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Age and stage-specific life table parameters of *Harmonia dimidiata* (Coleoptera: Coccinellidae) fed on *Rhopalosiphum padi* (Hemiptera: Aphididae) at different temperatures

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Abstract

Background: The life history and predation rate of the ladybird beetle, *Harmonia dimidiata* Fabricius (Coleoptera: Coccinellidae) were compared at four different temperatures (16, 20, 24, and 28 °C). The beetles were fed on the bird cherry-oat aphid, *Rhopalosiphum padi* Linnaeus (Hemiptera: Aphididae) and investigated at 70 ± 10% RH with a photoperiod of 14:10 h (L:D).

Results: The reproductive rates (R_0) were 20.07, 51.37, 66.95, and 14.54 beetle offspring at 16, 20, 24, and 28 °C, respectively. Results indicated that temperature had good impacts on the feeding potential, development, survivorship and fecundity, especially at 24 and 28 C compared with the other tested temperatures. In addition, the jackknife and bootstrap techniques were employed to estimate the population parameters' means. The obtained means of R_0 and other population parameters, using the bootstrap technique fit a normal distribution. Meanwhile, the jackknife technique generated biologically meaningless zero values for R_0. Both finite and predation rates were incorporated into limited predation rates for comparison of predation potential.

Conclusion: Both of the growth and predation rates indicated that *H. dimidiata* is more effective biocontrol agent for *R. padi* at 24 and 28 °C than at 20, 16 °C.

Keywords: Ladybird beetle, *Harmonia dimidiate*, Aphid species, Temperature, Life table parameters, Feeding response

Background

The bird cherry-oat aphid, *Rhopalosiphum padi* Linnaeus (Hemiptera: Aphididae), lives on a variety of flora as well as the bird cherry (*Prunus padus* Linnaeus) as a primary host and cereal crops as secondary hosts all over the world. It damages wheat foliage by sucking their juice and scanty the nutrients, which causes 40 to 60% of yield losses and indirect damage by transmitting (BYD) viruses (Papp and Mesterházy 1993). *R. padi* reduces the yield of wheat and barley without showing any obvious visual symptoms of damage.

The control of *R. padi* has usually relied on synthetic insecticides, but their extensive application has led to the development of resistance. Most of biocontrol agents received a high attention regarding the resistance problems with this pest species. The ladybird beetles are considered as very important aphid predators due to the

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wide host range of prey and show rapid functional and numerical responses (Blackman and Eastop 2000).

Coccinellids (Coleoptera: Coccinellidae) are very important predators for aphids, especially the genera of *Coccinella*, *Harmonia* and *Hippodamia.* Kuznetsov and Hong (2002) found a daily predation rate of approximately 200 aphid individuals by *Harmonia dimidiata* on *Aphis gossypii* (Hemiptera: Aphididae). They also stated that *H. dimidiata* could be kept at 15 °C for 4 months without prey. About 90% of these individuals could survive on a 10% honey solution only. The high voraciousness and ability of *H. dimidiata* to survive at lower temperature may make it a useful natural enemy for pest biocontrol.

The successful mass rearing of insect predators as biocontrol agents is necessary for determination their population characteristics, including growth, predation rate, fecundity, and stage differentiation. For most insects, the developmental rate is varied among individuals of the same species and between both sexes (Carey 1993). Neglecting the variation in the developmental rate and the population of male may cause errors in estimating the age-specific survival rate, and therefore, errors in estimated demographic parameters (Chi 1988). The age-stage, two-sex life table that considers stage differentiation and the male population were developed (Chi 1988). The age-stage, two-sex life table were used to estimate the population characteristics of many mite and insect species at various environmental conditions.

Influence of temperature on the development of insects has been investigated extensively. Improving the knowledge of the impacts of temperature on insect development is helpful in the mass production of beneficial insects and their use as biocontrol agents of pests. Previous investigations have determined that in terms of developmental time, fecundity, and functional response, the most suitable temperatures for rearing of *H. dimidiata* on *A. gossypii* are in a range of 20 to 25 °C (Agarwala et al. 2009). However, there is a lack of life table parameters related to the effect of temperature on this predator with its important prey (*R. padi*) whether in the laboratory or in the field. Therefore, in this study, data on the life history and predation rate of *H. dimidiata* reared on *R. padi* at various constant temperatures were analyzed using age and sex factors.

