and abundance. The mortality rate of *Bactrocera tau* (Walker) increased significantly when exposed to high temperatures (Huang et al. 2020). Lin et al. (2020) reported 85.3% mortality when the 3rd instar larvae of *B. dorsalis* were treated with 0.5–1 °C for 3 d.

In addition to mortality, temperature is one of the key stress variables reported to affect insect biological traits (Huang et al. 2020; Cutler et al. 2022). Le Bourg. (2007) documented the hormesis effects on longevity, behavioral aging, and heat and cold shock resistance in aged flies treated with low-temperature stress. The fitness, field performance, and tolerance of *Telenomus podisi* Ashmead were increased following exposure to fluctuating temperature regimes (Castellanos et al. 2019). The high temperatures cause oxidative damage by increasing the production of reactive oxygen species (ROS) (Zhang et al. 2014), and this oxidative stress increases the developmental duration and longevity of *H. armigera* and other insects (Zhang et al. 2017).

However,the effects of ongoing climate change on the life-history traits of *B. dorsalis* arepoorly studied. In this study, we used an age-stage, two-sex life table approach to evaluate the biological and demographic parameters of *B. dorsalis* under high (38 °C) and low-temperature stress (3 °C). These findings will provide in-depth knowledge about the impact of climate change on the biological parameters and population projection of *B. dorsalis*.

2 Materials and methods

2.1 Insect colony

Bactrocera dorsalis was collected from the colony maintained in the Insect Pest Management Program, National Agricultural Research Centre, Islamabad, Pakistan. The flies were cultured on an artificial diet in the laboratory for more than 10 generations. The colony was kept in the laboratory at 28 ± 1 °C with 65 ± 5% relative humidity (RH) under a 14:10 (L:D) photoperiod. Adults were maintained in screened Plexiglas insect rearing cages (45 cm × 45 cm × 45 cm) and provided with an adult diet containing protein hydrolysate yeast (MP Biomedicals Inc.) and sugar (1:3 by weight) and water ad libitum. The eggs were collected in perforated plastic bottles containing diluted guava juice. The eggs were incubated for 24 h and seeded on a standard wheat bran-based larval diet at the rate of 4–5 larvae/g. Pupae were collected in sawdust and placed in screened cages for the emergence of insects.

2.2 Impact of temperature stress on the mortality rate of *Bactrocera dorsalis*

The mortality of *B. dorsalis* at larval stage was evaluated following exposure to high temperature (HT: 38 °C) and low temperature (LT: 3 °C) as compared to control group. Thermal treatment was given in an incubator maintaining 65 ± 5% RH and 14:10 (L: D) h photoperiod. The larvae (4d old) were divided into five groups (one group for each day of treatment) that were exposed to either HT or LT for 1 to 5 days. The larvae of control group for each day treatment were placed under standard laboratory conditions of 28 ± 1 °C, 65 ± 5% RH, and a photoperiod of 14:10 L:D. Water was sprinkled externally to keep the diet wet. The treatment groups have three replicates, and each replicate contains 40 individuals. The larvae were kept in Petri dishes containing an artificial diet, and the Petri dishes were placed in plastic boxes containing sawdust for pupation. After each exposure time, the treated larvae were placed in standard laboratory conditions of 28 ± 1 °C, 65 ± 5% RH, and 14:10 L:D photoperiod, and the mortality were checked. The larvae that

could not show movement when touched or did not develop into the next instar were considered dead.

2.3 Life table experiments

The age-stage, two-sex life table was used to evaluate the biological and population parameters of *B. dorsalis* under high and low-temperature stress. For life table analysis, *B. dorsalis* eggs were collected from a plastic bottle with 1 mm holes that contained guava juice. The plastic boxes were put in the rearing cage for 3 h. Approximately 136, 132, and 135 eggs for HT, LT, and control treatments were transferred to Petri dishes containing a fresh larval artificial diet. Eggs were kept under standard laboratory conditions with a constant temperature of 28 ± 1 °C, 65 ± 5% RH, and 14 h light/10 h dark photoperiod. The larvae (4d old) were exposed to HT and LT for 1 and 2 d, respectively. After exposure to HT and LT, the survived and healthy larvae (87 for HT and 84 for LT) were placed individually in micro cages containing an artificial larval diet under standard laboratory conditions (28 ± 1 °C, 65 ± 5% RH, and 14 h light/10 h dark photoperiod). In control treatment, 80 larvae were reared under standard laboratory conditions of 28 ± 1 °C, 65 ± 5% RH, and 14:10 L:D photoperiod without exposure to temperature stress. The development duration and survival rate of larvae and pupae were recorded daily. After the adult emergence, we paired one male with one female and kept them in a small cage (15 × 15 × 20 cm). The couples were maintained on a protein adult diet, and water was provided *ad libitum*. The eggs were collected daily in a perforated plastic bottle containing commercially available guava juice. The fecundity and survival of adult flies were observed until complete mortality of adult flies.

2.4 Data analysis

The mortality data of *B. dorsalis* were statistically analyzed using one-way analysis of variance with Tukey's post hoc test (IBM, SPSS Statistics, version 22). Life table analysis of control, high temperature, and low temperature treated cohorts was performed using the age-stage, two-sex life table method (Chi & Liu. 1985; Chi. 1988; Chi et al. 2020). The TWOSEX-MSChart computer program (Chi. 2022b) was used to analyze the development duration, longevities of males and females, adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), oviposition days (O_d), and fecundity (F) (eggs/female) as well as the demographic parameters such as intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T) were determined following. The variances and standard errors were estimated through 100,000 bootstrap replicates (Akca et al. 2015). Paired bootstrap test was used to evaluate the differences among all life table parameters of the control and temperature treated groups at 5 % significance level based on the confidence interval of difference (Wei et al. 2020).

