Leaf selection and daily variation on feeding and oviposition of *Gratiana spadicea* (Klug) (Coleoptera, Chrysomelidae, Cassidinae)

Lenice Medeiros[1]
Gilson R.P. Moreira[2]

ABSTRACT: *Gratiana spadicea* (Klug) (Coleoptera, Chrysomelidae) is a monophagous beetle that feeds only on leaves of *Solanum sisymbriifolium* Lamarck (Solanaceae). We determined the portions of S. sisymbriifolium leaves that are used by the adults as feeding and oviposition sites. Daily variation on larval and adult feeding frequency, and on oviposition, was also registered under laboratory conditions (25°C; $70^{+}10\%$ rh). Larvae and adults were fed with *S. sisymbriifolium* leaves during photo (14 hours) and scotophase (10 hours). At the end of each phase, it was measured the leaf area they ate and registered position of their feeding marks on leaves. The oothecae were counted and noted, regarding their position on the leaf blade. Larvae and adults of *G. spadicea* showed feeding activity during photo and scotophase. Oviposition was restricted to photophase. Females leaf consumption rates were greater than those of the males. Adult feeding marks were most frequent on leaf margins. Oothecae were most frequently found near the central vein of the abaxial leaf surface. Daily ingestion rates grew exponentially through the larval stage; fifth instar ingested more than 60% of the total

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[1] *Departamento de Biologia Química, UNIJUI, Caixa Postal 560, 98700-000, Ijuí,RS and PPG Entomologia, UFPR, Caixa Postal 19020, 81531-990, Curitiba, PR, Brasil. lenicem@.unijui.tche.br*
[2] *Departamento de Zoologia, IB, UFRGS, Av. Bento Gonçalves, 9500, 91501-970, Porto Alegre, RS, Brasil. gilson.moreira@ufrgs.br*

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amount of food consumed by the larval stage. The possible adaptive mechanisms involved in such feeding and oviposition patterns are discussed.

Key words: *Gratiana*, Cassidinae, leaf selection, feeding behavior, oviposition behaviour.

INTRODUCTION

Gratiana spadicea (Klug, 1829) (Coleoptera, Chrysomelidae, Cassidinae) is found in the South of Brazil, North of Argentina and Uruguay, feeding exclusively on leaves of *Solanum sisymbriifolium* Lamarck, 1927 (Solanaceae) (FRERS, 1925; KVASINA & PONCE De LEÓN, 1985; BECKER & FRIEIRO-COSTA, 1988; BUZZI, 1994; JOLIVET & HAWKESWOOD, 1995; BECKER & FREIRE, 1996; BOROWIEC, 1996; PONCE De LEÓN *et al.*, 1999). This plant can reach up to two meters in height, and bears thin thorns on the stems, petioles and central vein of both sides of the leaves. It spontaneously grows in altered places, such as highways borders, fallow lands and pastures (MENTZ, 1998).

Solanum sisymbriifolium was accidentally introduced in South Africa where became an economically important weed, what stimulated the import of *G. spadicea* to be used as its biological control agent (HILL & HULLEY, 1995). Although considered a weed in some regions of Brazil (LORENZI, 1991), *S. sisymbriifolium* seems not to require intensive control practices, probably because *G. spadicea* keeps its populations under low densities. According to FREIRE (1982), *G. spadicea* populations can usually reach high-density level that imposes considerable damage for *S. sisymbriifolium* plants.

Many studies on *G. spadicea* biology have been accomplished in Rio Grande do Sul State (FREIRE, 1982; FRIEIRO-COSTA, 1984; ALBUQUERQUE & BECKER, 1986; BECKER & ROMANOWSKI, 1986; BECKER & FRIEIRO-COSTA, 1988; BECKER & FREIRE, 1996). All life stages are found from February to April. In May only the adults are found, when they enter in a state of reproductive quiescence. Then, they stay on hidden places throughout autumn and winter, from which they depart during spring, when a new cycle begins on *S. sisymbriifolium* (BECKER & FREIRE, 1996). The sexes can be recognized, in sexually mature individuals, through observation of the ventral region of the abdomen. In the females it is possible to visualize, by transparency, the white oviducts, while the males have orange testicles. The adult longevity varies between sexes. Males live more (about 198 days) than females (about 84 days). Each female produces an average of 640.95 eggs, distributed in 92.05 oothecae (ALBUQUERQUE & BECKER, 1986).

