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Short-Term Temperature Stress Modulates Fitness Traits in *Bactrocera zonata*, through Negative Impact on Larval Stage

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Abstract: The frequency and magnitude of climate extremes, especially temperature extremes (TE), are increasing, which are exposing insect populations. However, insect responses to TE are poorly understood. In this study, we investigated the impact of high-temperature (HT: 38 °C) and low-temperature (LT: 3 °C) stresses on demographic parameters and population projections of the peach fruit fly, *Bactrocera zonata*, a destructive pest of fruits and vegetables. Results show that the larval developmental stage was significantly increased by HT (8.30 d) and LT (8.10 d) compared with control (7.02 d). The preadult stage in the HT and LT stressed flies were 18.56 d and 18.40 d, respectively compared with control (17.37 d). Mean longevities of both males and females were also substantially prolonged in HT and LT treatments. Compared with control, the total pre-oviposition period (TPOP) and oviposition days of *B. zonata* were significantly increased in both stress conditions. Furthermore, female fecundity of flies significantly increased in both HT and LT (705.48 and 698.38 respectively) treatments compared with control (578.35). These findings show that temperature stresses in the larval stage delayed the larval development and increase the reproduction and life span of *B. zonata*. The temperature induces alteration in life-history traits that might have significant agricultural impacts on the control strategies for this key pest.

Keywords: climate change; heatwaves; invasive species; environmental changes; cold stress; Tephritidae

1. Introduction

Climate change affects all organisms, including insects, and only those that can adapt to it will have a greater chance of surviving. It is one of the variables that encourages the invasion of new ecologies. Invasive species have significant ecological and economic effects in the invaded regions [1,2]. Invasive species may benefit from climate change if previously unsuitable areas become more conducive to their establishment [1]. This is true for insects that depend on local environmental factors to survive and develop within their temperature limits. The effects of climate change on insect distribution are among the most important factors in determining their future risk to agricultural productivity and trade. Poikilothermic insects often experience population changes in response to temperature

changes. The physiological processes and ecological systems of insects are often affected by thermal variations such as sublethal or lethal extreme high temperatures [3]. Thermoregulation activity improves the survival of insects after exposure to high temperatures [4]. Many insects experience low temperatures that are consistently low enough to cause their bodily fluids to freeze. Insects use a variety of approaches to reduce this risk [5], such as behavioral avoidance, freezing risk reduction by promoting supercooling, removing freezable water [6], and altering fluid body composition to prevent ice crystallization [7]. Temperatures stress in the initial stages of insect life may impact the performance of later stages [8].

Insects require an optimal temperature range for their reproduction, growth, and biological and physiological processes [9–11]. The peach fruit fly, *Bactrocera zonata* Saunders (Diptera: Tephritidae), is among the most harmful species of Tephritidae that causes extensive damage in Asia and Africa. *Bactrocera zonata* is widely distributed in India, Pakistan, Bangladesh, Bhutan, Laos, Myanmar, Nepal, Sri Lanka, Thailand, and Vietnam. However, *B. zonata* is currently absent from China and is listed as one of the most important quarantine pests that needs serious attention on their invasion. This polyphagous pest infests more than 40 species of fruits and vegetables. *Bactrocera zonata* can cause 25 to 100% losses in peaches, apricots, guavas, and figs in India and 25 to 50% in guava alone in Pakistan [12]. Temperature is one of the most important abiotic factors affecting insects' biological and demographic parameters [13,14]. Insects change their phenology, geographic ranges, trophic interactions, population dynamics, and community structure in response to changing climates [15]. Previous studies focused on how temperature affects fecundity, survival rate, and growth of insects after treatment with various temperature stresses [16]. The mortality rate of *Zeugodacus tau* Walker (Diptera: Tephritidae) was dramatically enhanced following exposure to high temperatures [17].

Temperature is one of the most important abiotic stresses affecting insects' biological and demographic parameters [17–19]. Low temperature stress induces hormesis effects on longevity, behavioral aging, and resistance to heat and cold shock in aged flies [20]. Fluctuating temperatures increase the fitness and tolerance of *Telenomus podisi* Ashmead (Hymenoptera: Platygastridae) [21]. High temperatures improve the production of reactive oxygen species (ROS), which leads to oxidative damage [22]. As a result, insect development was delayed whereas longevity was increased [23].