2.5 Population projection

The population projection began with 10 *B. Dorsalis* eggs and was projected for 100 d. The total population size at time t was calculated with eq. 1:

$$N(t)=\sum_{j=1}^{\beta}\sum_{x=0}^{\infty}n_{xj,t} \quad (1)$$

where $n_{xj,t}$ is the number of individuals of age x and stage j at time t (Huang et al., 2018).

Then, we sorted the 100,000 bootstrap results of the λ to find the 2.5th and 97.5th percentiles (i.e., the 2,500th and 97,500th sorted bootstrap samples) to show the variability of both projections. We then used bootstrap life table samples that generated the 2.5th and 97.5th percentiles of the λ to project the population to represent the confidence interval of the projected populations (Huang et al. 2018). Projections were made by using TIMING-MSChart computer program (Chi. 2022a) based on the method of Chi & Liu (1985) and Chi (1990).

3 Results

3.1 Mortality of *Bactrocera dorsalis* under high and low temperature stress

The mortality of *Bactrocera dorsalis* at larval stage following exposure to HT and LT is shown in Fig. S1. The mortality rates of *B. dorsalis* increased significantly when exposed to high and low temperatures from 1 to 5 d. The high and low-temperature treatment for 1 day caused significantly higher mortality of 33.3 and 15.8 % in *B. dorsalis*, respectively (F = 29.293; df = 2, 6; P< 0.001) as compared to control (Fig. S1). The mortality was increased to 42.5 and 36.7 % following exposure to HT and LT for 2 d (F = 44.096; df = 2, 6; P< 0.001), while no mortality was observed in control group. After 3 d treatment, 66.7 and 68.3 % mortality was recorded for HT and LT (F = 56.586; df = 2, 6; P< 0.001), while 90 and 86.7 % mortality was observed after 4 d exposure, respectively (F = 69.952; df = 2, 6; P< 0.001) (Fig. S1). 100 % mortality was recorded in *B. dorsalis* following exposure to both treatments (HT and LT) for 5 consecutive days (F = 586.714; df = 2, 6; P< 0.001), as compared to control group 4.2 and 7.5%, respectively.

3.2 Developmental duration and adult longevity of *Bactrocera dorsalis*

The mean developmental duration and adult longevity of *B. dorsalis* under high and low temperature stress are shown in Table 1. The mean developmental duration of the larval stage significantly increased (P<0.05) in HT (6.82 d) and LT (7.80 d) as compared to the untreated group (6.33 d). The developmental time of pupae was also significantly

Table 1. Mean (± SE) duration of different developmental stages and total longevity (d) of *Bactrocera dorsalis* following exposure to high temperature (HT) and low temperature (LT).

Stages	Control	HT: 38 °C	LT: 3 °C
	Mean ± SE[b]	Mean ± SE[b]	Mean ± SE[b]
Eggs	2.13 ± 0.03 a	2.14 ± 0.04 a	2.07 ± 0.03 a
Larvae	6.33 ± 0.06 c	6.82 ± 0.10 b	7.80 ± 0.12 a
Pupae	9.19 ± 0.09 b	9.20 ± 0.12 b	9.73 ± 0.18 a
Preadult	17.51 ± 0.10 c	18.03 ± 0.17 b	19.57 ± 0.21 a
Adult longevity (Male)	48.15 ± 2.66 bA	57.18 ± 2.29 aA	59.20 ± 2.31 aA
Adult longevity (Female)	51.16 ± 2.40 bA	63.13 ± 2.92 aA	60.58 ± 1.89 aA

Standard errors were estimated by using the bootstrap technique with 100,000 resamplings. The difference was compared using the paired bootstrap test (P< 0.05). The means within a row followed by a different lowercase letters indicate significant differences between the treatments, while different uppercase letters within the same column indicate significant differences between female and male adult longevity

Table 2. Impact of high temperature (HT) and low temperature (LT) on the fecundity and demographic parameters of *Bactrocera dorsalis*.

Parameters	Control	HT: 38 °C	LT: 3 °C
	Mean ± SE	Mean ± SE	Mean ± SE
APOP (d)	14.93 ± 0.22 a	14.03 ± 0.27 b	14.16 ± 0.27 b
TPOP (d)	32.43± 0.29 b	31.55 ± 0.26 c	33.63 ± 0.41 a
Oviposition days (O_d)	18.67 ± 0.76 ab	20.62 ± 0.75 a	18.06 ± 0.50 ab
Fecundity (eggs/female) (F)	684.56 ± 39.80 b	846.90 ± 46.34 a	869.70 ± 34.44 a
Mean generation time (d)(T)	39.86 ± 0.35 b	40.64 ± 0.41 ab	41.71 ± 0.60 a
Intrinsic rate of increase (d^{-1}) (r)	0.1277 ± 0.0046 a	0.1295 ± 0.0048 a	0.1290 ± 0.0044 a
Finite rate of increase (d^{-1}) (λ)	1.1362 ± 0.0052 a	1.1383 ± 0.0054 a	1.1377 ± 0.0050 a
Net reproductive rate (offspring/individual) (R_0)	162.27 ± 26.71 a	193.04 ± 32.20 a	217.42 ± 33.79 a

