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Life table parameters and digestive physiology of *Aulacophora lewisii* Baly (Coleoptera: Chrysomelidae) on three *Luffa acutangula* (L.) Roxb. (Cucurbitaceae) cultivars

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Research Paper

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Abstract

Aulacophora lewisii Baly (Coleoptera: Chrysomelidae) is an important pest of *Luffa acutangula* (L.) Roxb. (Cucurbitaceae) in India. Larvae of *A. lewisii* feed on the roots, while adults consume leaves of *L. acutangula*. In the current study, effects of three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) on the life table parameters by age-stage, two-sex approach, and key digestive enzymatic activities (amylolytic, proteolytic, and lipolytic) of the larvae and adults of *A. lewisii* were determined. Further, nutrients (total carbohydrates, proteins, lipids, amino acids, and nitrogen content) and antinutrients (total phenols, flavonols, and tannins) present in the roots and leaves of three cultivars were estimated. The development time (egg to adult emergence) was fastest and slowest on Jaipur Long (31.80 days) and Abhiskar (40.91 days), respectively. Fecundity was highest and lowest on Jaipur Long (279.91 eggs) and Abhiskar (137.18 eggs), respectively. The intrinsic rate of increase (r) was lowest on Abhiskar (0.0511 day^{-1}) and highest on Jaipur Long (0.0872 day^{-1}). The net reproductive rate (R_0) was lowest on Abhiskar (23.32 offspring female^{-1}). The mean generation time (T) was shortest on Jaipur Long (52.59 days) and longest on Abhiskar (61.58 days). The amylolytic, proteolytic, and lipolytic activities of larvae and adults of *A. lewisii* were highest and lowest on Jaipur Long and Abhiskar, respectively. The lower level of nutrients and higher level of antinutrients influenced higher larval development time and lower fecundity of *A. lewisii* on Abhiskar than other cultivars. Our results suggest that Abhiskar cultivar could be promoted for cultivation.

Introduction

Luffa acutangula (L.) Roxb. (Cucurbitacea), commonly known as ridge gourd, is an annual crop having vine with a long taproot system and sharply angled 5-lobed leaves. The plant is grown for production of fruits, which is consumed as vegetable. The primary centre of origin of this plant is India, and now it is naturalised through tropics and subtropics (Shendge and Belemkar, 2018; Al-Snafi, 2019). The plant is widely cultivated in India, Bangladesh, Sri Lanka, Pakistan, China, Japan, Egypt, Africa, USA, Mexico, Brazil, Ecuador, Peru, Venezuela, and Australia (Al-Snafi, 2019; Kumari *et al.*, 2019; Panicker, 2020). The fruit is a rich source of iron, calcium, phosphorous, ascorbic acid, and carotene (Nagarajaiah and Prakash, 2014). In traditional medicine, the plant is used for the treatment of jaundice, diabetes, haemorrhoids, dysentery, headache, urinary bladder stone, splenitis, trachoma, ringworm infection, leprosy, etc. (Samvatsar and Diwanji, 2000; Shendge and Belemkar, 2018; S and Vellapandian, 2022). The whole plant has an immense medicinal value such as antidiabetic (Mohan Raj *et al.*, 2012; Juma *et al.*, 2013; Sharmin *et al.*, 2013; Panicker, 2020; Thatchinamoorthi *et al.*, 2021), antihyperlipidemic (Pimple *et al.*, 2011; Viviandhari *et al.*, 2020), anticancer (Dashora and Chauhan, 2015; Nallappan *et al.*, 2021), analgesic and anti-inflammatory (Dandge *et al.*, 2012; Iyyamperumal *et al.*, 2013; Ananthalakshmi *et al.*, 2021), immunomodulatory (Kalasakar and Surana, 2014; Belemkar *et al.*, 2021) and CNS depressants activity (Misar *et al.*, 2004; Belemkar *et al.*, 2021). The whole plant is also considered as a good source of antioxidants (Bulbul *et al.*, 2011; Dashora and Chauhan, 2015; Shendge and Belemkar, 2018; Nallappan *et al.*, 2021; S and Vellapandian, 2022).

Aulacophora lewisii Baly (Coleoptera: Chrysomelidae) is an important pest of the genus *Luffa* (Yong, 1993; Lewis and Metcalf, 1996; Abe *et al.*, 2000; Abe and Matsuda, 2005). The insect also feeds on towel gourd, bitter gourd, and other cucurbitaceous plants (LiYun *et al.*, 2009; Sarker *et al.*, 2019). The insect feeds on cucurbitaceous plants due to presence of four cucurbitacins (B, E, I, and E-glucoside) (Abe *et al.*, 2000). The first to fourth instars feed on the young roots, while adults consume leaves and flowers of the plant and causes economic damage, if their populations are not controlled (Dilipsundar *et al.*, 2022). The insect

is widely distributed in India, Bangladesh, Pakistan, China, Japan, Bhutan, Malaysia, Vietnam, and Taiwan (Ahmad *et al*., 2013; Lee and Beenen, 2015; Sarker *et al*., 2019). To date, literature on the biology of *A. lewisii* on *L. acutangula* is meagre.

Control of *A. lewisii* is mostly dependent on synthetic insecticides (endrin, lindane, malathion, dichlorvos, carbaryl, and carbofuran). These insecticides enter in the insect body through skin contact, ingestion, and inhalation. Organophosphates (malathion and dichlorvos) and carbmates (carbaryl and carbofuran) bind to the enzyme acetylcholinesterase at nerve endings throughout the bodies of insect, which causes overstimulation of the nervous system and subsequently, results death of the insect (Čolović *et al*., 2013). Organochlorine insecticides (endrin and lindane) produces a non-competitive inhibition of γ-aminobutyric acid (GABA)-regulated chloride transport, blocking the stimulation of chloride influx into the neuron, causing hyperexcitability of the central nervous system, and ultimately, results death of the insect (Jayaraj *et al*., 2016). Applications of pesticides can cause many problems such as environmental pollution, harmful pesticide residues in crops, pest resurgence, outbreak of secondary pests and pesticide resistance. In contrast to the chemical control, host-plant resistance is the most economical and effective approach to control an insect pest. Therefore, host plant resistance should be emphasised in integrated pest management programme (IPM) to control an insect pest. Crop plant resistance against an insect pest can be achieved through various ways such as antixenosis, antibiosis, and tolerance. Among them, antixenosis is the most important because by this mechanism, a phytophagous insect pest exhibits non-preference towards the resistant plant, which affects both feeding and reproduction of the insect pest (Golizadeh *et al*., 2017*a*, *b*). Crop plant cultivars of a species can vary in various physiological and morphological features including nutritional and anti-nutritional content, which can influence the development, longevity of adults and fecundity of an insect pest (Sarkar *et al*., 2016; Mukherjee *et al*., 2017; Golizadeh *et al*., 2017*a*, *b*; Debnath *et al*., 2020; Mobarak *et al*., 2020; Mitra *et al*., 2022).

Life table is a powerful and necessary technique to analyse and understand the effect of different host plants including different cultivars of a host plant on the growth, survival, reproduction, and intrinsic rate of an insect population (Das *et al*., 2019; Koner *et al*., 2019). Construction of life table is necessary to understand the population dynamics of an insect pest prior to implement effective control programme. The traditional age-specific life table is based on only the female age-specific population, which ignores the male population, stage differentiation and the variable developmental rates among individuals, and ignoring the variable developmental rate and male population may cause errors in calculating demographic parameters such as the intrinsic rate of increase, net reproductive rate and the mean generation time (Chi and Liu, 1985; Chi, 1988; Chi and Su, 2006; Chi *et al*., 2020; Wei *et al*., 2020). The age-stage, two-sex life table takes in to account of stage differentiation and male population, and it shows a solid relationship between mean fecundity and net reproductive rate (Chi and Liu, 1985; Chi *et al*., 2020; Yang *et al*., 2020). The demography of an insect pest population in different cultivars of a host plant is usually considered as eco-friendly approach to find resistant or partially resistant cultivars of a crop plant.

The aims of the present study were to (i) construct age-stage, two-sex life table of *A. lewisii* to study the biology and population dynamics of *A. lewisii* on three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long are currently grown in West Bengal, India due to high yielding potential. Abhiskar and Debsundari were originated from West Bengal, while Jaipur Long was originated from Hyderabad, India), (ii) determine the amylolytic, proteolytic, and lipolytic activities of the fourth instars and adults of *A. lewisii* by feeding on the roots and leaves of three *L. acutangula* cultivars, respectively, and (iii) understand the probable effect of various nutrients (total carbohydrates, proteins, lipids, amino acids, and nitrogen) and antinutrients (total phenols, flavonols, and tannins) present in the roots and leaves of three *L. acutangula* cultivars on the biology and population dynamics potential of *A. lewisii*. Findings of this current study could contribute to IPM programmes of *A. lewisii* on *L. acutangula*.

