Temperature-induced effects on development, reproduction, and predation of *Harmonia axyridis* fed on first instar larvae *Spodoptera litura*

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Abstract

Since metabolism, survival, and reproduction in hexapods are closely related to temperatures; changes in the mean and variance of temperature are major aspects of global climate change. In the typical context of biological control, understanding how predator–prey systems are impacted under thermal conditions can make pest control more effective and resilient. With this view, this study investigated temperature-mediated development and predation parameters of the predator *Harmonia axyridis* against the potential prey *Spodoptera litura*. The age-stage, two-sex life table of the predator was constructed at four temperatures (i.e. 15, 20, 25, and 30°C) by feeding on the first instar larvae of *S. litura*. Our results showed that the mean generation time (T) decreased but the intrinsic rate of increase (r) and the finite rate of increase (λ) increased with increased temperature. The mean duration of the total pre-adult stage decreased with higher temperatures. The T and r were 70.47 d and 0.0769 d^{-1} at 15°C; 58.41 d and 0.0958 d^{-1} at 20°C; 38.71 d and 0.1526 d^{-1} at 25°C; and 29.59 d and 0.1822 d^{-1} at 30°C, respectively. The highest net reproductive rate (R_0) and fecundity were obtained at 25°C. The highest λ (1.1998 d^{-1}) and lowest T (29.59 d) were obtained at 30°C, whereas the maximum net predation rate (C_0) was at 25°C. Total population and predation rates projections were the highest at 30°C. Based on these findings, we anticipate that biological control strategies for this predator release against *S. litura* should be attuned to warming scenarios to achieve better biocontrol functions.

Introduction

Climate change is having significant impacts on biodiversity and biotic interactions worldwide (Renault *et al.*, 2022). The initial 20 years of the 21st century saw global surface temperatures increase by 0.99°C (0.84–1.10°C) compared to 1850–1900 (Masson-Delmotte *et al.*, 2021). Such change can alter species composition (Lind *et al.*, 2022), change biotic interaction strength (Gaytán *et al.*, 2022), and shift species to higher altitudes and latitudes (Vaissi, 2022). Ectothermic animals, whose biology is heavily affected by variations in the natural setting and its severities, are probably across the organisms most vulnerable to the effects of climate change (Zhang *et al.*, 2022a). Arthropods have key ecological roles in maintaining ecosystem stability and resilience. Insect biodiversity, dynamics, and life histories are greatly impacted by variations in environmental temperature (Islam *et al.*, 2022a; Outhwaite *et al.*, 2022). In particular, insect predator metabolic rates and biological processes, which increase or decrease predation efficiency, are strongly impacted by temperature (Horn, 2019). It is now a high priority for researchers to study insect adaptation to climate and to use the results to modify control strategies accordingly (Hallman and Denlinger, 2019; Schowalter, 2022).

The tobacco caterpillar *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae) poses a pertinent threat as an insect pest, affecting over 120 host plants from 44 different plant families (Qin et al., 2004). This pest species is globally widespread but particularly problematic in Pakistan, China, Japan, and India. Routine pesticide use against this pest leads to health and environmental challenges as well as insecticide resistance (Zhang *et al.*, 2022b). Alternative approaches with lower risk to humans and the ecosystem such as biological control are thus needed (Blassioli-Moraes *et al.*, 2022). Biological control has long been used in agricultural pest management (Heimpel and Mills, 2017). Lady beetles stand out as one of the most noticeable and familiar useful biocontrol insects in agricultural crop ecosystems

(Hodek *et al.*, 2012). *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) is an excellent biological control agent for an enormous range of pests, particularly hemipterans and soft-bodies lepidopterans (Koch *et al.*, 2003; Lucas *et al.*, 2004; de Castro-Guedes *et al.*, 2016; Islam *et al.*, 2020; Di *et al.*, 2021). This predator has a wide geographic distribution, long lifespan, extensive host range, and high reproduction rate (Koch, 2003). Due to its dispersal capacity, voracity, multivoltinity (Koch, 2003), and ability to survive tropical and subtropical conditions, *H. axyridis* has been extensively reared in commercial settings and widely used as a predator (Roy *et al.*, 2016).

Assessing the effectiveness of predator-based biological control requires a comprehensive approach, which involves integrating growth, survival probabilities, reproductive capacity, and age-specific rates of predation (Yu *et al.*, 2013). Undoubtedly, a lot of literature has assessed the potential of *H. axyridis* as a biocontrol system against lepidopteran pests across different climatic scenarios (Koch *et al.*, 2003; Islam *et al.*, 2020, 2022a, 2022b; Di *et al.*, 2021). These studies primarily assessed the predation capacity and feeding strategies; but subsequent impacts on the predator development and reproduction rates are still unclear with respect to prey being fed to the predator. The current study extensively investigates how different temperatures influence the growth and biology of *H. axyridis* while feeding on *S. litura*. Additionally, it provides valuable insights into how global warming might affect the behaviour of this predator in the future. In this study, we assessed the influence of warming on the biology of this predator and its overall effectiveness as a biological control agent against *S. litura* first instar by integrating life table data with predation and population projection. This fundamental data will aid in comprehending the biological and population growth parameters and dynamics of *H. axyridis*, enabling better forecasts and the formulation of effective bio-based integrated pest management strategies targeting *S. litura*.

Materials and methods

Mass rearing of Harmonia axyridis and Spodoptera litura

Harmonia axyridis Pallas colonies were acquired from stock cultures in Huazhong Agricultural University (HZAU) (Wuhan, China) and subsequently raised in laboratory, feeding on *Acyrthosiphon pisum* Harris (Hemiptera: Aphididae). The *A. pisum* colony was reared on faba bean (*Vicia faba* L., var. 'Chenghu No. 10', Fabaceae) plants, maintaining specific conditions of 23 ± 1°C, 70 ± 5% relative humidity (RH), and a photoperiod of 16:8 (light:dark) h. The *H. axyridis* population was maintained in the laboratory under controlled conditions at 65 ± 5% RH, 23 ± 1°C, and a photoperiod of 16:8 (light:dark) h.

