Field Biology of *Edessa rufomarginata* (Hemiptera: Pentatomidae): Phenology, Behavior, and Patterns of Host Plant Use

DANIEL P. SILVA[1,2] AND PAULO S. OLIVEIRA[3]

ABSTRACT   Pentatomids may cause direct and indirect damage to important crop plants. Biological and ecological features of phytophagous stink bugs in natural environments, however, remain poorly documented. Here, we provide an ecological account of *Edessa rufomarginata* De Geer on *Caryocar brasiliense* (Caryocaraceae) in the Brazilian savanna. The phenology of *E. rufomarginata* matched that of its host plant, with immatures developing in the wet season simultaneously with the production of vegetative and reproductive plant tissue. Females do not exhibit parental care and lay eggs more frequently on larger plants. Oviposition frequency, however, does not differ between plants with and without flowers/fruits. Nymphs and adults usually feed on stem parts and more rarely on flower buds and fruits. First- and second-instar nymphs remain aggregated, but disperse as third-instar nymphs. Adults and nymphs were more abundant on mature stems of *C. brasiliense* compared with other plant locations. Ants visiting the plant to search for extrafloral nectar occasionally tap the abdomen of *E. rufomarginata* nymphs with their antennae to obtain honeydew. This is the first record of trophobiotic interactions between *Edessa* stinkbugs and ants, and one of the few for heteropterans. The interaction of the stink bug with other natural enemies, such as predaceous *Heniartes* (Reduviidae), was also observed. Given the pest status of *Edessa* species for crop plants, additional field studies on host plants, interaction with ants, and natural enemies in native habitats are needed for an effective management of these stink bugs in tropical agricultural systems.

KEY WORDS   ants, *Caryocar brasiliense*, cerrado savanna, myrmecophily, stink bugs

Species of Pentatomidae (Hemiptera: Heteroptera), also known as stink bugs, are well adapted to consume liquid food and the majority of the members in this family are phytophagous (Grimaldi and Engel 2005). Some species are considered important crop pests because they cause direct plant damage through the consumption of plant sap, and indirect damage by increasing the infestation of plant pathogens (Delabie 2001). Others, such as the predatory species in the subfamily Asopinae, may act as important agents of biological control against defoliating lepidopteran and coleopteran larvae (Grazia et al. 1999). Because of their economic interest, pentatomid species have been extensively studied in diverse regions but their biological and ecological features are documented mostly in agricultural environments (Panizzi et al. 2000 and references therein).

Plant reproductive structures are the main food resource of phytophagous pentatomids (Schuh and Slater 1995, Grazia and Schwertner 2008). Developing fruits, flower buds, and seeds are more attractive because they provide a high quality diet (Salisbury and Ross 1992) and ensure a higher reproductive success (Panizzi 2000), but plant vascular systems can also be used as feeding resources by some species (Schuh and Slater 1995, Grazia et al. 1999). At the end of the reproductive season of their preferred host plant species, adult pentatomids may start a reproductive diapause or quiescence under the leaf litter, bark, or other shelters (Jones and Sullivan 1981), or may disperse in search of secondary host plants (Grazia and Schwertner 2008). Despite the fact that some species are oligophagous, polyphagy seems to be the rule within the Pentatomidae, and their feeding behavior, performance, and survival may vary according with the host species (Panizzi 1997, 2000; Grazia and Schwertner 2008).

Egg masses can be laid over all plant parts above ground level or on surrounding plants near the main host (Grazia and Schwertner 2008). After emergence, first-instar nymphs remain aggregated and acquire mutualistic endosymbionts from their eggshells (Abe et al. 1995). During the first instar, nymphs do not feed from plant tissues (Schuh and Slater 1995). Gregariousness continues during second and third instars and dispersal over the host plant begins in the fourth instar onwards (Grazia and Schwertner 2008).

[1] Programa de Pós-Graduação em Ecologia, Departamento de Biologia Animal, Universidade Estadual de Campinas, 13083-970 Campinas SP, Brazil.

[2] Current address: Programa de Pós-Graduação em Ecologia e Evolução, Departamento de Ecologia, ICB, Universidade Federal de Góias, Rodovia Goiânia-Nerópolis, Km 5, Campus II, Setor Itatiaia, 74001–970 Goiânia GO, Brazil.

[3] Departamento de Biologia Animal, C.P. 6109, Universidade Estadual de Campinas, 13083-970 Campinas SP, Brazil (e-mail: pso@unicamp.br).

Despite general information concerning the biology and ecology of economically important pentatomids, specific data concerning Neotropical pentatomids in natural environments are lacking (Schuh and Slater 1995). Especially within the subfamily Edessinae, which includes the highly diverse genus *Edessa* (Fernandes and van Doesburg 2000a, b; Silva et al. 2004), basic data on ecology and field biology are clearly lacking. Field studies in natural habitats may reveal mutualistic partners as well as potential agents of biological control of *Edessa*, and thus provide relevant information for Integrated Pest Management Programs (IPMP).

