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Biology, ecology and demography of the tropical treehopper *Ennya maculicornis* (Hemiptera: Membracidae): relationships between female fitness, maternal care and oviposition sites

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Abstract. 1. Treehoppers (Hemiptera: Membracidae) exhibit a wide range of social behaviours related to maternal care and nymphal aggregation. Maternal care represents an investment in terms of time and energy leading to trade-offs which bear a strong relationship with parity and can thus affect population dynamics. These trade-offs can be modulated by biotic and abiotic features of the oviposition site.

2. Preliminary observations on *Ennya maculicornis* (Membracidae: Similinae: Polyglyptini) show that females generally lay a single egg mass, and occasionally two or three egg masses, and that maternal care is a plastic trait because some females abandoned their egg mass before it hatched while other females remained with their offspring after egg hatching. These features make this species an interesting model to study the relationship between female fitness, maternal care and ecological factors such as oviposition site.

3. The biology and natural history of *E. maculicornis* are described and the relationships in question analysed using demographic parameters estimated by matrix models. *Ennya maculicornis* showed sexual dimorphism and a longer developmental period than other species of the same tribe. Females exhibited maternal care that increased offspring survival, and preferred mature over young host leaves for oviposition. Finite rate of increase (λ) values were lower than 1, suggesting a tendency towards population decrease.

4. The results represent the first detailed description of the life history and ecology for a species of this genus. Additionally, new hypotheses for treehopper sexual dimorphism, oviposition site choice and the ecological effects on population dynamics are proposed.

Key words. Life cycle, polyglyptini, population matrix models, sociability, *Solanum maternum*.

Introduction

Treehoppers (Hemiptera: Membracidae) constitute a large group of sap-feeding insects that include over 3000 species distributed in all continents except the Antarctic (Godoy *et al.*, 2006). They exhibit a variety of life-history patterns, including social behaviours such as aggregation and maternal care associated with intra- and interspecific interactions such as cooperative brood care and ant mutualism (Godoy *et al.*, 2006; Lin, 2006). Species can be characterised as: (i) solitary – lacking maternal care and aggregation behaviours; (ii) gregarious – lacking maternal care but exhibiting nymphal aggregation and frequently ant mutualism; and (iii) subsocial – lacking ant mutualism but exhibiting extensive maternal care, and sometimes cooperative brood care (Eberhard, 1986; Zink, 2003a; Costa, 2006; Camacho *et al.*, 2014).

Because maternal care represents an investment in terms of time and energy, females of species exhibiting this behaviour are expected to face trade-offs related to fitness such as that between offspring survival and future fecundity (Zink, 2003b). These trade-offs are reflected in different reproductive strategies (Godoy *et al.*, 2006). Thus, females of many subsocial species exhibit semelparous reproduction, i.e. they deposit their entire reproductive potential in a single egg mass during a short period of time (~24 h), while females of gregarious and some subsocial species produce several egg masses over a longer period of time (days or weeks), and can thus be considered as iteroparous or moderately iteroparous (Wood, 1993; Lin, 2006). To the best of our knowledge, natural history including oviposition behaviour has not been described for solitary species.

In treehoppers, life-history traits such as maternal care can enhance individual fitness, for example by increasing hatching success and offspring survival, or can constrain individual fitness, for example by decreasing investment in future reproduction (Zink, 2003b). Furthermore, in some species, maternal care investment is modulated by ecological constraints such as features of the oviposition site (Zink, 2001, 2003a) and ant mutualism (Billick & Tonkel, 2003). Thus, to understand treehopper population dynamics, knowledge of the relationship between maternal care, female fecundity and ecological traits is desirable (Ratz *et al.*, 2016).

Ennya maculicornis Fairmaire belongs to the Polyglyptini tribe (Membracidae: Smilinae) that contains gregarious and subsocial species (Bristow, 1984; Cushman & Whitham, 1989; Billick & Tonkel, 2003). Preliminary field observations showed that females of *E. maculicornis* laid either single or multiple egg masses. Furthermore, maternal care does not seem to be a fixed trait as some females, after laying an egg mass, abandoned it before hatching occurred and went elsewhere to lay new egg masses; on the other hand, other females remained with their offspring until the first or second nymphal stage. These observations prompted us to: (i) describe the general biology and ecology of the treehopper *E. maculicornis*; (ii) determine the relationship between female fitness, maternal care and ecological factors such as oviposition site; and (iii) explore how these processes affect the finite rate of increase (λ) of the population.