In spite of being a relatively well known species, several basic aspects concerning the behavior of *G. spadicea* have not been studied yet, as for example those related to feeding and oviposition. Besides the ecological relevance, such kind of information is important to subsidize a varied assembly of laboratory experiments on *G. spadicea* feeding and oviposition (MEDEIROS & MOREIRA, 2002). In this sense, this study had as objective the determination of: 1) the daily rhythm of feeding and oviposition of *G. spadicea*; 2) the portions of *S. sisymbriifolium* leaves more often used by the adults, as feeding and oviposition sites, and 3) the daily leaf consumption rates of all larval instars.

MATERIALS AND METHODS

Plants used in this study were grown from seedlings of *S. sisymbriifolium* (about 100) that were transplanted into plastic pots, from the vicinity the Universidade Regional do Noroeste do Estado do Rio Grande do Sul (UNIJUI) campus, in Ijuí, Rio Grande do Sul State. These were filled with soil removed from the same places where the seedlings were taken. They were maintained in a green house, and were watered daily.

The insects were obtained from a *G. spadicea* rearing maintained on potted plants of *S. sisymbriifolium*, placed in a chamber (14 hour light, 25°C; 70±10% rh), located at UNIJUI entomology laboratory. In order to determine the daily *G. spadicea* feeding activity pattern, males (n=103) and females (n=92) were individualized in transparent non toxic plastic pots (9.5 cm height X 9.5 cm wide), containing moist filter paper, over which an intact leaf of *S. sisymbriifolium* (central vein varying from 9 to 12.6 cm in length) was placed. To keep the leaves fresh, their petiole apical portion was covered with a piece of moist cotton. The leaves were replaced at the end of each photo and scotophase. In the occasion, they were searched for the presence of feeding marks and oothecae, and the leaf area eaten determined. This was measured by placing the leaf against graph paper and counting the square millimeters corresponding to the area missing. The data were compared between sexes and light regime through Mann-Whitney tests, since it was not possible to fulfill the premises for using parametric analyses (ZAR, 1996). For recording the feeding mark positions, *S. sisymbriifolium* leaves were divided into three areas relative to the longitudinal axis. They corresponded to the distal, medium and proximal leaf portions. In addition, the leaf was also laterally divided into three regions, the central and the lateral veins, and the leaf margin (Fig. 1). The oothecae positions were determined only for the lateral regions at the adaxial and abaxial leaf sides. The corresponding frequencies between leaf sides were compared through Chi-square tests, in relation to sex and axes within leaf.

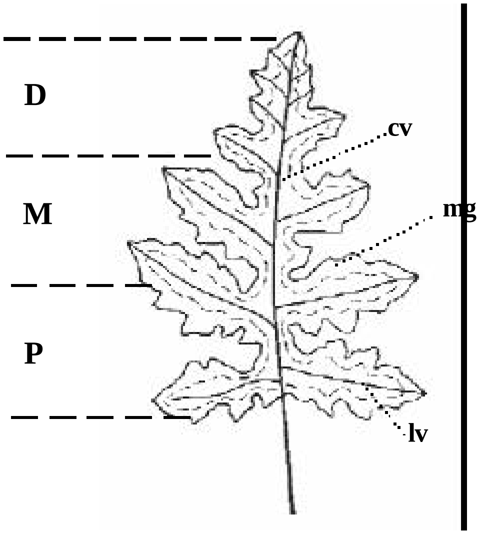

Fig. 1. Schematic representation of a *Solanum sisymbriifolium* leaf, showing the portions used for determining the distribution of Gratiana spadicea adult feeding marks. Longitudinal portions: (D, M, P) distal, median, and proximal, respectively; lateral portions: (cv) central vein, (lv) lateral vein, (mg) margin.

