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SHORT COMMUNICATION

OBSERVATIONS ON THE GROWTH AND LIFE TABLE ESTIMATES OF THE SLUG *MARIAELLA DUSSUMIERI* (L. PFEIFFER, 1855) (GASTROPODA: ARIOPHANTIDAE)

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Abstract. The life history features of the pestiferous slug *Mariaella dussumieri* (L. Pfeiffer, 1855) (Gastropoda: Ariophantidae) were studied in the laboratory. The growth and reproduction of *M. dussumieri* were studied using multiple cohorts of juveniles hatching from the eggs of field-collected and laboratory-reared individuals. About 18 out of 215 hatchlings survived to sexual maturity with a maximum life span of 401 days. The growth pattern was assessed for compliance with the von Bertalanffy growth equation for body weight, expressed as $BW_t = 9*(1-exp^{-0.09(t-0.11)})$. At the juvenile stage, mortality of the studied slugs was high and growth was rapid. However, when the individuals attained sexual maturity, growth slowed down and mortality decreased. The post oviposition period was very short, indicating semelparity. The characteristic life history features exhibited by *M. dussumieri* reflected its adaptation as a pestiferous slug.

INTRODUCTION

Terrestrial snails and slugs (Gastropoda: *Stylommatophora*) have enormous importance because of their pestiferous nature as they voraciously feed on twigs of seedlings and vegetables, thus causing economic damage (Raut and Ghose 1984; Barker 2002; Howlett 2012). However, most of the terrestrial gastropods are not pests and consume algae, fungi, lichen, and detritus as primary food resources (Barker 2004), aid in pollination (Sarma et al. 2007), and only a few of them are predators (Meyer et al. 2008). Thus, land snails and slugs perform multifunctional roles through the regulation of algae and fungi (Speiser 2001; Keller and Snell 2002; Maraun et al. 2003), lichen (Boch et al. 2015), endozoochory (Boch et al. 2011), litter decomposition (Mason 1970; Gupta and Oli 1998), facilitation of nutrient recycling (Skeldon et al. 2007) and by being prey to various invertebrates and vertebrates (Shachak et al. 1981; Barker 2004; Rosin et al. 2011). Further, the mucus of some snails and slugs has medicinal (Thomas 2013) and antimicrobial (Cilia and Fratini 2018) properties. In order to sustain the ecosystem services provided by land snails and slugs, as well as for the pest management, it is essential to evaluate their life history features so as to portray their population growth and prospective establishment in new habitats. The information on the general biology of land snails and slugs is essential for enhancing their functional roles and formulating appropriate strategies for pest management.

In terrestrial ecosystem, snails and slugs exploit a wide range of microhabitats including detritus and branches of woody plants (Wiktor et al. 2000). The life history traits of snails fit the habitat utility as is reflected in patterns of reproductive strategies and those of life cycle (Heller 2001). Many land slug species are simultaneous hermaphrodites, and many breed by cross-fertilization. Both reciprocal and non-reciprocal courtship and copulation are documented in terrestrial gastropods (Tompa 1984; Davison and Mordan 2007). Studies on the ecology of terrestrial slugs from Australia (South 1992), Europe (Howlett 2012), New Zealand (Barker 1989, 2002), and the USA (Capinera et al. 2011) are a handful, and most of them are restricted to pest species. In the Indian context, studies on slugs are also focused on pest species (Bhat and Shamanna 1972; Raut et al. 1990; Raut and Panigrahi 1990; Panigrahi 1995; Routray and Dey 2016) and on plant litter decomposition by the

terrestrial slug *Anadenus altivegus* (Theobald, 1862) from the Kumaon Himalaya (Gupta and Oli 1998).