The *S. litura* eggs were purchased online and kept inside the computer growth chamber at 25 ± 1°C and 65 ± 5% RH under a 16:8 photoperiod (light: dark). After hatching, the larvae were provided with a standard artificial diet following the method described by Saljoqi *et al.* (2015), and they were nurtured for till the last instar stage. The final instar larvae were separated and nurtured until maturity in identical containers containing soaked cotton buds as a medium for pupation and were provided with a diet comprising a 10% solution of glucose. A fresh/clean sheet of paper was positioned at base of the jar to serve as the oviposition substrate. Daily observation was conducted to monitor oviposition, and after the larvae emerged, they were kept together to ensure a homogeneous group of individuals of the same age.

Details of life table and predation rate studies

Prior to conducting the experiments, adult male and female *H. axyridis* were paired individually under each temperature regime to collect predator eggs. The paired *H. axyridis* individuals were placed in small Petri dishes (9 cm diameter), and they were provided with *A. pisum* as their food source. Regular daily observations were conducted on the Petri dishes, and 100 freshly laid eggs were transferred with a soft hairbrush to each dish at each temperature tested. The assays were carried out at four distinct constant temperatures (i.e. 15, 20, 25, and 30°C). The experiment was performed in a Petri dish (9 cm diameter) containing one leaf disc (9 cm diameter) of tomato, *Solanum lycopersicum* L. (Solanales: Solanaceae) kept on a 2 cm thick layer of 1.5% agar. Fifty predator eggs per temperature were used to create experimental cohorts. After egg hatching, about 350–400 first instar larvae of *S. litura* larvae (<6 h old) were placed on the tomato leaves every day. The larvae were gently transferred with brush. Before each lady beetle was fed, the number of *S. litura* larvae on the disc was counted. *H. axyridis* development duration and survival were examined daily. Exuvia was used to determine instar changes. The survival rate, the overall duration of development from larvae to pupae, and the time it took for hatching at every stage and across various temperature conditions. Adults were mated and separated by following the protocol described by Islam *et al.* (2022c). This protocol was repeated until all adults died. Daily recordings were made for adult fecundity (number of eggs produced), survival, and the count of *S. litura* larvae consumed (excluding mating hours) by the predators. Predation was noted by recording the number of larvae that were damaged and consumed. Adult mortality and fecundity, including cannibalised eggs, were recorded daily until all individuals/adults died. In case one individual of the pair killed/died, an alternate individual from the mother population was introduced.

Life table and predation rate analysis

The life table data were analyzed using the principles of age-stage two-sex life table theory (Chi, 1988; Chi *et al.*, 2020) using the TWOSEX-MSChart program (Chi *et al.*, 2022). The age-stage survival rate (s_{xj}) (equation 1), age-specific survival rate (l_x) (equation 2), age-specific fecundity (m_x) (equation 3), age-stage life expectancy (e_{xj}) (equation 4), age-stage reproductive value (v_{xj}) (equation 5), and population parameters *i.e.* net reproductive rate (R_0) (equation 6), finite rate of increase (λ) (equation 7), the mean generation time (T) (equation 8), and intrinsic rate of increase (r) (equation 9) were calculated from this program (Table 1). Female fecundity was computed based on the total number of eggs laid, irrespective of their fertility status.

Daily predation data were analyzed according to Chi and Yang (2003) by using the CONSUME-MSChart program (Chi, 2022a). The age-stage specific predation rate (c_{xj}, the mean predation rate of individuals at age x and stage j) (equation 10), age-specific predation rate (k_x, the number of prey consumed by the surviving individuals at age x) (equation 11), age-specific net predation rate (q_x) (equation 12), net predation rate (C_0) (equation 13), transformation rate (Q_p) (equation 14), and finite predation rate (ω) (equation 15) were calculated (Table 1).

Standard errors (SE) of all life table and predation parameters were determined using 100,000 bootstrap replications (Huang and Chi, 2012; Akca *et al.*, 2015; Polat Akköprü *et al.*, 2015). Paired bootstrap tests were employed to compare temperature differences

Table 1. Equations used in calculation of life table parameters, population, and predation projection of *Harmonia axyridis* preying upon 1st instar *Spodoptera litura* at four different temperatures