Methods

The experiment was carried out in a growth chamber under 60 ± 5% RH and 16:8 (L:D) photoperiod at four constant temperatures, 16, 20, 24 and 28 °C, with a variation of ± 1 °C. The experiment was carried out according to the procedures of Ali and Rizvi (2010), which involved determining the tested parameters using data from 100 eggs of the same generation. Following the method (Birch 1948) to assess and generate adult female life tables, the percentage of the start population was still alive. The adult female generated a mean number of female offspring at each age interval.

Age-specific life-table

Day by day, dead and alive insects from 100 eggs were documented. The following assumption was used to construct life table parameters of *H. dimidiate.*

$$100q_x = \text{Mortality during age interval } x \text{ and computed by formula } 100q_x = (d_x/l_x) \times 100$$

x = Insect age, l_x = at the start of each interval, insects survived, d_x = During each interval died, insects, e_x = life probability or average life left over for individual of age x and was computed by $e_x = T_x/l_x$ where l_x and T_x were computed as below:

$$L_x = \text{Individuals active between age } x \text{ and } x+1, \text{ and was determined by } T_x = l_x + (l_x+1) + (l_x+2) \ldots\ldots\ldots + lw), \text{ where } lw \text{ is the last age interval.}$$

Stage specific life-table

Data on the stage-specific life table was computed following the procedure (Ali and Rizvi 2008). The following standard heads were used.

x = Age (days) of the insect.
d_x = Mortality during age interval (x).

The information from the above statements was applied to calculate the following life table parameters.

Apparent mortality (100 q_x)

Apparent mortality was determined by the formula = $(d_x/l_x) \times 100$, which provide the record (%) died insect.

Survival fraction (S_x)

Stage-specific survival fraction (S_x) estimation of each phase data attained by apparent mortality with the equation of S_x of particular stage = l_x of succeeding stage/l_x of that particular stage.

Mortality survivor ratio (MSR)

It is the population enhancement and was determined by MSR = (Mortality in particular stage)/(l_x of subsequent stage).

Indispensable mortality (IM)

$$\mathrm{IM} = \left(\text{Number of emerging adults}\right) \times \left(\text{MSR of particular stage}\right)$$

K-values

Its significant element is answerable for number reduction or multiplication from one to another generation estimated for "log *lx*" as consecutive values variation. The insect's *k* values of various growth stages designated as "*K*" determine the total generation mortality.

$K = kE + kL1 + kL2 + kL3 + kL4 + kPP + kP$, where *kE*, *kL*1, *kL*2, *kL*3, *kL*4, *kPP*, and *kP* are the *k*-values at egg, 1st to 4th instars, pre-pupal, and pupal stages of *H. dimidiata.*

Female fecundity study

The fraction of individual initial population alive still and at each age interval, adult female produced a mean number of female progeny, followed the procedure adapted by Birch (1948) to determine and construct adult female life tables. The first column gives cohort (x) mean age. In such a table, the first column lists the mean age of the cohort (x), the second column gives initial population fractions (l_x) alive still each age interval (x) at the end, and in the third column, female offspring average number (m_x) at age x produced by per female per day. When (l_x) and (m_x) values once tabulated, then the different parameters of population, gross reproductive rate (GRR = Σm_x), Net reproductive rate ($R_o = \Sigma\ l_x m_x$), Approximate generation time (T_c) days, Innate capacity for increase (r_c), Intrinsic rate of natural increase (r_m), Finite rate of increase (λ), Corrected generation time (T) and doubling time (DT) were calculated.

Statistical analysis

The techniques of the bootstrap (Efron and Tibshirani 1993) and jackknife (Sokal and Rohlf 1995) were used for estimation of the population parameters. The means, variations, and standard errors of the predation rates were estimated with the bootstrap technique. Tukey–HSD test (Dunnett 1980) was used to compare the differences among treatments.

Results

Stage specific life table of *H. dimidiata*, fed on *R. padi* at four constant temperatures

Apparent mortality

The apparent (noticeable) mortality at the egg stage was the highest of (22%), at 16 °C. Similarly, mortality for second instar larvae was the highest of (14.93%) at 16 °C (Table 1). Furthermore, the apparent (noticeable) mortality at the egg stage was the lowest of (6%) at 24 ± 1 °C. The apparent mortality for the first instar was the minimum of (6.38%), while the second instar larvae was the lowest of (2.27%) at 24 °C. Similarly, for third instar larvae, it was the lowest of (2.33%), while for fourth instar larvae, it was the minimum of (1.19%) at 24 °C. Nevertheless, it was a minimum (2.17 and 2.41%) for prepupal and pupal stage at 20 °C and 24 °C (Tables 2, 3). The apparent mortality for the first instar was the maximum of (14.67%), while, for the third instar larvae, it was the highest of (10.53%). Meanwhile, it was the maximum of (7.84%) for fourth instar larvae at 28 °C (Table 4). Furthermore, it was the maximum for prepupal and pupal stage (17.02 and 17.95%) at 28 °C (Table 4). Therefore, the results indicated that the apparent mortality for all stages was the minimal at 24 °C (Table 3).