To determine the daily feeding activity of *G. spadicea* larvae, it was carried out an experiment similar to that described for the adults. In this case, instead of whole leaves, leaf disks (area=35.8 mm^2) of *S. sisymbriifolium* were used. The number of leaf disks offered per light phase varied from one (first and second instar) to four (fifth instar). At the end of each light phase, the leaf area eaten was determined as described for the adults. Based on these results, a daily consumption rate curve was determined in relation to the larval instar.

Seeking to determine the existence of variation within light phases on *G. spadicea* females feeding and oviposition, an additional experiment was accomplished. Females (n=20) were observed at every hour. In the occasion, the leaves offered as food and oviposition substrate were previously placed against graphic paper where their contour was drawn. The corresponding area eaten was determined later by subtraction, following the procedure already described. Also, the feeding marks and oothecal positions were noted. In order to avoid disturbing the insects during dark observations, an incandescent light, which was covered with a piece of red cellophane paper, was used. This experiment was accomplished in three consecutive days.

RESULTS

Feeding activity of *G. spadicea* was significantly greater in photophase than in scotophase, for both males ($\chi^2_{2,\,0.05} = 8.71$; $p<0.05$) and females ($\chi^2_{2,\,0.05} = 7.84$; $p<0.05$). The leaf area (mm^2/hour/individual) consumed did not differ between the sexes (Fig. 2 a, b). On the other hand, females consumed significantly greater leaf area than males, during both photo (Mann-Whitney test; U =2183; $p<0.05$) and scotophase (Mann-Whitney test; U =1321; $p<0.05$).

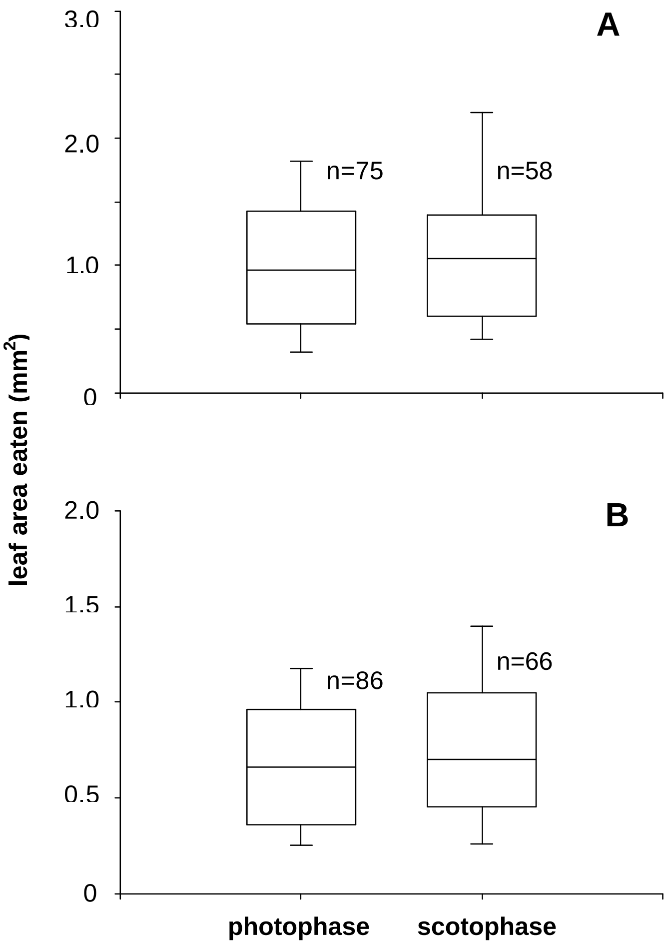

Fig. 2. Leaf area consumption (median and quartiles) of *Gratiana spadicea* females (A) and males (B), in relation to light phase (14 hours light and 10 hours dark). There was no significantly effect of the light phase on leaf consumption between sexes (Mann-Whitney tests, α =0.05).