Materials and methods

Study site and insect marking

Field work was performed in a cloud forest located at Incachaca (Cochabamba, Bolivia 17°15'17" S–65°48'54" W; 2359 m above sea level), situated within the Yungas biogeographical province. The only host of *E. maculicornis* observed in the study area was the small tree *Solanum maternum* Bohs and Nelson, an endemic plant from the Solanaceae family (Bohs & Nelson, 1997).

A total of 102 adult females of *E. maculicornis* with egg masses, distributed on 19 host individuals, were marked on their pronotum using a permanent marker. The petiole of the leaf where each egg mass was present was also tagged. Egg masses were observed every week from 11.00 to 16.00 hours between April and October 2014.

Biology of E. maculicornis

Life cycle duration was estimated by following 40 marked egg masses distributed on eight host individuals; these groups of individuals were chosen to observe developmental changes and to obtain a total count of nymphs. Nymphal stages were morphologically described in terms of body size and coloration patterns of the incipient pronotum. Determination of adult sex was based on observations of external genitalia (i.e. presence or absence of ovipositor) and coloration of the pronotum. Sexual dimorphism (Wood, 1993; Godoy *et al.*, 2006; Lin, 2006) was also characterised by the length of the pronotum of males ($n=23$) and females ($n=95$) measured with a digital caliper (0.01 mm precision) and compared using a *t*-test. The lower number of replicates for males was due to their high mobility and the difficulty in catching them. Female longevity during adulthood was estimated considering as proxy the period of time from the initial marking process until the last time it was observed.

Female fecundity

The number of egg masses laid by each of the females that were marked and later recaptured was determined. As females laid one, two or three egg masses, the fecundity of each female was determined as the sum of eggs in all the egg masses it laid. The number of eggs was estimated as described by Torrico-Bazoberry *et al.* (2016), based on a regression analysis between egg mass area (as the independent variable) and the number of eggs counted under a stereo microscope (as the dependent variable) using 15 egg masses collected from the same population. After adjusting the data to a normal distribution with the log function, the model obtained for *E. maculicornis* was $\log(\text{number of eggs}) = 23.0 + 2.4 \times \log(\text{egg mass area})$ ($R=0.764$, $P=0.001$). The effectiveness of the model was confirmed, as no difference was found between the real and the estimated number of eggs present in 15 egg masses ($T=248$, d.f. = 15, $P=0.559$).

As fecundity is usually related to female size (Honek, 1993), a relationship between both traits was evaluated with a Spearman correlation analysis using female volume as proxy of

female size. As the pronotum is the most prominent morphological feature of *E. maculicornis* females and its shape closely resembles that of a pyramid, female volume was estimated as $1/3 \times (1/2 \times \text{pronotum height}^2) \times \text{pronotum length}$.

Sociability

Sociability of *E. maculicornis* was described in terms of types of familiar aggregations (constituted by nymphs and/or adults) and of maternal care such as protective behaviours and feeding facilitation behaviours by a female towards its offspring (i.e. the female uses her ovipositor to make small perforations or slits around the egg mass which facilitate feeding by first-instar nymphs) (Lin, 2006; Torrico-Bazoberry *et al.*, 2014). Also, to determine the importance of maternal care on offspring survival, the duration of female presence (number of days in which the female stayed near the egg mass or nymphs) was compared between egg masses that hatched and those that did not with a Mann–Whitney rank-sum test. Additionally, a Spearman correlation analysis was performed between the proportion of hatched nymphs (number of first-instar nymphs/number of laid eggs estimated from egg mass size) and the duration of female presence.

Oviposition sites

The phenological state of the leaves (young or mature) where egg masses were laid was used to characterise the oviposition site. Oviposition preference based on leaf phenological state was determined by an exact binomial distribution test ($P = 0.5$) comparing the number of egg masses laid on each category. As offspring mortality values could depend on the phenological state of the leaf (Raupp & Denno, 1983; Piyasaengthong *et al.*, 2016), leaf category was related to nymphal survival parameters. Thus, the proportion of hatched egg masses (hatched egg masses/laid egg masses) and the proportion of hatched nymphs (as defined in the previous paragraph) on each leaf category (young or mature) were compared with Z and t tests, respectively.