Eq.	Equations	Parameters	References
1	$s_{xj} = \dfrac{n_{xj}}{n_{01}}$	Age-stage survival rate s_{xj}	Chi and Liu (1985), Chi (1988)
2	$l_x = \sum\limits_{j=1}^{\beta} s_{xj}$	Age-specific survival rate (l_x)	Chi and Liu (1985)
3	$m_x = \dfrac{\sum\limits_{j=1}^{\beta} s_{xj} f_{xj}}{\sum\limits_{j=1}^{\beta} s_{xj}}$	Age-specific fecundity (m_x)	Chi and Liu (1985)
4	$e_{xj} = \sum\limits_{i=x}^{\infty} \sum\limits_{y=j}^{\beta} s'_{iy}$	Age-stage life expectancy (e_{xj})	Chi and Su (2006)
5	$v_{xj} = \dfrac{e^{r(x+1)}}{s_{xj}} \sum\limits_{i=x}^{\infty} e^{-r(i+1)} \sum\limits_{y=j}^{\beta} s'_{iy} f_{iy}$	Age-stage reproductive value (v_{xj})	Tuan *et al.* (2014)
6	$R_0 = \sum\limits_{x=0}^{\infty} l_x m_x$	Net reproductive rate (R_0)	Chi and Liu (1985)
7	$\lambda = e^r$	Finite rate of increase (λ)	Chi and Liu (1985)
8	$T = \dfrac{\ln R_0}{r}$	Mean generation time (T)	Chi and Liu (1985)
9	$\sum\limits_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$	Intrinsic rate of increase (r)	Chi and Liu (1985)
10	$c_{xj} = \dfrac{\sum\limits_{i=1}^{n_{xj}} d_{xj,i}}{n_{xj}}$	Age-stage specific predation rate (c_{xj})	Chi and Yang (2003)
11	$k_x = \dfrac{\sum\limits_{j=1}^{\beta} s_{xj} c_{xj}}{\sum\limits_{j=1}^{\beta} s_{xj}}$	Age-specific predation rate (k_x)	Chi and Yang (2003)
12	$q_x = l_x k_x = \sum\limits_{j=1}^{\beta} s_{xj} c_{xj}$	Age-specific net predation rate (q_x)	Chi and Yang (2003)
13	$C_0 = \sum\limits_{x=0}^{\infty} \sum\limits_{j=1}^{\beta} s_{xj} c_{xj} = \sum\limits_{x=0}^{\infty} l_x k_x$	Net predation rate (C_0)	Chi and Yang (2003)
14	$Q_p = \dfrac{C_0}{R_0}$	Transformation rate (Q_p)	Chi and Yang (2003)
15	$\omega = \lambda \psi = \lambda \sum\limits_{x=0}^{\infty} \sum\limits_{j=1}^{\beta} a_{xj} c_{xj}$	Finite predation rate (ω)	Yu *et al.* (2013)
16	$N(t) = \sum\limits_{j=1}^{\beta} \sum\limits_{x=0}^{\infty} n_{xj,t}$	Total population size at time t	Huang *et al.* (2018)
17	$P(t) = \sum\limits_{j=1}^{\beta} \sum\limits_{x=0}^{\infty} c_{xj} n_{xj,t}$	Predation potential at time t	Huang *et al.* (2018)

at the 5% significance level, relying on the confidence interval of the variance (Wei *et al.*, 2020). SigmaPlot (version 12, Systat Software, Palo Alto, CA) was used to plot all the graphs.

Projection of population and predation

Population size projections (equation 16) and predation rates (equation 17) (Table 1) were initiated with ten pairs of *H. axyridis* for all tested temperatures. The calculations were carried out for 80 days, aiming to determine the total population size under the assumption of an unrestricted scenario without any influence from biotic or abiotic factors, and with an unlimited supply of first instar *S. litura* larvae as potential prey. We obtained confidence intervals of the λ with the 2.5th and 97.5th percentiles of the boot-strap samples (Huang *et al.*, 2018). Projections were generated

utilizing the TIMING-MSChart software (Chi, 2022b) following the approach outlined by Chi and Liu (1985) and Chi (1990).

Results

Development time and survival of H. axyridis

Temperature had a significant impact on the developmental time, longevity, the number of oviposition days, and fecundity of *H. axyridis*. The consumption of 1st instar of *S. litura* larvae by the predator and the completion of all developmental stages were observed across all four temperatures (Table 2). The developmental duration of various *H. axyridis* stages was significantly longer at lower temperatures compared to higher temperatures. The duration of each developmental stage in *H. axyridis* noticeably shortened as

Table 2. Mean (± SE) durations of each stage and preadult survival rate of *Harmonia axyridis* preying upon 1st instar *Spodoptera litura* at four different temperatures

	Temperature							
	15°C		20°C		25°C		30°C	
Stage	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
Egg (day)	50	6.00 ± 0.09 a	50	4.52 ± 0.10 b	50	2.98 ± 0.08 c	50	2.40 ± 0.07 d
First-instar larva (day)	50	7.10 ± 0.10 a	50	4.18 ± 0.09 b	48	2.94 ± 0.04 c	50	2.20 ± 0.06 d
Second-instar larva (day)	49	3.73 ± 0.10 a	49	3.67 ± 0.09 a	48	2.15 ± 0.05 b	49	1.43 ± 0.07 c
Third-instar larva (day)	48	6.10 ± 0.10 a	48	4.69 ± 0.10 b	48	2.77 ± 0.06 c	48	1.69 ± 0.07 d
Fourth-instar larva (day)	46	7.00 ± 0.11 a	48	5.35 ± 0.12 b	48	3.48 ± 0.07 c	47	3.23 ± 0.06 d
Pupa (day)	45	8.38 ± 0.11 a	48	5.79 ± 0.11 b	47	3.60 ± 0.09 c	44	3.20 ± 0.06 d
Total preadult stage (day)	45	38.36 ± 0.22 a	48	28.21 ± 0.23 b	47	17.89 ± 0.14 c	44	14.09 ± 0.10 d
Female longevity (day)	23	96.74 ± 3.13 a	23	89.39 ± 2.27 ab	24	86.38 ± 1.60 b	20	46.25 ± 1.31 c
Male longevity (day)	22	70.27 ± 1.21 a	25	66.70 ± 1.44 ab	23	63.32 ± 1.49 b	24	39.33 ± 0.96 c
Female Total longevity (day)	23	134.96 ± 3.05 a	23	117.74 ± 2.37 b	24	104.42 ± 1.53 c	20	60.10 ± 1.31 d
Male total longevity (day)	22	108.77 ± 1.12 a	25	91.40 ± 1.48 b	23	84.43 ± 1.44 c	24	53.63 ± 0.98 d

The means followed by different lowercase letters in each row are significantly different ($P < 0.05$, paired bootstrap test).

the temperature increased from 15 to 30°C. The preadult period of *H. axyridis* at 15, 20, 25, and 30°C were recorded as 38.36, 28.21, and 17.89 and 14.09 days, respectively. Notably, the developmental duration at 15°C was more than twice that at 30°C. With increasing temperature, the longevity of both female and male adults decreased significantly. Comparatively, at lower temperatures i.e. 15°C, both male and female lifespans were considerably longer than at higher temperatures i.e. 25–30°C.