Materials and methods

Host plants

Seeds of three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) were sown separately in pots (18 cm diameter, 20 cm height) containing sterilised soil (1500 cm^3) and were grown in natural condition during March–October 2022 at 30–37°C under natural photoperiod (13L:11D) at the Crop Research Farm (CRF) of the University of Burdwan (23°16′N and 87°54′E), West Bengal, India. Each plant with the pot was covered by a fine mesh nylon net (120 cm (height) × 65 cm (diameter)) to protect plants from insect attack and unintentional infection. Insecticides were not applied on these plants. Plants are watered once daily. Those plants which are not covered by nylon net are attacked by the adults of *A. lewisii* during early May.

Insect culture

Adults (males and females) of *A. lewisii* were collected from plants of each *L. acutangula* cultivar growing at the CRF of the University of Burdwan during May 2022. Adults (20 pairs of male and female) collected from a particular *L. acutangula* cultivar were fed on leaves of the same cultivar in glass jars (11 cm diameter × 22 cm height) as females could lay eggs on the leaves. The eggs (100) were allowed to hatch on moistened soil, and its larvae were fed on young tender roots of same *L. acutangula* cultivar on which adults of *A. lewisii* were also reared. For a particular cultivar, stock cultures containing 25 pairs of adults (males and females) were separately maintained for three generations in the laboratory at 27 ± 1°C, 70 ± 10% relative humidity and 12L:12D in biological oxygen demand incubators (ADS instruments and Tech., Kolkata, India) as the insects could habituate on each *L. acutangula* cultivar.

Life table study

Newly emerged fourth generation *A. lewisii* adults (antenna of male wider than female, and apical margin of abdominal ventrite V sinuate in female), which were fed on the leaves of same cultivar for three generations, were employed to construct life table. A pair of newly emerged adults (male and female) was placed in fine mesh nylon net cages (11 cm diameter × 22 cm height) for mating and egg laying (newly emerged males and females mate on the sixth day of emergence). After mating, each female was observed at 12 h interval to collect freshly laid eggs. Four eggs were randomly collected from a batch of newly laid eggs where a pair of male and female was paired on a particular *L. acutangula* cultivar

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($n = 25$ pairs of males and females). Eggs laid within 12 h by the females were used for life table study on a particular *L. acutangula* cultivar. Groups of 100 eggs collected from 25 mated females, on which particular cultivar they were maintained, were employed to construct age-stage, two-sex life table of *A. lewisii* on the roots of each *L. acutangula* cultivar. Each egg was placed in an earthen pot (5 cm diameter × 3 cm height) containing sterilised soil, which was moistened with distilled water. Before placing the soil in the Petri dish, a moistened Whatman No 41 filter paper was placed. Each larva was considered as an individual replicate containing young root (2 cm length and 0.5 cm diameter) of a particular *L. acutangula* cultivar until adult emergence. Larval mortality and moulting including pupation time and the time of adult emergence of each individual were recorded at 24 h interval. Each newly emerged adult was placed in a separate glass jar (8 cm diameter × 10 cm length) and covered with fine mesh nylon net. Newly emerged adults were fed on the leaves of a particular *L. acutangula* cultivar, the root of the same cultivar was provided to the larvae for rearing. Fresh leaves were provided daily for adult's feeding. The longevity of adults, i.e. from adult emergence to death of males and females was also recorded at 24 h interval.

The length and breadth of eggs, and instars by feeding on the roots of a particular cultivar (Abhiskar, Debsundari, and Jaipur Long) were measured to observe the growth of *A. lewisii* (egg, and first, second, and third instars were measured by microscope fitted with objective lens of 10× attached with oculometer ERMA Japan, while fourth instars were measured in millimetre graph paper) ($n = 10$). Further, length and breadth of the pupa and newly emerged adults were measured in millimetre graph paper ($n = 10$).

Fecundity of *A. lewisii* through lifetime was recorded on the leaves of each *L. acutangula* cultivar, on the roots of the same cultivar on which larvae were reared. The adult pre-oviposition period (APOP: the period between the emergence of an adult female and her first oviposition), total pre-oviposition period (TPOP: the time interval from birth to the beginning of oviposition), oviposition days, daily fecundity and total fecundity (number of eggs produced during the reproductive period) were recorded on the leaves of each cultivar (Chi, 1988; Chi and Su, 2006).

Raw data on the survival, development and oviposition of all individuals were analysed based on age-stage, two-sex life table theory (Chi and Liu, 1985; Chi, 1988) using the computer program TWOSEX-MSChart (Chi, 2022*a*). The parameters calculated were: age-stage specific survival rate (s_{xj}, x: age and j: stage), age-specific survival rate (l_x), age-stage specific fecundity (f_{xj}), age-specific fecundity (m_x), age-stage life expectancy (e_{xj}), and age-stage reproductive value (v_{xj}).

The potential population growth of *A. lewisii* on three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) was projected according to Chi and Liu (1985) and Chi (1990) to forecast the future population size and age-stage structure by using the TIMING-MSChart program (http://140.120.197.173/Ecology/Download/Timing-MSChart.rar) (Chi, 2022*b*).

Enzymatic activity of larvae and adults

Fourth generation fourth instars (2nd day) and adults (5 males and 5 females,10 days old) of *A. lewisii* that were fed on the roots and leaves, respectively, of three particular *L. acutangula* cultivars for three generations, were used to determine enzymatic activity. For each cultivar, fourth instars were ground with 100 mM sodium phosphate and 500 mM sodium chloride pH 7.6 (450 µl 10 mM Nacl), at a ratio of 45 µl larva^{-1}. Samples were shaken for 30 min at 4°C and centrifuged at 1700 × ***g*** for 5 min, and the supernatants were used as enzyme sources. Adults were placed in ice to prevent any movements, and after that adults ($n = 10$) were rapidly dissected under a stereomicroscope. The haemolymph was cleaned with precooled distilled water, and the extraneous tissues were removed from midguts. Midguts including contents were homogenised in 450 µl of 10 mM NaCl by a glass homogeniser. The solution was centrifuged at 12,000 ***g*** at 4°C for 15 min and the supernatant was collected for enzymatic assays (Mohammadzadeh *et al.*, 2013).

α-Amylase activity was determined according to Bernfeld (1955) with some modifications by Mohammadzadeh *et al.* (2013). The optimum pH on α-amylase activity was determined by incubation of the reaction mixture with pH set at 7–12. Soluble starch (1% w/v) as a substrate was added in 20 mM glycine–NaOH buffer (pH 7). One-hundred µl of the enzyme extract were added with glycine–NaOH buffer (500 µl; pH 7) at 37°C. Reaction began when 80 µl of 1% soluble starch were added and stopped 30 min later by addition of 100 µl of dinitrosalicylic acid (DNS) and heating in boiling water for 10 min. Each treatment was replicated five times including blanks in which substrate was added after DNS, and the absorbance was measured at 540 nm in the UV-visible spectrophotometer (Shimadzu, UV-1800240V). The result was expressed as mg maltose min^{-1} (one unit of α-amylase activity was defined as the quantity of enzyme required to produce 1 mg maltose at 37°C min^{-1}).

Total proteolytic activity was estimated by the protocol of Elpidina *et al.* (2001) using azocasein as a substrate at the pH optimum. The buffer (100 mM sodium acetate phosphate borate buffer) was used to determine the pH optimum of proteolytic activity over a pH range of 7–12. Azocasein (0.5% w/v) as a substrate was mixed in 100 mM sodium acetate phosphate borate buffer (pH 9.0). Enzyme extracts (100 µl) were added with 200 µl azocasein and 400 µl of 100 mM sodium acetate phosphate borate buffer (pH 9.0) at 37°C. The enzymatic reactions were stopped by addition of 12% of 300 µl trichloroacetic acid (TCA). The solution was centrifuged at 12,000 *g* for 15 min and the supernatant monitored spectrophotometrically at 440 nm. The absorbance from the supernatant was measured at 440 nm in the UV-visible spectrophotometer (Shimadzu, UV-1800240V). Each treatment was replicated five times including blanks in which substrate was added after TCA, and the result was expressed as mU min^{-1} (one unit is defined as the amount of enzyme that is required to hydrolyse azocasein to give 1 µg of tyrosine in 1 min at 37°C at certain pH).

The lipolytic activities were assayed as described by Choi *et al.* (2003). The standard reaction mixture (0.2 mM 2,3-dimercapto-1-propanol tributyrate (DMPTB) in 50 mM Tris-HCl, pH 7.2, 0.001% ethylenediaminetetraacetic acid, 0.06% Triton X-100 and 0.8 mM 5,5′-dithiobis(2-nitrobenzoic acid) (DTNB)) was prepared in a microcentrifuge tube. 50 µl of enzyme extract were added with 150 µl of standard reaction mixture and 800 µl of deionised water were added to make the total volume of the assay 1 ml. The final reaction mixture was incubated at 37°C for 30 min and the absorbance was measured at 400 nm in the UV-visible spectrophotometer (Shimadzu, Kyoto, Japan, UV-1800240V). We used a blank that contained no DMPTB. In the DMPTB–DTNB method, free thiol groups that are generated by the lipase hydrolysis of DMPTB reduce DTNB to create a yellow colour. Five samples were analysed for each experimental

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point. The assay was read to an end point and the molar extinction coefficient of DTNB 13.6 M^{-1} cm^{-1} was used for calculations.

