Developmental biology, polymorphism and ecological aspects of Stiretrus decemguttatus (Hemiptera, Pentatomidae), an important predator of cassidine beetles

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ABSTRACT. Developmental biology, polymorphism and ecological aspects of *Stiretrus decemguttatus* (Hemiptera, Pentatomidae), an important predator of cassidine beetles. *Stiretrus decemguttatus* is an important predator of two species of cassidine beetles, *Botanochara sedecimpustulata* (Fabricius, 1781) and *Zatrephina lineata* (Fabricius, 1787) (Coleoptera, Cassidinae), on the Marajó Island, Brazil. It attacks individuals in all development stages, but preys preferentially on late-instar larvae. Its life cycle in the laboratory was 43.70 ± 1.09 days, with an egg incubation period of six days and duration from nymph and adult stages of 16.31 ± 0.11 and 22.10 ± 1.67 days, respectively. The duration of one generation (*T*) was 12.65 days and the intrinsic population growth rate (*r*) 0.25. These data reveal the adjustment of the life cycle of *S. decemgutatus* with those of the two preys, but suggest greater impact on *Z. lineata*. However, no preference over cassidine species was shown in the laboratory. Up to 17 different color patterns can be found in adults of *S. decemguttatus*, based on combinations of three basic sets of color markings. Some of them resemble the markings of chrysomelids associated with *Ipomoea asarifolia* (Convolvulaceae) and are possibly a mimetic ring. Three color patterns were identified in nymphs, none of which was associated with any specific adult color pattern.

KEYWORDS. Asopinae; color pattern; Ipomoeae asarifolia; life table; predation.

Stiretrus decemguttatus (Hemiptera, Pentatomidae, Asopinae) is a South American polymorphic species (Thomas 1992) and a predator of Chrysomelidae. In 1953, Bondar recorded it attacking larvae and adults of Zatrephina lineata (Fabricius, 1787) on São Luis Island, Maranhão State, Brazil, while Van Doesburg (1970) detected its attacks on larvae and pupae of Paraselenus flava (Linnaeu, 1758) in Suriname.

Natural history data about this predator are unknown, probably due to the paucity of studies about its Cassidinae prey (Buzzi 1988; Buzzi, 1994; Moura & Grazia 2011). In 1990, the author of this paper observed *S. decemgutattus*, in the city of Salvaterra, attacking *Botanochara sedecimpustulata* (Fabricius, 1781) and *Zatrephina lineata*, chrysomelid leaf-eaters of *Ipomoea asarifolia* (Ders.) Roem. & Schult. (Convolvulaceae). Consequently, it is expected that the predator can play a fundamental role in the coexistence pattern of these Cassidinae beetles, according to the specific degree of vulnerability of each of these prey (Freeland 1983; Lawton 1986).

Investigations into the life cycle and aspects of the predation ability of *S. decemguttatus* on eggs, larvae, and pupae of *B. sedecimpustulata* and *Z. lineata* could evaluate the importance of this predator on populations of these prey and the consequences for community structure of herbivorous insects feeding on *Ipomoea asarifolia*. Because it is a polychromatic species (Thomas 1992; Van Doesburg 1970), whose color morphs exhibit very similar patterns to those of *Stiretrus decastigmus* morphs (Poncio *et al.* 2010), there is a need to study ecological genetics of *S. decemguttatus*, since differences in fecundity, viability, mating forms, seasonal frequencies, and mimetic relationships of individuals with different patterns, which have been detected for several species (Ford 1975; Bourdouxhe & Jolivet 1981; Vasconcellos-Neto 1988; Paleari 1994), may determine particular adjustments of the predator to each Cassidinae prey.

In the present study, a field survey was conducted to characterize the different color patterns of adults and nymphs *Stiretrus decemgutattus* found on the Marajó Island and laboratory data on the prey species and stage preference and on its life cycle are also given.

MATERIAL AND METHODS

The stages of research set out below and further described in specific items were developed in the city of Salvaterra (00° 45'12''S, 48° 31'00''W), at the Marajo Island, Pará State. Climatic data were recorded at the Meteorological Station of the National Institute of Meteorology, INMET (00°44'S, 48°31'W), in the city of Soure (Fig. 1).