The age-stage-specific survival rate (s_{xj}) of *H. axyridis* at four distinct temperatures is depicted in Supplementary Fig. S1. It refers to the probability that an egg will survive until age *x* and headway to reach stage *j*. At 15°C, the survival was 117 and 161 days for male and females, respectively. At 20°C the survival durations were 108 and 142 days for male and females. Lastly, at 25°C, the survival durations were 100 and 116 d and at 30°C the survival durations were 64 and 71 d for male and females, respectively (Supplementary Fig. S1).

### Reproduction and population parameters of H. axyridis

The mean fecundity increased with temperature, except at 30°C as shown in Table 3. The highest fecundity (765.33 eggs per female) was observed at 25°C, gradually decreasing as temperature exceeded (547.95 eggs) at 30°C. The number of oviposition days was the shortest (19.05 days) at 30°C and longest (27.83 days) at 15°C. Temperature significantly impacts when it comes to the adult pre-oviposition period (APOP) and the total pre-oviposition period (TPOP) (Table 3). The female beetles had the shortest APOP and TPOP at 30°C, i.e. 5.20 and 19.05 days respectively, and the longest APOP at 20°C, which was 9.26 days. The TPOP increased with colder temperatures: from 46.13 days at 15°C to 37.61 days at 20°C, and 24.17 days at 25°C.

The net reproductive rate (R_0), the intrinsic rate of increase (*r*), the finite rate of increase (*λ*), and the mean generation time (*T*) are presented in Table 3. As temperature increased from 15 to 30°

Table 3. Mean (± SE) life table parameters of *Harmonia axyridis* preying upon 1st instar *Spodoptera litura* at four different temperatures

	Temperature			
	15°C	20°C	25°C	30°C
Parameters*	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
R_0 (offspring/individual)	225.86 ± 35.26 b	268.76 ± 41.40 ab	367.36 ± 54.37 a	219.18 ± 38.22 b
r (day^{-1})	0.0769 ± 0.0028 d	0.0958 ± 0.0034 c	0.1526 ± 0.0053 b	0.1822 ± 0.0074 a
λ (day^{-1})	1.0799 ± 0.0030 d	1.1005 ± 0.0038 c	1.1648 ± 0.0061 b	1.1998 ± 0.0089 a
T (days)	70.47 ± 0.79 a	58.41 ± 0.76 b	38.71 ± 0.48 c	29.59 ± 0.36 d
F (eggs/female)	491.00 ± 15.15 d	584.26 ± 11.60 b	765.33 ± 13.31 a	547.95 ± 13.28 c
O_d (days)	27.83 ± 0.83 ab	30.13 ± 1.15 a	26.79 ± 0.49 b	19.05 ± 0.63 c
APOP (days)	7.91 ± 0.30 b	9.26 ± 0.28 a	6.13 ± 0.17 c	5.20 ± 0.17 d
TPOP (days)	46.13 ± 0.41 a	37.61 ± 0.43 b	24.17 ± 0.28 c	19.05 ± 0.23 d

The means followed by different lowercase letters in each row are significantly different ($P < 0.05$, paired bootstrap test). * R_0 = net reproductive rate; *r*= intrinsic rate of increase; *λ* = finite rate of increase; *T* = mean generation time; *F* = fecundity; O_d = oviposition days; APOP = adult preoviposition period; TPOP = total preoviposition period.
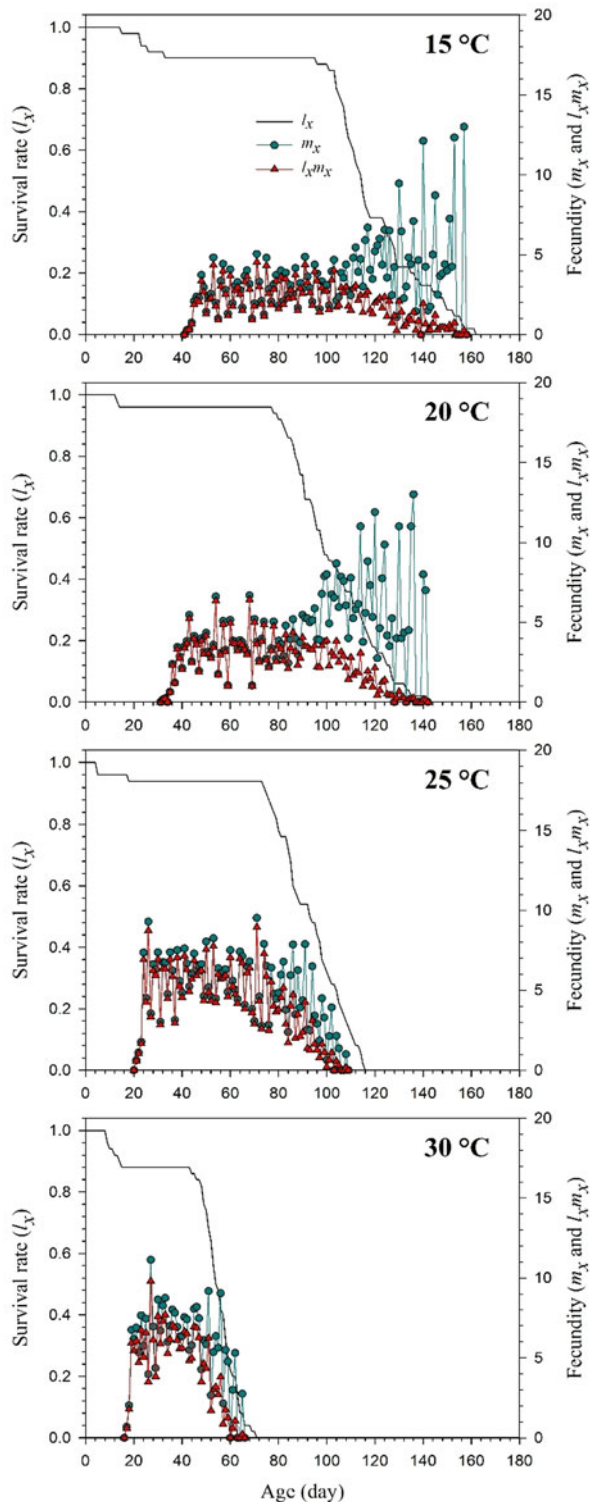
Figure 1. Age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity (l_xm_x) of the *Harmonia axyridis* preying on the 1st instar *Spodoptera litura* at different temperatures.