Standard errors were estimated by using the bootstrap technique with 100,000 resamplings. The difference was compared using the paired bootstrap test (P< 0.05). The means within a row followed by a different lowercase letters indicate significant differences between the treatments.

increased (9.73 d) under low-temperature stress (P< 0.05). However, no significant differences was observed in pupal duration following exposure to the HT as compared to control group (Table 1). The pre-adult stage was significantly increased (P< 0.05) when treated with LT (19.57 d) and HT (18.03 d) as compared to control insects (17.51 d). The mean longevity of the males increased significantly (P< 0.05) in LT (59.20 d) and HT (57.18 d) treatments compared to the control (48.15 d). Similarly, female longevity was also significantly prolonged (P< 0.05) following exposure to HT (63.13 d) and LT (60.58 d), as compared to control (51.16 d). The mean adult longevity was statistically similar between males and females of *B. dorsalis* (Table 1).

3.3 Fecundity and demographic parameters of *Bactrocera dorsalis*

The impact of HT and LT treatments on the fecundity and key demographic parameters of *B. dorsalis* is shown in Table 2. The low and high-temperature treatments affected the APOP and TPOP. The APOP of *B. dorsalis* was significantly (P< 0.05)decreased in HT (14.03 d) and LT (14.16 d) as compared to control (14.93 d) (Table 2). Similarly, TPOP was also significantly reduced following exposure to HT (31.55 d), while it increased in LT-treated insects (33.63 d) compared to control (32.43 d) (P< 0.05) (Table 2). Fecundity (eggs/female) of *B. dorsalis* was substantially increased (P< 0.05) under both stress conditions (Table 2). The number of eggs per female was significantly higher in LT (869.70 eggs) and HT treatments (846.90 eggs) compared to control (684.56 eggs). The oviposition days (O_d) were significantly increased in HT (20.62 d) as compared to LT (18.06 d) and control treatments (18.06 d) (P< 0.05). The mean generation time of *B. dorsalis* was also notably increased in LT (41.71 d) as compared to HT (40.64 d) and control insects (39.86 d) (Table 2). The key demographic parameters, including r, λ, and R_0, were increased in both HT and LT treatments compared to control, albeit the differences were not statistically significant (Table 2).

The detailed age-stage survival rates (s_{xj}) of *B. dorsalis* for different treatments are plotted in Fig. S2. The parameter s_{xj} shows the probability that a newly born egg will survive to age x and develop to stage j. The overlapping of s_{xj} curves

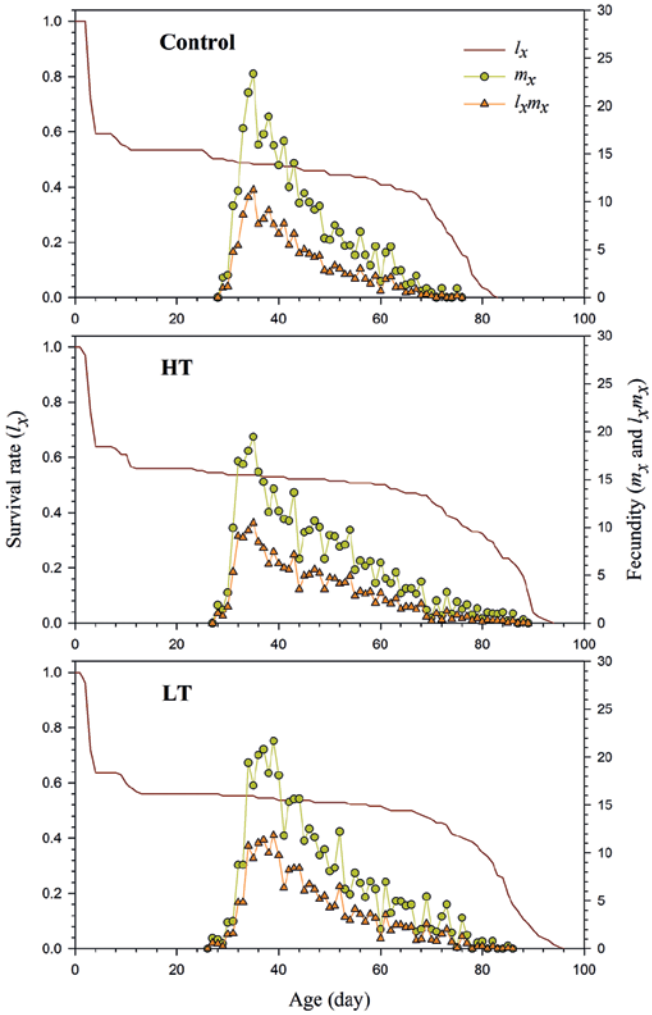

Fig. 1. Age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Bactrocera dorsalis* following exposure to high temperature (HT) and low temperature (LT).