The slug, *Mariaella dussumieri* (L. Pfeiffer, 1855) (Gastropoda: Ariophantidae) is considered to be endemic to the Western Ghats, India (Raheem et al. 2014), but introduced to Malaysia, Singapore (Godan 1983; Hoong 1995; Maassen 2001) and Sri Lanka (Maheshini et al. 2019). Although *M. dussumieri* was intercepted in the USA (Godan 1983), there is no evidence of its occurrence therein at present (Cowie et al. 2009). Being a voracious feeder, *M. dussumieri* is considered to be a pest of commercial plants as it impairs the quality and market value of crops, partly because of its excreta and mucus secretion (Tandon et al. 1975; Das et al. 2020). Besides, *M. dussumieri* was reported to consume coffee plants (Bhat and Shamanna 1972), cabbage (Tandon et al. 1975), leaves, and succulent buds of vanilla plants (Mavinkurve et al. 2004) in southern India, and young rubber plants in Sri Lanka (Naggs et al. 2003). In addition to commercial plants, the herbivory of *M. dussumieri* has also been reported to harm weed plants, eg., it caused delayed flowering and reduced dry matter yield in such weed plants as *Galinsoga ciliata* and *G. parviflora* (Rai and Tripathi 1985). Taking into consideration its pestiferous nature, the observation of the growth pattern and life table estimates of *M. dussumieri* was continued (previous observations were performed by Raut et al. 1990) under laboratory conditions in our study. The observations on the life history features of *M. dussumieri* are expected to be helpful in evaluating its population dynamics and pest management in the future.

MATERIALS AND METHODS

Specimen collection and rearing

Live specimens of *M. dussumieri* were collected during the rainy season (July to September 2017) from semi-managed gardens near a human settlement in Coochbehar, West Bengal, India (26°22'35.7" N, 89°25'41.1" E). The species was identified by their external morphological characters (Pfeiffer 1855). Sixty-seven specimens were collected by handpicking with a wet paintbrush early in the morning and late in the evening because of a greater chance of encounter (Raut and Ghose 1984). The collected specimens were kept in a plastic jar with a sufficient amount of wet coco peat at the inner base to maintain high moisture and humidity and brought to the laboratory for rearing and study of life-history parameters. The collected specimens were released in five terraria (38 × 31 × 31 cm in size) with a maximum density of fifteen slugs/ terrarium. The terrarium was provided with a moist mixture of soil and coco peat (1:2 by volume) at the base, a banana (*Musa acuminata*) pup with moist soil in a plastic bowl (volume – 2 litre), and a chunk (~315 cm^2) of scutch grass (*Cynodon dactylon*). The top of the terrarium was covered with a transparent plastic sheet with minute holes to allow air circulation whilst ensuring a moist atmosphere. The study was conducted in the laboratory from July 2017 to June 2019 at room temperature (27°–34°C).

Experimental design

In the rearing terrarium, the specimens were fed *ad libitum* with slices of bottle gourd, button mushroom, and lettuce. The leftover food and faeces were removed from the terrarium at regular intervals to prevent bacterial and fungal growth. Water was sprayed inside the terrarium daily using a water sprayer so as to maintain high moisture and humidity. Each terrarium was inspected daily for the presence of eggs. Once the eggs were found, the oviposition was recorded, and egg clutches were transferred to a plastic bowl (volume – 100 ml) with moist soil and coco peat mixture at the inner base. The clutches were observed daily till hatching to determine the incubation period and hatchability.

The juveniles that hatched from different clutches on the same day were grouped together to constitute a particular cohort. The cohort was transferred to a plastic bowl (2 litre volume) with a moist soil-coco peat mixture and a banana leaf at the inner base on the day of hatching. A total of nine cohorts (n = 51, 18, 11, 18, 31, 34, 10, 32 and 10 individuals) were considered in this experiment. The hatched juveniles were supplied with the same food items as the collected specimens within the bowls for two months. To maintain the cohort combinations, two-month-old juveniles were transferred to nine terraria (36 × 29 × 19.5 cm) and were provided with soil-coco peat mixture, a banana pup, and scutch grass as the collected specimens mentioned above. From the age of two months, the body weight of a maximum of ten live specimens from each cohort was measured to the nearest 0.1 g with an electronic balance (Afcoset, India). From the beginning of the experiment, life-history traits such as longevity (days), age of sexual maturity (days), fecundity, the incubation period of the eggs (days), hatching rate (%), and post oviposition time (days) were recorded.