However, the impact of ongoing climate change on the demographic parameters and population projections of *B. zonata* is poorly studied. In this study, we used an age-stage, two-sex life-table method to investigate the life history traits of *B. zonata* when the larval stage was exposed to high temperature (HT: 38 °C) and low temperature (LT: 3 °C). These results will give detailed information about how climate change affects the biological parameters and population projection through the carryover effects of *B. zonata*.

2. Material and Methods

2.1. Study Insects

The population of *B. zonata* was collected from the maintained colony at the Insect Pest Management Program, National Agricultural Research Center, Islamabad, Pakistan. The population was cultured using an artificial diet at 28 ± 1 °C with 65 ± 5% relative humidity (RH) in a 14:10 (L:D) photoperiod.

2.2. Life-Table Experiments

The demographic parameters and population projections of *B. zonata* were evaluated under high temperature (HT: 38 °C) and low temperature (LT: 3 °C) stresses using an age-stage, two-sex life table and the TWOSEX-MSChart computer program. *Bactrocera zonata* eggs were collected from a 1 mm holed plastic bottle that contained commercially available guava juice. These plastic bottles were placed in the rearing cages for 3 h. For life-table experiments, 120 eggs were collected for each treatment (HT, LT, and control) and transferred to Petri dishes containing fresh artificial larval 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. When the larvae reached 4 days old, they were exposed to HT and LT for 1 and 2 days, respectively. After treatment with HT and LT, the surviving larvae (56 for HT and 62 for LT) were individually transferred to microcages containing artificial larval diet under standard laboratory conditions. In the control group, 58 healthy larvae were reared under standard laboratory conditions as mentioned above without exposure to HT or LT stress. Data on the developmental duration and survival rate of larvae and pupae were recorded daily. We paired one male and one female after adult emergence and kept them in a small cage (15 × 15 × 20 cm). All couples were maintained on a protein-rich adult diet. Water was provided ad libitum. Perforated plastic bottles containing commercially available guava juice were used for egg collection. The longevity and fecundity of adult flies were continuously observed until complete mortality.

2.3. Life-Table Data Analysis

Life-table data from the HT, LT, and control cohorts were analyzed using the age-stage, two-sex life-table method [24–26]. 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 statistically analyzed using the TWOSEX-MSChart computer program [27]. Standard errors and differences were calculated through 100,000 bootstrap replicates [28,29]. The variances between life-table parameters of all cohorts (HT, LT, and control) were evaluated by paired bootstrap test at a 5% significance level based on the confidence interval of difference [30]. Details of the life-table analysis is given in the Supplementary File.

2.4. Population Projection

The population projection simulation based on life-table parameters of *B. zonata* started with 10 eggs and was projected for 90 days. The total population size at the time t was estimated by Equation (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 [31].

We sorted the 100,000 bootstrap results of the λ to find the 2.5th and 97.5th percentiles (i.e., the 2500th and 97,500th sorted bootstrap samples) to check the variability of the projections. Samples from the bootstrap life table were used to generate the 2.5th and 97.5th percentiles of the λ to project the population to represent the confidence interval of the projected populations [31]. The projection of *B. zonata* was analyzed using the TIMING-MSChart computer program [32] following the method of [24,33].

3. Results

3.1. Developmental Duration and Adult Longevity of Bactrocera zonata

The mean duration of different developmental stages and longevity of *B. zonata* following exposure to HT and LT are shown in Table 1. The larval developmental duration of *B. zonata* was significantly increased ($p < 0.05$) by 8.30 days in HT and 8.10 days in LT treatments compared with control insects (7.02 d). No significant differences were observed in the pupal stage among all treatments. The preadult stage was substantially ($p < 0.05$) prolonged in HT (18.56 days) and LT (18.40 days) treatments compared with control (17.37 days). The mean longevities of both male and female *B. zonata* were significantly increased ($p < 0.05$) following exposure to HT (i.e., 65.15 days for males; 68.08 days for females) or LT (i.e., 63.10 days for males; 65.23 days for females) compared with untreated control insects (i.e., 54.18 days for males and 56.04 days for females). No significant differences were observed between longevities of males and females (Table 1). The total longevity

of HT-treated *B. zonata* was 85.12 days; for LT-treated *B. zonata* it was 82.47 days. Both were significantly prolonged compared with the untreated control which was 72.39 days.