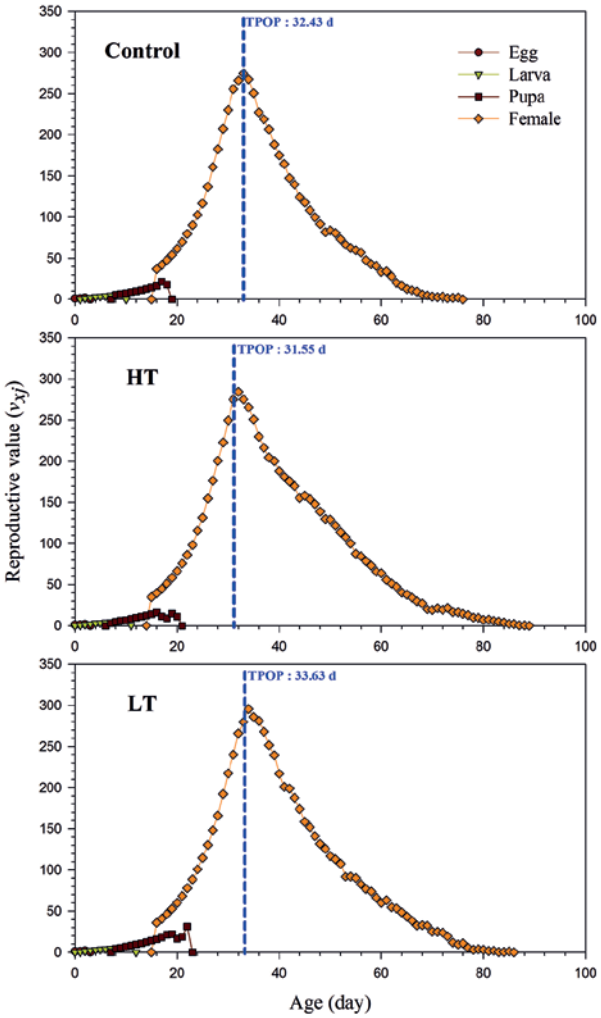

Fig. 2. Age-stage-specific reproductive value (v_{xj}) of *Bactrocera dorsalis* following exposure to high temperature (HT) and low temperature (LT).

represents variations in developmental stages of HT, LT, and control groups (Fig. S2). The survival rate and developmental duration of larval and pupal stages were significantly increased in HT, and LT-treated *B. dorsalis* cohorts (Fig. S2). The adult longevities of male and female were also substantially increased in HT and LT as compared to control cohorts (Fig. S2).

The age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *B. dorsalis* cohorts following exposure to HT and LT are plotted in Fig. 1. The l_x curves show the probability that an egg will survive to age x by ignoring stage differentiation (Fig. 1). The l_x curves started to decline from 0.4 after 76 d in LT and 72 d in HT, as compared to control cohort (60 d). The m_x and $l_x m_x$ curves show that reproduction began in LT cohort at the age of 25 d and ended at 85 d. In HT cohort, the reproduction started at the age of 27 and ended at 89 d. However, in control cohort, the reproduction began at the age of 28 d and ended at 75 d (Fig. 1).

The age stage-specific life expectancy (e_{xj}) of *B. dorsalis* after exposure to HT and LT are plotted in Fig. S3. Based on the age-stage, two-sex life table, the e_{xj} shows the expected life span that an individual of age x and stage j can live after age x (Fig. S3). The e_{xj} curves shows the longer life expectancy of male and female in HT and LT cohorts as compared to control (Fig. S3). The age-stage-specific reproductive value (v_{xj}) of *B. dorsalis* following exposure to HT and LT are presented in Fig. 2. The maximum v_{xj} values were 300 and 288 for *B. dorsalis* females in LT and HT cohorts respectively, which is higher than in control group (276).

3.4 Population projection

The original, 2.5th and 97.5th percentile of projected *B. dorsalis* population after short-term exposure to HT and LT, together with the control, were plotted in Figure 5. The total population size of *B. dorsalis* was highest in HT exposed *B. dorsalis* and projected to almost 500,000 individuals after