Data analysis

Data on the survivorship were applied to estimate life table parameters (Krebs 1999), and the age-specific survivorship (l_x) and life expectancy at age x (e_x) were calculated, while slug growth was assessed through changes in the body weight (Faberi et al. 2006). Data on the body weight (BW, in g) were represented as a function of time (months) and were subsequently assessed for compliance with the von Bertalanffy growth equation $BW_t = BW_\infty(1 - (e^{-k(t - t_0)}))$, where BW_t is the

bodyweight of the slug at time t, and BW_∞ and k are the von Bertalanffy growth parameters assuming that the relation between BW_{t+1} and BW_t will yield a straight line equation (y = a + bx), with the slope (b) being $e^{(-k)}$ and the intercept (a) being $BW_\infty = [1 - e^{(-k)}] = BW_\infty(1\text{-}b)$, thereby enabling determination of BW_∞ and k, the parameter of the von Bertalanffy growth parameters (King 2007). The time (t) is set as the instantaneous time (in months), whilst t_0 is obtained as $t_0 = t + (1/k) \ln ((BW_\infty - BW_t)/(BW_\infty))$. Data on the expected and observed values of body weight were compared using the student's *t*-test to assess the fit between the growth data and the von Bertalanffy growth equation.

The fecundity table was estimated using the suitable formulae as mentioned below (Krebs 1999; Smith and Smith 2001) with the modification due to the hermaphroditic nature of the slug. The m_x value (number of individuals produced per individual of age x, in months) was considered without any variations in the sex ratio, assuming the species to be hermaphroditic. The calculations were made using the summation of the eggs produced by the survivors, gross reproductive rate (GRR) = $\sum_{x=10}^{13} m_x$. Subsequent calculations were made to determine the net reproductive rate (R_0) = $\sum_{x=10}^{13} l_x m_x(R_0)$, based on the survival of the individuals at a particular age x (in months). In the above equations, the values 10 and 13 represent the reproductive period (in months) of the cohorts, and the value of m_x was equal to all the eggs oviposited by *M. dussumieri* at age x (without dividing into male and female). The cohort generation time, T_c, was calculated as $T_c = \sum x l_x m_x / R_0$, while the intrinsic rate of the population increase (r_m) as $r_m = \frac{\sum l_x m_x \log e^{\sum l_x m_x}}{\sum x l_x m_x}$ (Krebs 1999; Smith and Smith 2001). The post-oviposition period was determined from the last deposited egg till mortality of the last individual in the cohort. The data of the experiments were subjected to statistical analysis (Zar 1999) using excel software. Selection of the statistical test was made following Krebs (1999) and Zar (1999).

RESULTS

Longevity and survivorship

Individuals of only four out of the nine cohorts considered in this study survived beyond the age of sexual maturity. At juvenile stages, mortality of individuals was considerably high, and individuals of four out of the nine cohorts did not survive beyond the age of 7 days. One of the rest five cohorts comprised a single individual which survived for a considerable time (270 days) but did not attain sexual maturity. The four cohorts were continually monitored for survival, growth, and fecundity data. As in other cohorts, mortality of individuals in these cohorts was high, but a certain number of them, i.e., 5, 5, 5, and 3 individuals per cohort, respectively, survived beyond the age of sexual maturity (i.e., the day of the first oviposition). In these cohorts, the individuals exhibited varying degrees of longevity, with a maximum longevity of 401 days with the post-oviposition period ranging from 2 to 21 days. The survivorship pattern (type III) and the life expectancy of the slug *M. dussumieri* are presented in Figure 1. The post-hatching longevity of the studied slugs was 68.06 ± 16.33 (mean ± SE) days (range 3 to 401 days), and longevity of the sexually matured slugs was 369.5 ± 11.35 days (range 347 to 401 days).