Survival fraction

Survival fraction (S_x) for an egg, first, second, third and fourth instars larvae was the maximum of (0.94, 0.94, 0.98, 0.98 and 0.99) at 24 °C (Table 3), While, at the prepupal and pupal stage, the survival fraction (S_x) was the highest of (0.98, 0.98) at 24 °C (Tables 2, 3). On the other hand, the survival fraction (S_x) for

Table 1 Stage-specific life table of *H. dimidiata* on *R. padi* at 16 ± 1 °C

Stage X	l_x	d_x	l_x	$100q_x$	S_x	T_x	MSR	IM	Log l_x	e_x	*k*-values
Egg	100	22	89.0	22	0.78	442	0.30	13.65	2	4.42	0.108
1st instar	78	11	72.5	14.1	0.86	353	0.18	7.98	1.89	4.53	0.066
2nd instar	67	10	62	14.93	0.85	280.5	0.19	8.33	1.83	4.19	0.071
3rd instar	57	6	54	10.53	0.89	218.5	0.12	5.45	1.76	3.83	0.048
4th instar	51	3	49.5	5.88	0.94	164.5	0.06	2.87	1.71	3.23	0.026
Pre-pupa	48	2	47	4.17	0.96	115	0.04	1.98	1.68	2.40	0.019
Pupa	46	1	45.5	2.17	0.98	68	0.04	2.0	1.66	1.48	0.009
Adult	45	45	22.5						1.65		K = 0.347

Table 2 Stage-specific life table of *H. dimidiata* on *R. padi* at 20 ± 1 °C

Stage X	l_x	D_x	l_x	$100q_x$	S_x	T_x	MSR	IM	Log l_x	e_x	*k*-values
Egg	100	11	94.5	11	0.89	535	0.13	7.42	2	5.35	0.051
1st instar	89	12	83	13.48	0.87	440.5	0.16	8.96	1.95	4.95	0.063
2nd instar	77	4	75	5.19	0.95	357.5	0.06	3.20	1.89	4.64	0.023
3rd instar	73	6	70	8.22	0.92	282.5	0.09	5.13	1.86	3.87	0.043
4th instar	67	3	65.5	4.48	0.96	212.5	0.04	2.51	1.83	3.17	0.02
Pre-pupa	64	5	61.5	7.81	0.92	147.0	0.09	4.87	1.81	2.30	0.036
Pupa	59	3	57.5	5.08	0.95	85.5	0.11	6.00	1.77	1.45	0.022
Adult	56	56	28						1.75		$K = 0.258$

Table 3 Stage-specific life table of *H. dimidiata* on *R. padi* at 24 ± 1 °C

Stage X	l_x	D_x	*lx*	100 q_x	S_x	T_x	MSR	IM	Log l_x	e_x	*k*-values
Egg	100	6	97	6	0.94	644	0.07	5.14	2	6.44	0.027
1st instar	94	6	91	6.38	0.94	547	0.07	5.38	1.97	5.82	0.029
2nd instar	88	2	87	2.27	0.98	456	0.02	1.84	1.94	5.18	0.01
3rd instar	86	2	85	2.33	0.98	369	0.02	1.87	1.93	4.29	0.01
4th instar	84	1	83.5	1.19	0.99	284	0.01	0.95	1.92	3.38	0.005
Pre-pupa	83	2	82	2.41	0.98	200.5	0.03	1.96	1.92	2.42	0.011
Pupa	81	3	79.5	3.70	0.96	118.5	0.08	6.00	1.91	1.46	0.016
Adult	78	78	39						1.89		$K = 0.108$