General observations on the natural history of *S. decemgutattus*, in vacant lots in the cities of Salvaterra and Soure, took place in 1990. In 1991, a field survey was carried out in the city of Salvaterra to observe polymorphism and ecological aspects of this predator. In parallel, to better understand and analyze behavioral aspects of *S. decemgutattus*, a broad study was conducted on the biology and popu-

lation dynamics of their Cassidinae prey, *Botanochara* sedecimpustulata and Zatrephina lineata, which will be the subject of future papers.

Color polymorphism. Color patterns of *S. decemgutattus* observed for thirty-four months in field and laboratory were described and some were also photographed and drawn. A reference collection was organized and deposited at the Museum of Zoology "Professor Adão José Cardoso", State University of Campinas.

In the field, from May 1991 to May 1993, data on *S. decemgutattus* were obtained during surveys of Cassidinae prey, according to the methodology of Paleari (1997), which included examining *I. asarifolia* once a month in: a) an area of 100 m² of a farm located in the vicinity of Salvaterra, b) within thirty patches which were growing in sidewalks and streets of Salvaterra. Nymphs and adults of *S. decemgutattus* were recorded and their color patterns were also described.

Laboratory experiments. In December 1993, four females of the predator were used to start a laboratory population, which was kept in captivity until March 1994, in a balcony surrounding the building. This balcony was protected with mosquito screen and it was under ambient temperature and relative humidity.

Food preference tests. Ten males and 10 females of *S. decemguttatus* were starved during 12 h and individualized on Petri dishes (10 cm diameter) covered with moist filter paper. Each dish contained a portion of *I. asarifolia* leaf (3.5 cm diameter) with a clutch of eggs, a pupa, and a larva from each instar of *B. sedecimpustulata*, the most abundant species at the site. This set was renewed seven times for each one of the 20 bugs tested. Observations and data records of each series were carried out once a day, for up to 4h, in the afternoon, and referred to the behavioral aspects and the phase

of the first Cassidinae caught by the 140 adult *S. decemguttatus*. This period was based on previous observations of *S. decemgutattus* towards their prey, which were often attacked and consumed after two to three hours.

Adults of *B. sedecimpustulata* were excluded from the tests because of the rarity of attacks on individuals in this stage. The preference of *S. decemgutattus* for *B. sedecimpustulata* and the *Z. lineata* prey was tested using the same Petri dishes described above, each with one fifth-instar larvae of each cassidine species. Preparations were also renewed in each of the seven repetitions, after observation and record of the first predated species in the 4-hour period.

Developmental biology. Egg clutches with 60 eggs from four females (Patterns 2, 3 and 5 – Table I) of *S. decemguttatus* collected in vacant lots in Salvaterra were placed in labeled transparent jars (4 cm high by 2.5 cm in diameter).

After hatching, the nymphs were kept for one day with the chorion and, after the first molt, placed in individual plastic boxes (10 cm length by 7 cm width and 4 cm height). To provide ventilation, an area of 12.5 cm² was cut out of the lids and replaced with organza. The bottom of each box was lined with slightly moistened absorbent paper upon which was placed a leaf of *Ipomoea asarifolia*, the food of the Cassidinae prey.

Molt of each individual at the end of each day was recorded, the box was cleaned, and a fresh *I. asarifolia* leaf and 4 fifth instar larvae of *B. sedecimpustulata* offered to *S. decemgutattus* were placed in it. All prey offered to the asopine nymphs and adults in captivity were collected in the field.

Upon emerging, the adults of *S. decemgutattus* were identified and characterized per sex and color pattern. Then, 24 pairs were organized and each one was kept in a box similar

Table I. Descriptions of color patterns of variegated and non-variegated adults of *Stiretrus decenguttatus* found in Salvaterra and Soure, Pará State, Brazil and offspring phenotypes in the developmental biology study (see table IV).

