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Biology and life history of *Lema praeusta* (Fab.) (Coleoptera: Chrysomelidae), a biocontrol agent of two Commelinaceae weeds, *Commelina benghalensis* and *Murdannia nudiflora*

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Abstract

We examined previous reports of *Lema praeusta* (Fab.) (Coleoptera: Chrysomelidae) as a minor pest of turmeric, eggplant, bottle gourd and pumpkin leaves, but no feeding damage by larvae and adults of *L. praeusta* were recorded by us on these leaves. We observed feeding by the larvae and adults of *L. praeusta* on ten species of Commelinaceae plants in no-choice tests. The biology, fecundity and life table parameters of *L. praeusta* on two Commelinaceae weeds, *Commelina benghalensis* L. and *Murdannia nudiflora* (L.) Brenan were determined under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D). Total larval development times of *L. praeusta* were 6.36 ± 0.07 and 7.28 ± 0.11 days (mean ± SE) on *C. benghalensis* and *M. nudiflora*, respectively. Adult females lived 106.25 ± 1.17 and 77.65 ± 0.91 days (mean ± SE) on *C. benghalensis* and *M. nudiflora*, respectively. Each female laid 272.95 ± 2.39 and 224 ± 1.74 eggs (mean ± SE) during a lifetime on *C. benghalensis* and *M. nudiflora*, respectively. The net reproductive rate (R_o), intrinsic rate of increase (r_m), generation time (T_c), doubling time (*DT*) and finite rate of increase (λ) were 136.48, 0.14, 36.17, 5.10 and 1.41 on *C. benghalensis*, respectively, whereas R_o, r_m, T_c, *DT* and λ were 112, 0.20, 23.64, 3.47 and 1.51 on *M. nudiflora*, respectively, suggesting that *L. praeusta* could be a potential biocontrol agent against *C. benghalensis* and *M. nudiflora* in the fields of rice, maize, sorghum, soybean, mung bean, peanut and cotton.

Keywords: biological control, Commelinaceae, weed, Coleoptera, Chrysomelidae, fecundity and life table

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Introduction

Commelina benghalensis L. (Commelinaceae), a perennial herb, is a weed of 25 crops in 28 countries (Wilson, 1981; Caton *et al*., 2010). It was first reported from the USA during 1928 and was recognized as a noxious weed in 1983 (Faden, 1993; Webster *et al*., 2006). It has become a major weed in the southeastern coastal plain of the USA in various crops such as cotton (*Gossypium* sp.) and peanut (*Arachis hypogaea* L.) (Webster *et al*., 2006). It is listed as a Federal Noxious weed in Florida and Georgia in cotton, peanut, maize (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], nursery stock and orchards (Webster *et al*., 2006). In the South Burnett region of southeastern Queensland, the weed is found extensively in cultivation and is associated with peanut, navy or dry bean (*Phaseolus vulgaris* L.), sorghum [*Sorghum bicolor* (L.) Moench] and maize (Walker & Evenson, 1985). *Commelina benghalensis* is considered as a major weed of rice, maize, sorghum, soybean, mung bean [*Vigna radiata* (L.) R. Wilczek] and peanut in Southeast Asia (Holm *et al*., 1977). It is also one of the most

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noxious weeds of rice in India (Wilson, 1981). It is currently controlled by applying herbicides such as Axiom® (flufenacet + metribuzin), Dual Magnum®Canopy SP® (metribuzin + chlorimuron) during pre-emergence, while herbicides such as Basagran®, Classic® (acetochlor) and Pursuit® (Imazethapyr) are used during post-emergence. But, it has been reported that applying herbicides with soil residual activity is crucial for the management of *C. benghalensis* (Webster *et al.*, 2006; Issac *et al.*, 2013).

Murdannia nudiflora (L.) Brenan (Commelinaceae) is also a perennial herbaceous weed in Indian rice-fields (Moody, 1989; Waterhouse, 1993). It infests 16 crops in 23 countries (Holm *et al.*, 1977), and has been reported from China, Bangladesh, Nepal, Sri Lanka, Pakistan, Thailand, Vietnam, Philippines, Japan, Africa, Central, North and South America (Holm *et al.*, 1977; Waterhouse, 1993). It has also been reported as a weed in cocoa (*Theobroma cacao* L.) and rubber (*Hevea brasiliensis* Müll. Arg.) in Malaysia, tea [*Camellia sinensis* (L.) Kuntze] in Indonesia, pineapples [*Ananas comosus* (L.) Merr.] in Guinea, Hawaii and the Philippines, sugarcane (*Saccharum* spp.) in Angola, Hawaii, Indonesia, Brazil, Philippines and Taiwan, and coffee (*Coffea arabica* L.) in Venezuela (Holm *et al.*, 1977). It has become an invasive species in the USA from Texas to North Carolina, where it is common in cotton and soybean. It is also recorded as a weed in peanut, maize, banana (*Musa* sp.), citrus [*Citrus limon* (L.) Burm. f] (Ahmed *et al.*, 2015). It is well adapted to wet-dry climates typical of tropical and subtropical Asian regions and is abundant throughout the year. Growers apply herbicides (bentazone, metribuzin, triazines and 2,4-D) to control it (Wilson, 1981).