The Study System

Edessa rufomarginata De Geer (Hemiptera: Heteroptera) is widely distributed from Mexico to Argentina (Silva et al. 2004) and is a secondary pest of several crop plants, mostly within the family Solanaceae (Panizzi et al. 2000). The most economically important host plants of this stink bug are tobacco, potato, eggplant, soybean, sunflower, rice, and corn (Silva et al. 1968, Rizzo and Saini 1987). Surprisingly, however, very little is known about the biology and ecology of this pentatomid species (e.g., Rizzo and Saini 1987). In the Brazilian "cerrado" savanna, Oliveira (1997) observed *E. rufomarginata* feeding and reproducing on *Caryocar brasiliense* Cambessèdes (Caryocaraceae), also known as "pequizeiro," an important commercial tree species whose fruits are widely used in culinary culture (Prance and Freitas da Silva 1973). The plant is commonly visited by numerous ant species that search for extrafloral nectar on flower buds and shoot tips (Oliveira and Brandão 1991, Oliveira and Freitas 2004).

In the current study, we addressed the following questions concerning *E. rufomarginata* in the savanna environment: (1) What is the phenological relationship between *E. rufomarginata* and the host plant *C. brasiliense*? (2) Is plant size an important feature for host plant selection? (3) Which parts of *C. brasiliense* are selected for oviposition? (4) What is the pattern of host plant use by nymphs and adults?

Materials and Methods

The study was carried out in a cerrado area in Itirapina, State of São Paulo, south-eastern Brazil (22° 15′S, 47° 49′W, 770 m of altitude). A dry season occurs from April to September (fall-winter), and a wet season from October to March (spring-summer). The vegetation at the study site consists of a dense scrub of shrubs and trees, corresponding to the cerrado *sensu stricto* (Oliveira-Filho and Ratter 2002). *C. brasiliense* is very abundant in the area, reaching up to 300 individuals per hectare (Oliveira 1997). Data on *E. rufomarginata* and its host plant were obtained from September 2008 to February 2009, and complement previous observations gathered from June 1986 to July 1987 at the same study site (Oliveira 1988). Insect voucher specimens are deposited in the Museu de Zoologia da Universidade Estadual de Campinas, Brazil (ZUEC).

The Phenologies of *E. rufomarginata* and *C. brasiliense*. Comparative phenological records of plants and herbivores are important to evaluate to what degree a plant's pattern of leaf, flower, and fruit production is matched by the insect's developmental stages and population variation during a given time period (Del-Claro and Torezan-Silingardi 2009). From August 1986 to July 1987, the phenologies of the stink bug and its host plant were recorded every 2 wk by checking tagged shrubs of *C. brasiliense* ($N = 80$; 0.5–1.0 m tall) along a trail in the cerrado (Oliveira 1988). The variables recorded for the stink bug were: (1) number of adults; (2) number of nymphs; and (3) number of egg masses. The plant variables were: (1) number of leaves; (2) number of inflorescences; (3) number of flower buds, flowers and fertilized flowers; and (4) number of fruits. From September 2008 to February 2009, the same variables were also registered for another set of tagged *C. brasiliense* shrubs ($N = 75$; 0.5–2.0 m tall) and infesting stink bugs.

Biological and Ecological Features of *E. rufomarginata*. From September 2008 to February 2009, 75 shrubs of *C. brasiliense* (0.5–2.0 m tall) were used to test whether host plant size and plant reproductive status were important variables affecting host plant selection by *E. rufomarginata* females. The number of leaves, flower buds, and fruits of each shrub were counted monthly.

To investigate patterns of host plant use by *E. rufomarginata*, as well as the oviposition behavior of females, the crown of *C. brasiliense* shrubs was categorized in three parts, as follows: (1) Mature stems: brown-grayish stems produced in previous years, and possessing cracks and holes on the bark; (2) young stems: light green stems (not lignified; no cracks or holes) produced by the plant during the study period; and (3) leaves: new leaves continuously produced by the shrubs during the study period. Egg masses and *E. rufomarginata* individuals (nymphs and adults) found on each plant part were counted once a week, through daytime snapshot scan samplings. Behavioral interactions between *E. rufomarginata* and other organisms were also observed.

Forty *E. rufomarginata* adults were collected in the field and reared in the laboratory under controlled conditions ($25 \pm 2°C$ and 12L:12D). Couples ($N = 17$) were reared in 300 ml plastic cups, and were fed *ad libitum* with tangerine, peanuts, and bean pods. A wet cotton kept adequate humidity levels inside rearing cups, and food was replaced three times a week to avoid mold proliferation. Couples were checked three times a day (8:00, 12:00, and 18:00 h) to record mating, oviposition behavior, number of eggs laid, and number of newly hatched nymphs.