Pattern	Dorsal aspect				Pattern	Offspring phenotype		
	Spot design	Spot color	Background (scutelum-corium)/Head-leg		number	Male	Female	Nymphs
Variegated		Black or Median-brown	Whitish		1	19	0	3C 1-2
	Elongated		Whitish with median-brown stains		2	4	3	3C 1-2
			Red		3	0	2	3C 1
		Dark red	Whitish		4	1	0	3C 2
		Median-brown	Whitishwith plenty of median-brown		5	0	0	0
	Circular	~	Wine		6	1	0	3C 3
		Creme – sometimes with	Dark red		7	2	0	3C 3
		Teu Sireak	Black		8	0	0	0
		Red	Black		9	0	0	0
Not variegated	Not motallia		Madian brown	head and legs ochre	10	0	6	3C 1
	Not metame		Wiedian-Diown	head and legs black	11	0	4	3C 1-2
			Green	head and legs ochre	12	0	5	3C 1
				head and legs black	13	0	2	3C 1-2
	Matallia		Dhua	head and legs blue	14	0	1	3C 2
	Wietanie		Blue	head and legs ochre	15	1	0	3C 2
			Violet	head and legs violet	16	0	2	3C 1
				head and legs ochre	17	0	0	0

to the one used for the nymphs, with the same feeding routine, 9^{th} and 12^{th} day pupae. Subsequently, with the scarcity of immature stages, each breeding box received a pair of *B*. *sedecimpustulata*.

Daily records kept for each of these pairs consisted of the behavioral aspects, number of clutches, and their respective number of eggs and hatchings, sex and color pattern of the descendants, as well as the number of larvae consumed during the first four days after mating.

RESULTS

Climatic conditions and ecological aspects of the predator and their cassidine prey. All the adults and nymphs of *Stiretrus decemguttatus* observed in the field were found on patches of *Ipomoea asarifolia*, with cassidine populations of *Botanochara sedecimpustulata* and *Zatrephina lineata*, especially in the rainy season (Fig. 1). The asopine bugs were found feeding mainly on late instar cassidine larvae (Fig. 2E and 3C). In only one situation a female adult of *B*.



Fig. 1. Mean monthly values of temperature (°C) relative humidity (%) and rainfall (mm) from January 1993 to December 1994 in Soure (00°44'S, 48°31'W), Marajó Island, Pará State, Brazil (Source: National Institute of Meteorology – INMET).

sedecimpustulata was attacked by *S. decemgutattus* (Fig. 2D). The only egg clutches (Fig. 3A) detected in the field were camouflaged in dry calyxes of *Sida* sp. (Malvaceae) growing in a patch of *I. asarifolia*. These two cassidines were the most abundant prey of *S. decemguttatus* in Salvaterra and Soure. *Botanochara impressa* and *Chelymorpha* aff. *alternans*, other vulnerable species, were observed sporadically in the field, usually as solitary adults.

Around mid-December, *B. sedecimpustulata* restarted their feeding and breeding activities, after diapause that kept them inactive for up to nine months. Around March, the population of this cassidine prey had greatly increased, with an abundance of larvae damaging the host plant *Ipomoea asarifolia*. Population size of *Z. lineata*, a species that does not undergo diapause, had also increased, but its number remained below that of *B. sedecimpustulata*. The increase in the number of larvae was followed by the number of nymphs and adults of *S. decemgutattus*.

Color patterns of S. decemgutattus recorded. Color patterns of hundreds of adults observed could be classified into 17 morphs, showing uniform (without spots) or variegated patterns (Fig. 2). The former comprise metallic (Fig. 2A 15 and 2F pair) and non-metallic (Fig. 2A 9 and 10) colors (Table I, patterns 10 to 17), while variegated adults display variable patterns, i.e., circular (Figs. 2A 1, 2B 2 and 2E) or elongated (Figs. 2A 2 to 8 and 11 to 14; 2B 3 to 6; 2 D) maculae on the dorsal area (Table I, patterns 6 to 9 and 1 to 5, respectively). Depending on the degree of fusion of the elongated maculae, individuals will present eight to 10 maculae, while individuals with circular designs invariably present 10 maculae. Patterns 2, 4 (Figs. 2A 2 to 8 and 11 to 14), 10 (Fig. 2A 9 and 10), and 11 were the most common in the field and laboratory (Table I, offspring phenotype). The rarest, 8 and 9 (Fig. 2E), observed only in 1991 and 1994, respectively, seem to be phenotypes more common in males.

In the period of drought (Fig. 1) and diapause of *B.* sedecimpustulata prey, we recorded the appearance of a large number of adults of an Eumolpinae (Chrysomelidae), rare at other times of the year, which was also feeding on the tender leaves of *I. asarifolia*, and whose color patterns resembled patterns 14 to 17 of *S. decemguttatus* (Fig. 2F).