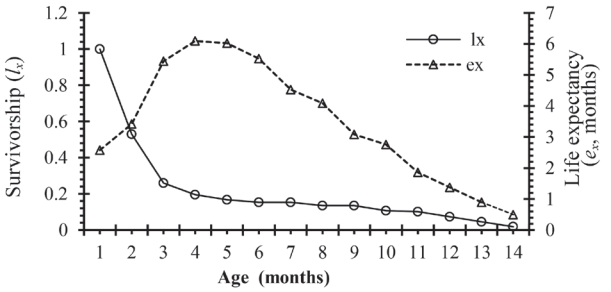

Figure 1. The survivorship and life expectancy of *Mariaella dussumieri* (n = 215), reared under laboratory conditions. The data of the different cohorts were cumulatively taken together for the analysis.

Growth parameters

There were noticeable changes in slug colour (from creamy white to saffron yellow) observed as they grew and matured. The saffron yellow pigmentation continued to become darker with time, and black pigmentation appeared as slugs got older (Figure 2). The growth of slugs is shown through changes in their body weight over the time period (Figure 3) derived from the von Bertalanffy growth equation $BW_t = 9*(1\text{-}\exp^{-0.09(t-0.11)})$. Changes in body weight were a decreasing function of the time period, following a linear regression equation (Figure 3). The comparison of the observed and expected BW_t values did not show significant differences indicating a fit between the growth curve and the von

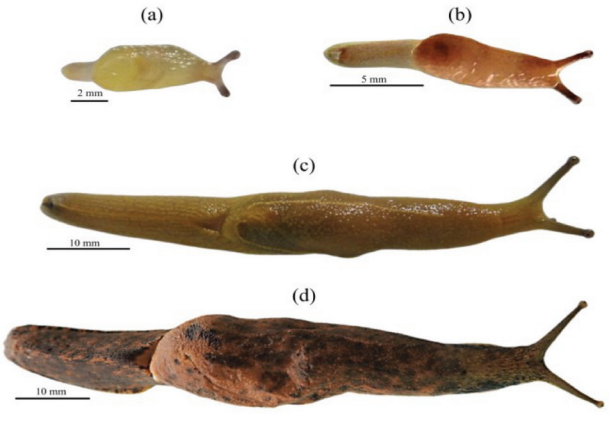

Figure 2. The slug *Mariaella dussumieri* at different life stages (a – 3 days, b – 4 weeks, c – 10 months and d – 13 months) reared under laboratory conditions.

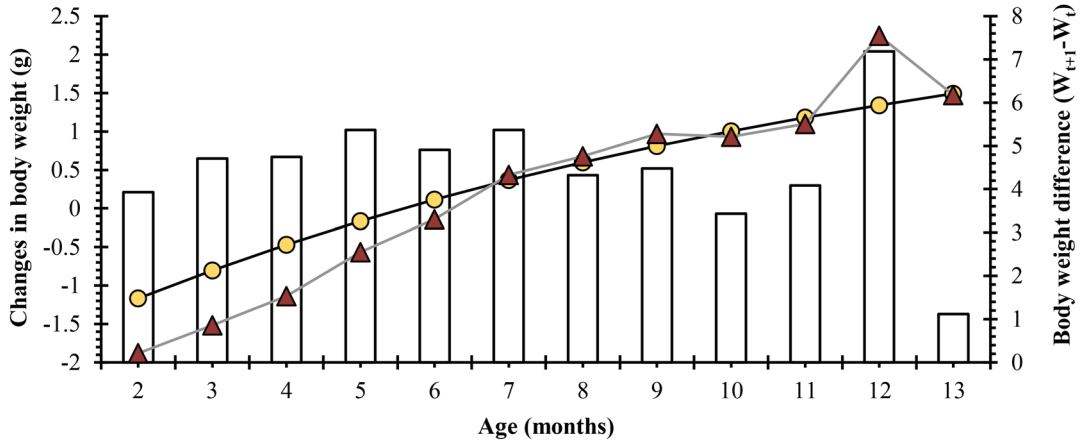

Figure 3. The growth of *Mariaella dussumieri* in terms of body weight, reared under laboratory conditions [triangles represent values of body weight observed in specific month, the circles represent the expected values following the von Bertalanffy growth equation, and monthly changes in body weight are represented through the bars].