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

Parameters	Control	High Temperature (HT)	Low Temperature (LT)
	Mean ± SE	Mean ± SE	Mean ± SE
Eggs	2.04 ± 0.02 a	2.08 ± 0.02 a	2.10 ± 0.03 a
Larvae	7.02 ± 0.10 b	8.30 ± 0.08 a	8.10 ± 0.09 a
Pupae	8.29 ± 0.09 a	8.13 ± 0.10 a	8.23 ± 0.12 a
Preadult	17.37 ± 0.15 b	18.56 ± 0.14 a	18.40 ± 0.16 a
Adult longevity (Male)	54.18 ± 1.74 bA	65.15 ± 1.89 aA	63.10 ± 1.72 aA
Adult longevity (Female)	56.04 ± 2.63 bA	68.08 ± 2.27 aA	65.23 ± 2.52 aA
Total Longevity	72.39 ± 1.50 b	85.12 ± 1.44 a	82.47 ± 1.52 a

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

3.2. Fecundity and Demographic Characteristics of Bactrocera zonata

The effects of HT and LT treatments on *B. zonata* fecundity and demographic traits are shown in Table 2. No statistical differences were observed in key demographic parameters (i.e., r, λ, and R_0) when *B. zonata* were exposed to HT and LT (Table 2). The mean generation time (T) was significantly increased ($p < 0.05$) in HT (49.23 days) and LT (47.86 days) exposed flies as compared with controls (45.66 days). Similarly, the fecundity (eggs/female) of *B. zonata* was significantly higher ($p < 0.05$) in the HT- and LT-exposed groups with 705.48 and 698.38 eggs, respectively, as compared with untreated control individuals (578.35 eggs). Although no significant differences were observed in the oviposition period, the number of oviposition days (O_d), which corresponds to the actual number of days that an insect has produced eggs, were 38.32 and 36.65 days in HT- and LT-treated insects, respectively, which were significantly increased compared with the untreated insects (30.83 days; $p < 0.05$). The total preoviposition period was also substantially prolonged ($p < 0.05$) in HT (31.44 days) and LT (31.15 days) compared with controls (30.43 days). However, no significant differences were observed in the adult preoviposition period between all treated groups (Table 2).

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

Parameters	Control (Mean ± SE)	High Temperature (HT) (Mean ± SE)	Low Temperature (LT) (Mean ± SE)
Intrinsic rate of increase (d^{-1}) (r)	0.1031 ± 0.0048 a	0.1014 ± 0.0042 a	0.1049 ± 0.0042 a
Finite rate of increase (d^{-1}) (λ)	1.1086 ± 0.0053 a	1.1067 ± 0.0046 a	1.1106 ± 0.0046 a
Net reproductive rate (offspring/individual) (R_0)	110.85 ± 21.15 a	146.98 ± 26.84 a	151.32 ± 27.11 a
Mean generation time (days) (T)	45.66 ± 0.56 b	49.23 ± 0.52 a	47.86 ± 0.49 a
Fecundity (eggs/female) (F)	578.35 ± 22.25 b	705.48 ± 28.58 a	698.38 ± 31.38 a
Oviposition period (days) (O_p)	39.00 ± 6.28 a	50.00 ± 5.21 a	48.00 ± 5.29 a
Oviposition days (days) (O_d)	30.83 ± 1.67 b	38.32 ± 1.48 a	36.65 ± 1.63 a
APOP (days)	13.13 ± 0.07 a	13.16 ± 0.07 a	13.19 ± 0.08 a
TPOP (days)	30.43 ± 0.27 b	31.44 ± 0.21 a	31.15 ± 0.24 a

Standard errors were estimated by using the bootstrap technique with 100,000 resampling. Difference was compared using the paired bootstrap test ($p < 0.05$). The means within a row followed by a different lowercase letter indicate significant differences between the treatments. APOP: adult pre-oviposition period, TPOP: total pre-oviposition period.

The s_{xj} of *B. zonata* following exposure to HT and LT are shown in Figure 1. The s_{xj} curves shows the probability of newly laid eggs to survive to age x and develop to stage j. The overlapping of these curves shows the differences among developmental stages of all treated groups, i.e., HT, LT, and control (Figure 1). The adult longevities of males and females of *B. zonata* were prolonged in the HT and LT groups compared with the control cohort (Figure 1).