The insect *Lema praeusta* (Fab.) (Coleoptera: Chrysomelidae) is broadly distributed in India, Sri Lanka, South China, Indochina, Indonesia (Sumatra), Hainan Island and Taiwan (Warchałowski, 2011). Sengupta & Behura (1957) recorded *L. praeusta* from Orissa, India as a minor pest on turmeric and stated that it also fed on eggplants and cucurbits, but Kalaichelvan *et al.* (2003) recorded *L. praeusta* on *Commelina* species. We observed that first and second instar *L. praeusta* larvae feed on the undersides of *C. benghalensis* and *M. nudiflora* leaves, which gives the leaves a net-like appearance. Third and fourth instar larvae completely defoliate both weeds (personal observation). Adults feed on leaves of both *C. benghalensis* and *M. nudiflora* (fig. 1). After defoliating plants, third and fourth instar larvae and adults of *L. praeusta* will also feed on stems of both weeds (personal observation).

In the current study, we offered leaves of Zingiberaceae (turmeric, cardamom, ginger and mango ginger), Solanaceae (potato and eggplant) and Cucurbitaceae (bottle gourd, ridge gourd and pumpkin) to observe feeding damage by larvae and adults of *L. praeusta*. We tested ten species of Commelinaceae plants as hosts, and also studied the biology, fecundity table and life table parameters of *L. praeusta* on *C. benghalensis* and *M. nudiflora* to understand its potential as a biological control agent against both these weeds.

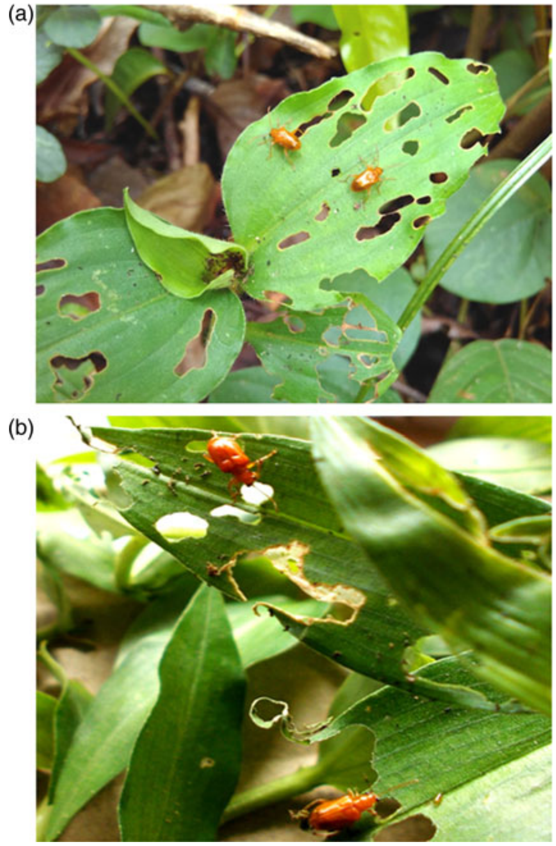

Fig. 1. Adults of *Lema praeusta* engaged in feeding on *Commelina benghalensis* (a) and *Murdannia nudiflora* (b) leaves.

Materials and methods

Plant and insect materials

All plants were sourced from the vicinity of the University of Burdwan (23°16′ N & 87°54′ E), West Bengal, India (table 1). Each uninfested plant (table 1) was 1 week old (ca. 12 cm height) and was planted separately in pots containing ~1500 cm^3 of soil. Each whole plant (ca. 12 cm height) and the pot was covered with a fine mesh nylon net cage [80 cm (height) × 60 cm (diameter)] to prevent insect attack. Plants that were 3–4 weeks old (ca. 45 cm height) were used for the host-specificity study.

Lema praeusta was identified by Dr J. Poorani, Principal Scientist, National Research Centre for Banana, Tamilnadu and confirmed by following the keys of Warchałowski (2011) and Lee & Matsumura (2013).

Two separate cultures of *L. praeusta* (one reared on *C. benghalensis* leaves and the other on *M. nudiflora*) were maintained at 27 ± 1°C, 65 ± 5% RH and 12L:12D photoperiod in a biological oxygen demand incubator (ADS instruments and Tech., Calcutta, India) for five generations. Sixth generation males and females were used to study developmental duration and construct fecundity and life table parameters.

Host-specificity studies

The host-specificity study was performed by exposing first instar larvae and adults of *L. praeusta* on plants mentioned in table 1. In no-choice and choice tests, light trap collected *L. praeusta* adults were starved for 24 h before use. Newly emerged first instar larvae were used in no-choice tests.

In no-choice tests, 20 *L. praeusta* adults were placed separately on each of five plants per plant species (table 1). Ten first instar larvae of *L. praeusta* were also placed separately on each of five plants per species (table 1). The plants were examined

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Table 1. Plants used for the host-specificity study (no-choice tests) of *Lema praeusta*.

Family	Plants	Common name
Commelinaceae	*Commelina benghalensis* L.	Tropical spiderwort
	C. obliqua Vahl	
	C. maculata Edgew.	Spotted dayflower
	Murdannia nudiflora (L.) Brenan	Doveweed
	M. vaginata (L.) G. Brückn.	
	M. spirata (L.) G. Brückn.	Asiatic dewflower
	Tradescantia zebrina (Schinz) D. R. Hunt	Wandering jew
	T. pallida (Rose) D. R. Hunt	Purple heart plant
	T. spathacea Sw.	Moses-in-the-cradle plant
	Cyanotis cristata (L.) D. Don	Crested cat ears plants
Solanaceae	*Solanum melongena* L.	Eggplant
	Solanum tuberosum L.	Potato
Cucurbitaceae	*Lagenaria sicerar*ia (Molina) Standl.	Bottle gourd
	Luffa acutangula (L.) Roxb.	Ridge gourd
	Cucurbita pepo L.	Pumpkin
Zingiberaceae	*Curcuma longa* L.	Turmeric
	Zingiber officinale Roscoe	Ginger
	Elettaria cardamomum (L.) Maton	Cardamom
	Curcuma amada Roxb.	Mango ginger
Poaceae	*Oryza sativa* L.	Rice

24 h after the experiment began, and feeding was recorded on a subjective visual scale.