Biochemical analysis of roots and leaves

The nutritional parameters from the roots and uninfested leaves of each *L. acutangula* cultivar (Abhiskar, Debsundari, and Jaipur Long) were estimated by using 1 g young tender roots and fresh leaves, respectively, to various biochemical analysis such as total carbohydrates (Dubois *et al*., 1956), total proteins (Lowry *et al*., 1951), total lipids (Folch *et al*., 1957), total amino acids (Moore and Stein, 1948), total phenols (Bray and Thorpe, 1954) and total flavonols (Howell *et al*., 1976). Dried roots and leaves were used for determination of total tannins (Scalbert, 1992) and total nitrogen (Vogel, 1958) as water content in young roots and fresh leaves may interfere satisfactory estimations. Each biochemical analysis was replicated five times.

Estimation of moisture content

One-gram young tender roots or fresh leaves from each *L. acutangula* cultivar (Abhiskar, Debsundari and Jaipur Long) was placed in a hot-air oven for 72 h at 50 ± 1°C and the dried roots or leaves were weighed in a balance (±0.01 mg). The water content was determined by recording the difference between fresh and dry weights of roots or leaves ($n = 5$). The moisture content for roots or leaves of three cultivars was replicated five times (Debnath *et al*., 2020).

Statistical analysis

The means and standard errors of life table parameters were estimated by bootstrap technique (Efron and Tibshirani, 1993) with 100,000 replications, which is present in the TWOSEX-MS Chart program to observe whether the data are normally distributed (Chi, 2022*a*). The paired bootstrap (Chi, 2022*a*, 2022*b*) was used to evaluate the differences at the 5% significance level in the development time, adult longevity, adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period and fecundity, and life table parameters (r, λ, R_0, and T) among three *L. acutangula* cultivars. Data on enzymatic activity of the fourth instars and adults among treatments, and the biochemical properties of three *L. acutangula* cultivars were subjected to one-way analysis of variance followed by Tukey's test (HSD) (Zar, 1999). The Pearson correlation coefficient analysis was applied to observe the relationship between the life table parameters of *A. lewisii* and chemical properties (nutrient and antinutrients) of the roots and leaves of three *L. acutangula* cultivars. All the statistical analyses were performed by using SPSS (version 25.0) software.

Results

Development, survival and oviposition of A. lewisii

The effect of three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) on larval development time and longevity of *A. lewisii* adults is given in table 1. Significant differences were recorded in the incubation period of eggs, which was the longest on Abhiskar followed by Debsundari and the shortest on Jaipur Long. Incubation period was 1.14 times longer on Abhiskar than Jaipur Long. The larval duration for the first two instars was the longest on Abhiskar followed by Debsundari and the shortest on Jaipur Long. However, the larval duration of third and fourth instars was longer on Abhiskar and Debsundari compared to Jaipur Long. The durations of first, second, third, and fourth instars were 1.61, 1.59, 1.26, and 1.23 times longer, respectively, on Abhiskar compared to Jaipur Long. The pupal duration was the longest on Abhiskar and the shortest on Jaipur Long, which is 1.30 times longer on Abhiskar than Jaipur Long. Moreover, the immature development (from egg to adult emergence) was different among cultivars, which was the longest on Abhiskar followed by Debsundari and the shortest on Jaipur Long. The preadult duration was 1.29 times longer on Abhiskar than Jaipur Long. The longevities of adult males and females were the longest on Jaipur Long, intermediate on Debsundari and the shortest on Abhiskar. Adult females lived 1.63 times longer on Jaipur Long compared to Abhiskar, while males survived 1.58 times longer on Jaipur Long in comparison to

Table 1. Development time and adult longevity (Mean ± SE) of *Aulacophora lewisii* on three *Luffa acutangula* cultivars

	Abhiskar		Debsundari		Jaipur Long	
Parameters	*n*	Duration (day)	*n*	Duration (day)	*n*	Duration (day)
Egg	96	12.79 ± 0.14a	80	11.91 ± 0.11b	85	11.25 ± 0.15c
1st instar	89	3.24 ± 0.07a	72	2.56 ± 0.07b	77	2.01 ± 0.01c
2nd instar	80	3.51 ± 0.07a	65	3.08 ± 0.07b	71	2.21 ± 0.05c
3rd instar	67	3.66 ± 0.07a	61	3.46 ± 0.07a	67	2.90 ± 0.04b
4th instar	53	4.06 ± 0.01a	58	3.86 ± 0.06a	62	3.29 ± 0.08b
Pupa	43	13.40 ± 0.13a	50	12.16 ± 0.14b	60	10.32 ± 0.15c
Preadult	43	40.91 ± 0.32a	50	36.94 ± 0.25b	60	31.80 ± 0.29c
Adult longevity						
Female	17	35.35 ± 2.30a	24	43.36 ± 2.86b	35	57.63 ± 1.99c
Male	26	34.89 ± 0.58a	26	40.92 ± 1.17b	25	54.96 ± 0.61c

Standard errors were estimated using 100,000 bootstrap resampling. Data followed by different lower-case letter within the row were significantly different based on a paired bootstrap test at 5% level of significance.

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Abhiskar. The proportion of female adults were significantly highest on Jaipur Long (N_f /N = 35%) followed by Debsundari (N_f /N = 24%) and the lowest on Abhiskar (N_f /N = 15%).

Different morphological features of *A. lewisii* fed on three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) are shown in table 2. The length and breadth of eggs, and first two instars of *A. lewisii* were the highest on Jaipur Long and the shortest on Abhiskar. The length and breadth of eggs were 1.23 and 1.45 times greater, respectively, on Jaipur Long than Abhiskar. The length of third instar was the shortest on Abhiskar than the other two cultivars, but the breadth was the highest on Jaipur Long followed by Debsundari and the shortest on Abhiskar. The length and breadth of fourth instar were the highest on Jaipur Long, intermediate on Debsundari and the shortest on Abhiskar. The length of first, second, third, and fourth instars were 1.07, 1.11, 1.08, and 1.05 times longer, respectively, on Jaipur Long compared to Abhiskar; whereas the breadth of first, second, third, and fourth instars were 1.26, 1.18, 1.19, and 1.23 times greater on Jaipur Long compared to Abhiskar. The data on head capsule width from first to fourth instars of *A. lewisii* fed on three *L. acutangula* cultivars (Abhiskar, Debsundari, and Jaipur Long) are presented in Supplementary table 1. The head capsule width of first, second, third, and fourth instars were 1.19, 1.10, 1.09, and 1.09 times greater, respectively, on Jaipur Long compared to Abhiskar. The length and breadth of pupa, and newly emerged adults (male and female) were the longest on Jaipur Long followed by Debsundari and the shortest on Abhiskar (table 2). The length and breadth of pupa were 1.07 and 1.12 times greater, respectively, on Jaipur Long than Abhiskar. The length and breadth of newly emerged female were 1.19 and 1.18 times greater, respectively, on Jaipur Long compared to Abhiskar; whereas the length and breadth of newly emerged male were 1.19 and 1.27 times greater, respectively, on Jaipur Long compared to Abhiskar. Newly emerged females were longer than males when *A. lewisii* were fed on three *L. acutangula* cultivars. Average fresh weight of newly emerged adults were the highest on Jaipur Long (16.16 ± 0.28 mg adult^{-1}) followed by Debsundari (14.25 ± 0.27 mg adult^{-1}) and the lowest on Abhiskar (12.29 ± 0.25 mg adult^{-1}) ($F_{2,27}$ = 52.179, P < 0.0001).

Three *L. acutangula* cultivars significantly influenced APOP, TPOP, oviposition days and fecundity of adult *A. lewisii* (table 3). The APOP and TPOP were the highest on Abhiskar followed by Debsundari and the lowest on Jaipur Long. The oviposition days were the longest on Jaipur Long, intermediate on Debsundari and the shortest on Abhiskar. The highest fecundity was recorded for females fed on Jaipur Long followed by Debsundari and the lowest on Abhiskar.

Figure 1 displays age-stage specific survival rates (s_{xj}), which shows the rate of individuals surviving to age x and stage j. The s_{xj} curves varied prominently on three *L. acutangula* cultivars and overlaps were observed in the s_{xj} curves, which revealed the variable development rates among individuals. The female curves emerged at age 37, 33, and 27 days on Abhiskar, Debsundari, and Jaipur Long, respectively; whereas male curves emerged at age 36, 33, and 27 days on Abhiskar, Debsundari, and Jaipur Long, respectively (fig. 1a, b and c), suggesting development of *A. lewisii* was delayed on Abhiskar.