Table 4 Stage-specific life table of *H. dimidiata* on *R. padi* at 28 ± 1 °C

Stage X	l_x	D_x	l_x	100 q_x	S_x	T_x	MSR	IM	Log l_x	e_x	*k*-values
Egg	100	15	87.5	15	0.75	415	0.22	6.91	2	4.15	0.125
1st instar	75	11	69.5	14.67	0.85	327.5	0.18	5.82	1.88	4.37	0.069
2nd instar	64	7	60.5	10.94	0.89	258	0.13	4.15	1.81	4.03	0.051
3rd instar	57	6	54	10.53	0.89	197.5	0.12	3.92	1.76	3.46	0.048
4th instar	51	4	49	7.84	0.92	143.5	0.09	2.98	1.71	2.81	0.035
Pre-pupa	47	8	43	17.02	0.83	94.5	0.23	7.21	1.67	2.01	0.081
Pupa	39	7	35.5	17.95	0.82	51.5	0.44	14.0	1.59	1.32	0.086
Adult	32	32	16						1.51		$K = 0.495$

an egg, first, second, third, and fourth instars larvae was minimum (0.75, 0.85, 0.89, 0.89 and 0.92); however, at the prepupal and pupal stage, the survival fraction (S_x) was the lowest of (0.83 and 0.82) at 28 °C (Table 4).

Mortality survivor ratio

Mortality survival ratio (MSR) at the egg stage was highest (0.30) at 16 °C (Table 1). While the mortality survival ratio (MSR) at the same stage was the smallest (0.07) at 24 °C. Similarly, MSR was the least for first, second, third, and fourth instars larvae at 24 °C. Furthermore, for the prepupa, MSR was minimum (0.03) at 24 °C (Table 3), while the maximum was 0.23 at 28 °C (Table 4).

Indispensable mortality

Indispensable mortality (IM) for the egg stage was the almost of (13.65). However, it was highest for the second instar larvae (8.33). Furthermore, for third instar larvae, it was a maximum of (5.45). In contrast, IM for the fourth instar larvae was almost (2.87). Similarly, IM for the fourth instar larvae was the least (0.95). Likewise, IM for the prepupa was the minimum of (1.96). However, it was lowest (2.0) for pupae at 16 °C (Table 1). Simultaneously,

the IM for the first instar larvae was at the upper limit (8.96) at 20 ± 1 °C (Table 2). On the other hand, Indispensable Mortality (IM) for the egg stage was the least (5.14). Meanwhile, the IM for first instar larvae was at a lower limit of (5.38). However, it was the lowest for the second instar larvae (1.84). Furthermore, The IM value for the same phases was the lowest. On the other hand, IM for third instar larvae was minimum (1.87) at 24 °C (Table 3). Similarly, IM for the prepupal stage was maximum (7.21). For pupae, it was the highest of (14.0) at 28 °C (Table 4).

Life expectancy

The life expectancy for the pupal stage was on the higher side (1.48 days) at 16 °C (Table 1). However, the egg stage's life expectancy was the highest of (6.44) at 24 °C. While, for the first instar larvae, it was the highest of (5.82 days) at 24 °C. Furthermore, it was at the upper limit (5.18 days) for second instar larvae at 24 °C. However, it was a maximum of (4.29 days) for third instar larvae at 24 °C. Consequently, it was a maximum (3.38 days) for fourth instar larvae at 24 °C. On the other hand, it was the highest for the prepupa (2.42 days) at 24 °C (Table 3). Furthermore, the egg stage's life expectancy was the smallest (4.15 days) at 28 °C (Table 4). While for first instar larvae (4.78 days) at 28 ± 1 °C. However, for second instar larvae, it was at lower limits (4.03 days) aphid at 28 ± 1 °C. Furthermore, it was minimum (3.46 days) for third instar larvae at 28 °C. Moreover, it was the minimum of (2.81 days) for fourth instar larvae at 28 °C. Consequently, for the prepupa, it was the lowest of (2.01 days) at 28 °C. Besides, it was on the lower side (1.32 days) at 28 °C (Table 4).

K-values

The *k*-value at the egg stage was the lowest (0.027) at 24 °C, but the highest (0.128) was at 28 °C. The minimum *k* value for the 1st larval instar was 0.029 at 24 °C. However, it was a maximum (0.069) at 28 °C. For the 2nd larval instar, this value was highest (0.071) at 16 °C and the lowest (0.01) at 24 °C. However, for the 3rd instar, it was minimum (0.01) at 24 °C and it was the maximum (0.048) at 16 °C. For the 4th instar, it was the lowest (0.005) at 24 °C and it was the maximum (0.026) at 16 °C. Furthermore, the k value for prepupa and pupal stage was the least (0.011 and 0.016) at 24 °C (Table 3). For adults, *K* value was the highest (0.495) at 28 °C, while the minimum was 0.108 at 24 °C.