Color patterns of nymphs (Figs. 3C and 3D) were divided in three phenotypes, with types C1-D1 and C2-D2 being the most common and involving warning colors. Type C1-D1 consists of a black head, thorax, wing pads, legs, and abdominal markings, with the rest of the abdomen red or reddish-orange. Type C2-D2 differs from C1-D1 only by the presence of two reddish markings on the thorax, and the head that may be all red. Nymphs of the third phenotype (Figs. 3C 3 and 3D 3) are rarer and completely orange. Nymphs with this pattern collected in the field, resulted in adults with the color pattern eight. Nymphs with different phenotypes in the fifth instar may originate adults with a similar pattern, while a pair with a given pattern may produce offspring with individuals of different color patterns, even from the same egg clutch.

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Fig. 2. Adults of *Stiretrus decemgutattus*: Color patterns variegated (A 1–8, 11–14 and B 2–6) and not variegated (A 9, 10, 15 and B 1); Ventral aspect of adults (C); Three adults preying on a female of *Botanochara sedecimpustulata* (D); adult color pattern very similar to the *B. sedecimpustulata* (E); pair very similar to adult (right) of crysomelid Eumolpinae (F); for details of adult color patterns see Table I.

Food preference tests. Botanochara sedecimpustulata predation by S. decemgutattus in laboratory, during the four hours (Table II), showed 57 predated larvae, corresponding to 40.7% of the 67 attacks, 75.44% of individuals in fourth and fifth instars. First to third instars larvae, eggs, and pupae sustained 14, six and four attacks, respectively, represent the development stages of least interest to S. decemgutattus. In these experiments, in which the preference of S. decemguttatus for one of the stages of development of the prey was investigated, 56 males and 17 females did not attack any prey during 4 h of observation. However, in this interval of time, many of them fed on a portion of I. asarifolia leaf placed on the respective dishes.

Table II. Eggs, larvae, and pupae of *Botanochara sedecimpustulata* preyed by *Stiretrus decemgutattus* in laboratory.

Total consumption		
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* Males and females did not attack any prey.

Offered a choice between larvae of *B. sedecimpustulata* and of *Z. lineata* (Table III), males and females of *S.*

decemguttatus did not demonstrate a preference for either of these Cassidinae species ($\chi^2 = 1.8346/GL = 1$; P > 0.05), nor was the higher predation of *Z. lineata* larvae by the males statistically significant ($\chi^2 = 1.0362$; GL = 1; P > 0.05).

Table III. Fifth instar larvae of *Botanochara sedecimpustulata* and *Zatrephina lineata* consumed by *Stiretrus decemgutatus* adults in laboratory.

Adults	Fifth-instar lavae					
S. decemguttatus	B. sedecimpustulata	Z. lineata	Total consumption			
Male (N = 70)	29	41	70			
Female $(N = 70)$	37	33	70			
Total consumption	66	74	140			

Developmental biology. The predator's courting ritual, which was observed in the laboratory, usually takes place in the late afternoon soon after an oviposition. Sexually mature male faces and approaches the female, stimulating her with the ventral spine (Fig. 2C) that individuals of both sexes have, touching the female's cervical region several times prior to copulation. Copulation occurs with individuals facing away each other, the pair then remains in this position for several hours, during which the male is dragged by the female whereever she goes and does not feed, while she does it normally.

The preoviposition period of *S. decemgutattus* lasts about three and a half days and the average number of eggs per female was 52.42 ± 5.85 , with 41.25 ± 5.60 viable eggs, with typically 13 clutches (Fig. 3A), but up to 14, on moist paper covering the dishes. There was no parental care. The egg incubation period of *S. decemgutattus* in the laboratory was six days (Table IV). Although there was uniformity among the individuals monitored in this phase, cases were found of hatching in five days.

S. decemgutattus nymphs began preying on larvae only in the second instar, when they were also observed sucking on *I. asarifolia* leaves. During this instar, four of them did not prey on larvae but fed exclusively on the sap of the leaves, without death or delayed development.