In choice tests, light trap collected *L. praeusta* females engaged in copulation were used to observe egg laying preference as females begin laying eggs 24 h after they have finished mating. After mating, 20 females were placed in a net cage (1.52 m length, 1.52 m breadth and 1.22 m height) containing *C. benghalensis* and *M. nudiflora* plants in separate pots placed 0.61 m apart to record the oviposition preference of *L. praeusta*. Numbers of eggs laid by *L. praeusta* on *C. benghalensis* and *M. nudiflora* leaves were observed after 24 h of mating (each replicate contained 20 adults, $N = 5$). After each replicate, plants and insects were discarded.

Fecundity table

This experiment was conducted by taking newly emerged sixth generation virgin male and female *L. praeusta* adults that had been reared on either *C. benghalensis* or *M. nudiflora*. For egg laying, a pair of newly emerged virgin male and female were kept together in a 15 cm (length) × 8 cm (diameter) sterilized glass jar containing leaves of the same plant species on which they had been reared ($N = 20$). The petioles of fresh mature leaves were inserted into a moist piece of cotton, which was wrapped with aluminium foil to prevent moisture loss, and provided daily both for feeding and egg laying. Data were collected as pre-oviposition, oviposition and post-oviposition periods of *L. praeusta* fed on either *C. benghalensis* or *M. nudiflora* leaves. During the oviposition period, the number of eggs laid was recorded at 24 h intervals. Fecundity tables of *L. praeusta* fed on each host plant were separately constructed following Krebs (1999) and Smith & Smith (2001). The fecundity table includes x = the age categories, l_x = age-specific survivorship from the female life table, m_x = age-specific productivity and the mean number of female young produced by each female of age $x = l_x m_x$, which is m_x weighted by survivorship. Further, xl_xm_x was obtained by multiplying the l_xm_x by the appropriate age. The eggs laid by *L. praeusta* of a particular age class and the survivorship of females in that age class were used to calculate the net reproductive rate ($R_o = \Sigma\ l_xm_x$), mean generation time ($T_c = \Sigma\ xl_xm_x/R_o$), intrinsic rate of increase ($r_m = \log_e R_o/T_c$), finite rate of increase ($\lambda = e^r$ by using Euler r), and doubling time ($D.T. = \log_e 2/r_m$).

Growth duration of L. praeusta

The larval development of *L. praeusta* was conducted using 100 eggs laid on the same day by 20 different sixth generation females that had been reared on either *C. benghalensis* or *M. nudiflora*. Larvae were reared at 27 ± 1°C, 65 ± 5% RH and 12L:12D in a biological oxygen demand incubator on the same species of plant leaves and on which oviposition had occurred. One hundred eggs were randomly divided into ten batches to record total larval and pupal duration, and male and female longevity on each type of leaf. During development time, dead larvae were replaced with same age larvae from rearing stock that had been fed on the same plant species. Larval length, breadth and head capsule width for all the instars along with pupal length and breadth of *L. praeusta* were measured for each type of leaf separately. Furthermore, length and breadth including fresh and dry weights of newly emerged adults were recorded. Date of death of the adult males and females were recorded.

Life table study

Eggs ($N = 250$) laid within a 12 h period by 30 *L. praeusta* females were collected randomly for separate life table studies on *C. benghalensis* and *M. nudiflora*. The larvae were fed on the same species of plant leaves on which adults had been reared for five generations and on which oviposition had occurred. Twenty-five eggs from each plant species were kept in each of ten glass jars (15 cm length × 8 cm diameter) and maintained at 27 ± 1°C, 12L:12D and 65 ± 5% RH. The larvae surviving in each instar were counted at 24 h intervals until they pupated, and mortality of pupae and adults was also recorded at 24 h intervals. Data obtained from egg hatch to adult death of *L. praeusta* on each type of leaf were collectively used to construct the life tables following Southwood & Henderson

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(2000). The life table parameters considered were: x = age interval of age class, n_x = number of survivors at the start of age interval x, l_x = proportion of organisms surviving to start age interval x, d_x = number or proportion dying at age interval x to $x+1$, q_x = rate of mortality during the age interval x to $x+1$, L_x = number of individuals alive on the average during the age interval x to $x+1$, T_x = total number of individuals of stage units beyond stage x, and e_x (life expectancy) = T_x/l_x.

Statistical analysis

Student's *t* test was applied to compare data on life history parameters of *L. praeusta* (each instar, total larval and pupal duration, and longevity of males and females) and length, breadth and head capsule width of all instars of *L. praeusta* (Zar, 1999). The net reproductive rate (R_o), the intrinsic rate of increase (r_m), the generation time (T_c), Euler equation, Euler r (r – adjusted), the doubling time (*DT*) and the finite rate of increase (λ) were also estimated using jackknife and bootstrap ($m > 1000$) techniques (Meyer *et al.*, 1986; Efron & Tibshirani, 1993).