The curves of age-stage specific fecundity (f_{xj}) demonstrated variation in the egg laying performance of *A. lewisii* on three *L. acutangula* cultivars (fig. 2). The f_{xj} and age-specific fecundity (m_x) on Abhiskar, Debsundari, and Jaipur Long started at 46, 38, and 32 days, respectively (fig. 2a, b and c). The females started

Table 2. Morphological features of *Aulacophora lewisii* (n = 10, mean (mm) ± SE) fed on three *Luffa acutangula* cultivars under laboratory conditions (27 ± 1°C, 65 ± 5% r.h. and 12L:12D)

	Length					Breadth				
	Abhiskar	Debsundari	Jaipur Long	$F_{2,27}$	P value	Abhiskar	Debsundari	Jaipur Long	$F_{2,27}$	P value
Egg	0.31 ± 0.01a	0.34 ± 0.005b	0.38 ± 0.01c	19.223	0.0001	0.20 ± 0.01a	0.25 ± 0.01b	0.29 ± 0.01c	23.230	0.0001
First instar	2.26 ± 0.02a	2.36 ± 0.01b	2.41 ± 0.01 b	20.877	0.0001	0.35 ± 0.01a	0.40 ± 0.01b	0.44 ± 0.01b	15.893	0.0001
Second instar	3.25 ± 0.07a	3.46 ± 0.03b	3.62 ± 0.02c	19.126	0.0001	0.50 ± 0.01a	0.55 ± 0.01b	0.59 ± 0.01c	16.383	0.0001
Third instar	4.13 ± 0.07a	4.35 ± 0.02b	4.46 ± 0.02b	16.038	0.0001	0.64 ± 0.01a	0.70 ± 0.01b	0.76 ± 0.01c	23.718	0.0001
Fourth instar	9.00 ± 0.05a	9.28 ± 0.02b	9.46 ± 0.02c	42.994	0.0001	1.38 ± 0.03a	1.53 ± 0.02b	1.70 ± 0.04c	30.680	0.0001
Pupa	5.04 ± 0.04a	5.23 ± 0.02b	5.41 ± 0.02c	43.895	0.0001	2.32 ± 0.03a	2.43 ± 0.01b	2.59 ± 0.03c	40.885	0.0001
Female[a]	6.02 ± 0.11a	6.50 ± 0.16b	7.15 ± 0.11c	19.158	0.0001	3.59 ± 0.02a	3.93 ± 0.03b	4.25 ± 0.04c	95.086	0.0001
Male[a]	5.02 ± 0.12a	5.59 ± 0.14b	5.96 ± 0.03c	20.204	0.0001	2.62 ± 0.04a	3.03 ± 0.04b	3.32 ± 0.04c	79.253	0.0001

Means followed by different letters for length or breadth of *A. lewisii* within the rows are significantly different by Tukey's test at 5% level of significance.
[a]Newly emerged.

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Table 3. Fecundity parameters (Mean ± SE) of *Aulacophora lewisii* emerging from larvae reared on three *Luffa acutangula* cultivars

Parameters	*n*	Abhiskar	*n*	Debsundari	*n*	Jaipur Long
APOP (day)	17	10.60 ± 0.31a	24	9.19 ± 0.32b	35	8.17 ± 0.25c
TPOP (day)	17	51.60 ± 0.73a	24	46.14 ± 0.52b	35	40.06 ± 0.49c
Oviposition period (day)	17	23.07 ± 0.70a	24	27.91 ± 1.84b	35	32.69 ± 1.32c
Proportion of female adults (N_f /N) (%)	100	15 ± 0.36a	100	24 ± 0.43b	100	35 ± 0.48c
Fecundity (eggs)	17	137.18 ± 14.06a	24	195.62 ± 19.00b	35	279.91 ± 12.42b

Standard errors were estimated using 100,000 bootstrap resampling. A paired bootstrap test was used to detect differences between treatments. The sample size (n) is the number of individuals included in the calculation of the respective statistics.

to oviposit on 46 days and continued up to 81 days on Abhiskar, while females started to oviposit on 38 days and ended at 89 days on Debsundari but females began to oviposit on 32 days and ended on 87 days on Jaipur Long. The highest f_{xj} and m_x peaks of *A. lewisii* on Abhiskar were 66, 59, and 44 days on Abhiskar, Debsundari, and Jaipur Long, respectively (fig. 2a, b and c). We recorded the highest age-specific maternity (l_xm_x) on 53, 59, and 44 days on Abhiskar, Debsundari, and Jaipur Long, respectively (fig. 2a, b and c). The f_{xj}, m_x and l_xm_x were lower on Abhiskar compared to other two cultivars, suggesting that a diet of two cultivars (Debsundari and Jaipur Long) were more conducive to the development and reproduction of *A. lewisii*.

The age-stage specific life expectancy (e_{xj}) is the probability that an individual of age x and stage j is expected to live. The value of e_{xj} showed a downward trend on three *L. acutangula* cultivars, with maximum average longevity values at age zero (e_{01}) were 43.98, 45.35, and 57.16 days on Abhiskar, Debsundari, and Jaipur Long, respectively (fig. 3). The maximum life expectancies of female and male *A. lewisii* on Abhiskar were 83 and 86 days, respectively (fig. 3a). The maximum life expectancies of female and male on Debsundari were 93 and 85 days, respectively (fig. 3b), while the maximum life expectancies of female and male were 99 and 94 days, respectively, when fed with Jaipur Long (fig. 3c). The values of e_{xj} was the lowest on Abhiskar followed by Debsundari and the highest on Jaipur Long, suggesting *A. lewisii* developed more slowly on Abhiskar.

The age-stage reproductive value (v_{xj}) represents the contribution of age x and stage j to the future population. The reproductive value of a new born individual (v_{01}), finite rate of increase, on Abhiskar, Debsundari, and Jaipur Long were 1.052, 1.067, and 1.091 day^{-1}, respectively (Supplementary fig. 1a, b, and c), which are close to λ. Females began to emerge at age 37, 33, and 27 days on Abhiskar, Debsundari, and Jaipur Long, respectively, and subsequently, reached its peak values to 85.07, 91.58, and 97.47 day^{-1} at 52, 54, and 44 days on Abhiskar, Debsundari, and Jaipur Long, respectively, indicating Abhiskar is less suitable cultivar for reproduction of *A. lewisii*. The reproductive values were zero at age 82, 90, and 89 days on Abhiskar, Debsundari, and Jaipur Long, respectively, as the aged adults did not produce eggs.

The population growth parameters of *A. lewisii* reared on three *L. acutangula* cultivars are shown in table 4. The insect population reared on Jaipur Long had the highest net reproductive rate (R_0 value) and those reared on Abhiskar had the lowest R_0 value (table 4). The value of intrinsic rate of increase (r) was the highest when *A. lewisii* was reared on Jaipur Long followed by Debsundari. The lowest r resulted from rearing the *A. lewisii* on Abhiskar (table 4). The variations in finite rate of increase (λ) were similar to the intrinsic rate of increase. The mean generation time (T) was also different among the tested three *L. acutangula* cultivars with the cultivar Jaipur Long promoting the fastest generation times followed by Debsundari and the longest generation times on Abhiskar. The value of gross reproductive rate (*GRR*) was the highest on Jaipur Long followed by Debsundari and the shortest on Abhiskar (table 4).

Population projection

The stage structures of *A. lewisii* are projected with an initial population of 10 eggs using the TIMING-MSChart program (Supplementary fig. 2). After 120 days of simulation, the population growth was the highest on Jaipur Long followed by Debsundari and the slowest on Abhiskar. There are 36,641 preadults and 2245 adults (1287 females and 958 males) on Jaipur Long, while the numbers of preadults on Debsundari were 6025 and adults were 193 (88 females and 105 males). The numbers of preadults on Abhiskar were 1646 and adults were 95 (36 females and 59 males).

Enzymatic activity of larvae

Amylolytic activity in the fourth instars of *A. lewisii* was the highest in larvae when fed on Jaipur Long (0.45 ± 0.01 mg maltose min^{-1}) followed by Debsundari (0.32 ± 0.01 mg maltose min^{-1}) and the lowest on Abhiskar (0.22 ± 0.01 mg maltose min^{-1}) ($F_{2,12}$ = 87.540, P < 0.0001) (fig. 4). Proteolytic activity in the fourth instars of *A. lewisii* was the highest in larvae fed with Jaipur Long (0.91 ± 0.04 mU min^{-1}) followed by Debsundari (0.74 ± 0.03 mU min^{-1}) and the lowest on Abhiskar (0.50 ± 0.02 mU min^{-1}) ($F_{2,12}$ = 52.059, P < 0.0001) (fig. 5). Lipolytic activity in the fourth instars of *A. lewisii* was the highest in larvae fed with Jaipur Long (0.0413 ± 0.001 mU min^{-1}) followed by Debsundari (0.0324 ± 0.001 mU min^{-1}) and the lowest on Abhiskar (0.0257 ± 0.001 mU min^{-1}) ($F_{2,12}$ = 34.362, P < 0.0001) (fig. 6).