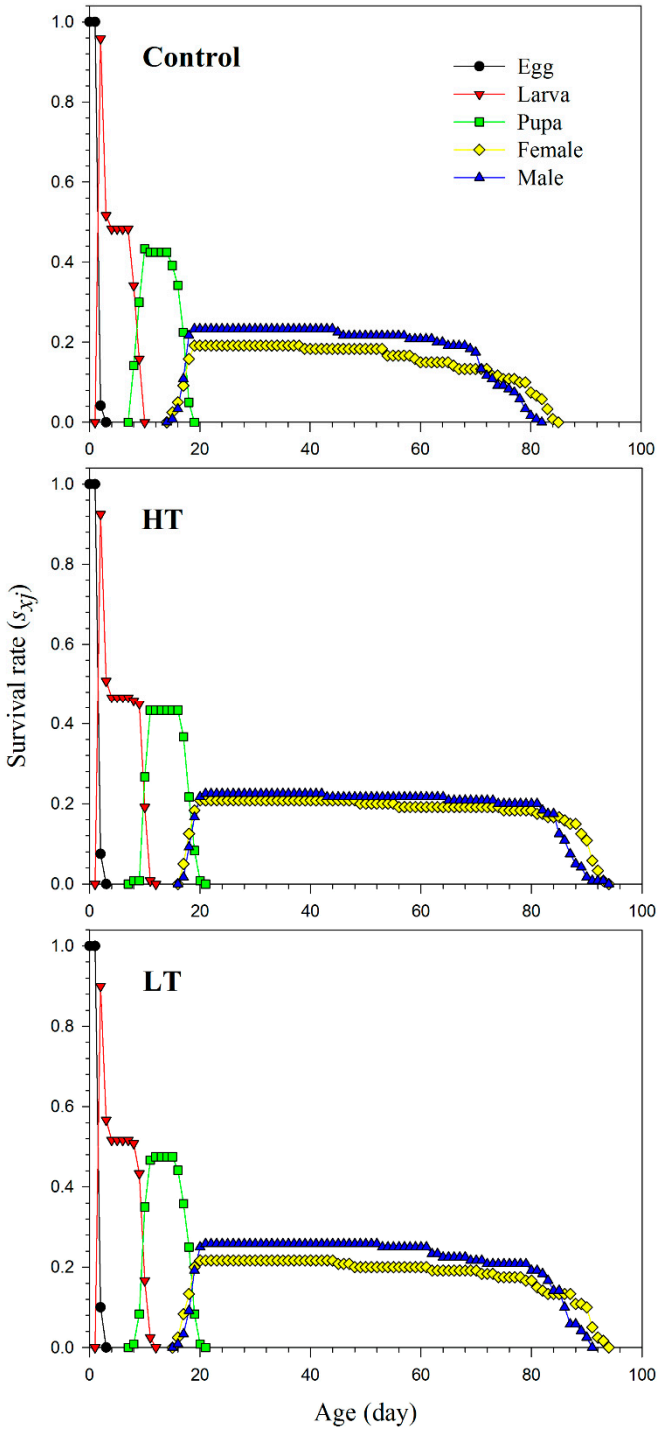

Figure 1. Age-stage-specific survival rate (s_{xj}) of *Bactrocera zonata* following exposure to high temperature (HT) and low temperature (LT).

The l_x, m_x, and l_xm_x of *B. zonata* after HT or LT treatments are shown in Figure 2. The plotted curves of l_x represent the probability for the egg to survive to age x by neglecting stage differentiation (Figure 2). The l_x curves started to decline from 0.4 after 53 d in control cohorts, whereas in the HT and LT groups it started to decline after 73 days and 71 days, respectively. This shows that the survival rates in the HT and LT cohorts were significantly higher than for control insects (Figure 2). The highest m_x values in the HT and LT groups were nearly 16, observed at age 52 days and 49 days, respectively, which were much higher than the control cohort (~12 at the age of 53 days). The peak values of net maternity (l_xm_x) were highest at the age of 52 days and 49 days, which were higher than untreated control insects at the age of 53 days. Furthermore, the plotted curves of m_x and l_xm_x indicated that the reproduction ended in the HT and LT groups at the age of 90 days and 89 days, respectively, which was longer than in controls (83 days) (Figure 2).