Fertility life table parameters of adult female *H. dimidiate*

gross reproductive rate

The gross reproductive rate ($\sum m_x$) of adult female *H. dimidiata* beetle was maximum (215.87) at 24 °C and minimum (82.755) at 28 °C. The gross reproductive rate was significantly different among all tested temperatures. The temperature, as well as the host insects, had a significant effect on GRR. Moreover, the net reproductive rate was maximum (66.95) at 24 °C and minimum (14.54) at 28 °C. Statistically significant differences were recorded in net reproductive rates at different temperatures. The results indicate that R_o is greater than > 1 at all measured temperatures; hence, the population grows. However, the approximate generation time (T_c) was significantly maximum (89.01) days at 16 °C and minimum (36.66) days at 28 °C. Furthermore, the innate capacity for increase (r_c) was maximum (0.0772) at 24 °C and minimum (0.0337) at 16 °C. It was significantly different at all measured temperatures. The results showed that the values of (r_c) were positive at all measured temperatures, which indicates that the population growth rate of *H. dimidiata* increased at all measured temperatures. The intrinsic rate of natural increase was maximum (0.07 and 0.07). In comparison, the value of λ was a maximum of 1.0730 and 1.0730. The temperature had a significant effect on the finite rate of population increase except for 24 and 28 °C. Meanwhile, the mean generation time was maximum (99.97) days at 16 °C and minimum (38.24) days at 28 °C. Mean generation time was significantly different at different temperatures. At 20 and 24 °C, the mean generation time was non-considerably different. Nevertheless, the population doubling time was maximum (20.575) days at 16 °C and minimum (9.263) days at 24 °C. DT was non-significantly different at different temperatures except for 16 °C, which was significant from all other tested temperatures (Table 5).

Adult female fertility (m_x) and survival (l_x) at four constant temperatures specific fertility (m_x) and survival (l_x) at 16 °C

The first specific fertility (m_x) was observed after 22 days. It was the maximum at day (54). The fertility was observed up to day (70) in the case of both aphid species. After this duration, although some female remained live, they cannot develop. The female remained live up to 86 days. The survivorship curve indicated that the first mortality was observed at day (21). The population decreased gradually up to the age of (51) days. After this period, a steep down decrease was observed in the female population (Fig. 1).

Specific fertility (m_x) and survival rate (l_x) at 20 °C

The first specific fertility (m_x) was observed at day (14). The fertility was maximum at the age of (33) days. The fertility was observed up to the age of (54) days. After this duration, although some female remains live, they cannot

Table 5 Estimated life table parameters of *H. dimidiata,* fed on *R. padi* aphids at four constant temperatures

Life table parameters	Temperatures			
	16 ± 1 °C	20 ± 1 °C	24 ± 1 °C	28 ± 1 °C
Gross reproductive rate, GRR	128.57 ± 2.03c	203.0 ± 3.24b	215.87 ± 2.18a	82.75 ± 1.83d
Net reproductive rate, R_o	20.07 ± 0.82c	51.37 ± 1.52b	66.95 ± 0.95a	14.54 ± 1.53c
Approximate generation time, T_c	89.01 ± 1.34ba	63.54 ± 2.12b	56.21 ± 1.24c	36.66 ± 0.97d
Innate capacity for increase, r_c	0.0337 ± 2.67d	0.0377 ± 2.18c	0.0772 ± 4.22a	0.0731 ± 3.98b
Intrinsic rate of natural increase, r_m	0.03 ± 0.01c	0.06 ± 0.01b	0.07 ± 0.01a	0.07 ± 0.01a
Finite rate of increase, λ	1.0309 ± 5.15c	1.0620 ± 3.78b	1.0730 ± 1.89a	1.0730 ± 4.23a
Mean generation time, T	99.97 ± 2.32a	65.66 ± 0.97b	60.06 ± 1.25b	38.24 ± 1.41c
Doubling time, DT	20.575 ± 1.33a	11.014 ± 0.49b	9.263 ± 0.35b	9.487 ± 0.50b

Means within the rows with different lowercase letters are significantly different from each other at *P value* ≤ 0.05 (two-way ANOVA) using Tukey-HSD test