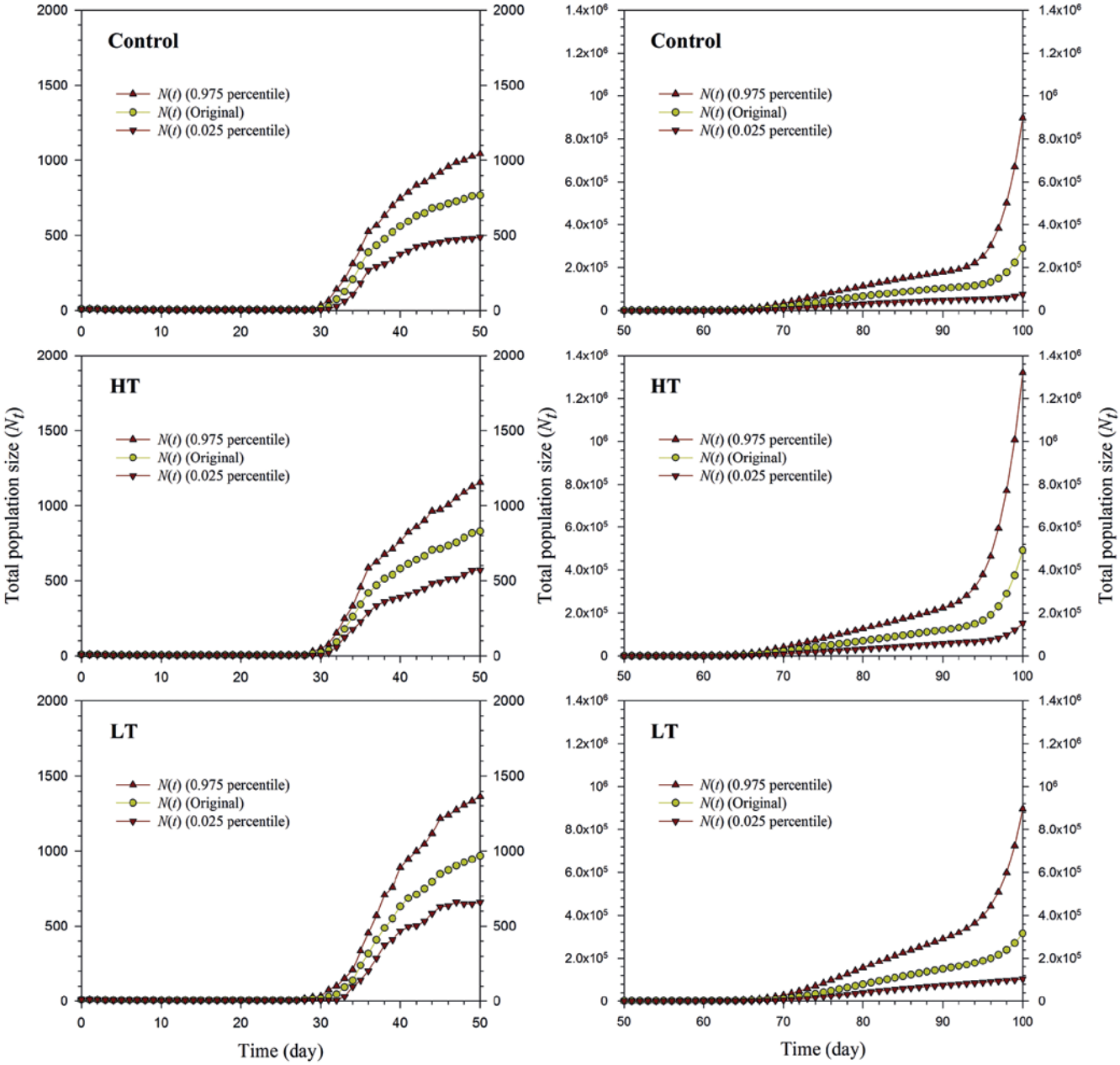

Fig. 3. Total population size (*Nt*) after population projection of *Bactrocera dorsalis* following exposure to high temperature (HT) and low temperature (LT) for 100 d (0-50 d and 50-100 d) using the life table data of the original cohort and the cohorts constructed based on the 2.5 and 97.5% percentiles of *λ*, finite rate of increase.

100 d. The population size of control yielded the lowest population size estimate ~ 290,000, while the LT exposed population was projected to be nearly 315,000 individuals (Fig. 3).

4 Discussion

Insects change their phenology, geographic ranges, trophic interactions, population dynamics, and community structure in response to changing climates (Han et al. 2019). Thermal extremes influence insect responses to climate change, significantly impacting pest control and biodiversity conservation (Ma et al. 2021). In this study, we reported the impact of short-term temperature stress (HT and LT) on key biological and demographic parameters of *B. dorsalis*. Results showed that high and low-temperature stress increased larval duration, adult life span, and female fecundity of *B. dorsalis*. High temperatures are usually associated with oxidative damage through increased generation of reactive oxygen species (ROS) (Zhang et al. 2014), and oxidative stress slows down the development and prolongsthe lifes-

pan of *H. Armigera* and other insects (Zhang et al. 2017). These results, combined with our study, imply that developmental delay leading to lifespan extension under various stresses may be a common phenomenon in insects. In several studies, the intriguing concept of hormesis was raised to explain the fact that a toxic chemical has a lethal effect at high concentrations and can be beneficial for insects at a sublethal concentration (Ullah et al. 2019; Cutler et al. 2022). Furthermore, cold stress causes oxidative damage in insects, and then a warm recovery time activates the antioxidant system, allowing repair of damage caused by cold stress, resulting in increased lifespan (Lalouette et al. 2011). Zhang et al. (2015) reported that thermal stress (above 37 °C) is one of the factors that cause oxidative stress in insects. Jia et al. (2011) showed that low (–5, –2.5, 0, and 5 °C) and high (35, 37.5, and 40 °C) temperature stresses induce oxidative damage in *B. dorsalis*. In our study, temperature stresses might induce oxidative stress, which extended the developmental period, lifespan, and fecundity of *B. dorsalis*. As the larval stage of *B. dorsalis* causes great damage, the prolonged larval duration would potentially have significant agricultural impacts, and increased fecundity may also affect the population of *B. dorsalis*. Taken together, our results suggest that global warming can substantially affect the *B. dorsalis* population and pest severity level, while cold acclimation helps this key pest to survive in temperate areas.

The mortality rate of *B. dorsalis* at the larval stage significantly increased when exposed to HT and LT stress. Our results of high-temperature stress are in line with (Huang et al. 2020) that the mortality rate of *B. tau* was significantly increased when exposed to high temperature. Wang et al. (2014) reported 98.90 and 100 % mortality in the 3rd instar *B. dorsalis* larvae following exposure to 0 °C for 1 and 2 days, respectively. The mortality rate of 3rd instar *B. dorsalis* was 85.3% after treatment with 0.5–1 °C for 3 d (Lin et al. 2020). These results showed that temperature stress causes mortality in the larval stage. However, the survived larvae benefit in the subsequent life stages after temperature stress conditions. In this study, we choose 38 °C as HT for 1 day and 3 °C as LT for 2 d exposure, which causes 33.3 and 36.7 % mortality, respectively, to check the impact of temperature stress on the subsequent life stages of survived larvae following exposure to these stress conditions.