Bertalanffy equation (differences = 0.25; observed z score = 0.32; $p = 0.75$; n = 20 paired data). At the time of sexual maturity, the body weight of *M. dussumieri* was recorded to be 5.95 ± 0.81 g.

Oviposition

Individuals of four cohorts (with the number of individuals, n = 5, 5, 5, and 3, respectively) out of the nine cohorts studied attained the age of sexual maturity, cumulatively contributing to the 1243 eggs deposited throughout the period between February and May. The cohort with a single specimen did not produce any eggs. The eggs were deposited in various places within the terrarium, mainly in the soil groove and crevices of scutch grass chunks, at the base of dead grass, beneath banana pups, and occasionally on banana pups and on the inner wall of the terrarium (Figure 4). The age of sexual maturity ranged between 296 and 367 days and the oviposition period ranged from 10 to 60 days (40 ± 11.34 days on average). On average, 33.75 ± 22.75 eggs were produced in the first clutch, and 20 ± 3 eggs were recorded in the last clutch. The number of egg clutches (0.46 ± 0.08 clutches/individual) laid during the reproductive period varied in different months, with the number of eggs per clutch ranging between 1 and 98 eggs. Depending on the number of survivors, the total number of eggs oviposited per month varied between 70 and 681 eggs, with a peak recorded during the 11th month (Figure 5). Taking into consideration the hermaphroditic nature and self-fertilization of *M. dussumieri*, the net reproductive rate (R_0) was observed to be 5.78, which can be considered as the number of the offspring produced by an individual during the lifetime. The cohort generation time (T_c) was 11.53 months and the rate of *M. dussumieri* increase under these conditions, represented through the intrinsic rate of increase (r_m) was estimated to be 0.152. The finite rate of increase (λ) was 1.164 (Table 1), as deduced from the equations $\lambda = e^r$ ($r = \ln\lambda$).

Incubation period and hatchability

The incubation period of the eggs of *M. dussumieri* ranged from 10 to 16 days with an average of 14.16 ± 1.3 SE days with a hatchability of 46.85 ± 6.64 SE per hundred eggs. Following the first hatching of eggs, the rest of the eggs of a single egg clutch hatched within 2 to

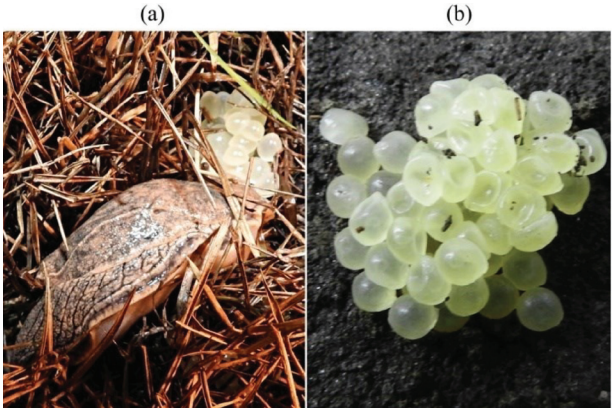

Figure 4. (a) The slug, *Mariaella dussumieri*, laying eggs on the scutch grass (b) egg clutch of *M. dussumieri.*

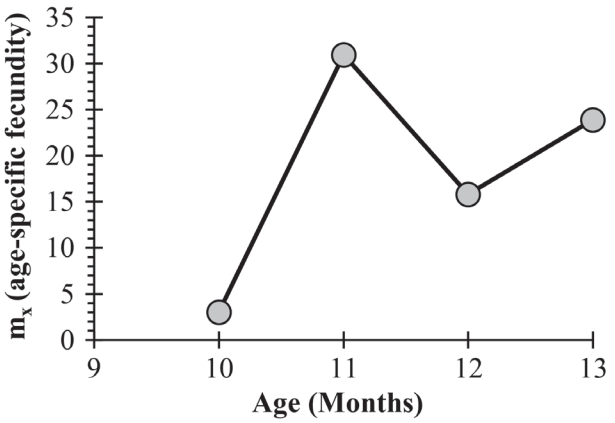

Figure 5. Age-specific fecundity (m_x) of *Mariaella dussumieri* under laboratory conditions.