Results

Host-specificity

Twenty-four hours after placing first instar larvae on Zingiberaceae (turmeric, cardamom, ginger and mango ginger), Solanaceae (potato and eggplant), Cucurbitaceae (bottle gourd, ridge gourd and pumpkin) and rice plants, all the larvae died. No feeding damage was noticed on any of the plants tested in this study. However, adults laid eggs on the upper side of the leaves of *C. benghalensis* and *M. nudiflora*.

In choice assays between *C. benghalensis* and *M. nudiflora* plants, significantly more adults were engaged in feeding on *C. benghalensis* leaves compared with *M. nudiflora* (table 2). Mated females laid significantly more eggs after 24 h of release on *C. benghalensis* compared with *M. nudiflora* leaves (table 2). In the laboratory, mated females generally started to lay eggs 3–4 days after mating began. Some females laid eggs after 24 h of release on the leaves, suggesting that light trap collected females had already mated in the field.

Fecundity table

Newly emerged *L. praeusta* males and females started to mate after 1 or 2 days. On average, one female mated three times during its life span, and a few females also mated a fourth time. The preoviposition period of newly emerged *L. praeusta* females varied between 3 and 10 days (6.1 ± 0.23 days, mean ± SE) when fed on *C. benghalensis* and *M. nudiflora* leaves. A single mating for *C. benghalensis*- and *M. nudiflora*-fed *L. praeusta* continued for 44.95 ± 1.03 (mean ± SE) minutes.

The period of reproductivity of *C. benghalensis*-fed *L. praeusta* females varied between 5 and 72 days (58.45 ± 1.01, mean ± SE days), whilst the period of reproductivity of *M. nudiflora*-fed females continued from 4 to 44 days (33.85 ± 0.66, mean ± SE days). Females fed on *C. benghalensis* and *M. nudiflora* leaves laid an average of 272.95 ± 2.39 (mean ± SE) eggs (range 245–284) and 224 ± 1.74 (mean ± SE) eggs (range 209–235) during their life time, respectively. The postoviposition period of females fed on *C. benghalensis* and *M. nudiflora* leaves was 38.9 ± 0.71 (mean ± SE) days. Fecundity of *L. praeusta* was age-dependent when they were fed on either *C. benghalensis* or *M. nudiflora*. Most of the *C. benghalensis*-fed females began to lay eggs when they were 8 days old, and there were eggs laying peaks at 8–12, 23–28, 36–41 and 57–62 days (fig. 2). Most *M. nudiflora*-fed females began to lay eggs when they were 8 days old, and there were eggs laying peaks at 6–12, 17–24 and 31–40 days (fig. 2). The mean number of eggs laid per day per *C. benghalensis*- and *M. nudiflora*-fed female over their lifetime was 2.76 ± 0.03 (mean ± SE) (range 0–29). Freshly laid eggs were yellow and sticky but later turned brown. Just before hatching, one end of the egg turned dark brown, indicating the cephalic side of the emerging larva.

The age-specific maternity ($l_x m_x$) of *L. praeusta* on *C. benghalensis* and *M. nudiflora* is shown in fig. 2. The net reproductive rate (R_o), generation time (T_c), intrinsic rate of increase (r_m), doubling time (*DT*) and the finite rate of increase (λ) of *C. benghalensis*- and *M. nudiflora*-fed *L. praeusta* population are presented in table 3. The means and standard errors of R_o, T_c, r_m, *DT* and λ of *C. benghalensis*- and *M. nudiflora*-fed *L. praeusta* estimated by jackknife and bootstrap methods are also presented in table 3. The R_o, T_c and *DT* were higher both in jackknife or bootstrap estimates for *L. praeusta* when fed on *C. benghalensis* compared with *M. nudiflora*, whereas r_m and λ of *L. praeusta* were higher both in jackknife or bootstrap estimates when fed on *M. nudiflora* compared with *C. benghalensis* (table 3).

Growth duration of L. praeusta

The development of 100 *L. praeusta* larvae on *C. benghalensis* and *M. nudiflora* leaves are separately reported. The incubation period and duration of each of the four instars and total larval developmental period of *L. praeusta* were higher on *M. nudiflora* compared with *C. benghalensis* (table 4). Before pupation, late fourth instar larvae left the plant and moved down plant stems in search of moist soil where pupation took place over 8–9 days. The pupal period was longer on *M. nudiflora* compared with *C. benghalensis* (table 4). Generally, adult females lived longer on both types of leaves compared with adult males (table 4). Longevity of *L. praeusta* males and females were higher on *C. benghalensis* compared with *M. nudiflora* (table 4).

The length and breadth of the egg were significantly greater on *C. benghalensis* compared with *M. nudiflora* (table 5). The first instar larvae were yellow, second and third instars larvae were black, while fourth instar larvae were white (fig. 3). Except for third instar larvae where larval head capsule width did not significantly differ between the two plant species, the length, breadth and head capsule widths of all four instars of *L. praeusta* larvae fed on *C. benghalensis* were greater compared with larvae fed on *M. nudiflora* (table 5). The cocoon

Table 2. Feeding (number of insects engaged in feeding) and egg laying preference (number of eggs laid ± SE) of light trap collected *Lema praeusta* adults (n = 20) 24 h after being released in net cages containing *Commelina benghalensis* and *Murdannia nudiflora* plants (n = 5 per species).

L. praeusta	*C. benghalensis*	*M. nudiflora*	t_8	*P*
Feeding preference[1]	14.8 ± 0.37	5 ± 0.44	16.807	0.0001
Oviposition preference	9.80 ± 0.58	5.40 ± 0.50	5.68	0.0001

[1]For feeding preference, males and females were released in equal numbers.