Enzymatic activity of adults

The amylolytic activity of *A. lewisii* adults was recorded greatest when fed on Jaipur Long (0.80 ± 0.03 mg maltose min^{-1}) followed by Debsundari (0.66 ± 0.02 mg maltose min^{-1}), while the lowest enzymatic activity was observed when the adults were fed on Abhiskar (0.53 ± 0.04 mg maltose min^{-1}) ($F_{2,12}$ = 19.292, P < 0.0001) (fig. 4). The highest proteolytic activity was observed in homogenates of *A. lewisii* adults when fed with Jaipur Long (1.31 ± 0.12 mU min^{-1}) followed by Debsundari (0.84 ± 0.03 mU min^{-1}), while the lowest value of proteolytic activity was

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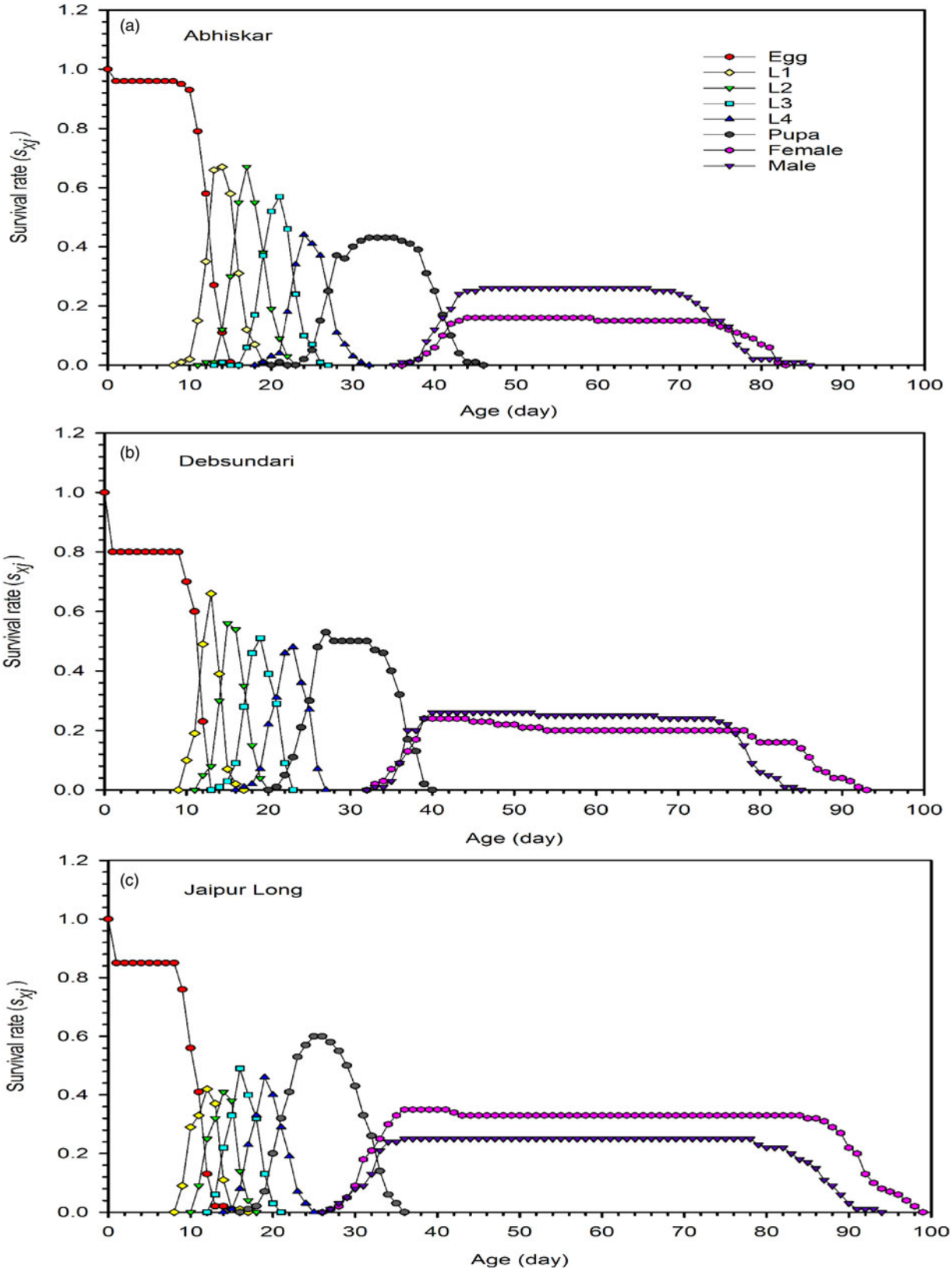

Figure 1. Age-stage specific survival value (s_{xj}) of *Aulacophora lewisii* fed on three *Luffa acutangula* cultivars.

recorded on Abhiskar (0.59 ± 0.02 mU min^{-1}) ($F_{2,12} = 26.031$, $P < 0.0001$) (fig. 5). Adults fed on Jaipur Long (0.200 ± 0.008 mU min^{-1}) showed the highest lipolytic activity followed by Debsundari (0.138 ± 0.007 mU min^{-1}) and the lowest on Abhiskar (0.087 ± 0.007 mU min^{-1}) ($F_{2,12} = 58.551$, $P < 0.0001$) (fig. 6).

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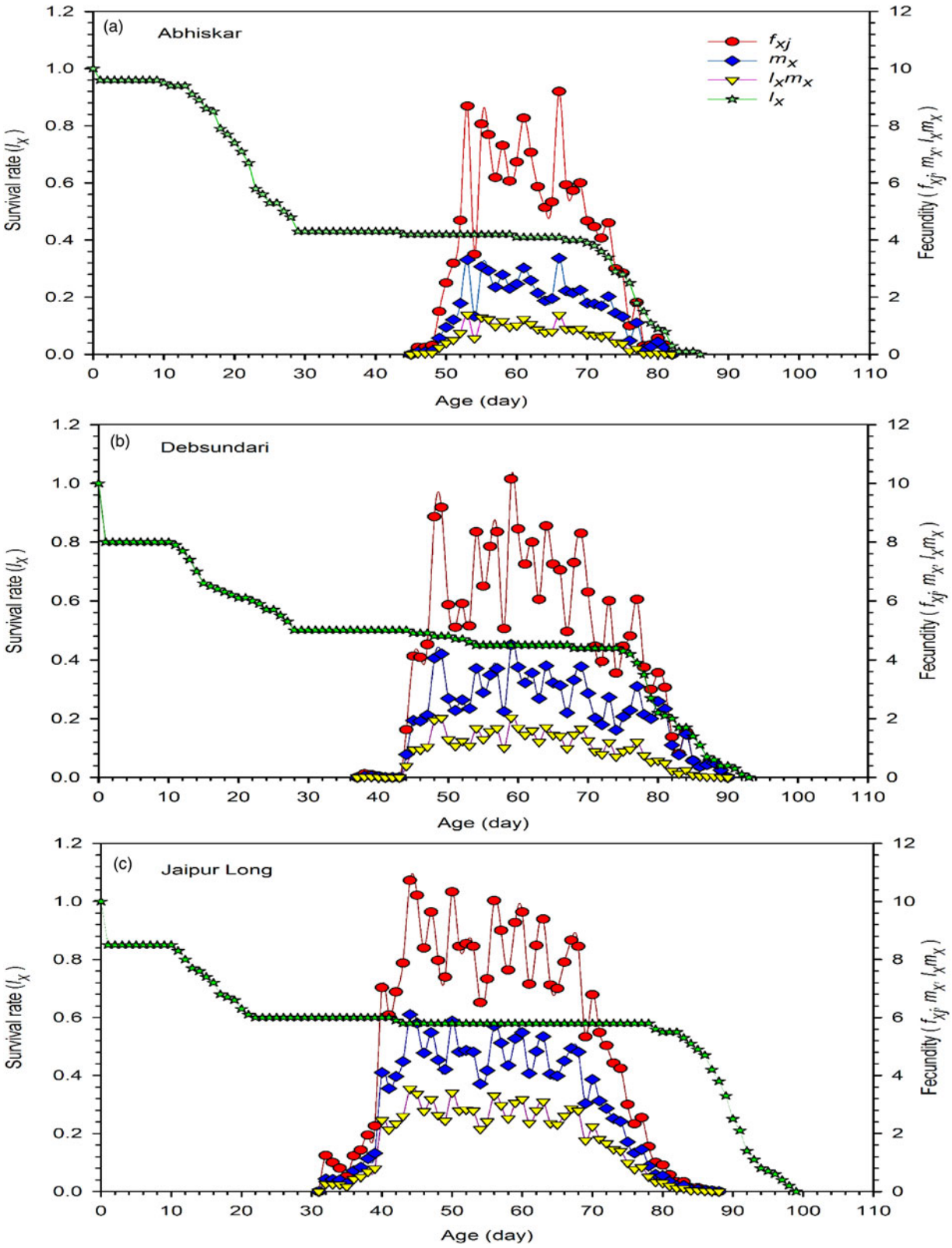

Figure 2. Age-specific survival rate (l_x), age-stage specific fecundity (f_{xj}), age-specific fecundity (m_x) and age-stage specific maternity ($l_x m_x$) of *Aulacophora lewisii* fed on three *Luffa acutangula* cultivars.