It was registered 1137 feeding marks, from which 652 (57.34%) were made by *G. spadicea* females, and 485 (42.66%) by the males. The distribution of the feeding marks in relation to the leaf portions did not differ between the sexes ($\chi^2_{2,0.05} = 2.156$; $p>0,05$). For both sexes, the highest frequency of marks occurred on the margin of the distal portion of the leaf (Fig. 3a,b).

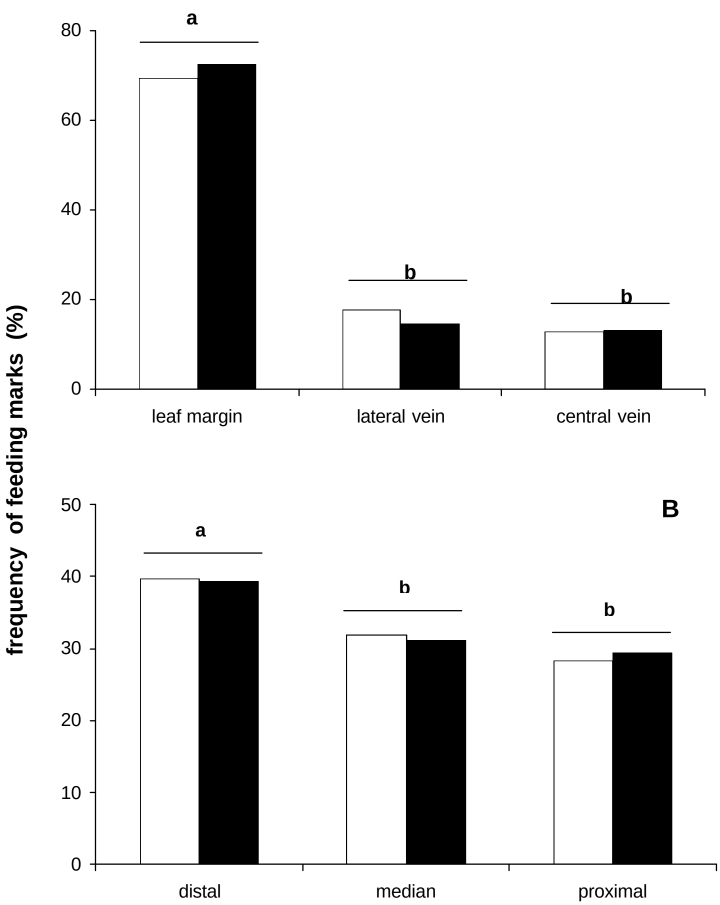

Fig. 3. Feeding mark frequencies (n=1137) of *Gratiana spadicea* males (dark bars) and females (white bars) in relation to the longitudinal (A) and lateral (B) portions of Solanum sisymbriifolium leaves. There was no sex effect on feeding mark frequency for any leaf portion. Leaf portions followed by the same letters do not differ significantly (Chi-square tests, α=0.05).

The oothecae (n=94) were most frequently deposited (55.3%) at the central vein (Fig. 4). The frequency of oothecae was significantly higher ($\chi^2_{2,0.05} = 8.34$; $p<0.05$) at the abaxial (64.9%) side of the leaf, compared to the adaxial (25.1%).

As verified for the adults, the number of *G. spadicea* larvae on feeding activity was significantly higher in photophase. The amount of food (mm^2/hour/individual) consumed by the first, second and third larval instar was significantly greater in photophase than in scotophase. For the remaining larval instars there was no difference in food consumption regarding variation in light regime (Tab. 1).

Table 1. Leaf area ingestion rate (average ± standard error) of *Gratiana spadicea* larvae under photo (14h) and scotophase (10h).

Instar	**Photophase**		**Scotophase**	
	n	**mm²/hour**	**n**	**mm²/hour**
I	79	0.19 ± 0.01 [a]	67	0.14 ± 0.01 [b]
II	52	0.49 ± 0.04 [a]	40	0.33 ± 0.04 [b]
III	77	1.08 ± 0.07 [a]	57	0.74 ± 0.07 [b]
IV	75	1.63 ± 0.11 [a]	53	1.41 ± 0.15 [a]
V	61	4.91 ± 0.32 [a]	55	4.33 ± 0.39 [a]

Averages followed by the same letters do not significantly differ, for a given instar (Student *t* tests; $\alpha = 0.05$).