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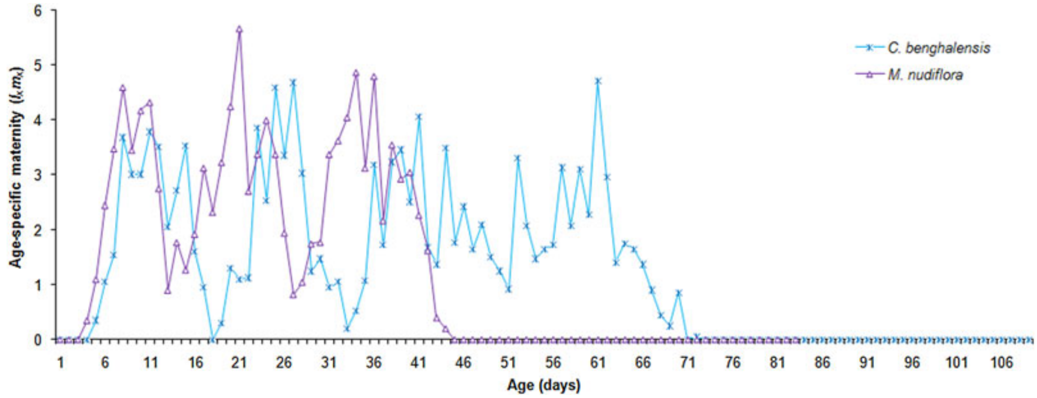

Fig. 2. Age-specific maternity ($l_x m_x$) of *Lema praeusta* fed on *Commelina benghalensis* and *Murdannia nudiflora* leaves calculated under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

was creamy white and the pupa was pale yellow (fig. 3). The cocoon and pupal length and breadth of *L. praeusta* were longer when fed on *C. benghalensis* compared with *M. nudiflora* (table 5). The sex ratio of newly emerged males and females on both the plant species was 1 male : 2 females. The length and breadth of newly emerged females were greater compared with males when fed on both types of leaves, but the length and breadth of newly emerged males and females were higher on *C. benghalensis* compared with *M. nudiflora* (table 5). Generally, newly emerged females were heavier compared with males on both *C. benghalensis* and *M. nudiflora* (table 6). The fresh and dry weights of newly emerged males and females of *L. praeusta* fed on *C. benghalensis* were heavier compared with males and females that emerged from *M. nudiflora* (table 6).

Life table study of L. praeusta

Commelina benghalensis-fed *L. praeusta* survived up to 129 days, whilst *M. nudiflora*-fed *L. praeusta* survived up to 103 days. The survival rate of *C. benghalensis*-fed *L. praeusta* from egg to adult was 38.8%, whereas 33.2% adults emerged from eggs when *L. praeusta* were fed on *M. nudiflora*. The l_x (age-specific survival rate) of *C. benghalensis*-fed *L. praeusta* were 51.2% at day 20, 28.8% at day 30, 26.4% from day 50 to 90, 23.6% at day 103, 11.2% at day 120 and last adult died on day 129 (fig. 4). The l_x of *M. nudiflora*-fed *L. praeusta* was 44% at day 20, 24.8% from day 30 to 50, 18.8% at day 80, 11.2% at day 90 and last adult died on day 103 (fig. 4). Twenty-nine females and 21 males were alive at day 114 when *L. praeusta* were fed on *C. benghalensis*, but at day 122 all males were dead and 16 females were still alive. Eighteen females and

Table 3. Life table parameters estimated with jackknife and bootstrap techniques (mean ± SE) calculated for *Lema praeusta* on *Commelina benghalensis* and *Murdannia nudiflora* leaves under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

	Original population size		Estimation techniques			
			Jackknife		Bootstrap	
Parameter	*C. benghalensis*	*M. nudiflora*	*C. benghalensis*	*M. nudiflora*	*C. benghalensis*	*M. nudiflora*
Net reproductive rate (R_o)	136.48	112.0	137.30 ± 0.05	112.0 ± 0.05	135.96 ± 1.38	111.74 ± 2.77
Intrinsic rate of increase (r_m)	0.14	0.20	0.14 ± 0.00[1]	0.20 ± 0.00[2]	0.13 ± 0.00[3]	0.20 ± 0.00[4]
Generation time (T_c) (days)	36.17	23.64	35.96 ± 0.03	23.64 ± 0.04	38.95 ± 0.26	24.03 ± 0.30
Euler equation	8.33	5.88	8.23 ± 0.33	5.91 ± 0.65	8.51 ± 0.18	6.52 ± 0.28
Euler *r* (*r* – adjusted)	0.35	0.41	0.34 ± 0.00[5]	0.39 ± 0.00[6]	0.35 ± 0.00[7]	0.46 ± 0.02
Doubling time (*DT*) (days)	5.10	3.47	5.06 ± 0.00[8]	3.47 ± 0.00[9]	5.50 ± 0.04	3.54 ± 0.05
Finite rate of increase (λ)	1.41	1.51	1.41 ± 0.00[10]	1.48 ± 0.00[11]	1.43 ± 0.01	1.59 ± 0.02

[1]0.0001.
[2]0.0003.
[3]0.0009.
[4]0.0027.
[5]0.0005.
[6]0.0013.
[7]0.0077.
[8]0.0036.
[9]0.0058.
[10]0.0007.
[11]0.0019.
The means of population parameters of *C. benghalensis* and *M. nudiflora* under jackknife or bootstrap were significantly different ($P < 0.01$) using the Mann–Whitney *U* test using SPSS software.