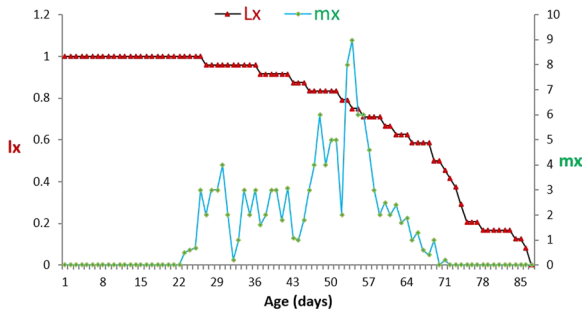

Fig. 1 Age specific survival (l_x) and fertility (m_x) of adult female *H. dimidiata* fed on *R. padi* aphid at 16 ± 1 °C

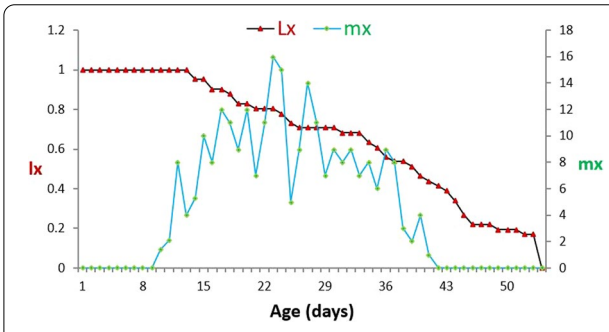

Fig. 3 Age specific survival (l_x) and fertility (m_x) of adult female *H. dimidiata* fed on *R. padi* aphid at 24 ± 1 °C

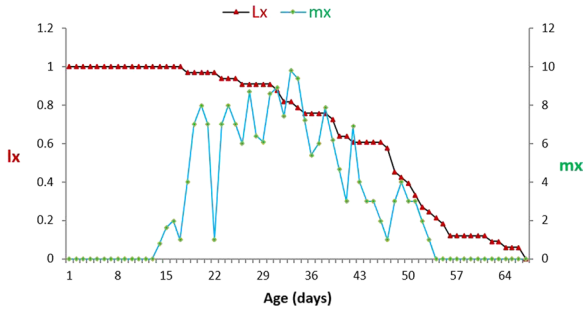

Fig. 2 Age specific survival (l_x) and fertility (m_x) of adult female, *H. dimidiata* fed on *R. padi* aphid at 20 ± 1 °C

breed. The female remains live up to the age of (66) days. The survivorship curve indicates that the first mortality was observed at day (17). The population decreased gradually up to the age of (46) days. After this period, a steep down decrease was observed in the female population (Fig. 2).

Specific fertility (m_x) and survival rate (l_x) at 24 °C

The first specific fertility (m_x) was observed at the age of (10) days. The fertility was maximum at the age of (22) days. The fertility was observed up to the age of (42) days. Although some females remained alive, they could not develop after this period. The maximum (m_x) was observed between (12–35) days. The female remained live up to the age of (53) days. The survivorship curve indicated that the first mortality was observed at day (14). The population decreased gradually up to the age of (35) days. After this period, a steep down decrease was observed in the female population (Fig. 3).

Specific fertility (m_x) and survival rate (l_x) at 28 °C

The first specific fertility (m_x) was found at day (8). The fertility was maximum at the age of (20) days. The fertility was observed up to the age of (27) days. After this, although some female remained alive, they could not develop. The maximum (m_x) was observed between

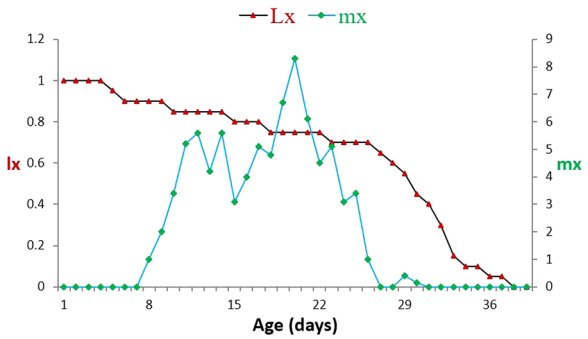

Fig. 4 Age specific survival (l_x) and fertility (m_x) of adult female *H. dimidiata* fed on *R. padi* aphid at 28 ± 1 °C

(11–23) days. The female remained live up to the age of (38) days. The first mortality was observed at the age of 5 days. The population decreased gradually up to the age of (26) days. After this period, a steep down decrease was observed in the female population (Fig. 4).