Results showed that temperature stress influenced the duration of different developmental stages and the total longevity of *B. dorsalis*. The duration of the preadult stage was significantly increased when treated with low and high-temperature stress compared to control. The mean longevities of *B. dorsalis* females and males were significantly increased following low and high-temperature exposure. Huang et al. (2020) reported that the developmental duration of *B. tau* increased significantly following exposure to high-temperature stress (34 °C to 42 °C). The developmental durations of the egg, larval, and pupal stages of *B. tau* increased significantly when treated to 42 °C compared to control (Huang et al. 2020). The developmental stage of insects increased when the ambient temperature was raised to an unsuitable temperature. Liu et al. (2005) also reported that the developmental duration of *B. tau* was significantly prolonged when the ambient temperature exceeded 34 °C. The developmental duration of *B. dorsalis* larvae was significantly increased when exposed to high and low-temperature stress compared to control (25 °C)(Yang et al. 1994). Le Bourg. (2007) reported the hormetic effects on longevity, behavioral aging, and heat and cold shock resistance in aged flies following exposure to repeated cold shocks. Khazaeli et al. (1997) documented the extension of longevity in *Drosophila melanogaster* following exposure to 36 °C. The total adult longevities of male and female *B. tau* were gradually extended with increasing temperatures (from 24 to 34 °C). However, the longevities were significantly decreased when the temperature increased (from 38 to 42 °C) compared to the control (Huang et al. 2020). Wang et al. (2014) reported cold tolerance of different geographic populations of *B. dorsalis* with 34.4, 26.7, 21.2, and 14.4% mortality of 3rd instar larvae of Guangzhou (23.1 N), Xiamen (24.3 N), Fujian (26.0 N), and Wuxi (31.6 N) populations, respectively after the treatments of 5°C for 6 h. Moreover, they demonstrated that *B. dorsalis* adapt to cold climates while expanding its northern distribution in China. However, the occurrence of this key pest substantially changed when it invaded and inhabited the more temperate zone of Wuxi.

According to Lithgow et al. (1995), heat exposure may increase longevity and thermotolerance in *Caenorhabditis elegans* (Maupas) by inducing the activity of *hsps*, which affects the ability of cells to cope with the degenerative effects of age and the environment. Considering the association between *hsp70* and thermotolerance in *Drosophila melanogaster* Meigen (Feder 1995), some *hsps* might be involved in the increased longevity of adults associated with heat stress. However, further studies are needed to fully understand the potential effects of *hsps* on insect longevity.

The adult preoviposition period of *B. dorsalis* was significantly decreased in both high and low-temperature treated insects, while the oviposition was considerably increased following exposure to high-temperature stress. In contrast, the preoviposition period of *B. tau* was significantly increased when exposed to different short-term hightemperatures (24, 34, 36, 38, and 40 °C) for 12 h (Huang et al. 2020). Moreover, the field performance and tolerance of *T. podisi* against low and high temperatures increased following exposure to temperature stress (Castellanos et al. 2019). The population and predation projections of *Harmonia axyridis* Pallas were proportional to the temperature (Islam et al. 2022). The overall life table of *B. dorsalis* in this study shows that low and high-temperature stress stimulates key biological parameters that allow them to withstand stress conditions. However, there are several unresolved questions regarding temperature-induced longevity extension and increased fecundity in *B. dorsalis*. Therefore, future investigations are necessary to validate these results at the molecular level, since increased transcriptional level of several genes during preconditioning

is often linked with stimulation of reproduction, longevity, and development of insects.

5 Conclusion

The results showed the impact of temperature stress on key biological and demographic parameters of *B. dorsalis*, using the age-stage, two-sex life table approach. The developmental duration and total longevities of males and females were significantly increased following temperature stress. Moreover, the adult preoviposition period was decreased while the oviposition, fecundity, and total population size increased dramatically when treated with both stress conditions. Taken together, the present study suggests that prolonged larval duration and increased fecundity of *B. dorsalis* during heat waves conditions could alter the pest severity level of *B. dorsalis*in the field. Using molecular techniques, future studies are necessary to investigate the functional analysis of genes responsible for altering the key biological traits of *B. dorsalis* during heat stress.

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References

Akca, I., Ayvaz, T., Yazici, E., Smith, C. L., & Chi, H. (2015). Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): with additional comments on life table research criteria. *Journal of Economic Entomology, 108*(4), 1466–1478. https://doi.org/10.1093/jee/tov187

Castellanos, N., Bueno, A., Haddi, K., Silveira, E., Rodrigues, H., Hirose, E., … Oliveira, E. (2019). The fitness and economic benefits of rearing the parasitoid *Telenomus podisi* under fluctuating temperature regime. *Neotropical Entomology, 48*(6), 934–948. https://doi.org/10.1007/s13744-019-00717-1

Chi, H (1988): Life-table analysis incorporating both sexes and variable development rates among individuals. *Environmental Entomology, 17*(1): 26–34. https://doi.org/10.1093/ee/17.1.26