Table 4. Development time (mean ± SE, day) of eggs, larvae, pupae and longevity of *Lema praeusta* on *Commelina benghalensis* and *Murdannia nudiflora* leaves under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

	C. benghalensis	*M. nudiflora*	t_{198}	*P*
Incubation time	3.44 ± 0.05	3.65 ± 0.05	−2.92	0.004
First instar	2.54 ± 0.05	2.68 ± 0.05	−2.04	0.043
Second instar	1.47 ± 0.05	1.88 ± 0.04	−6.664	0.0001
Third instar	1.31 ± 0.05	1.47 ± 0.05	−2.34	0.02
Fourth instar	1.04 ± 0.02	1.25 ± 0.04	−4.4	0.0001
Total larval duration	6.36 ± 0.07	7.28 ± 0.11	−7.079	0.0001
Pupa	8.13 ± 0.04	9.16 ± 0.04	−18.481	0.0001
Male longevity	98 ± 0.58	69.25 ± 0.49	37.980	0.0001
Female longevity	106.25 ± 1.17	77.65 ± 0.91	19.302	0.0001

12 males were alive at day 86 when *L. praeusta* were fed on *M. nudiflora*, at day 98 all males were dead, but all 18 females were still alive. The life expectancy (e_x) of *L. praeusta* when fed on *C. benghalensis* and *M. nudiflora* are shown in fig. 5.

Discussion

Our observations and data conflict with published accounts of *L. praeusta* as a minor pest on turmeric in Orissa (Sengupta & Behura, 1957) because we did not observe any feeding damage by larvae and adults of *L. praeusta* on turmeric leaves. We did not notice *L. praeusta* larvae and adults on leaves of eggplant, bottle gourd, ridge gourd and pumpkin in the Crop Research Farm of our University during 2 years of observation, but we observed both larvae and adults of *L. praeusta* feeding on *C. benghalensis* and *M. nudiflora* in rice-fields. Eggplant, bottle gourd, ridge gourd and pumpkin plants were within 9 m of both weeds, suggesting that the previous report of *L. praeusta* as a pest of eggplant, bottle gourd, ridge gourd and pumpkin was wrong (Sengupta & Behura, 1953, 1957). The developmental time and biology of the insect on which Sengupta & Behura (1957) worked also differed from our observations. Sengupta & Behura (1957) reported that the full-grown larva pupated under the covering of the excreta, whereas, we observed that full-grown larvae of *L. praeusta* pupate under white salivary froth. Further, Sengupta & Behura (1957) reported *L. praeusta* to be bicolorous, but identification keys of Warchałowski (2011) and Lee & Matsumura (2013) suggest that bicolorous species belong to a different group of *Lema* species (Auxiliary group E); *L. signatipennis* is in this group and it feeds on turmeric (Warchałowski, 2011). In contrast, the species we studied has key characters consistent with those of *L. praeusta*: 'elytra unicolorous' and 'pronotum differently coloured than elytra, reddish, fulvous, brownish or black with hind part reddish' (Warchałowski, 2011). Also, the length of *L. signatipennis* is 5 mm, whereas *L. praeusta* is between 5.3 and 6.7 mm long (Warchałowski, 2011). Sengupta & Behura (1957) specimens were about 5 mm long, which also suggests that their identification was wrong. Most importantly, we did not observe feeding damage by larvae and adults of *L. praeusta* on the leaves of cardamom, ginger, mango ginger and potato in the laboratory.

Lema praeusta appears to have potential as a biocontrol agent of *C. benghalensis* and *M. nudiflora* in the field. *Lema praeusta* had four larval instars and is a multivoltine species. Larvae and adults of *L. praeusta* fed on other species of Commelinaceae in the laboratory such as *Commelina obliqua*, *Commelina maculata*, *Murdannia vaginata*, *Murdannia spirata*, *Tradescantia zebrina*, *Tradescantia pallida*, *Tradescantia spathacea* and *Cyanotis cristata*. Kalaichelvan *et al*. (2003) noted *L. praeusta* on several *Commelina* species. The short development time and oviposition behavior of *L. praeusta* on both *C. benghalensis* and *M. nudiflora* will likely lead to overlapping generations in the field. The current study indicates that the biology of *L. praeusta* was similar to other chrysomelid species such as *Altica cyanea* on the rice-field weed *Ludwigia adscendens* (Nayek & Banerjee, 1987), *Agasicles hygrophila* on *Alternanthera philoxeroides* (Buckingham, 1996; Pemberton, 1999), *Gratiana graminea* on *Solanum viarum* (Medal *et al*., 2010), *Galerucella birmanica* on *Trapa natans* (Ding *et al*., 2006) and *G. placida* on *Polygonum orientale* (Malik *et al*., 2016).

Our results suggested that *C. benghalensis* has better nutritional quality for *L. praeusta* than *M. nudiflora*. Insects fed *C. benghalensis* had shorter developmental times of immatures and higher fecundity. Further, the mortality of *L. praeusta* adults was greater on *M. nudiflora* compared with *C. benghalensis*. It is widely known that host plants serve an important role in regulating insect development, survival and reproduction (Awmack & Leather, 2002; Schoonhoven *et al*., 2005; Roy & Barik, 2012, 2013).