When each breeding box of the *S. decemguttatus* pairs received a pair of *B. sedecimpustulata* due to the scarcity of immature stages in late January, some *B. sedecimpustulata* females oviposited and in these conditions, as in the field, their eggs were attacked, not the females. In general, few adult Cassidinae were predated, and the asopine bug restricted their feeding to *I. asarifolia* kept in the breeding boxes. After offering these adult preys in early February, no marked change was found in the survival of *S. decemguttatus*; oviposition continued for another five days (Fig. 4). The two longest living individuals lived another 21 and 23 days, up to the end of February and the beginning of March, when almost all *B. sedecimpustulata* adults were already in diapause.

From the first to the fourth instars, the development time increases, varying from 2.36 ± 0.06 to 3.31 ± 0.06 (Table IV), which were relatively short increases compared to that of the fifth instar, 5.95 ± 0.08 , which is expected due to the

greater morpho-physiological changes taking place in this phase. Proportionally, an increase was found in the consumption of larvae, which went from 1.58 ± 0.09 in the second instar to 5.20 ± 0.21 in the fifth (Table IV). The accumulated mortality rate during the juvenile stages was 8.33%, with the highest number of deaths in the fifth instar (Table IV).

Table IV. Duration of the developmental stages of *Stiretrus decemgutattus* and their consumption, respectively, of the *Botanochara sedecimpustulata* larvae (5th instar), in laboratory.

		-			
Developmental stage	n	Developmental time $(x \pm sd)$	Larvae consumption		
Egg	59	6.00 + 0.00 (6-6)	0		
N1	59	2.36 + 0.06 (2-3)	0		
N2	58	2.62 + 0.07 (2-4)	$1.58 + 0.09 \ (0-2)^1$		
N3	57	2.67 + 0.35 (2-4)	$1.95 + 0.11 (0-4)^1$		
N4	55	3.31 + 0.06 (2-4)	$2.61 + 0.14 (0-4)^1$		
N5	55	5.95 + 0.08 (5-8)	$5.20 + 0.21 \ (0-9)^1$		
Adult	53	22.10 + 1.67 (2-40)	_		
Male	28	20.29 + 1.53 (6-9)	$1.70 + 0.22 \ (0-3)^2$		
Female	25	23.91 + 1.75 (2-40)	$3.70 + 0.39 (1-7)^2$		
Total		43.70 + 1.09 (24-62)	_		

¹ Total prey consumption in the period; ² Average number of prey in the first four days after emergence.

The reproductive peak of the population occurred in late January at the beginning of the adult stage (Fig. 4 and Table V) and a higher average contribution of eggs per female between the 10th and 15th days. *S. decemgutattus* showed a high growth potential in the laboratory at the end of a generation (T = 12.7; with r = 0.26), with a net contribution of $R_0 = 26.3$ eggs per female (Table V).

Table V. Life table of *Stiretrus decemgutattus*: x, age at beginning of interval (days); n, number of alive females at the beginning of each interval; lx, proportion of females alive at the beginning of age interval; dx, proportion of female deaths in each interval; qx, proportion of dead females in relation to the number starting each interval; Fx, the sum of eggs; mx, expected daughters; lxmx, reproductive expectation.

. 66.7	, · r · ·	8	-, ,	P	r		
х	n	lx	dx	qx	Fx	mx	lxmx
0	24	1.0000	0	0	0	0	0
5	24	1.0000	0.1250	0.1250	73	3.0	3.0
10	21	0.8750	0	0	263	12.5	11.0
15	21	0.8750	0.0833	0.0952	186	8.9	7.8
20	19	0.7917	0.0417	0.0526	102	5.4	4.3
25	18	0.7500	0.5417	0.7222	4	0.2	0.2
30	5	0.2083	0.1250	0.6000	2	0.4	0.1
35	2	0.0833	0.0417	0.5000	0	0	0
40	1	0.0417	0.0417	1.0000	0	0	0
45	0	0	0	0	0	0	0
Total					630	30.4	26.3

Net replacement rate: $R_0 = 26.3$; Mean generation time: T = 12.7; Instantaneous rate of population increase: r = 0.26.



Fig. 3. Immature stages of Stiretrus decemgutattus: egg clutch (A); color patterns among nymphs (5th instar) of Stiretrus decemgutattus (B-D).



Fig. 4. Fecundity and survivorship curve of Stiretrus decemgutattus.