Chi, H (1990): Timing of control based on the stage structure of pest populations: a simulation approach. *Journal of Economic Entomology, 83*(4): 1143–1150. https://doi.org/10.1093/jee/83.4.1143

Chi, H., You, M., Atlıhan, R., Smith, C. L., Kavousi, A., Özgökçe, M. S., … Liu, T.-X. (2020). Age-Stage, two-sex life table: An introduction to theory, data analysis, and application. *Entomologia Generalis, 40*(2), 103–124. https://doi.org/10.1127/entomologia/2020/0936

Chi, H. (2022a). *TIMING-MSChart: a computer program for the population projection based on age-stage, two-sex life table*. http://140.120.197.173/ecology/Download/TIMING-MSChart-new.rar

Chi, H. (2022b). TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. http://140.120.197.173/ecology/Download/TWOSEX-MSChart-B100000.rar

Chi, H., & Liu, H. (1985). Two new methods for the study of insect population ecology. *Bulletin of the Institute of Zoology, Academia Sinica, 24*(2), 225–240.

Cutler, G. C., Amichot, M., Benelli, G., Guedes, R. N. C., Qu, Y., Rix, R. R., … Desneux, N. (2022). Hormesis and insects: Effects and interactions in agroecosystems. *The Science of the Total Environment, 825*, 153899. https://doi.org/10.1016/j.scitotenv.2022.153899

Danjuma, S., Thaochan, N., Permkam, S., & Satasook, C. (2014). Effect of temperature on the development and survival of immature stages of the carambola fruit fly, *Bactrocera carambolae*, and the Asian papaya fruit fly, *Bactrocera papayae*, reared on guava diet. *Journal of Insect Science, 14*(1), 126. https://doi.org/10.1093/jis/14.1.126

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. *Science, 289*(5487), 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Feder, M. E., Parsell, D. A., & Lindquist, S. L. (1995). The stress response and stress proteins. *Cell biology of trauma,* 177–191.

Fiaboe, K. K., Kekeunou, S., Nanga, S. N., Kuate, A. F., Tonnang, H. E., Gnanvossou, D., & Hanna, R. (2021). Temperature-based phenology model to predict the development, survival, and reproduction of the oriental fruit fly *Bactrocera dorsalis*. *Journal of Thermal Biology, 97*, 102877. https://doi.org/10.1016/j.jtherbio.2021.102877

Feder, M., Blair, N., & Figueras, H. (1997). Natural thermal stress and heat-shock protein expression in *Drosophila* larvae and pupae. *Functional Ecology, 11*(1), 90–100. https://doi.org/10.1046/j.1365-2435.1997.00060.x

Han, P., Becker, C., Sentis, A., Rostás, M., Desneux, N., & Lavoir, A.-V. (2019). Global change-driven modulation of bottom–up forces and cascading effects on biocontrol services. *Current Opinion in Insect Science, 35*, 27–33. https://doi.org/10.1016/j.cois.2019.05.005

Huang, H.-W., Chi, H., & Smith, C. L. (2018). Linking demography and consumption of *Henosepilachna vigintioctopunctata* (Coleoptera: Coccinellidae) fed on *Solanum photeinocarpum* (Solanales: Solanaceae): With a new method to project the uncertainty of population growth and consumption. *Journal of Economic Entomology, 111*(1), 1–9. https://doi.org/10.1093/jee/tox330

Huang, Y., Gu, X., Peng, X., Tao, M., Chen, G., & Zhang, X. (2020). Effect of short-term high-temperatures on the growth, development and reproduction in the fruit fly, *Bactrocera tau* (Diptera: Tephritidae). *Scientific Reports, 10*(1), 6418. https://doi.org/10.1038/s41598-020-63502-w

Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology, 46*(1), 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Islam, Y., Güncan, A., Fan, Y., Zhou, X., Naeem, A., & Shah, F. M. (2022). Age-stage, two-sex life table and predation parameters of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), reared on *Acyrthosiphon pisum* (Harris)(Hemiptera: Aphididae),

at four different temperatures. *Crop Protection, 159*, 106029. https://doi.org/10.1016/j.cropro.2022.106029

Jia, F.-X., Dou, W., Hu, F., & Wang, J.-J. (2011). Effects of thermal stress on lipid peroxidation and antioxidant enzyme activities of oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *The Florida Entomologist, 94*(4), 956–963. https://doi.org/10.1653/024.094.0432

Khazaeli, A. A., Tatar, M., Pletcher, S. D., & Curtsinger, J. W. (1997). Heat-induced longevity extension in *Drosophila*. I. Heat treatment, mortality, and thermotolerance. *The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences, 52*(1), 48–52. https://doi.org/10.1093/gerona/52A.1.B48

Lalouette, L., Williams, C., Hervant, F., Sinclair, B. J., & Renault, D. (2011). Metabolic rate and oxidative stress in insects exposed to low temperature thermal fluctuations. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology, 158*(2), 229–234. https://doi.org/10.1016/j.cbpa.2010.11.007

Liu, Y. H. (2005). Effects of temperature and supplementary nutrition on population growth of *Bactrocera tau* (Walker). *Southwest Agricultural University*.