C, both r and λ rose, whereas, T notably decreased. The peak R_0 was observed at 25°C. The highest r and λ, and the shortest T were all recorded at 30°C.

Figure 1 illustrates l_x (age-specific survival rate), m_x (total fecundity of population), and l_xm_x (net maternity) of *H. axyridis*

population fed with 1st instar of *S. litura* larvae. The l_x represents the fundamental version of the s_{xj} curves. The l_x of the *H. axyridis* population, decreased to 0.90 on the 42nd day at 15°C when the first birth occurred. At 20°C, the first birth occurred on the 32nd day with survival rate of 0.96. Fecundity of the population was observed early at 25°C on the 21st day with a l_x of 0.84, and on the 17th day with l_x dropping to 0.88 at 30°C. The l_xm_x curves values depended on l_x and m_x values. The peak l_xm_x values for *H. axyridis* populations were 4.54 on 71st day, 6.42 on 68th day, 8.96 on the 71st day and 9.80 on the 27th day at 15, 20, 25, and 30°C, respectively (fig. 1).

The e_{xj} (age-stage life expectancy) of *H. axyridis* fed with *S. litura* larvae at four constant temperatures are depicted in Supplementary Fig. S2. The e_{xj} calculates the duration or length of time for a newly hatched individual. Temperature had a distinct impact on the e_{xj} curve of *H. axyridis* for both males and females. The highest life expectancy values were observed for females and males reaching 99.96 and 72.77 days at 15°C, 92.74 and 65.40 days at 20°C, 88.42 and 68.43 days at 25°C and 47.10 and 40.62 days at 30°C (Supplementary Fig. S2).

In Supplementary Fig. S3 presents age-stage-specific reproduction (v_{xj}) of *H. axyridis* fed with *S. litura* larvae at four constant temperatures. The v_{xj} represents the contribution that each individual will make to the subsequent generation. The curves clearly show that temperature significantly influences the age stage-specific reproduction. The highest v_{xj} value of *H. axyridis* female fed with 1st instar of *S. litura* larvae was 80.32 eggs/d (on the 71st day) at 15°C increasing to 86.11 eggs/day (on the 60th day) at 20°C, 88.32 eggs per day (on the 41st day) at 25°C, and reaching 100.47 eggs per day (on the 27th day) at 30°C (Supplementary Fig. S3).

Predation rate of H. axyridis

The mean daily consumption of *H. axyridis* while feeding on 1st instar of *S. litura* larvae increased with rising temperature across all larval stages and the total preadult stage (Table 4). For preadult *H. axyridis,* the daily consumption was 23.29, 37.89, 45.83, and 56.69 prey at 15, 20, 25, and 30°C, respectively. Female beetles consumed significantly more than males at all temperature conditions. The highest daily predation rate was observed in female *H. axyridis* at 25°C, consuming 184.06 prey/day, although this was not significantly different from the daily consumption at 30°C with 180.84 prey/day. The highest consumption for males was at 30°C. the consumption of 1st instar *S. litura* larvae was highest at 30°C and not significantly different from 25°C when considering all adults regardless of sex. Conversely, *H. axyridis* consumed fewer prey at lower temperatures, i.e. 84.16 and 130.83 prey per day at 15 and 25°C, respectively.

The age-stage specific daily predation rate (c_{xj}) of *H. axyridis* feeding on 1st instar *S. litura* larvae increased, and the duration of the *H. axyridis* stages was shortened with temperature increased (Supplementary Fig. S4). Predation in adult stages was higher than on preadult stages.

Table 5 provides the predation rate parameters, including net predation (C_0), transformation (Q_p), finite predation (ω), and stable predation (ψ) rate, for *H. axyridis* feeding on 1st instar *S. litura* larvae. The highest net predation rate was found at 25°C with 12,995.08 preys per individual, while lowest net predation rate was found at 15°C with 7207.10, although this was not significantly different from the net predation rate at 30°C, which was 7230.68 1st instar *S. litura* larvae per *H. axyridis*. There were no

Table 4. Stage daily predation (D_j) (preys/individual) (mean ± SE) of *Harmonia axyridis* preying upon 1st instar *Spodoptera litura* at four different temperatures

	Temperature			
	15°C	20°C	25°C	30°C
Stages	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
First-instar larva	6.27 ± 0.21 d	12.12 ± 0.29 c	14.43 ± 0.98 b	18.65 ± 0.57 a
Second-instar larva	15.66 ± 0.32 d	24.36 ± 0.60 c	29.20 ± 1.01 b	34.92 ± 1.29 a
Third-instar larva	34.70 ± 0.77 d	62.04 ± 1.03 c	69.95 ± 1.86 b	105.84 ± 3.20 a
Fourth-instar larva	84.23 ± 1.89 d	121.54 ± 1.50 c	152.21 ± 4.50 b	166.69 ± 5.56 a
Preadult	23.29 ± 0.50 d	37.89 ± 0.60 c	45.83 ± 1.25 b	56.69 ± 1.76 a
Adult (female)	89.24 ± 0.74 cA	156.43 ± 1.94 bA	184.06 ± 1.73 aA	180.84 ± 1.78 aA
Adult (male)	76.85 ± 0.77 dB	97.58 ± 1.19 cB	148.88 ± 1.14 bB	164.41 ± 2.86 aB
Adults	84.16 ± 1.05 c	130.83 ± 4.43 b	169.10 ± 2.76 a	172.54 ± 2.07 a

The means followed by different lowercase letters in each row indicate significant differences among the temperatures, while different uppercase letters within the same column indicate significant differences between female and male adult stage daily predation are significantly different ($P < 0.05$, paired bootstrap test).