Table 1. The fecundity schedule of the *Mariaella dussumieri* reared under laboratory condition for the estimation of generation time and fecundity (x – age in months, l_x – the proportion of individual surviving at age x, m_x – number of offspring at age x, R_0 – net reproductive rate, T_c – cohort generation time, r_m – the intrinsic rate of natural increase and λ – the finite rate of increase).

x	l_x	m_x	l_xm_x	xl_xm_x
1	1			
2	0.53			
3	0.26			
4	0.2			
5	0.17			
6	0.15			
7	0.15			
8	0.13			
9	0.13			
10	0.11	3.04	0.33	3.26
11	0.1	30.96	3.17	34.84
12	0.07	15.81	1.18	14.12
13	0.05	23.9	1.11	14.45
14	0.02	0	0	0
		R_0	5.78	66.67
		T_c	11.53	
		r_m	0.15	
		λ	1.16	

4 days, and unhatched eggs were observed to be infected with fungus and damaged within 7–10 days. Although not significant, the hatchability was positively correlated with the oviposition sequence (r = 0.27, p = 0.32). The first clutch exhibited hatchability of 36.22 ± 16.78 SE juveniles per hundred eggs, which thereafter inconsistently increased to reach hatchability of 57.96 ± 12.39 SE juveniles per hundred eggs, for the last clutch.

DISCUSSION

The life history of slugs is diverse in terms of the fertilization pattern, clutch size, developmental pattern, and seasonality of reproduction (Heller 2001). This proposition is supported by the life history patterns of the slugs, *A. altivagus* (Gupta and Oli 1998), *Semperula birmanica* (Panigrahi 1995, 1998), and *Laevicaulis alte* (Nagabhushanam and Kulkarni 1971), observed in the Indian context. Apart from being reported as a pest (Bhat and Shamanna 1972; Tandon et al. 1975; Mavinkurve et al. 2004), the information available on the life history features of *M. dussumieri* in India is fragmentary (Raut et al. 1990) with inadequate details of its longevity, oviposition patterns and reproductive strategies. Although in the present instance, the culture of *M. dussumieri* in the laboratory was continuous, the observation period of reproductive aspects including oviposition was limited to a certain period of the year, i.e., February–May. However, the subsequent developmental pattern appeared to be similar to that of different slugs from West Bengal, India (Panigrahi 1995, 1998), i.e., the reproduction including mating and oviposition, which was restricted to the winter period with a temperature lower than 20° C (Raut et al. 1990). In natural conditions, *M. dussumieri* was observed to be active from March to November and to overcome the rest of the winter through hibernation (Raut et al. 1990). However, under laboratory conditions, the slug remained active throughout the year. The oviposition time of slugs varies with species and geographic area (Heller 2001). For example, an Indian slug, *A. altivagus,* lays eggs throughout late September – early October in Kumaon Himalayan forests, India (Gupta and Oli 1998), and the invasive garden slug *Laevicaulis alte* (Ferussac, 1822) lays eggs throughout July–October in West Bengal, India (Panigrahi 2000). In the present instance, *M. dussumieri* laid eggs from late February to May in the laboratory, although in nature it is reported to breed throughout March–November (Raut et al. 1990). *M. dussumieri* attained sexual maturity between 296 and 367 days, which remained similar to the data reported in an earlier study (Raut et al. 1990). However, *Limax valentianus* (Férussac, 1821) was reported to attain sexual maturity between 151 and 179 days (Hommay et al. 2001) and *Deroceras reticulatum* (Müller, 1774) within merely 3 months (Billman-Jacobe et al. 2020).