The net reproductive rate (R_o, the total female offspring produced per female) of *L. praeusta* was higher when fed on

Table 5. Length, breadth and head capsule width of *Lema praeusta* (mm ± SE) larval instars and length and breadth of egg, pupa, newly emerged male and female of *L. praeusta* feeding on *Commelina benghalensis* and *Murdannia nudiflora* under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

	Length				Breadth				Head capsule width			
	C. benghalensis	*M. nudiflora*	t_{18}	*P*	*C. benghalensis*	*M. nudiflora*	t_{18}	*P*	*C. benghalensis*	*M. nudiflora*	t_{18}	*P*
Egg	1.11 ± 0.02	1.03 ± 0.01	3.8	0.001	0.48 ± 0.02	0.43 ± 0.01	2.45	0.03				
First instar	1.12 ± 0.02	0.95 ± 0.02	5.85	0.0001	0.52 ± 0.01	0.48 ± 0.01	2.28	0.04	0.32 ± 0.01	0.29 ± 0.01	2.605	0.02
Second instar	2.91 ± 0.02	2.85 ± 0.02	2.17	0.04	1.86 ± 0.03	1.78 ± 0.02	2.21	0.04	0.75 ± 0.02	0.69 ± 0.01	2.882	0.01
Third instar	3.95 ± 0.03	3.86 ± 0.01	2.53	0.03	2.81 ± 0.03	2.69 ± 0.03	2.6	0.02	0.82 ± 0.03	0.80 ± 0.02	1.41	0.18
Fourth instar	5.51 ± 0.03	5.27 ± 0.04	3.743	0.001	3.51 ± 0.05	3.32 ± 0.05	2.54	0.02	1.08 ± 0.03	0.99 ± 0.03	2.32	0.03
Cocoon	6.52 ± 0.13	6.16 ± 0.08	2.35	0.03	3.70 ± 0.11	3.35 ± 0.10	2.28	0.04				
Pupa	5.22 ± 0.04	4.94 ± 0.05	2.7	0.02	2.59 ± 0.04	2.44 ± 0.05	2.33	0.03				
Male[1]	5.57 ± 0.03	5.41 ± 0.02	3.99	0.001	2.27 ± 0.04	2.16 ± 0.03	2.21	0.04				
Female[1]	5.89 ± 0.03	5.59 ± 0.03	7.59	0.0001	2.56 ± 0.04	2.44 ± 0.03	2.36	0.03				

[1]Means: newly emerged.

Fig. 3. Different stages of *Lema praeusta* from egg to adult emergence.

Table 6. Fresh weight and dry weight (mg ± SE) of a newly emerged male and female *Lema praeusta* fed on *Commelina benghalensis* and *Murdannia nudiflora* under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

	Fresh weight				Dry weight			
	C. benghalensis	*M. nudiflora*	t_{18}	*P*	*C. benghalensis*	*M. nudiflora*	t_{18}	*P*
Male	6.33 ± 0.07	5.42 ± 0.08	8.56	0.0001	1.60 ± 0.08	1.37 ± 0.05	2.32	0.03
Female	9.23 ± 0.09	8.37 ± 0.10	6.29	0.0001	2.50 ± 0.06	2.20 ± 0.06	3.50	0.003

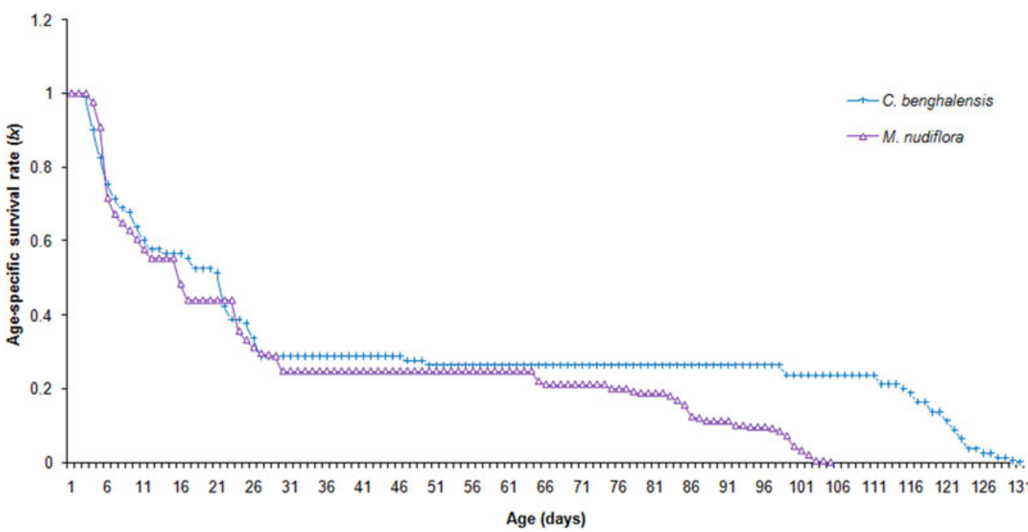

Fig. 4. Age-specific survivorship (l_x) of *Lema praeusta* fed on *Commelina benghalensis* and *Murdannia nudiflora* leaves calculated under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

C. benghalensis compared with *M. nudiflora*. *Lema praeusta* laid eggs between day 5 and 72 when fed on *C. benghalensis*, and produced an average of 272.95 ± 2.39 (mean ± SE) eggs, whereas *M. nudiflora*-fed *L. praeusta* laid eggs between day 4 and 44, and produced an average of 224 ± 1.74 (mean ± SE) eggs. This is the reason for the higher $\Sigma l_x m_x$ of *L. praeusta* on *C. benghalensis* compared to *M. nudiflora*. A population of *C. benghalensis*-fed *L. praeusta* will multiply 136 times, while the population of *M. nudiflora*-fed *L. praeusta* will multiply 112 times, which suggests that more *L. praeusta* will be available to consume *C. benghalensis* compared with *M. nudiflora* in a biocontrol program. The generation time (T_c) (the mean age