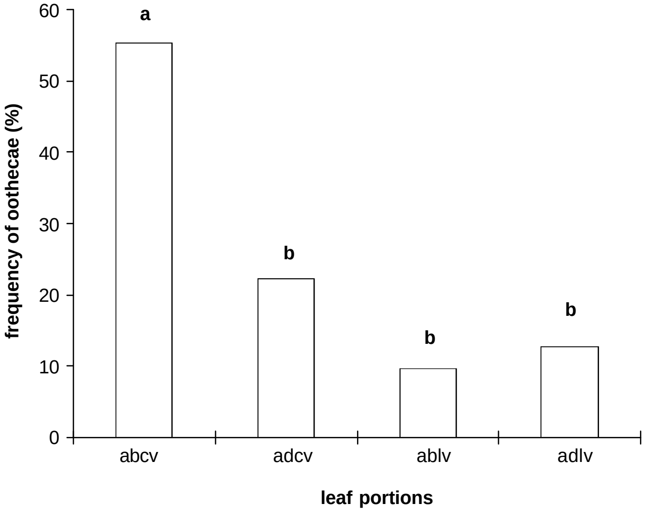

Fig. 4. Variation in *Gratiana spadicea* oothecal (n=94) position on *Solanum sisymbriifolium* leaf portions. (ab) abaxial surface; (ad) adaxial surface; (cv) central vein, and (lv) lateral vein. Bars followed by the same letters do not significantly differ (Chi-square tests, α=0.05).

Gratiana spadicea food consumption rates increased exponentially throughout the larval stage. The fifth instar larvae were responsible for the ingestion of more than 60% of the leaf area consumed in this stage of the life cycle (Fig. 5).

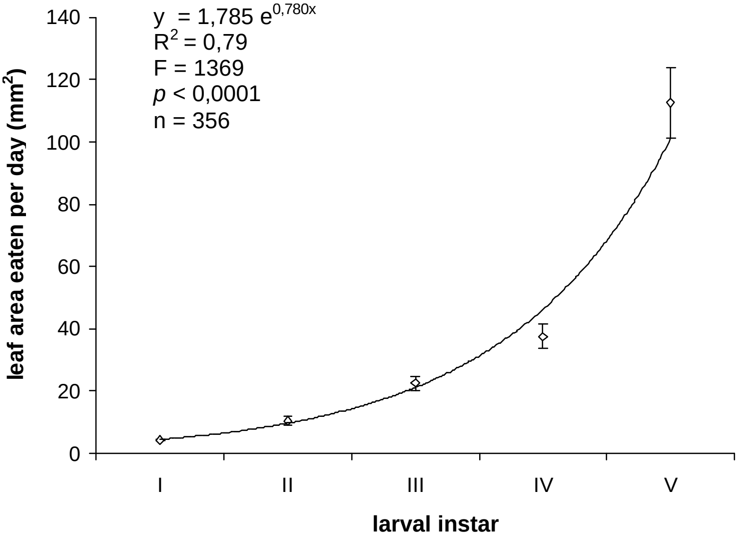

Fig. 5. Leaf consumption (mm²/individual/day) of *Gratiana spadicea* larvae on *Solanum sisymbriifolium* leaves. The dots represent the averages and their respective 95% confidence intervals.

All the oothecae were deposited during photophase. The egg laying activity started at the second hour of photophase and finished two hours before the scotophase beginning (Fig. 6a). There was a coincidence between the peak of egg deposition and female food consumption, as both occurred at 6:00 p.m. (Fig. 6b).