Table 5. Predation rates (mean ± SE) of *Harmonia axyridis* preying upon 1st instar *Spodoptera litura* at four different temperatures

	Temperature			
	15°C	20°C	25°C	30°C
Predation rate parameters	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Net predation rate, C_0 (preys/individual)	7207.10 ± 420.00 c	10,568.20 ± 658.24 b	12,995.08 ± 642.01 a	7230.68 ± 409.63 c
Transformation rate, Q_p (C_0/R_0)	31.91 ± 4.13 a	39.32 ± 4.37 a	35.37 ± 4.37 a	32.99 ± 5.51 a
Finite predation rate, ω (preys)	17.78 ± 0.49 d	33.34 ± 0.75 c	42.26 ± 1.26 b	56.83 ± 2.08 a
Stable predation rate, ψ (preys)	16.46 ± 0.44 d	30.29 ± 0.63 c	36.28 ± 1.02 b	47.36 ± 1.60 a

The means followed by different lowercase letters in each row are significantly different ($P < 0.05$, paired bootstrap test).

significant differences in transformation rate among temperatures. Both finite predation and stable predation rates were highest at 30°C, while the lowest values were at 15°C (Table 5).

Age-specific survival rate (l_x), age-specific predation rate (k_x), age-specific net predation rate (q_x), and cumulative net predation rate (C_0) for *H. axyridis* fed on first instar *S. litura* larvae are presented in fig. 2. The k_x represents the mean number of prey consumed by *H. axyridis* at age x, while q_x signifies the weighted number of prey consumed by *H. axyridis* at age x. Predation of 1st instar *S. litura* larvae by *H. axyridis* during larvae and adult stages reveals an association between age-specific predation rate (k_x) and age-specific net predation rate (q_x) values, leading to an increase in survival rates until the adult stages. However, a stepwise decline in age-specific net predation rate was observed starting at the adult stage. The cumulative predation rates were 7207 on the 162nd day, 10,568 on the 143rd day, 12,995 on the 117th day, and 7230 on the 71st day at temperatures of 15, 20, 25, and 30°C, respectively (fig. 2).

Population and predation projection

The initial population and predation projection began with 10 pairs of *H. axyridis* across all temperature conditions, as shown in fig. 3. The maximum predicted population size of *H. axyridis* was projected to exceed 1.45×10^8 individuals at 30°C. In contrast, at 15°C the population was estimated to surpass 4.49×10^4 individuals. The total population size at 20°C and 25°C were 1.22×10^5 and 1.08×10^7, respectively. Notably, a significant increase in the total population at 25°C and 30°C compared to 15°C and 20°C was observed after 80 days (fig. 3, A1:A4). Regarding consumption, the highest estimated consumption of 1st instar *S. litura* larvae was projected to reach 6.44×10^9 at 30°C, while the lowest consumption was estimated to be approximately 5.26×10^5 prey at 15°C. The predation potential of *H. axyridis* was estimated 4.24×10^6 and 4.42×10^8 preys at 20 and 25°C, respectively (fig. 3, B1:B4).

Discussion

Recently, we determined the predatory functional response of this predator to larvae *S. litura* (Islam *et al.*, 2020; Islam *et al.*, 2022b) and showed that predation increased with temperature, typically when feeding on first instar. Here we evaluated the impacts of foraging on 1st instar larvae *S. litura* on the subsequent biology, reproduction, and predation parameters of *H. axyridis*. Our findings showed that development, growth, reproduction, and population parameters varied in magnitude across four temperatures tested. The time it takes for the immature and adult stages of *H. axyridis* to develop appears to decrease as temperature increases, likely due to temperature's direct impact on metabolism. The reduced length of each developmental stage, both in the immature and adult phases of *H. axyridis* under higher
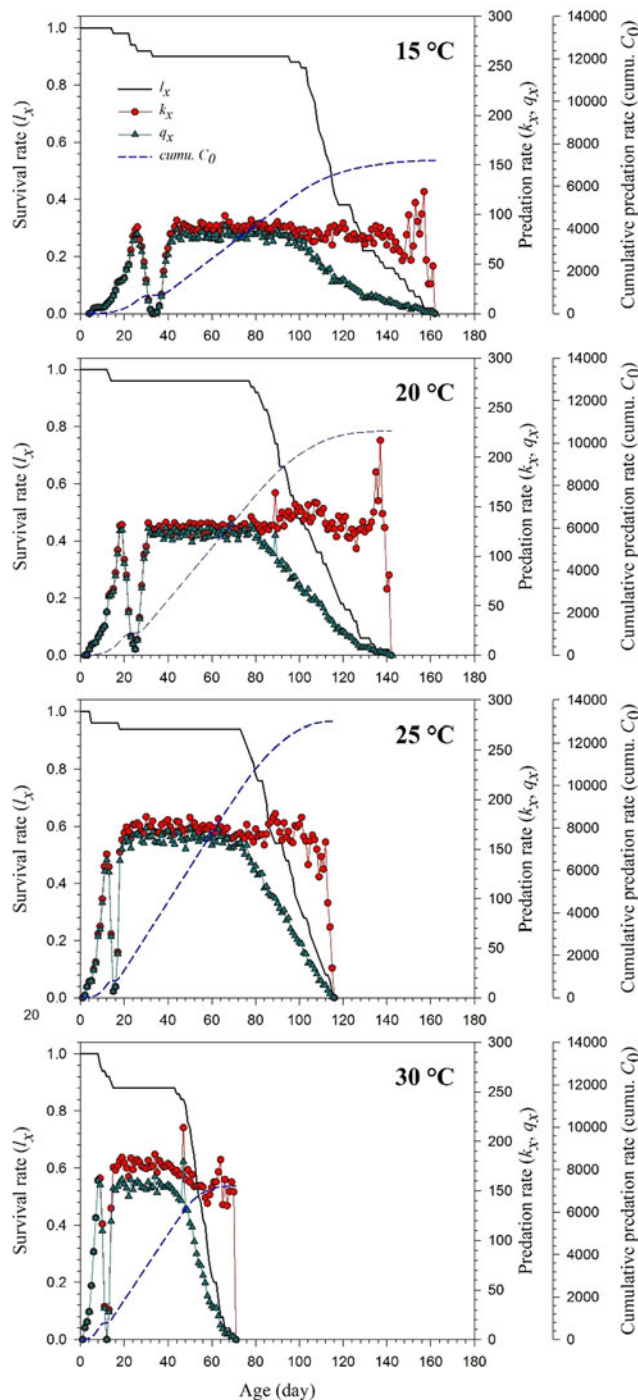
Figure 2. Age-specific survival rate (l_x), age-specific predation rate (k_x), age-specific net predation rate (q_x) cumulative net predation rate (C_0) of *Harmonia axyridis* preying on the 1st instar *Spodoptera litura* at different temperatures.