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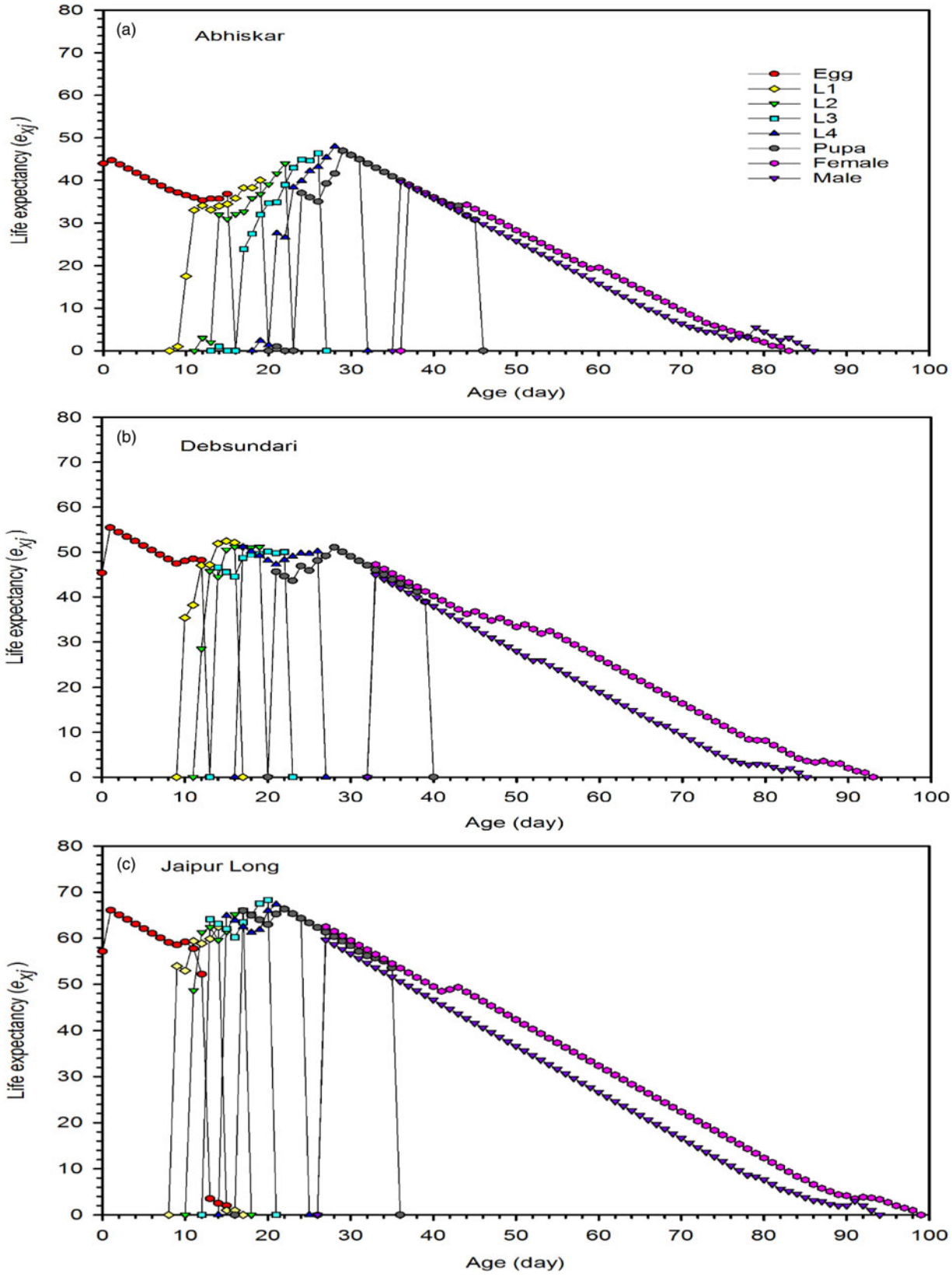

Figure 3. Age-stage specific life expectancy (e_{xj}) of *Aulacophora lewisii* fed on three *Luffa acutangula* cultivars.

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Table 4. Mean (± SE) of intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0: offspring/individual), mean generation time (T) and gross reproductive rate (*GRR*, number of offsprings) of *Aulacophora lewisii* reared on three *Luffa acutangula* cultivars

Parameters	*n*	Abhiskar	*n*	Debsundari	*n*	Jaipur Long
r (day^{-1})	15	0.0511 ± 0.0043a	22	0.0648 ± 0.0037b	35	0.0872 ± 0.0032c
λ (day^{-1})	15	1.0525 ± 0.0045a	22	1.0670 ± 0.0039b	35	1.0911 ± 0.0035c
R_0	15	23.32 ± 5.67a	22	46.95 ± 9.48b	35	97.97 ± 14.05c
T (day)	15	61.58 ± 0.57a	22	59.39 ± 0.54b	35	52.59 ± 0.67c
GRR	15	59.78 ± 12.29a	22	111.30 ± 17.40b	35	168.52 ± 19.54c

Standard errors were estimated using 100,000 bootstrap resampling. A paired bootstrap test was used to detect differences between treatments. The sample size (n) is the number of couples included in the calculation of the respective statistics.

Biochemical properties of roots and leaves

Total carbohydrates, proteins, lipids and amino acids were the highest in the roots and leaves of Jaipur Long, intermediate in Debsundari and the lowest in Abhiskar (table 5). The nitrogen content was the highest in the roots and leaves of Jaipur Long, and the lowest in Abhiskar (table 5). Total phenols, flavonols, and tannins were the highest in the roots and leaves of Abhiskar, intermediate in Debsundari and the lowest in Jaipur Long (table 5). The highest and lowest water content was recorded in the roots and leaves of Jaipur Long and Abhiskar, respectively (table 5).

Correlation analysis

Duration of immature stages of *A. lewisii* fed with the roots of three *L. acutangula* cultivars displayed negative correlations with nutrients (total carbohydrates, proteins, lipids, amino acids, and nitrogen) and moisture content, while positive correlations were observed with antinutrinets (total phenols, flavonols, and tannins) (Supplementary table 2). Longevity of males and females including fecundity showed positive correlations with nutrients (total carbohydrates, proteins, lipids, nitrogen, and amino acids) as well as moisture content, while negative correlations were observed with antinutrients (total phenols, flavonols, and tannins) (table 6). Positive correlations were observed for *GRR*, r, λ, and R_0 with nutrients (total carbohydrates, proteins, lipids, nitrogen, and amino acids) and moisture content, while negative correlations were observed with antinutrients (total phenols, flavonols, and tannins) (table 6). The T was negatively and positively correlated with nutrients (total carbohydrates, proteins, lipids, nitrogen, and amino acids) and antinutrients (total phenols, flavonols, and tannins), respectively (table 6). Proteolytic, amylolytic, and lypolytic activities of adults or larvae were positively correlated with nutrients (total carbohydrates, proteins, lipids, nitrogen, and amino acids) and moisture content, while negative correlations were observed with antinutrients (total phenols, flavonols, and tannins) (table 6, Supplementary table 2).

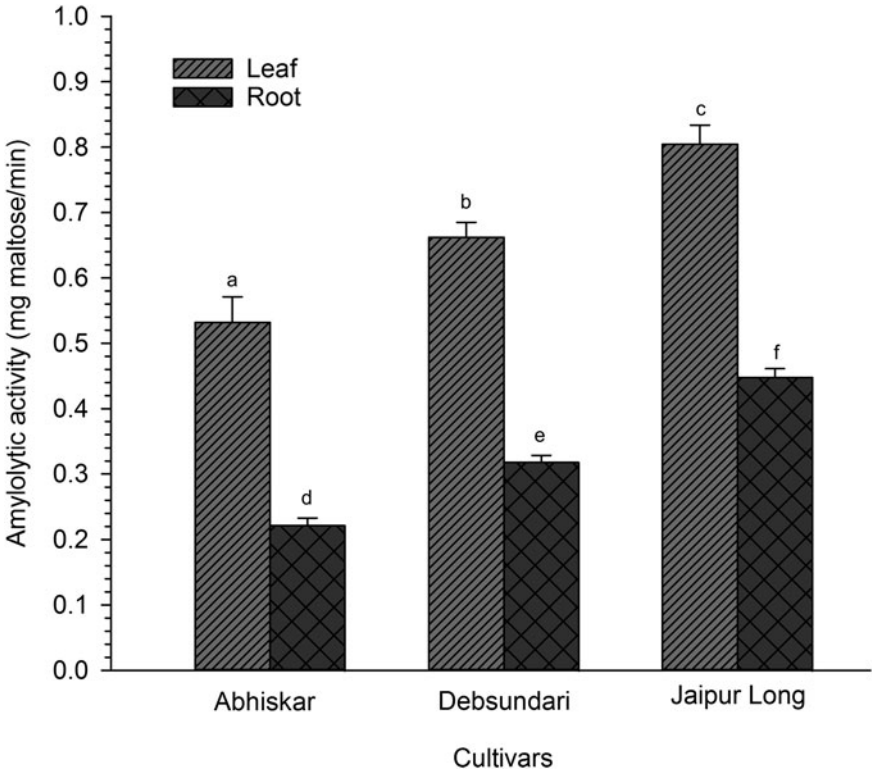

Figure 4. Amylolytic activity of fourth instars and adults of *Aulacophora lewisii* ($n = 5$) fed on roots and leaves of three *Luffa acutangula* cultivars, respectively. Means followed by different letters for amylolytic activities of either larvae or adults are significantly different by Tukey's test at 5% level of significance.