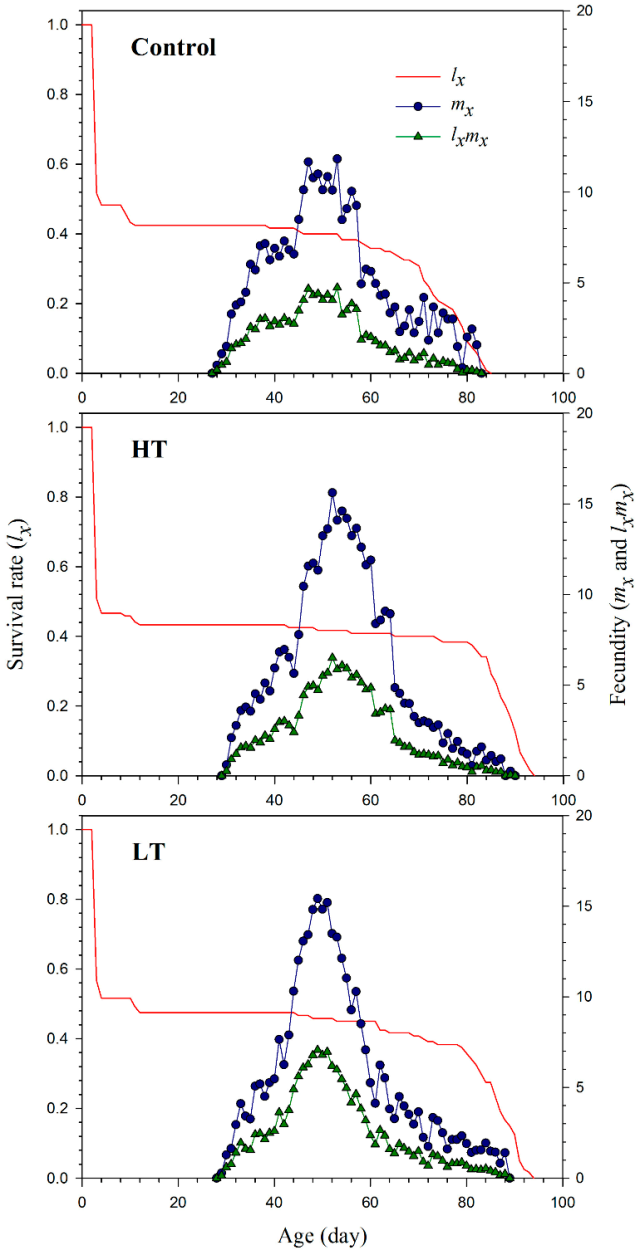

Figure 2. Age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity (l_xm_x) of *Bactrocera zonata* following exposure to high temperature (HT) and low temperature (LT).

The e_{xj} of *B. zonata* after treatment with HT or LT are shown in Figure 3. The plotted curves of e_{xj} represent the predicted life span of an individual of age x and stage j that lives after age x (Figure 3). These curves indicated the prolonged life expectancy of male and female *B. zonata* in the HT and LT cohorts as compared with the controls.