temperatures, could be attributed to heightened metabolism, increased consumption of food, and greater energy levels, which facilitated rapid moulting to the subsequent stage. The number of *H. axyridis* instars was similar to that observed for this predator when fed on *A. pisum* (Islam *et al.*, 2022c), *Cinara atlantica* (Castro *et al.*, 2011), *Aphis fabae* Scopoli, *Dysaphis crataegi* Kalt. (Stathas *et al.*, 2011) (All Hemiptera: Aphididae), *S. litura* eggs (Islam *et al.*, 2022a), *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (de Oliveira Ramos *et al.*, 2014)

and *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae) (Abdel-Salam and Abdel-Baky, 2001). All developmental times of preadult stages were significantly lower at low temperatures (15–20°C) and increased with warmer temperatures (25–30°C). Previous studies showed that *H. axyridis*, when fed on eggs of *C. atlantica*, *A. fabae*, *D. crataegi*, and *A. kuehniella*, exhibited maximum development times (i.e. 43.1, 70.2, 56.5, and 39.3 days, respectively) at 15°C, which started to decrease as the temperature increased. For example, when *H. axyridis* immature stages were fed *A. kuehniella* eggs daily, their development time was 39.3 days at 15°C, but it notably decreased to 15.2 days when the temperature rose to 30°C (de Oliveira Ramos *et al.*, 2014). Our results corroborate these earlier reports. The maximum development time (i.e. 38.3) of immature stages was at 15°C, and development time then decreased with warmer temperatures (i.e. 14.09). These findings indicate that temperature significantly influences the development of *H. axyridis*.

Similar to immature development, adult longevity was also significantly different across temperatures for both males and females. The maximum longevity of both adults (i.e. females and males) of the predator occurred at 15°C. The longevity of females and males predator at 15°C was 96.7 days for females and 70.2 days for males. Lower temperatures resulted in an increase in the longevity of adults, which indicated decreased activity or decreased energy consumption during the reproductive phase. The longevity of adults decreased as the temperature increased from 15 to 30°C. The longevity of females and males at 30°C was 46.2 days for females and 39.3 days for males. As reported previously, the longevity of *H. axyridis* adults decreased at higher temperatures, indicating that constant high temperatures have detrimental effects. A similar trend in adult's longevity was observed when *H. axyridis* was fed with the eggs of *S. litura* and the nymphs of *C. atlantica* (Castro *et al.*, 2011). Female longevity was 95.3 and 89.1 days at 15 and 25°C, respectively, when *H. axyridis* was fed on *C. atlantica*. Another study by Islam *et al.* (2022c) showed that the longevity of female *H. axyridis* feeding on *A. pisum* at 20°C was 87.7 days, which was compatible with our findings at 20°C (89.3 days). At various temperatures, the adult females had a longer lifespan compared to the males. Our findings align with earlier research results where *H. axyridis* was offered different types of prey (Castro *et al.*, 2011; Islam *et al.*, 2022a, 2022c).