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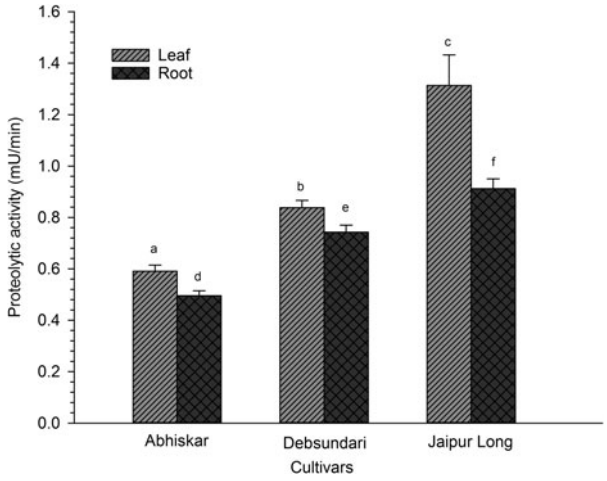

Figure 5. Proteolytic activity of fourth instars and adults of *Aulacophora lewisii* ($n = 5$) fed on roots and leaves of three *Luffa acutangula* cultivars, respectively. Means followed by different letters for proteolytic activities of either larvae or adults are significantly different by Tukey's test at 5% level of significance.

Discussion

Age-stage, two-sex life table is a helpful tool to measure the effect of external factors such as effect of different host plants including various cultivars of a host plant on the growth and development including reproduction of an insect population (Debnath *et al.*, 2020; Mobarak *et al.*, 2020). It presents an amalgamated and extensive depiction of an insect population's development, survival and reproduction, thus we may get an accurate estimation of the growth rate of an insect pest population. It is well established that the performance of an insect pest is influenced by host plants, be it different cultivars of the same plant and can enlighten the development of eco-friendly pest management strategies. The quality of host plants serves an important role in the growth, development and reproduction of an insect, which reflects the appropriateness of a particular host plant for the sustenance of an insect's life cycle. To date, no reports are in record on *A. lewisii*

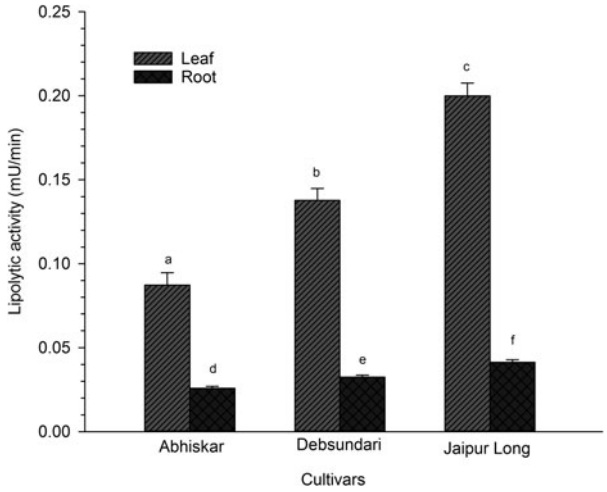

Figure 6. Lipolytic activity of fourth instars and adults of *Aulacophora lewisii* ($n = 5$) fed on roots and leaves of three *Luffa acutangula* cultivars, respectively. Means followed by different letters for lipolytic activity of either larvae or adults are significantly different by Tukey's test at 5% level of significance.

Table 5. Biochemical analyses (Mean ± SE) of the roots and leaves of three *Luffa acutangula* cultivars

Parameters	Abhiskar		Debsundari		Jaipur Long		$F_{5,24}$	*P* value
	Roots	Leaves	Roots	Leaves	Roots	Leaves		
Carbohydrate (mg g^{-1} DW[a])	9.28 ± 1.10a	8.78 ± 0.86a	16.57 ± 1.59bd	13.54 ± 1.14b	24.84 ± 1.75c	17.09 ± 0.70d	22.807	0.0001
Protein (mg g^{-1} DW)	43.14 ± 2.06a	23.19 ± 1.85b	54.66 ± 2.64c	32.47 ± 2.03d	65.19 ± 2.93e	40.76 ± 1.89a	44.098	0.0001
Lipid (mg g^{-1} DW)	35.39 ± 1.61a	33.06 ± 1.87a	45.65 ± 2.03b	42.36 ± 1.90b	56.89 ± 2.63c	51.19 ± 1.47c	21.841	0.0001
Amino acid (mg g^{-1} DW)	1.93 ± 0.13ac	1.30 ± 0.14a	2.89 ± 0.19b	2.05 ± 0.18c	3.66 ± 0.19d	2.75 ± 0.13b	26.492	0.0001
Nitrogen (% DW)	4.02 ± 0.21ac	3.04 ± 0.18b	4.72 ± 0.22c	3.74 ± 0.18ae	5.51 ± 0.28d	4.54 ± 0.20ce	15.856	0.0001
Phenol (mg g^{-1} DW)	1.94 ± 0.18ac	2.77 ± 0.14b	1.34 ± 0.14c	2.14 ± 0.11a	0.73 ± 0.07d	1.51 ± 0.13c	27.936	0.0001
Flavonol (mg g^{-1} DW)	0.10 ± 0.01a	0.69 ± 0.03b	0.07 ± 0.01a	0.31 ± 0.03c	0.03 ± 0.001d	0.14 ± 0.01a	184.962	0.0001
Tanin (mg g^{-1} DW)	1.25 ± 0.08a	3.01 ± 0.17b	0.74 ± 0.07c	2.40 ± 0.13d	0.41 ± 0.03e	1.69 ± 0.12f	81.935	0.0001
Moisture content (%FW[b])	84.75 ± 0.31a	83.65 ± 0.35a	86.57 ± 0.32b	84.76 ± 0.45a	89.07 ± 0.49c	86.27 ± 0.47b	22.126	0.0001

Means followed by different letters within the rows are significantly different by Tukey's test at 5% level of significance.
[a]DW, Dry weight.
[b]FW, Fresh weight.

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Table 6. Correlation coefficients (r) of the life table parameters of adults of *Aulacophora lewisii* reared on the leaves of three *Luffa acutangula* cultivars with the nutrients, moisture content and antinutrients

Parameters	Carbohydrate		Protein		Lipid		Amino acid		Nitrogen		Phenol		Flavonol		Tannin		Moisture	
	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}	r	P_{value}
Male longevity	0.840	0.0001	0.833	0.0001	0.859	0.0001	0.868	0.0001	0.822	0.0001	−0.851	0.0001	−0.852	0.0001	−0.871	0.0001	0.741	0.002
Female longevity	0.851	0.0001	0.870	0.0001	0.879	0.0001	0.867	0.0001	0.833	0.0001	−0.889	0.0001	−0.908	0.0001	−0.888	0.0001	0.769	0.001
Fecundity	0.878	0.0001	0.878	0.0001	0.886	0.0001	0.850	0.0001	0.846	0.0001	−0.923	0.0001	−0.932	0.0001	−0.877	0.0001	0.750	0.001
GRR	0.882	0.0001	0.868	0.0001	0.902	0.0001	0.863	0.0001	0.847	0.0001	−0.899	0.0001	−0.913	0.0001	−0.851	0.0001	0.735	0.002
r	0.826	0.0001	0.766	0.001	0.849	0.0001	0.806	0.0001	0.830	0.0001	−0.880	0.0001	−0.865	0.0001	−0.806	0.0001	0.691	0.004
λ	0.769	0.001	0.768	0.001	0.864	0.0001	0.817	0.0001	0.826	0.0001	−0.867	0.0001	−0.913	0.0001	−0.785	0.001	0.713	0.003
R_0	0.814	0.0001	0.826	0.0001	0.866	0.0001	0.834	0.0001	0.840	0.0001	−0.893	0.0001	−0.870	0.0001	−0.825	0.0001	0.697	0.004
T	−0.812	0.0001	−0.824	0.0001	−0.825	0.0001	−0.856	0.0001	−0.831	0.0001	0.832	0.0001	0.823	0.0001	0.866	0.0001	−0.764	0.001
Amylolytic activity	0.781	0.0010	0.796	0.0001	0.806	0.0001	0.802	0.0001	0.738	0.002	−0.742	0.002	−0.819	0.0001	−0.799	0.0001	0.640	0.010
Proteolytic activity	0.745	0.001	0.806	0.0001	0.743	0.002	0.859	0.0001	0.732	0.002	−0.694	0.004	−0.816	0.0001	−0.905	0.0001	0.740	0.002
Lipolytic activity	0.837	0.0001	0.788	0.0001	0.929	0.0001	0.852	0.0001	0.771	0.001	−0.846	0.0001	−0.887	0.0001	−0.788	0.0001	0.854	0.0001

using age-stage, two-sex life table, and further, the biology of *A. lewisii* on *L. acutangula* is reported for the first time. In the current study, the longest preadult duration (egg to adult emergence) was recorded on Abhiskar (40.91 days) followed by Debsundari (36.94 days) and the shortest on Jaipur Long (31.80 days), while females of *A. lewisii* adults lived the longest on Jaipur Long (57.63 days) followed by Debsundari (43.36 days) and the shortest on Abhiskar (35.35 days). These observations suggest that the variation in the nutritional quality of the roots and leaves of three *L. acutangula* cultivars influenced the development of larvae and adults of *A. lewisii*, respectively. Moreover, this study suggests that roots and leaves of Abhiskar is of poor nutritional quality for the development of *A. lewisii* than the other two cultivars because larval development was longer and longevity of adults was shorter on Abhiskar.