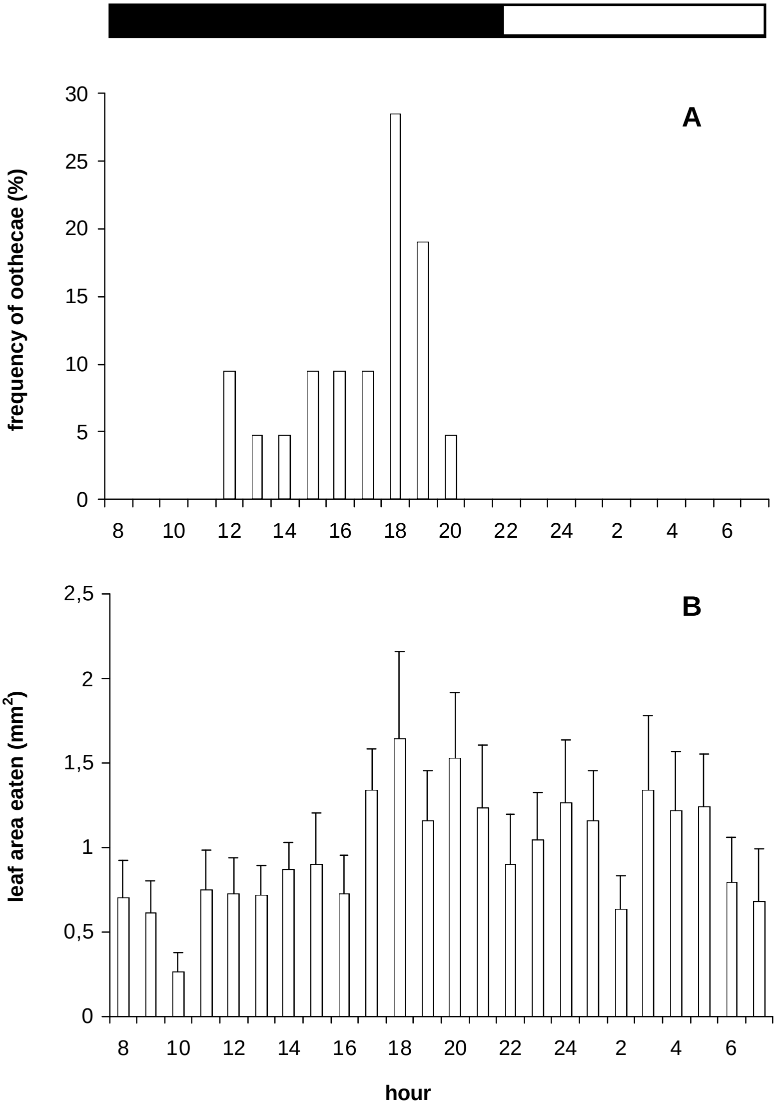

Fig. 6 . Oviposition (A) and feeding (B) daily rhythm of *Gratiana spadicea* females on *Solanum sisymbriifolium*. White and dark upper bars indicate photo and scotophase, respectively. Data in Figure B correspond to the average (± standard error) activity of 20 females during three consecutive days.

DISCUSSION

Our data have demonstrated that feeding activity of larvae and adults of *G. spadicea* occurs under both photo and scotophase, and that oviposition behavior is markedly affected by variation in light regime, being restricted to the photophase. The influence of the photoperiod on animals and plants is a relatively well-known phenomenon. It allows the organisms to distinguish between long days of summer and short days of winter (SAUNDERS, 1982; BECK, 1980). The distinction between and/ or duration of daily phases of brightness and darkness mediates a series of seasonal behaviors (*e.g*., flowering and fruiting in plants, diapause in animals), and also influences some life history traits, such as the development rates of several species (SAUNDERS, 1982). Photoperiod also exerts influence on the organism daily activities (or routine) when under either light or dark phases. This kind of influence dictates the organism circadian rhythm, which is responsible for the time allocation that characterizes the species as being either of the day, night or twilight type (BECK, 1980; MARQUES *et al*., 1997).

No animal can use the totality of its time in feeding activities, because this is incompatible with other important behaviors, such as mating, defense against natural enemies, oviposition, or simply rest. Feeding, as well as any other activity of an organism, involves costs and risks and, therefore, it is reasonable to suppose that there are trade-offs between rates of consumption, processing and assimilation of the food (CUTHILL & HOUSTON, 1997).