Fertility life table parameters of adult female *H. dimidiata*

Gross reproductive rate

The gross reproductive rate ($\sum m_x$) of adult female of *H. dimidiata* beetle was maximum (215.87) at 24 °C and minimum (82.755) at 28 °C. The gross reproductive rate was significantly different among all tested temperatures (Table 5).

Net reproductive rate (R_o)

The net reproductive rate was maximum (66.95) at 24 °C and minimum (14.54) at 28 °C (Table 5). Statistically significant differences were recorded in net reproductive rates at different temperatures. The results indicated that R_o was greater > 1 at all measured temperatures; hence, the population grows.

Approximate generation time (Tc)

The approximate generation time (T_c) was significantly maximum (89.01 days) at 16 °C and minimum (36.66 days) at 28 °C (Table 5).

Innate capacity for increase (rc)

The innate capacity for increase (r_c) was maximum (0.0772) at 24 °C and minimum (0.0337) at 16 °C (Table 5). It was significantly different at all measured temperatures. The results showed that the values of (r_c) were positive at all measured temperatures, which indicated that the population growth rate of *H. dimidiate* increased at all tested temperatures.

Intrinsic rate of natural increase (rm)

The intrinsic rate of natural increase was maximum (0.07 and 0.07) (Table 5).

Finite rate of population increase (λ)

The value of λ was a maximum of 1.0730. The temperature had a significant effect on the finite rate of population increase, except for 24 °C and 28 °C (Table 5).

Mean generation time

The mean generation time was a maximum (99.97) days at 16 °C and a minimum of (38.24) days at 28 °C. Mean generation time was significantly different at different temperatures. At 20 and 24 °C, the mean generation time was non-considerably different (Table 5).

Population doubling time (DT)

The population doubling time was maximum (20.575) days at 16 °C and minimum (9.263) days at 24 °C. DT was non-significantly different at different temperatures, except for 16 °C, significant from all other tested temperatures (Table 5).

Discussion

Comparison between traditional life tables and the two-sex life table is the best method for vital and basic research in ecological investigations (Ali et al. 2020; Govindan and Hutchison 2020). Obtained results indicated shorter life spans than the 81.0 d for *H. dimidiata* when fed on *R. padi* at 28 °C (Gillani et al. 2007) who reported also a larger fecundity of 422 eggs/female for *H. dimidiata* when fed on *B. brassicae* at 25 °C. At 24 and 28 °C, the curves of m_x and $l_x m_x$ indicated roughly periodic reproduction peaks those were very close to those obtained by another ladybird beetle, *Lucidina biplagiata* (Yu et al. 2005). This result may be attributed to the different temperatures (suitable for females) to complete metabolic reactions in the predator body and also egg laying (Ali et al. 2020).

For an insect's development, and survival, r is very important demographic parameter (Chen et al. 2017). According to the theory of demographic life tables, if r is greater than zero, therefore, the temperature is suitable for population growth (Chen et al. 2017). This theory supported the findings of the present study.

The R_0 is a significant indicator for the development of population, where the maximum rate of population is dependent on the fecundity (Sayyed et al. 2008). The GRR is a sign of a rapid increase in the insect population that depends on fecundity and adult emergence percentage. In general, these parameters are highly affected

by temperature and food source (Chen et al. 2018). The present study achieved the highest net reproductive rates (GRR and R_0) when *H. dimidiata* was fed on *R. padi* at 20 and 24 °C. The temperature affected the biotic potential (R_0, *r*, and GRR at 24 °C) of *H. dimidiata*. The population increased when R_0 was more than one (Chen et al. 2017), and the present finding was also according to this theory.

Our data for *N*, *Nf*, *F*, and R_0 were consistent with Chi Equation. However, when the bootstrap technique was used for calculating R_0, minor difference was appeared due to the use of the resampling technique. The use of a jackknife technique resulted in degrees of a discrepancy between the estimated means and their definitions (Chi and Yang 2003).

The temperature-dependent attributes of the intrinsic rate of increase (*r*) and the finite rate of increase (*k*) were clear. Also, the R_0 was lower, and the mean generation time (*T*) was shorter at the tested higher temperatures..

The age-specific predation rate (k_x) and the age-specific net predation rate (q_x) demonstrates the importance and advantage of both in biological control (Kuroda and Miura 2003) and can be useful for estimating the release interval in a biocontrol programs.