DISCUSSION

During the thirty-four months of observations, nymphs and adults of *S. decemguttatus* fed mainly on cassidine lar-

vae of late instar in the field and in the laboratory, when compared to early-instar larvae, pupae, and adults. Only one female adult B. sedecimpustulata was attacked by S. decemgutattus. A similar finding was reported for adults and nymphs of the predator Oplomus dichrous (Herrich-Schaeffer, 1838) (Pentatomidae) on Leptinotarsa decemlineata (Say, 1824) (Chrysomelidae) (Drummond et al. 1987). In addition to S. decemguttatus obtaining a larger quantity of food per attack (see Krebs & Davies 1996), it probably is also able to penetrate the integument of these individuals more easily than the egg chorion. Another advantage of the preferential predation on late-instar larvae is that they are solitary and their exuvio-fecal annex (Buzzi 1988) is already loose due to the partial or complete loss of the exuviae attached to the anal furculae. In addition, grouped larvae from first to third instars of B. sedecimpustulata and Z. lineata were observed repelling S. decemgutattus by cycloalexic behavior (Jolivet *et al.* 1990; Vasconcellos-Neto & Jolivet 1988, 1994), as has been reported by Eisner *et al.* (1967) and Noerdjito *et al.* (1992). Pereira *et al.* (2009) observed *Harpactor angulosus* (Lepeletier and Serville, 1825) (Hemiptera, Reduviidae) preying *Hylesia* spp. (Lepidoptera) larvae, which were also mainly isolated. The predator could achieve greater success by avoiding massive defense of the larvae, which is very aggressive with strong body movements associated with the release of a regurgitated with greenish color (Specht *et al.* 2006). Adult beetles, on the other hand, might offer the predator substantial amounts of nutritious material, but besides being well protected, especially on the abdomen covered with elytra, they can fly and escape the threat of an attack.

Neither males nor females of *S. decemguttatus* preferred any of these Cassidinae species, even though under attack, *B. sedecimpustulata* larvae moved their bodies more vigorously than *Z. lineata* larvae, repelling the predator, which sometimes attacked other species. Although, it seems that *S. decemguttatus* can get similar quality and quantity of resources from both species, by not showing any preference in the laboratory, its preference or effects on the dynamics of prey populations in the field was not studied.

Stiretrus decemgutattus nymphs began preying on larvae from the second instar, when they also suck I. asarifolia leaves or fed exclusively on sap of the leaves, without subsequent death or delayed development. Although, a strong preference of adult S. decemguttatus for one of the stages of the prey was found in the present study, over half individuals did not attack any beetle larva and many of them, on the other hand, sucked a portion of I. asarifolia leaf on the respective dishes. This habit of consuming plant and prey (omnivory) is common to many arthropods (Coll & Guerson 2002). The implications of this behavior on the biology and ecology of these animals are poorly studied (Eubanks & Stryrsky 2005; Kaplan & Thaler 2011). However, based on functional and numerical responses of omnivorous predators Eubanks (2005) stated that knowing the role of diet on development and reproduction of these species may add relatively little about the dynamics of its interactions. Other predatory Hemiptera also benefit from the host plant of their prey (Castañe et al. 2011; Lykouressis et al. 2008; Naranjo & Stimac 1985; Salas-Aguilar & Ehler 1977; Valicente & O'Neil 1995). The survival of Podisus maculiventris (Say, 1832) (Pentatomidae) increases and its development time and preoviposition period decrease when it feeds on potato leaves (Ruberson et al. 1986). However, this predator does not survive the second instar exclusively on plant diet, in this regard differing from nymphs of S. decemguttatus. In the dry season, which in Marajó begins to be felt in March and reaches its height between September and November (OAS 1974), the prey population is so reduced (Paleari 1997) that I. asarifolia may assume an important role in the maintenance of the asopine bugs. However, physiological conditions of this host plant need to be studied because its leaves become more coriaceus and with reduced water content.