Le Bourg, E. (2007). Hormetic effects of repeated exposures to cold at young age on longevity, aging and resistance to heat or cold shocks in *Drosophila melanogaster. Biogerontology, 8*(4), 431–444. https://doi.org/10.1007/s10522-007-9086-6

Lithgow, G. J., White, T. M., Melov, S., & Johnson, T. E. (1995). Thermotolerance and extended lifespan conferred by single-gene mutations and induced by thermal stress. *Proceedings of the National Academy of Sciences of the United States of America, 92*(16), 7540–7544. https://doi.org/10.1073/pnas.92.16.7540

Lin, K. W., Lin, H. L., Shiesh, C. C., Hsu, Y. L., Lin, C., Chen, S. C., & Yeh, W. B. (2020). Cold treatment for guava fruits infested with oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Applied Entomology and Zoology, 55*(1), 37–44. https://doi.org/10.1007/s13355-019-00651-z

Lumbierres, B., Madeira, F., Roca, M., & Pons, X. (2021). Effects of temperature and diet on the development and reproduction of the ladybird *Oenopia conglobata. Entomologia Generalis, 41*(2), 197–208. https://doi.org/10.1127/entomologia/2020/1077

Ma, C.-S., Ma, G., & Pincebourde, S. (2021). Survive a warming climate: Insect responses to extreme high temperatures. *Annual Review of Entomology, 66*(1), 163–184. https://doi.org/10.1146/annurev-ento-041520-074454

Nika, E. P., Kavallieratos, N. G., & Papanikolaou, N. E. (2021). Linear and non-linear models to explain influence of temperature on life history traits of *Oryzaephilus surinamensis* (L.). *Entomologia Generalis, 41*(2), 157–167. https://doi.org/10.1127/entomologia/2020/1088

Ullah, F., Gul, H., Desneux, N., Gao, X., & Song, D. (2019). Imidacloprid-induced hormesis effects on demographic traits of the melon aphid, *Aphis gossypii. Entomologia Generalis, 39*(3-4), 325–337. https://doi.org/10.1127/entomologia/2019/0892

Vargas, R. I., Piñero, J. C., & Leblanc, L. (2015). An overview of pest species of *Bactrocera* fruit flies (Diptera: Tephritidae) and the integration of biopesticides with other biological approaches for their management with a focus on the Pacific region. *Insects, 6*(2), 297–318. https://doi.org/10.3390/insects6020297

Wang, J., Zeng, L., & Han, Z. (2014). An assessment of cold hardiness and biochemical adaptations for cold tolerance among different geographic populations of the *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Journal of Insect Science, 14*(1), 292. https://doi.org/10.1093/jisesa/ieu154

Wang, S., Chen, X., Li, Y., Pan, B., Wang, S., Dai, H., … Tang, B. (2020). Effects of changing temperature on the physiological and biochemical properties of *Harmonia axyridis* larvae. *Entomologia Generalis, 40*(3), 229–241. https://doi.org/10.1127/entomologia/2020/0917

Wei, M., Chi, H., Guo, Y., Li, X., Zhao, L & Ma, R (2020): Demography of *Cacopsylla chinensis* (Hemiptera: Psyllidae) reared on four cultivars of *Pyrus bretschneideri* (Rosales: Rosaceae) and *P. communis* pears with estimations of confidence intervals of specific life table statistics. *Journal of Economic Entomology, 113*(5): 2343–2353. https://doi.org/10.1093/jee/toaa149

Woods, H. A., Dillon, M. E., & Pincebourde, S. (2015). The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology, 54*, 86–97. https://doi.org/10.1016/j.jtherbio.2014.10.002

Yang, P., Carey, J. R., & Dowell, R. V. (1994). Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Environmental Entomology, 23*(4), 971–974. https://doi.org/10.1093/ee/23.4.971

Yao, F.-L., Ding, X.-L., Mei, W.-J., Zheng, Y., Desneux, N., He, Y.-X., & Weng, Q.-Y. (2020). Impact of heat stress on the development of egg and adult coccinellid *Serangium japonicum*: Evidence for cross-stage and cross-generation effects. *Entomologia Generalis, 40*(4), 365–376. https://doi.org/10.1127/entomologia/2020/1096

Zhang, S., Fu, W., Li, N., Zhang, F., & Liu, T.-X. (2015). Antioxidant responses of *Propylaea japonica* (Coleoptera: Coccinellidae) exposed to high temperature stress. *Journal of Insect Physiology, 73*, 47–52. https://doi.org/10.1016/j.jinsphys.2015.01.004

Zhang, G.-H., Liu, H., Wang, J.-J., & Wang, Z.-Y. (2014). Effects of thermal stress on lipid peroxidation and antioxidant enzyme activities of the predatory mite, *Neoseiulus cucumeris* (Acari: Phytoseiidae). *Experimental & Applied Acarology, 64*(1), 73–85. https://doi.org/10.1007/s10493-014-9806-y

Zhang, X.-S., Wang, T., Lin, X.-W., Denlinger, D. L., & Xu, W.-H. (2017). Reactive oxygen species extend insect life span using components of the insulin-signaling pathway. *Proceedings of the National Academy of Sciences of the United States of America, 114*(37), E7832–E7840. https://doi.org/10.1073/pnas.1711042114

Zhang, W., Chang, X.-Q., Hoffmann, A., Zhang, S., & Ma, C.-S. (2015). Impact of hot events at different developmental stages of a moth: The closer to adult stage, the less reproductive output. *Scientific Reports, 5*(1), 10436. https://doi.org/10.1038/srep10436

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