Demographic analyses

The life cycle of *E. maculicornis* consists of seven stages: egg, five nymphal instars and adult. The first two nymphal stages of *E. maculicornis* are sedentary while the last three are mobile, similar to *Alchisme grossa* (Membracidae, Hoplophorionini) (Pinto, 2015); hence, the life cycle of *E. maculicornis* was modelled as a four-stage matrix for demographic analyses: egg (E), nymph 1 (N1, which comprises the sedentary nymphs of the first and second instars), nymph 2 (N2, which comprises the mobile nymphs of the third, fourth and fifth instars) and adult (A) (Fig. 1a). Sex proportion for *E. maculicornis* was determined as the mean proportion on each host individual used to characterise nymphal stages and life cycle duration. The number of E, N1, N2 and A was multiplied by the proportion of females in order to work only with the female component of the population

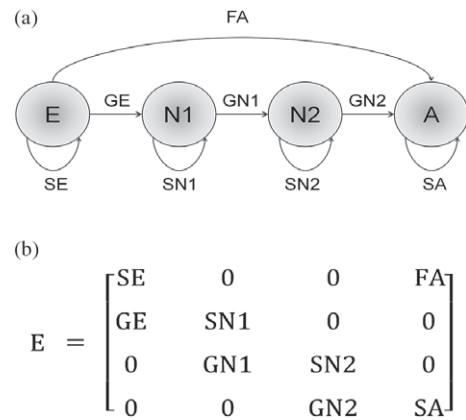


Fig. 1. Stage-classified life cycle of *Ennya maculicornis*. (a) Graphic representation: E, eggs; N1, nymph 1 (first and second nymphal instars); N2, nymph 2 (third; fourth and fifth nymphal instars); A, adults. (b) Demographic matrix based on a four-stage life cycle: SE, probability of surviving and remaining as an egg; GE, probability of surviving and reaching the next stage for eggs; SN1, probability of surviving and remaining as nymph 1; GN1, probability of surviving and reaching the next stage for nymph 1; SN2, probability of surviving and remaining as nymph 2; GN2, probability of surviving and reaching the next stage for nymph 2; FA, adult fecundity; SA, probability of surviving and remaining as an adult.

(Caswell, 2001). As nymphs of *E. maculicornis* only move within the host individual where they were born, demographic parameters were determined by following all individuals of *E. maculicornis* on different plant individuals ($N = 8$) (Pinto, 2015). Hence, eight four-stage demographic matrixes were constructed (one for each host individual) which included the following demographic parameters: the probabilities of surviving and remaining at the same stage (stasis) for an egg, nymph 1, nymph 2 and adult (SE, SN1, SN2 and SA, respectively); the probabilities of surviving and reaching the next stage (growth) for an egg, nymph 1 and nymph 2 (GE, GN1 and GN2, respectively); and the fecundity of adults (FA) (Fig. 1a). The latter parameter (FA) was determined as the mean number of eggs deposited by the females present on each individual plant. Growth and stasis were estimated following Caswell (2001).

A single matrix model was constructed for each individual plant (Fig. 1b), and two analyses were conducted: the first to estimate λ , calculated as the dominant eigenvalue of the matrix (Caswell, 2001; Hood, 2010), and the second to estimate the elasticity matrix, which includes the proportional contribution of each demographic parameter to variations in λ (Caswell, 2001).

An average λ value and a mean elasticity matrix were obtained for *E. maculicornis* using the eight host individuals as replicates. To determine which of the demographic parameters contributed more to variations in λ , an ANOVA comparison followed by a Holm–Sidak *post hoc* test were performed, considering the type of demographic parameter (fecundity, stasis or growth) as a factor, and using the total sum of each demographic parameter of the matrix as the dependent variable (i.e. stasis = SE + SN1 + SN2 + SA, growth = GE + GN1 + GN2, fecundity = FA) (Pfister, 1998).

Statistical analyses

All statistical analyses were performed with the SIGMAPLOT 11.0 software, except for the binomial test which was performed on <http://vassarstats.net/>, and the calculation of λ and elasticity matrix, which was performed using POPTOOLS (Hood, 2010).