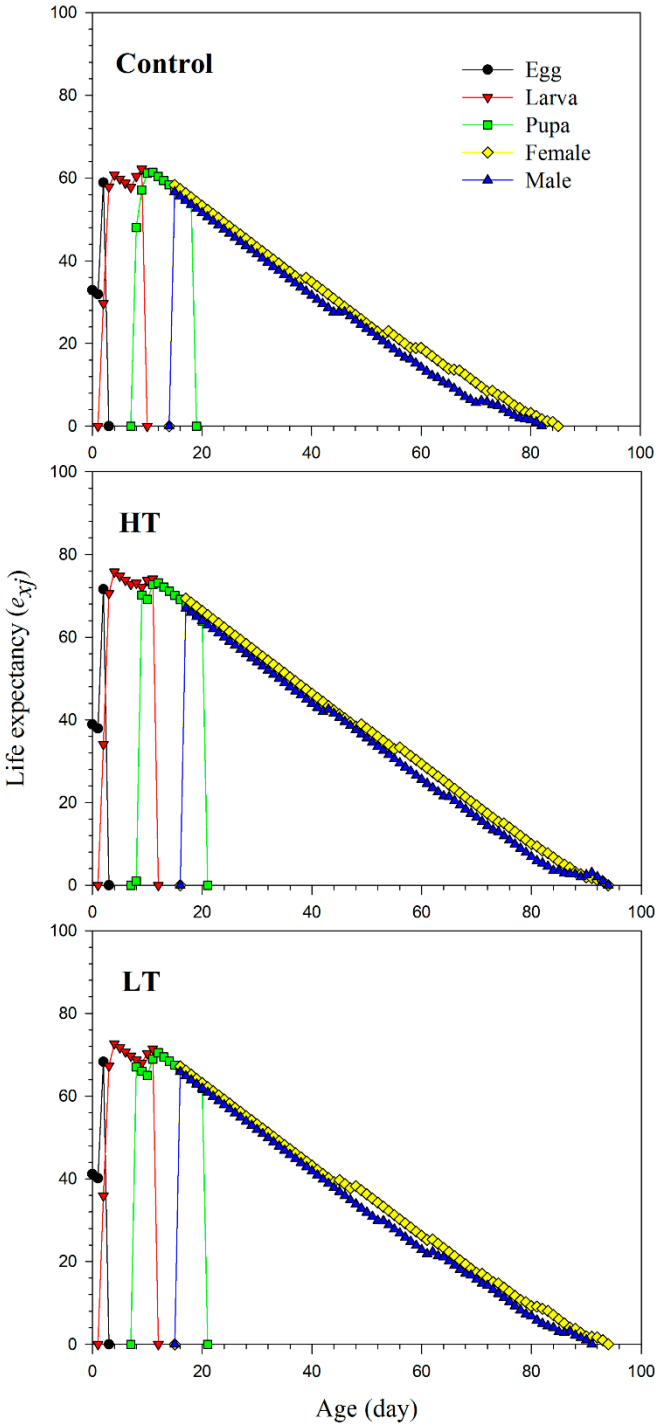

Figure 3. Age-stage-specific life expectancy (e_{xj}) of *Bactrocera zonata* following exposure to high temperature (HT) and low temperature (LT).

The v_{xj} of *B. zonata* after exposure to HT or LT are plotted in Figure 4. The maximum v_{xj} values of *B. zonata* females in the HT and LT groups were 231.7 (at 49th d) and 242.2 (at 45th d), respectively, which is higher than the control cohort with 181 at 45th d. Further-

more, the duration of total preoviposition in HT- and LT-treated insects were longer than the control insects (Figure 4).

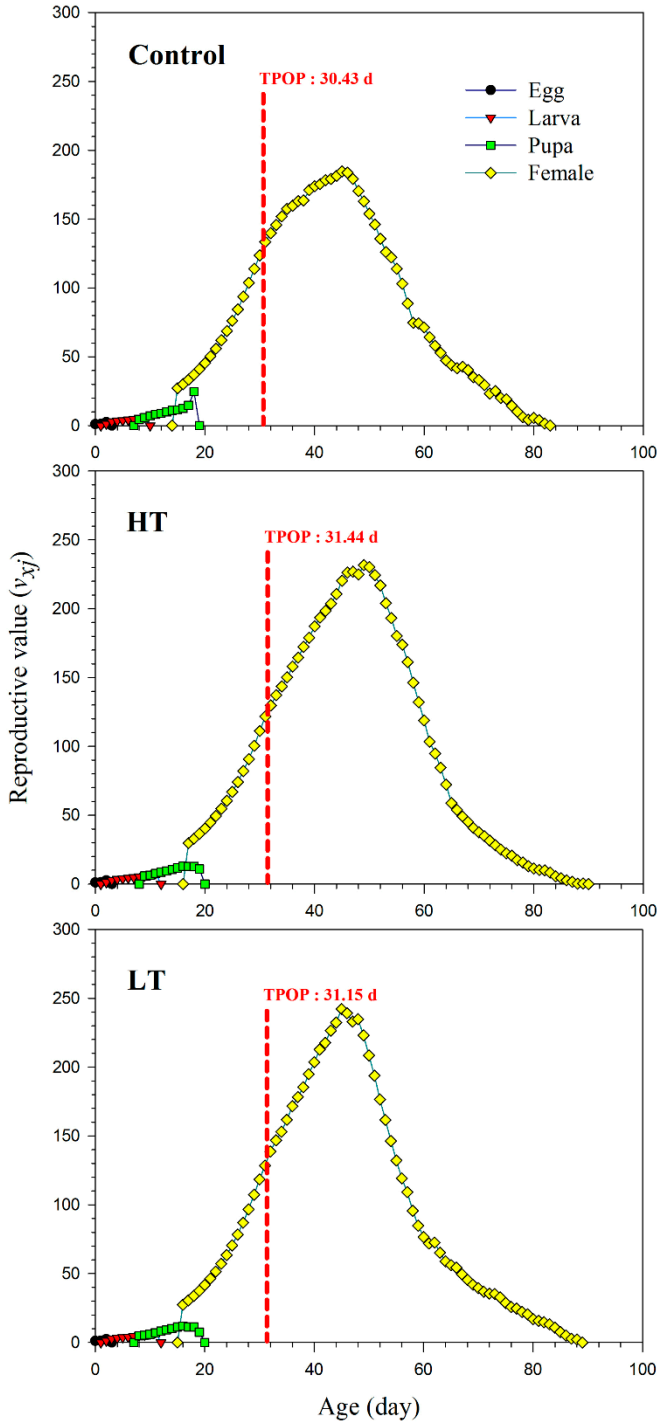

Figure 4. Age-stage-specific reproductive value (v_{xj}) of *Bactrocera zonata* following exposure to high temperature (HT) and low temperature (LT). TPOP: total pre-oviposition period.