According to SLANSKY (1983), folivorous insects usually dedicate at least 20% of their daily time for feeding. To a herbivore as *G. spadicea* the relative low mobility (mainly in the larval stage) determines the whole life cycle to be passed on the same plant. So, to this beetle, one can consider that the energy costs related to the food searching is practically null, what theoretically allows them to feed continually, at least under experimental conditions. It is important to consider that such conditions exclude the exogenous risks associated to the feeding activity of the insect, as for example, the exposure to variation on abiotic (mainly temperature and humidity) and biotic factors (e.g. natural enemies). Thus, it is probable that feeding activity of *G. spadicea* is even more restricted under natural conditions. In the laboratory, the first three larval instars showed a decrease in food consumption during scotophase, which may be associated to a decrease of the feeding frequency. On the other hand, the two last larval instars need to accumulate energy for the pupal stage, what possibly justifies the fact that they continually feed, in both photo and scotophase. Some authors observed that larvae of some Lepidoptera species dedicate up to 50% of their daily time for feeding during the fifth instar (HEINRICH, 1979; RAUSHER, 1981; SCHMIDT *et al*., 1988).

The daily feeding curve of *G. spadicea* larvae followed the pattern found for many other holometabolous insects, where most of the food consumption occurs in the last larval instar (SCRIBER & SLANSKY, 1981; SLANSKY, 1983). In general, these larvae consume near 60% of the total food ingested in this development phase, which is associated to the necessity of energy accumulation that guarantees the survival in the pupal stage (SLANSKY, 1983).

Differences between the amount of food ingested by male and female insects are relatively common, mainly in direction of the sex that presents the largest size (SCRIBER & SLANSKY, 1981; SLANSKY, 1983). This seems to be the case of *G. spadicea*. PONCE De LEÓN *et al*. (1999) showed for a population of this cassidine in Uruguay that females are significantly larger than the males. Although we have not made any measure relative to size of *G spadicea* adults used in the experiments, apparently females presented larger size than the males. All the adults that we used had reached sexual maturity and we suppose they were in reproductive activity. In this sense, it is possible that the reproduction *per se* contributes to the greatest food consumption by the females, since they request greater energy for oogenesis and oviposition.

Unlike feeding activity, *G. spadicea* females only oviposited in photophase. According to MARQUES *et al*. (1997), the organisms tend to establish stable relationships with their environmental cycles, choosing either a light or dark phase as a reference to execute certain activities. They present a rhythmic pattern of operation related to light regime, which was probably settled down along to their evolution (MARQUES *et al*., 1997).

Additional studies are necessary to a better understanding of the role of environmental factors in the establishment and maintenance of this pattern in *G. spadicea*.

FRIEIRO-COSTA (1984) and MEDEIROS (2000) have also found a higher frequency of oothecae on the abaxial side of *Solanum sisymbriifolium* leaves under field conditions. Oviposition site selection, both at the inter- and intra-specific levels, has been demonstrated for many species of herbivore insects (FEENY *et al*., 1983; SINGER, 1986; JONES, 1991; RENWICK & CHEW, 1994). Such selectivity is, in many cases, related to greatest larval performance (THOMPSON, 1988; 1996). In this sense, new experimental studies are necessary to detect if there is some adaptative advantage for *G. spadicea* related to the oothecae differential positions on the leaves of *S. sisymbriifolium*. In the same way, the adaptative value related to the higher frequency of the adults feeding near the leaf edges must be better evaluated. Both larvae and adults of *G. spadicea* feed in the same host plant and it is reasonable to consider that, at least in some occasions, they compete for feeding sites. If it is so, as the adults move away from the sites where the larvae are born, they may indirectly guarantee prompt, suitable food for newly hatched individuals, which in consequence do not have to move early to other intact feeding sites. This is a potentially energy costly and risky activity, since the stellate trichomes that cover *S. sisymbriifolium* leaves mechanically lead to heavy mortality and slow down first instar movement in this cassidine beetle (MEDEIROS, 2000; MEDEIROS & MOREIRA, 2002).

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