Results

Biology of *E. maculicornis*

Marked females laid a total of 124 egg masses distributed on 19 host individuals during the study period; 83 females laid a single egg mass, 16 laid two egg masses, and three laid three egg masses. Egg masses were slightly covered with a waxy secretion. Life cycle duration from egg to adult stage lasted 94 ± 9 days (mean \pm SD). Eggs took 25 ± 9 days to hatch, first instars lasted 15 ± 4 days, second instars 15 ± 4 days, third instars 13 ± 5 days, fourth instars 12 ± 4 days, and fifth instars took 14 ± 5 days to reach to adult stage. First-instar nymphs emerged with entirely black body colouration, and measured around 1 mm. Second-instar nymphs had a black upper side and a green lower side of the body, and measured approximately 2 mm. Third-instar nymphs measured around 3 mm, had a notorious green circle in the union of the abdomen and the anal tube, and showed an incipient green circle in the union of the thorax and the abdomen. Fourth-instar nymphs measured around 4 mm, had the same notorious green circle in the union of the abdomen and the anal tube as the third-instar nymphs but had an incipient pronotal process. Fifth instars measured around 5 mm and had a notorious pronotal process and wing pad apices.

Sex of adults was determined by the presence of an ovipositor on females. Adults also presented sexual dimorphism in coloration (green in females and black in males) and pronotum length [shorter in males (7.49 ± 0.29 mm) than in females (8.10 ± 0.42 mm; $T = 8.41$, d.f. = 47, $P < 0.001$]. Newly emerged and young adult females had a bright green pronotum, while apparently older females (i.e. the ones recaptured later in the season) had a yellow pronotum. Sex proportion in the study area was 1.19:1 (female:male) and the estimated female longevity during adulthood was 77 days.

Mating ($n = 15$ observations) occurred between pairs of individuals separated from the aggregations of nymphs and adults (see later) and positioned on the upper side of the leaf close to the union of the petiole with the leaf.

Female fecundity

Seventy-seven (62%) of the 124 continuously observed egg masses hatched. Egg hatching was identified when an opening at the top of the eggs was found; non-hatched eggs did not have an opening on the top. Furthermore, non-hatched eggs showed black coloration or evidence of a fungus cover or desiccation. For females with a single oviposition event ($n = 83$), only 47 (57%) egg masses hatched. For females ($n = 16$) with two oviposition events, 23 (72%) of the 32 laid egg masses hatched: nine females (56%) had both of their egg masses hatched, five

females (31%) had only one egg mass hatched (usually the first egg mass), and two females (13%) had no egg masses hatched. For females ($n = 3$) with three oviposition events, seven (78%) of the nine laid egg masses hatched: one female had its three egg masses hatched while the other two females had only two egg masses hatched each. Considering all the hatched egg masses ($n = 77$), only 21 (27%) had more than 50% of their eggs hatched. Additionally, a positive correlation was obtained between female size and its fecundity, i.e. the total number of eggs it laid ($n = 89$, $R = 0.24$, $P = 0.02$).

Sociability

Two kinds of aggregations of *E. maculicornis* were identified on the underside of leaves: individual familiar aggregations conformed by a single female and its nymphs, and mixed familiar aggregations consisting of either nymphs and adults from different families or only nymphs of different instars (mostly from the third, fourth and fifth stages) from different families. On two of the 19 plants being followed, nymphs of *E. maculicornis* were observed in mixed aggregations with nymphs and adults of *Ennya chrysurus* Fairmaire.

In individual familiar aggregations, behaviours observed were related to maternal care, and occurred when a predator approached or when they were disturbed (i.e. the approach of observers to the egg mass). Maternal care behaviour consisted in wing-fanning, kicking with methatoracic legs and fast lateral movements of the pronotum. No feeding facilitation behaviours (i.e. feeding slits made by the female) were observed.

Most females ($n = 76$; 62% of the egg masses continuously observed) stayed with their progeny for less than 1 week after oviposition; thus, maternal care mostly occurred during the egg instar. Moreover, egg masses that hatched had longer maternal care (17 ± 14 days, $n = 76$) than did egg masses that did not hatch (9 ± 6 days, $n = 39$) ($n = 124$, $T = 1755.5$, $P < 0.001$). Additionally, a positive correlation between maternal care duration and proportion of hatched nymphs (number of first-instar nymphs/number of laid eggs estimated from egg mass size) was found ($n = 62$, $R = 0.39$, $P < 0.001$). Both patterns suggest that the occurrence of maternal care increases offspring survival.