Stiretrus decemgutattus maintains a complex interaction with both Cassidinae prey and *I. asarifolia*. This is partially due to specific phenology of B. sedecimpustulata prey that restarts its reproductive activities in December, when a significant growth of the population is recorded, and declines sharply between February and March (Paleari 1997). The diapause of B. sedecimpustulata represents a negative impact on the predator due to the increase consumption of larvae, greater morpho-physiological changes from the first to the fifth instar, the reproductive peak of the S. decemgutattus population at the beginning of the adult stage and its high growth potential in the laboratory at the end of a generation, with a net contribution of $R_0 = 26.3$ eggs per female. This feature should result in a further negative impact on populations of Z. lineata, which becomes the main target of the asopine bugs, with the onset of diapause of B. sedecimpustulata. Although S. decemguttatus did not prefer either prey species in the laboratory, it is more easily found in the environment after diapause, not only due to its high density but also because it exposes itself and its eggs more, both usually conspicuous on the younger leaves that stand out in patches of Ipomoea asarifolia.

A large variety of color patterns of *S. decemguttatus* adults and nymphs (Figs. 2 and 3) was found in Ilha do Marajó. *S. decemguttatus* preying on *Paraselenis flava* (Linnaeus, 1758) (Chrysomelidae) larvae and pupae in Suriname, showed only two patterns (Van Doesburg 1970) resembling those of Figs. 2A 9 and 10 (nonmetallic), 2A 15 (metallic) and 2A 1 (circular spots design). The pattern of circular designs was unique and found only in males. If this finding is not an artifact of the brevity of author's survey, it may represent the genetic composition of that population, which is different than those found in the present study, since in Salvaterra males are not monomorphic and most common patterns are those of Figs. 2A 9 and 10 (nonmetallic) and Figs. 2A 2 to 8 and 11 to 14, which Van Doesburg (1970) observed only in females.

The presence of a well-developed scutellum allied to the color patterns recorded makes S. decemguttatus very similar to the Cassidinae that feed on *I. asarifolia* (Fig. 2E and 2F; Table I - 9, 14, 17) and suggests the possible existence of mimicry, according to the hypothesis put forward by Van Doesburg (1970) after finding close similarities between S. decemguttatus and Chrysomelidae, especially Doryphora aestuans Linnaeus, 1758, which coexisted in Suriname. This explanation is more exciting considering that certain patterns (3, 4, 6, 7, 8 and 9, see Table I and Fig. 2E) involve colors generally found on aposematic insects (Brower & Brower 1964; Rothschild 1972 a, b), and that this asopine bug complements its food with I. asarifolia sap, which has toxic effects when ingested by cattle (Barbosa et al. 2005; Tortelli et al. 2008). It is possible that S. decemputattus acquires defense against natural enemies by storing secondary toxic products in its body (Duffey 1980), or by synthesizing new compounds from sap of the plant (Pasteels et al. 1983). On the other hand, the patterns of individuals 10 and 11 (Table I) are similar to those of adult Z. lineata in the dry period of the year, when the latter take on a reddish brown color resembling

that of the vegetation, which provides a certain degree of camouflage. Fifth instar nymphs with different phenotypes (Fig. 3B-C) may originate adults with a similar pattern, while a pair with a given pattern may produce individuals with different color patterns, even from the same egg clutch, a phenomenon also found by Van Doesburg (1970).

Aposematism and/or mimicry signals in *S. decemgutattus* are interesting evolutionary problems and can play an important role, especially given its common pleiotropic effect (Ford 1975), by acting upon other characteristics determined by the same genes responsible for color patterns.

Natural enemies of adult *S. decemguttatus* were not found during this study. It is possible that they may include a species of reduviid predator of adult *B. sedecimpustulata*, as well as reptiles and birds, which are very common in the region.

In conclusion, our data support that *S. decemguttatus* is an omnivorous and polymorphic species, whose high growth potential should cause a greater impact on the populations of *Z. lineata* than *B. sedecimpustulata*, and thus favor the population growth of the latter cassidine after diapause, due to an important egg parasitoid being also negatively affected.

The variegated and non-variegated adults of this asopinae bug, whose morphs differ in viability and fecundity – some resembling the markings of chrysomelids associated with *Ipomoea asarifolia* – integrate a complex system involving much more than simple advantages related to aposematism and/or mimicry of *S. decemguttatus*. For this, mating forms, type of genetic inheritance, viability, fecundity and frequency of the different patterns throughout the year are interrelated aspects which should be studied and analyzed as a whole in order to understand the ecological significance of this polychromism.

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