3.3. Population Projection

Simulations of HT and LT exposure and control population growth for 90 days and projected population size ±95% confidence intervals after 90 days were plotted in Figure 5. Similar population growth was observed on growth curves (logarithmic scale) for 90 days (Figure 5a). The total population size exceeded 24,000 individuals for LT-exposed insects,

whereas the HT-treated population had almost 16,000 flies at the 90th day. The projected insect population was ~18,600 in the control group after 90 days (Figure 5b).

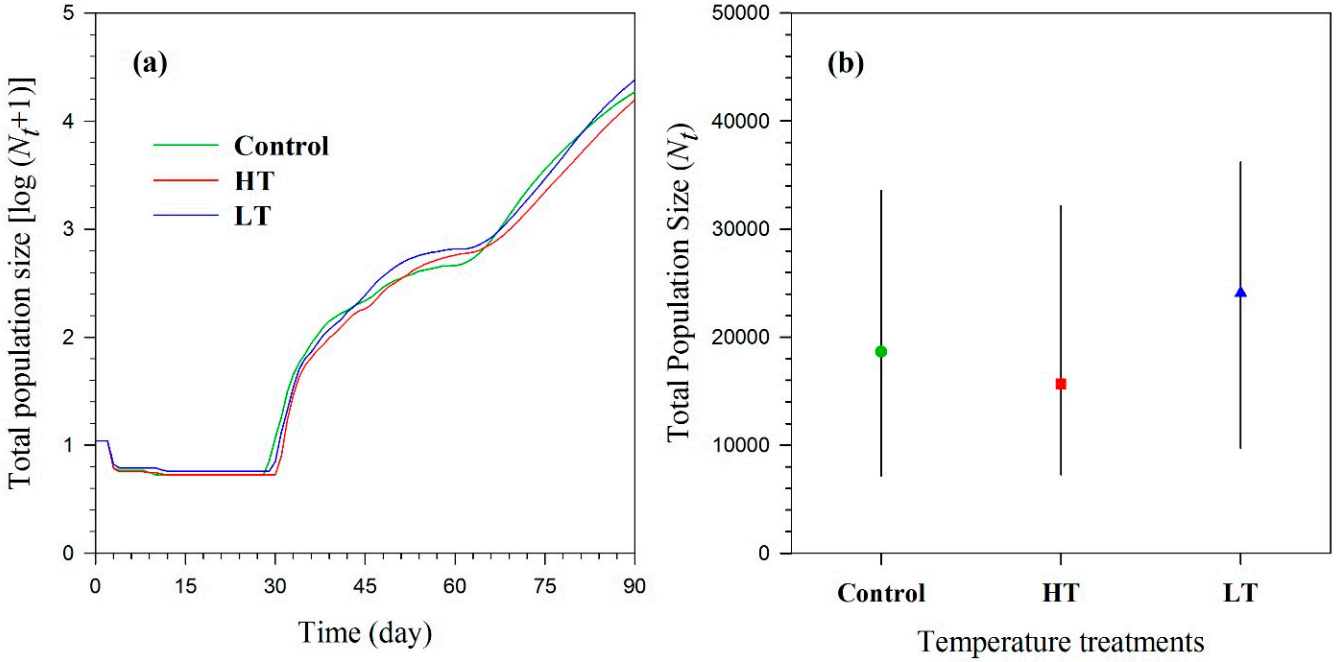

Figure 5. Total population size [log(N_t + 1)] (**a**) and (*Nt*) (**b**) after population projection of *Bactrocera zonata* following exposure to high temperature (HT) and low temperature (LT) for 90 days using the life-table data of the original cohort and the cohorts constructed based on the 2.5 and 97.5% percentiles of λ, finite rate of increase.