Oviposition sites

In all, 118 of the 124 tagged egg masses (95%) were on the underside of a leaf; the rest were on the upper side, the stem or the petiole. Among these 118 egg masses, 71 (60%) were laid on a mature leaf and 47 (40%) on a young leaf; the ratio of mature to young leaves in host plants was approximately 3:1. Comparison between both leaf categories indicated a higher use of mature leaves as oviposition sites ($n = 118$, $P = 0.04$). The proportion of hatched egg masses was 89% for young leaves, and 33% for mature leaves. Additionally, the proportion of hatched nymphs was 33% and 35%, respectively. Neither the proportion of hatched egg masses ($n = 82$, $Z = 1.559$, $P = 0.119$) nor the proportion of hatched nymphs ($n = 82$, $T = 0.96$, d.f. = 65, $P = 0.339$) differed between leaf categories.

Table 1. Elasticities of parameters in a demographic matrix of *Ennya maculicornis* based on four-stage life cycle on eight individual host-plants.

Demographic parameter	Mean \pm SD
SE	0.2572 \pm 0.4356
SN1	0.1768 \pm 0.3087
SN2	0.5252 \pm 0.4538
SA	0.0002 \pm 0.0002
GE	0.0101 \pm 0.0102
GN1	0.0101 \pm 0.0102
GN2	0.0101 \pm 0.0102
FA	0.0101 \pm 0.0102

SE, probability of surviving and remaining as an egg; GE, probability of surviving and reaching the next stage for eggs; SN1, probability of surviving and remaining as nymph 1; GN1, probability of surviving and reaching the next stage for nymph 1; SN2, probability of surviving and remaining as nymph 2; GN2, probability of surviving and reaching the next stage for nymph 2; FA, adult fecundity; SA, probability of surviving and remaining as an adult.

Demographic analyses

Lambda (λ) values were lower than 1 (0.82 ± 0.13 , ranging from 0.52 to 0.96) for the eight host individuals used by *E. maculicornis*, indicating a tendency of the population to decrease.

The proportional contribution (elasticity) of each demographic parameter to variations in λ on the average elasticity matrix is shown in Table 1. Stasis of nymph 2 (SN2, 52.5%), stasis of eggs (SE, 25.7%) and stasis of nymph 1 (SN1, 17.7%), were the parameters that contributed the most (95.9%) to variations in λ . Contribution of the type of demographic parameters to λ also differed ($F = 3873.496$, d.f. = 23, $P < 0.001$), the contribution of stasis being higher and different from those of growth ($T = 75.612$, $P < 0.001$) and fecundity ($T = 76.823$, $P < 0.001$). There were no differences between growth and fecundity ($T = 1.211$, $P = 0.239$).

Discussion

Biology and ecology of *E. maculicornis*

Sexual dimorphism (colour and size) now reported for *E. maculicornis* is a well-documented phenomenon for many treehopper species (Wood, 1993; Wallace, 2008). In the case of body size difference, intersexual selection and specifically male preference can explain the larger body of females, particularly as larger females are generally associated with greater fecundity (Bonduriansky, 2001; Clutton-Brock, 2008; Stillwell *et al.*, 2010). However, in the case of *E. maculicornis*, male mating preference for larger females has yet to be confirmed. On the other hand, the smaller body size of *E. maculicornis* males could be explained by the gravity hypothesis, which proposes a negative correlation between moving ability on vertical surfaces and body size (Blanckenhorn, 2005; Corcobado *et al.*, 2010).

For most subsocial treehopper species, maternal care lasts until the offspring reach adulthood (Godoy *et al.*, 2006; Lin, 2006; Torrico-Bazoberry *et al.*, 2014). By contrast, for

gregarious treehopper species, maternal care lasts until mutualistic ants begin to attend the offspring (Perotto *et al.*, 2002; Lin, 2006). Although ant mutualism is frequent among Polyglyptini species (Bristow, 1984; Cushman & Whitham, 1989; Billick & Tonkel, 2003), *E. maculicornis* was not found interacting with ants, probably due to the absence of ants in the study site, owing to its high altitude (Wood, 1993); instead, it displayed the same maternal care behaviours described for subsocial species (Godoy *et al.*, 2006; Lin, 2006). Furthermore, *E. maculicornis* exhibited metathoracic leg kicking, a behaviour attributed only to species of the tribe Hoplophorionini (McKamey & Deitz, 1996), which includes species with the highest degree of maternal investment. Additionally, long developmental time has been attributed to high levels of subsociality (Lin, 2006). *Ennya maculicornis* presents the longer life cycle reported for a Polyglyptini species with an average of 94 days, in contrast to *Publilia concava* Say (25–75 days; Cushman & Whitham, 1989; Billick & Tonkel, 2003), *P. reticulata* Van Duzee (40–50 days; Bristow, 1984) and *Entylia bactriana* Germar (30–40 days; Whitehead, 1915). Thus, maternal care behaviour and duration of nymphal development suggest that *E. maculicornis* could be considered as a subsocial species, and the most social among previously described Polyglyptini species.