The intrinsic rate of increase (r) represents the rate at which an insect population grows at low abundance, taking into account survival, development, and reproduction factors. We observed that as temperatures rose, the r values for *H. axyridis* also increased. The net reproductive rate (R_0) was highest at 25°C. The findings indicate that *H. axyridis* populations experience the fastest growth at 25°C, which could elucidate the preference for rearing *H. axyridis* populations in regions where the average monthly temperature remains around 25°C, typically during the months of June, July, and August. In our findings, female fecundity increased with temperature except 30°C, suggesting a lower female life span. In this research, the peak average fecundity of *H. axyridis* was found at 25°C, which differed from the temperature (15°C) at which *H. axyridis* exhibited its maximum fecundity when feeding on *C. atlantica*, *A. pisum*, and *S. litura* eggs (Castro *et al.*, 2011; Islam *et al.*, 2022a, 2022c). Similarly, another coccinellid, *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae), laid the most eggs at 15°C when offered with *Aphis gossypii* Glover (Hemiptera: Aphididae) at various temperatures (Yu *et al.*, 2013). Such differences could be due to prey mobility and nutritional value of the given prey.
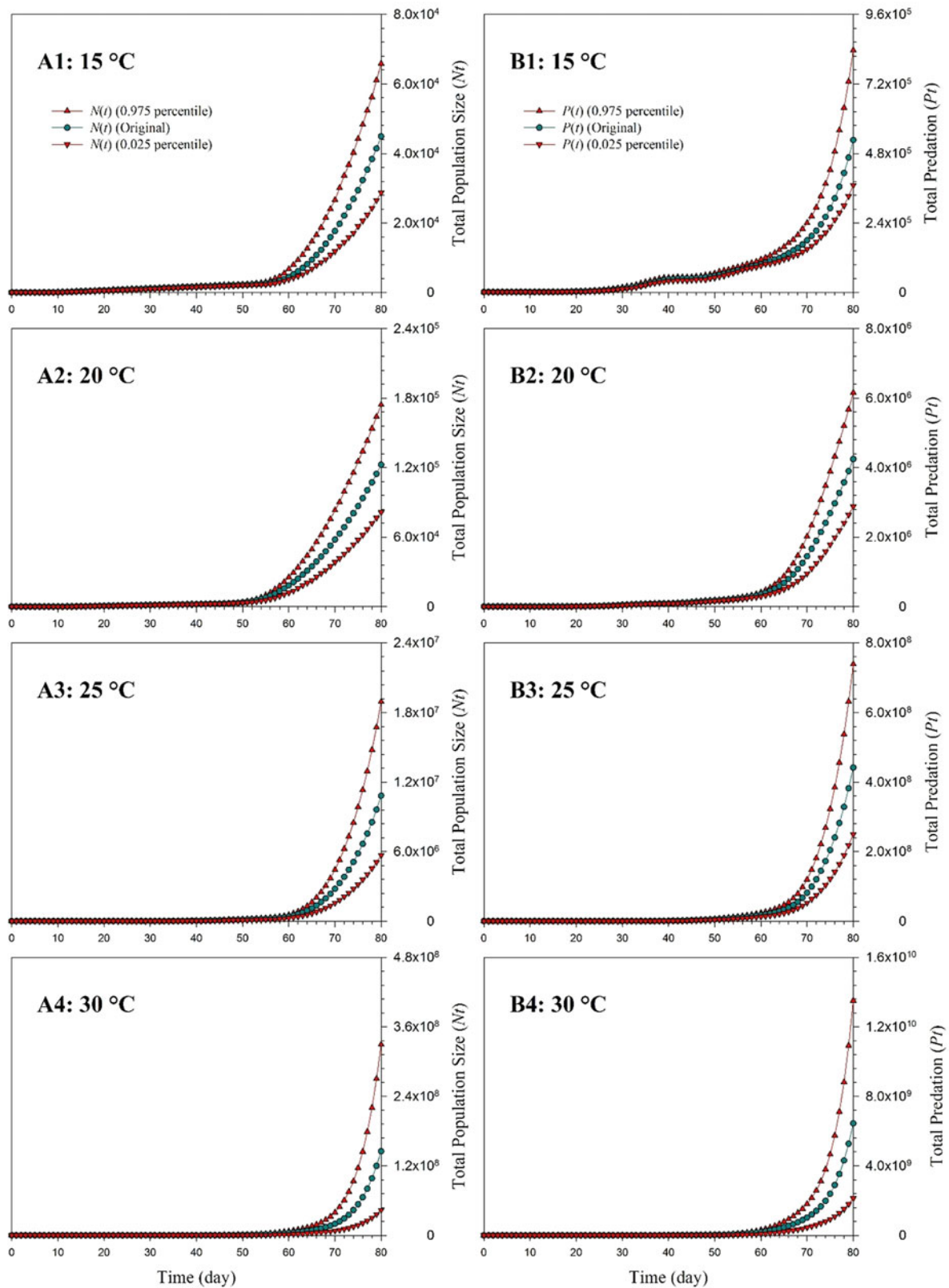
Figure 3. Population and predation projection over an 80-day period of *Harmonia axyridis* preying on the 1st instar *Spodoptera litura* at different temperatures (the original cohort and the cohorts constructed based on the 2.5 and 97.5% percentiles of *λ,* finite rate of increase are all in log base 10). A1, A2, A3, and A4 represent the total population size at 15, 20, 25, and 30°C, respectively. B1, B2, B3, and B4 represent the total predation potential at 15, 20, 25, and 30°C, respectively.

The rates of predation are heavily influenced by attributes of the given prey, such as density, activity level, and distribution, as well as attributes of the predator, including its stage, age, and nutritional status (de Lourdes Ramírez-Ahuja *et al.*, 2017). In previous findings, researchers reported that *H. axyridis* predation rates were positively affected by the predator age and temperature (Xue *et al.*, 2009; Ge *et al.*, 2019; Gao *et al.*, 2020; Islam *et al.*, 2020, 2021, 2022b). In this research, elevated temperatures had a pronounced effect, leading to a substantial increase in predation rates for both the immature and adult stages. Furthermore, the predatory stages of *H. axyridis* may display sensitivity to a particular aspect of the prey, such as its nutritional quality. However, to validate these findings, choice experiments are necessary to assess the predator's preferences when exposed to various developmental stages of the prey.

Conclusion

For effective implementation of bio-based pest control strategies, it is crucial to consider phenological, ecological, and environmental variable impacts towards predator–prey systems. The current study findings clearly showed that thermal surroundings have profound impacts on the population responses and predation parameters of *H. axyridis* feeding on first instar larvae *S. litura*. For effective pest suppression, it is thus recommended that this predator release strategy should be customised according to warming scenarios. Further research should consider resources (Yang *et al.*, 2015), light (Tu *et al.*, 2014), humidity (Yang *et al.*, 2015), and other essential variables impacts to make bases for predictive models according to real-world scenarios.

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