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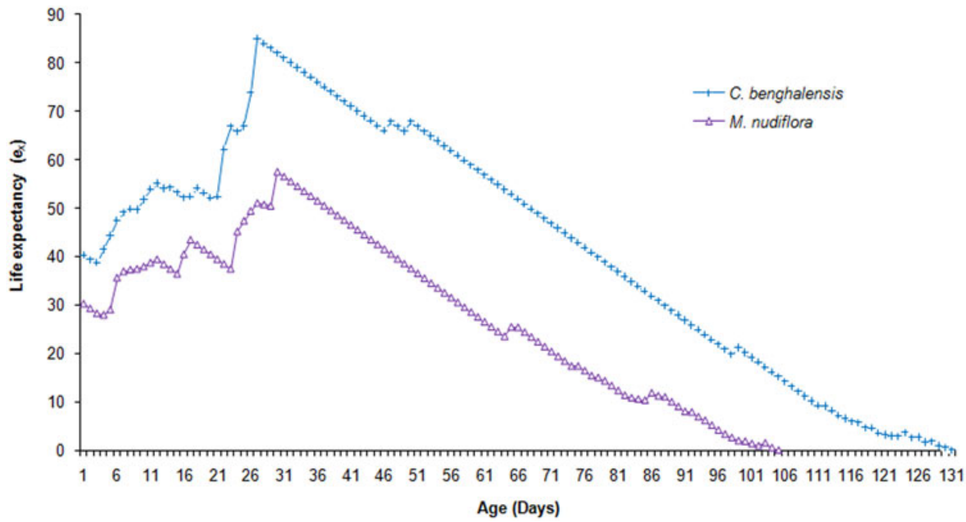

Fig. 5. Life expectancy (e_x) of *Lema praeusta* fed on *Commelina benghalensis* and *Murdannia nudiflora* leaves calculated under laboratory conditions (27 ± 1°C, 65 ± 5% RH and 12L:12D).

of the mothers in a cohort at the birth of female offspring) of *C. benghalensis*-fed and *M. nudiflora*-fed *L. praeusta* were 36 and 24 days, respectively, which indicates that *M. nudiflora*-fed *L. praeusta* will produce female offspring at an earlier age than *C. benghalensis*-fed *L. praeusta*. The explanation is that the $\Sigma x l_x m_x$ of *L. praeusta* on *C. benghalensis* is greater due to higher $\Sigma l_x m_x$ and longer survivability of adult females, which influenced higher T_c.

The intrinsic rate of natural increase (r_m) indicates how fast the *L. praeusta* population can increase on either *C. benghalensis* or *M. nudiflora*. The r_m for *L. praeusta* on *C. benghalensis* (0.14) is lower compared with *M. nudiflora* (0.20), which suggests that a *L. praeusta* population will increase faster on *M. nudiflora*, but this is due to the higher T_c of *L. praeusta* on *C. benghalensis* compared with *M. nudiflora*. The higher r_m for *L. praeusta* on *M. nudiflora* compared with *C. benghalensis* influenced the greater finite rate of increase (λ, number of females per female per day) on *M. nudiflora* (1.51) compared with *C. benghalensis* (1.41). The *DT* (number of days required by a population to double) of *C. benghalensis*-fed and *M. nudiflora*-fed *L. praeusta* were 5.1 and 3.47 days, respectively. However, this is only due to the lower r_m of *L. praeusta* on *C. benghalensis* compared with *M. nudiflora*.

The higher intrinsic rate of increase (r_m) and finite rate of increase (λ), and lower generation time (T_c) and doubling time (*DT*) of *L. praeusta* on *M. nudiflora* compared with *C. benghalensis* suggests that *L. praeusta* will perform better as a biological control agent on *M. nudiflora* compared with *C. benghalensis*. But the $\Sigma x l_x m_x$ of *L. praeusta* on *C. benghalensis* is greater due to higher $\Sigma l_x m_x$ and longer survivability of adult females, which influenced higher T_c and DT, and lower r_m and λ of *L. praeusta* on *C. benghalensis* compared with *M. nudiflora*. The longer survival and higher fecundity of adult females on *C. benghalensis* compared to *M. nudiflora* will result in more feeding damage and the production of more females in the next generation on *C. benghalensis*. Thus, *L. praeusta* should be a better candidate for biocontrol of *C. benghalensis* than *M. nudiflora*. Moreover, our fecundity life table results will help to predict the population dynamics of *L. praeusta* in any future weed biocontrol program (Medeiros *et al*., 2000). Our fecundity life tables may also be helpful for estimating potential production of *L. praeusta* on *C. benghalensis* and *M. nudiflora* in mass rearing and release programs.

We conclude that *L. praeusta* is not a pest of turmeric, cardamom, ginger, mango ginger, eggplant, potato, bottle gourd, ridge gourd and pumpkin plants, but is an excellent candidate for biological control of *C. benghalensis* and *M. nudiflora* in rice, maize, sorghum, soybean, mung bean, peanut and cotton. Future research is needed for a more complete evaluation of the potential of *L. praeusta* such as searching behaviour, intraguild predation and development on different host plants.

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