In a recent report, eggs of *E. chrysura* were observed parasitised by Myrmaridae wasps *Gonatocerus anomocerus* Crawford and *Schizophragma* sp. Ogloblin (Miranda, 2016). Furthermore, egg masses of *E. chrysura* without guarding females were more parasitised than egg masses with guarding females (Miranda, 2016). As egg masses of *E. maculicornis* without maternal care or with shorter maternal care duration had lower proportion of hatched eggs, and as small parasitoid wasps were also observed in the field (L. Caceres-Sanchez *et al.*, unpublished), it is possible that the low proportion of hatched eggs could be explained by egg parasitism. However, specific studies would be necessary to validate this hypothesis.

Leaves used as oviposition sites can be selected by females based in their preferences for specific chemical plant features (Piyasaengthong *et al.*, 2016), which in turn are often associated with offspring performance (Awmack & Leather, 2002). The genus *Solanum* L. is rich in alkaloids, a family of secondary metabolites involved in plant defence against herbivores (Eltayeb *et al.*, 1997; Nenaah, 2010; Fürstenberg-Hägg *et al.*, 2013). Alkaloids are differentially distributed in the plant tissues, usually occurring in higher concentrations in younger leaves (Eltayeb *et al.*, 1997). However, as no differences in hatching success were found between young and mature leaves, it is possible that other factors, such as physiological features of plants, or ecological constraints such as the presence of natural enemies, can determine oviposition site preference (Piyasaengthong *et al.*, 2016). However, it is also possible that the preference of *E. maculicornis* for mature leaves as oviposition sites may be simply explained by their higher availability in the field.

Demographic analyses

Lambda (λ) was < 1 in *E. maculicornis*, indicating that this population is decreasing. This could be due to intrinsic factors

(such as low fecundity, low egg hatching success, etc.) or ecological factors such as predation, competition or chemical defences of the host. Given that *E. maculicornis* and *E. chrysur* use the same host species, competition for best feeding or oviposition areas could occur and also affect λ (Morris *et al.*, 2004). Furthermore, the host of *E. maculicornis* could be suboptimal (Vanbergen *et al.*, 2003) or it could have chemical defences that affect the life cycle and hence the population dynamics of this treehopper, as has been reported for other solanaceous hosts (Alves *et al.*, 2007; Arab *et al.*, 2012). In order to clarify the ecological causes responsible for the population decrease, detailed life table response experiments (LTRE) (Caswell, 2001) should be pursued for this species.

Elasticity analysis revealed that stasis contributed to λ more than growth or fecundity. Pfister (1998) found similar results in several widely different taxa (vertebrates, invertebrates and plants). Our result may be biased by the reduction of the number of stages considered in the model used, which causes more individuals to remain at the same stage for a longer period of time instead of moving to the next stage (growth) (Enright *et al.*, 1995). In any case, fecundity does not contribute much (<1%; Table 1) to changes in λ , which also raises the question as to why some *E. maculicornis* females lay several egg masses instead of investing in maternal care, especially as maternal care occurs mostly when offspring are at the egg stage.

The results presented herein demonstrate that reproductive strategies and related behavioural traits such as maternal care may not be species-specific traits but rather plastic traits that change in response to the environment. Comparative studies focusing on insect reproductive strategies and factors related to the variation of egg mass production should be pursued in order to verify the generality of this conclusion.

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CFP conceived and designed the study. LCS, DTB and HMN wrote the paper with contributions from CFP. LCS, RC, KR and SA conducted fieldwork and data collection. LCS, DTB, RC, KR and SA analysed the data. All authors read and improved the manuscript and agreed its final content. The authors declare that they have no conflict of interest.

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