In the present study, the survivorship curve (l_x) and mortality (d_x) of preadult stages, in general, showed a similar pattern with a higher mortality happening in the initial phases, egg, first, and second instar larvae. While in third and fourth instar larvae, the mortality was minimum. This showed that early instars were susceptible to temperature. The stage and age-specific life table parameters of immature stages indicated that apparent mortality for different stages was minimal, survival fraction and high life expectancy. *K* value was minimum at 24 ± 1 °C, out of the tested temperatures. Different workers carried out a comprehensive work on the life table parameters of various coccinellid beetles under other environmental conditions, but *H. dimidiata* was the least studied species, particularly in Pakistan. No such type of study was carried out in the past. Ali and Rizvi (2010) reported that (24 ± 1 °C) was the most suitable temperature for rearing *Coccinella septempunctata* when fed on *Lipaphis. erysimi* aphid based on superior development, maximum survival, and minimum mortality. Similarly, Auad et al. (2014) reported a shortened developmental period for *Harmonia axyridis*, fed on *R. padi*, when reared at the higher temperature of 28 °C as compared to low temperature of 16 °C. In the present study, the developmental period was temperature-dependent and shortened at high temperatures.

Obtained results are matched with the findings of Castro et al. (2011) who reported that temperature influenced the life table parameters including r_m, r_c, DT, *T* and λ by changing developmental time, survival rate, and fecundity rate of *H. axyridis*, fed on *Cedrus. atlantica*. Yu et al. (2013) reported that the (R_o) value of *H. dimidiata* was maximum at 15 °C when fed on *A. gossypii* aphid. While in the present studies, the maximum (R_o) value was found at 24 ± 1 °C. The results regarding (R_o) in the present study and that of the past worker, Yu et al. (2013) indicated a massive variation at the same temperature levels. This variation may be due to different strains and biotypes or geographical populations of *H. dimidiata*.

Similarly, the innate capacity for increase (r_c) was maximum at 24 ± 1 °C and minimum at low temperature. The intrinsic rate of increase is a fundamental parameter as an indicator for population growth potential (Robert and Miller 2000). In the present study, the natality was higher than the mortality at all tested temperatures. Among the tested temperature, the (r_m) value was maximum at 24 ± 1 °C. The (r_m) values were positive at all tested temperatures, which indicated the population increase. The present results conform the results of Yu et al. (2013), who reported that the intrinsic rate of increase (r_m) and finite rate of increase (λ) was maximum at 25 °C and minimum at the low temperature of 15 °C. The same trend was obtained in the present study where r_m and λ were minimum at low temperature and maximum at 24 ± 1 °C. The mean generation time (*T*) was maximum at low temperatures and minimum at high temperatures in the present study. The results are closely associated with Yu et al. (2013), who reported that mean generation time was maximum at low temperatures. With increasing temperature, the generation time decreased significantly. The doubling time was maximum at low temperature and minimum at 24 ± 1 °C. The doubling time (DT) was significantly different at low temperatures of 16 ± 1 °C and it was non-significantly different at all other tested temperatures. Similarly, the host insects had a non-significant effect on doubling time.

Conclusion

Results indicated that temperature had impacts on the developmental potential and the reproductive capacity of *H. dimidiata*, where the feeding potential, development, survival and fecundity at 24 and 28 °C were higher than those at the other investigated temperatures. Also, results demonstrated that an accurate description of a predator's development, survival, and predation capacity can be achieved with the age-stage, two-sex life table. These findings could be useful to estimate the suitability of *H. dimidiata* as a biocontrol agent under various environmental conditions. The present findings would be helpful to determine the suitable rearing of *H. dimidiata* for effective pest control under different greenhouse and field conditions.

Abbreviations
100 q_x: Mortality during age interval; x: Insect age; l_x: At the start of each interval, insects survived; d_x: During each interval died, insects; e_x: Life probability or average life left over for individual of age; L_x: Individuals active between age x and $x+1$; S_x: Stage-specific survival fraction; MSR: Mortality in particular stage; IM: Number of adults emerged.

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Author contributions
JK conceived the idea and designed the study. JK and AK performed wet lab. experimentation. SS, MA and NA provided technical and financial assistance for the study. JK and AK did statistical analysis. JK, NA and FU wrote the original draft of the manuscript. JK and AK did the insect rearing, the bioassay experiments in addition to the statistical analysis. NA, SS, SKA, AAA and PA, technically proofread the manuscript. All authors have read and approved the final version of the manuscript. All authors read and approved the final manuscript.

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Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
This study does not contain any individual person's data.

Competing interests
The authors declare not to have any competing interests regarding the publication of this work.

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