4. Discussion

In response to changing climates, insects alter their phenology, geographic ranges, trophic interactions, population dynamics, and community structure [15]. Thermal extremes substantially affect pest management and biodiversity preservation by influencing how insects react to climate change [9,34]. Temperature stress at the initial stages of insect life may stimulate the performance of later stages, which could be due to the carryover effects resulting in population growth [35]. In this study, we evaluated the key demographic parameters and population projections of *B. zonata* following exposure to HT and LT stresses.

The results showed that the duration of larval developmental and preadult stage were significantly increased when insects were treated with HT and LT compared with controls. The fecundity and mean longevities of *B. zonata* males and females were also notably increased following exposure to HT or LT. The developmental duration of *Z. tau* egg, larval, and pupal stages, was substantially enhanced when treated at 34 °C to 42 °C [17]. Ullah et al., [35] reported that in the preadult stage, longevities of males and females and total longevity of *B. dorsalis* was increased dramatically after exposure to high and low temperature stress (38 and 3 °C) at their larval stage. The developmental duration of *Z. tau* was prolonged when the temperature exceeded 34 °C [36]. Repeated cold shocks induce hormetic effects on longevity, behavioral aging, and heat and resistance to cold shock in aged flies [20]. Khazaeli et al. [37] reported prolonged longevity in *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) when treated with a 36 °C temperature. The *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) population and predation projections were proportional to the temperature [38].

The high- and low-temperature stresses usually cause oxidative damage in insects through increased generation of reactive oxygen species (ROS) [22,39]. The oxidative

damage delays the larval development and prolongs the lifespan of insects [23]. Combined with our findings, these studies imply that developmental suppression leading to longevity extension under various stresses may be a common phenomenon in insects. Cold stress induces oxidative damage, and then a warm recovery time activates the antioxidant system, allowing insects to repair the damage caused by cold stress and resulting in prolonged longevity [39]. Heat stress is one of the important factors that induces oxidative stress [8], whereas low (−5, −2.5, 0, and 5 °C) and high (35, 37.5, and 40 °C) temperature stresses induce oxidative damage in insects [8]. In addition, Lithgow et al. [40] explained the possible mechanism of increased longevity and thermotolerance in *Caenorhabditis elegans* Maupas (Nematoda: Rhabditida), by showing heat stress induces the *hsps* activities, which affects the cell's ability to cope with degenerative effects of age and the environment. The association between *hsp70* and thermotolerance in *Drosophila melanogaster* Meigen showed that some *hsps* might be linked with prolonged longevity of adults following heat stress [41]. These findings show that high or low temperature stresses might induce oxidative stress, delay development, prolong longevity, and increase fecundity in *B. zonata*. The increased life span and fecundity of *B. zonata* may have effects on population growth and would potentially have significant agricultural impacts. Furthermore, global warming affects the population growth and pest severity level of *B. zonata*, whereas cold acclimation helps this key pest to survive in stress conditions. The overall *B. zonata* life table indicated that low and high temperature stress at initial life stages stimulates the performance of later stages, allowing them to cope with subsequent stress conditions. However, there are still several unresolved questions especially related to the underlying mechanisms of prolonged longevity and increased fecundity. Therefore, further detailed studies are necessary to validate these carryover effects at the molecular level, especially the underlying mechanisms of prolonged longevity and increased fecundity after temperature stress. This is because in preconditioning, the transcriptional level of several genes increases, often associated with stimulation of reproduction, longevity, fertility, and development of insects.

5. Conclusions

Together, we investigated the key demographic parameters and population projections of *B. zonata* following exposure to HT and LT using age-stage, two-sex life-table approach. The results showed that the developmental durations, fecundity, and mean longevities of males and females of *B. zonata* were significantly increased when the insects were exposed to HT and LT compared with controls. These findings suggest that temperature stress, either high or low, at larval stages of *B. zonata* might benefit the performance of later stages. However, further studies are needed to examine the functional analysis of the genes responsible for altering the critical biological characteristics of *B. zonata* during temperature stress.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12112903/s1.

Author Contributions: Z.L. and F.U. conceived research. F.U. conducted experiments. Z.L. and I.u.H. contributed materials. A.G. and F.U. analyzed data and conducted statistical analysis. F.U., A.G. and H.G. wrote the manuscript. Z.L., F.U., A.G., N.D., K.T. and M.H. revised the manuscript. Z.L. secured funding. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The authors confirm that the data supporting the findings of this study are available in the article.

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Conflicts of Interest: The authors declare that they have no conflict of interest associated with this paper or the study they describe.

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