Following the attainment of sexual maturity, the number of *M. dussumieri* eggs per clutch varied between 1 and 98, compared to 1–50 in the case of *A. altivagus* (Gupta and Oli 1998) and 38–53 in the case of *L. valentianus* (Hommay et al. 2001). The hatching of *M. dussumieri* occurred between 10 and 16 days at room temperature (27°C–34°C), which is within the range of 9–21 days reported for *L. alte* (Subba Rao et al. 1989) and shorter than the hatching period of *A. altivagus* (70–80 days) (Gupta and Oli 1998). The fact that the incubation period of *M. dussumieri* is shorter than that of *A. altivagus* could be explained by a comparatively higher temperature. In the present observation, the hatching rate of *M. dussumieri* eggs was 46.85%, which is comparatively higher than that of *L. valentianus* (Hommay et al. 2001) and lower than those of *A. altivagus* (Gupta and Oli 1998), *D. leave* (Faberi et al. 2006) and *Milax gagates* (Clemente et al. 2010) under different laboratory conditions. Like in several species of the arionid slug (Foltz et al. 1982), cross-fertilization might be indispensable for *M. dussumieri*, as the aged, single individuals in the cohort did not lay eggs in this study.

In this study, *M. dussumieri* exhibited a maximum survival of 401 days, which is lower than that of *A. altivagus* (720 days) (Gupta and Oli 1998), *L. valentianus* (Hommay et al. 2001), but higher than that of

D. laeve (~380 days) (Faberi et al. 2006), as observed in earlier studies. It is possible that these slugs differ in body size and habitat preferences. For instance, compared to the highest size of *M. dussumieri*, the body size of the slug *D. laeve* is small, while *A. altivagus* is characteristically bigger in size. Thus, the movement and the feeding pattern of these slugs are likely to be different, which may be the reason for the corresponding differences in their reproduction strategies. As a general rule, it is possible that the reproduction of the slug *D. laeve* is fast, in contrast to that of the slugs *M. dussumieri* and *A. altivagus*. At the early stages of life, the pattern of body weight increase with age was fast in *M. dussumieri*. However, during oviposition, it attained maximum and gradually declined in the post oviposition period. Similar patterns were determined in *D. reticulatum* (Zotin 2007), *D. leave* (Mohamed and Ali 2011) and *L. flavus* (Mohamed and Ali 2013). In the present study, the net reproductive rate of *M. dussumieri* (R_0 = 5.78) was found to be low compared to that of *M. gagates* (7.2–33.2) (Clemente et al. 2010), and the cohort generation time (T_c = 11.53 months, ~345 days) was high compared to those of *M. gagates* (181–206 days) and *D. leave* (231.7–115.5 days) (Faberi et al. 2006). This study indicates that *M. dussumieri* is "semelparous" (reproducing only once in a lifetime), "short-lived" (life duration is up to 2 years; in comparison to other slugs), and the survivorship follows the type III survivorship curve. The preferred oviposition microhabitats of *M. dussumieri* are characterized by retention of moisture and maintenance of high humidity that ensure non-desiccation and successful development of eggs. As the eggs of *M. dussumieri* were laid in clusters, the drying rate per unit of weight (of egg) may have been lower than that of the species laying single scattered eggs (Bayne 1968). These features of *M. dussumieri* reproduction including its semelparity may be related to unstable and changing habitats that favour comparatively short life with maximum reproductive output. Rapid growth with high mortality at juvenile stages, slow growth rate at sexual maturity, and very short post oviparous life may be attributed to the semelparous life history strategy. As life history strategies are influenced by climatic conditions, intra and interspecific competition, and food quality, further study should be carried out to explore how these factors influence the life history of the studied slug *M. dussumieri*.

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Conflicts of interest

As authors of this article, we declare that we have no conflict of interest.

Authors' contributions

HB and GA conceived the work; survey and collection were performed by HB; analysis and compilation by GA, HB and PP.

Data availability

The data used in this research article can be made available upon authentic and reasonable request.

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