In this study, the fecundity of *A. lewisii* was the highest on Jaipur Long (279.91 eggs), intermediate on Debsundari (195.62 eggs) and the lowest on Abhiskar (137.18 eggs), suggesting variations in fecundity among different cultivars of a host plant are due to differences in quality and quantity of food consumed by the larvae and adults of *A. lewisii* (Awmack and Leather, 2002). We observed a negative correlation between the fecundity of *A. lewisii* and antinutrients of three *L. acutangula* cultivars, suggesting antinutrients (total phenols, flavonols and tannins) of roots and leaves played an inhibitory role which influenced the negative impact of egg laying performance of *A. lewisii*. Similarly, a negative correlation was observed between fecundity of *Galerucella placida* Baly (Coleoptera: Chrysomelidae) and antinutrients of leaves of *Rumex dentatus* L. and *Polygonum glabrum* Willd. (Koner *et al.*, 2019). The lowest fecundity of *A. lewisii* on Abhiskar suggested that higher amounts of antinutrients in Abhiskar than the other two *L. acutangula* cultivars results the lower egg laying performance of *A. lewisii* on Abhiskar.

The intrinsic rate of increase (r) is the most important population growth parameter, which can be used to evaluate plant resistance to insect pests (Carey, 1993). In this investigation, the highest r of *A. lewisii* was observed on Jaipur Long, which is due to quicker larval developmental time, and high immature survival and fecundity as compared with other two *L. acutangula* cultivars. At the same time, lower r, R_0, and λ, and higher T values on Abhiskar can be attributed to the longer development time, poorer immature survival and lower fecundity of *A. lewisii* on this cultivar (Debnath *et al.*, 2020; Mobarak *et al.*, 2020; Mitra *et al.*, 2021). According to the correlation analysis, there were a negative correlation between total phenols, flavonols, and tannins of tested *L. acutangula* cultivars and r, R_0, λ values of *A. lewisii* that supported the role of the root and leaf antinutrients as inhibiting factor for increase of the insect population. Phenols serve as defensive agents against feeding by herbivores, while tannins reduce the digestibility of substances (Harborne, 2003) and flavonols help to protect plants from insect attack by influencing their behaviour, and growth and development (Treutter, 2006; War *et al.*, 2012). Here, phenols, flavonols, and tannins were higher in Abhiskar than other two *L. acutangula* cultivars, suggesting higher amounts of these antinutrients resulted longer development time, lower immature survival and lower fecundity of *A. lewisii* which caused lower increase of the insect population on Abhiskar. The *GRR* indicates rapid increase in the insect population, which depends on the fecundity and adult emergence percentage (Mobarak *et al.*, 2022). Here, *GRR* showed positive correlations with the nutrients and negative correlations with antinutrients, suggesting *GRR* is dependent on nutrients and

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antinutrients of the food source. The present study achieved the lowest *GRR* when *A. lewisii* were fed on Abhiskar than other cultivars, implicating lower nutrients and higher antinutrients in Abhiskar resulted the lowest *GRR* on Abhiskar. This study revealed that *T* of *A. lewisii* fed with three *L. acutangula* cultivars were positively correlated with the antinutrients of roots and leaves (total phenols, flavonols, and tannins), suggesting the antinutrients of roots and leaves influenced prolonged generation time of *A. lewisii* (Koner *et al.*, 2019). In the current investigation, *T* was the highest on Abhiskar than other *L. acutangula* cultivars, suggesting lower nutrients and higher antinutrients in Abhiskar influenced higher generation time (Mitra *et al.*, 2021). The above results suggested that Abhiskar is the least suitable cultivar for the development and reproduction of *A. lewisii* due to lower amount of nutrients and higher amount of antinutrients.

Plant-insect interactions are the consequential of quality and quantity of nutrients and antinutrients which are consumed by the insect herbivore (Cates, 1980). Primary metabolites (carbohydrates, proteins, and lipids) of the host plant influence survival and development of an insect herbivore (Harborne, 2003). In the current research, total carbohydrates, proteins, lipids, amino acids and nitrogen content showed a significant negative correlation with larval development period, suggesting higher amounts of these compounds cause better survival and development of *A. lewisii* resulting increased susceptibility to host plant. Here, the biochemical properties of leaves of three *L. acutangula* cultivars demonstrated that Abhiskar is of poor nutritional quality than Jaipur Long and Debsundari because nutrients such as total carbohydrates, proteins, lipids, amino acids, and nitrogen content were the lowest in Abhiskar than the other two cultivars, suggesting survival, growth, and development of *A. lewisii* will be lower on Abhiskar. The suboptimal ratio between carbohydrates and proteins reduces the insect growth and development (Simpson and Raubenheimer, 2009; Roeder and Behmer, 2014). This could be another explanation for lower growth and development of *A. lewisii* feeding on Abhiskar than Jaipur Long and Debsundari. Low water content in the leaves of host plants reduces survivability of insect herbivores. The lowest water content in the roots and leaves of Abhiskar than Jaipur Long and Debsundari could be another explanation for lower survivability of *A. lewisii* on Abhiskar (Mattson and Scriber, 1987; Roy and Barik, 2012, 2013; Mobarak *et al.*, 2020).

Insects exploit optimal levels of carbohydrates, proteins, and lipids in their diets for their efficient growth, development, survival, and reproduction (Awmack and Leather, 2002). These primary metabolites should be properly digested by the appropriate enzymes for ingestion and assimilation into body tissues (Awmack and Leather, 2002). α-Amylase is the major hydrolysing enzyme of carbohydrates while proteases breaks down proteins into amino acids in addition inactivation of toxic proteins ingested during feeding. Lipases hydrolase intracellular triglyceride into diacylglyceride as digested component or energy demands (Terra and Ferreira, 2005). Therefore, host plant cultivars in terms of nutritional quality play an important role in the growth, reproductive performance and population dynamics of an insect herbivore (Awmack and Leather, 2002; Malik *et al.*, 2018; Mason *et al.*, 2022). The midgut amylolytic, proteolytic, and lipolytic activities of larvae and adults of *A. lewisii* fed with three *L. acutangula* cultivars were positively correlated with nutrients, suggesting the nutritional quality of roots and leaves played an important role in the synthesis and secretion of enzymes as well as digestion of consumed foods by the larvae and adults of *A. lewsii*. The amylolytic, proteolytic, and lipolytic activities of the larvae and adults of *A. lewisii* were the highest on Jaipur Long and the lowest on Abhiskar, implicating larvae and adults of *A. lewisii* had a high ability to utilise the roots and leaves of Jaipur Long, respectively, than the roots and leaves of Abhiskar. This observation suggested that digestive performance of insects fed with Abhiskar would lead to lower survival and reduced biological fitness (Mardani-Talaee *et al.*, 2015). The poor performance of *A. lewisii* on Abhiskar is due to presence of enzyme inhibitors, which inhibits uptake of nutrients by *A. lewisii* and subsequently, growth, development and fecundity of *A. lewisii* are affected.

Based on the current findings, it can be concluded that Jaipur Long and Debsundari are susceptible cultivars than Abhiskar to *A. lewisii* based on the results of population parameters and activities of key digestive enzymes. The prolonged larval development time and lowest fecundity of *A. lewisii* resulted lower intrinsic rate of increase and net reproductive rate of *A. lewisii* on Abhiskar, suggesting the lower population growth of *A. lewisii* could result lower subsequent infestations. Therefore, the use of partially resistant Abhiskar cultivar is a way to reduce *A. lewisii* infestation. However, the understandings of differences in food quality, presence of secondary components and possible inhibitors from a wider range of *L. acutangula* cultivars are necessary to design the stable planting systems which could lead to lower infestations caused by *A. lewisii* on *L. acutangula*.

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Author's contributions. A. B. designed experiments. S. D. and S. K. performed experiments. S. D. and R. D. analysed data. S. D. made the Figs. A. B. wrote the manuscript. All authors edited the manuscript and approved the final version of the manuscript.

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