A logistic regression based on the Quasi-Newton iterative method was applied to test whether the number of leaves influenced host plant selection by egg-laying females. Chi-square tests were used to test whether females had preference to oviposit on plants with or without floral buds, and to investigate
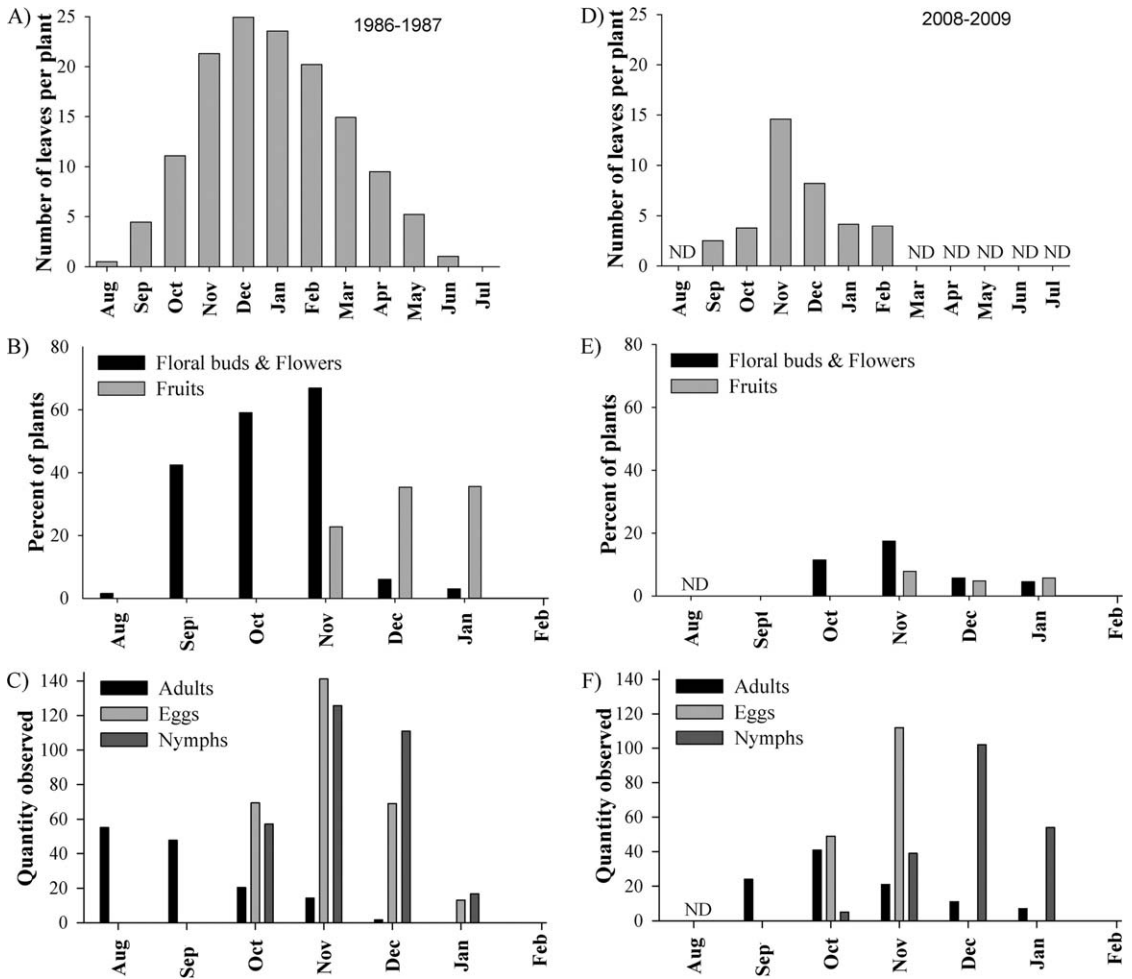
Fig. 1. Phenological relationships between *C. brasiliense* and *E. rufomarginata* from August 1986 to July 1987 (A–C) and from September 2008 and February 2009 (D–E), in the cerrado savanna of Itirapina, SE Brazil. ND = No data.

preferred plant locations. The use of different plant parts by *E. rufomarginata* was evaluated with a General Linear model (GLM) module via a one-way analysis of variance (ANOVA), followed by Tukey *post hoc* comparisons. The assumptions for all tests were followed and the data were transformed whenever it did not follow the tests' assumptions.

Results

The Phenologies of *E. rufomarginata* and *C. brasiliense*. Except for fruit development and maturation during the wet season, most of the phenological events of *C. brasiliense* occurred in the dry season of 1986–1987. Leaves started to senesce and fall in the beginning of February. In the dry season all shrubs had just few or no leaves at all (Fig. 1A), and during this period both mature and young stems shriveled out. By the end of August, growing shoots of mature stems became active again, and young stems, new leaves and floral buds developed until the beginning of the wet

season (Figs. 1A, B). During October–November all flowers were completely opened. Fruit maturation occurred in the end of the wet season, 3 to 4 mo after flowers had opened, but no new fruit was produced until February–March 1987 (Fig. 1B). The same general phenological pattern was observed from September 2008 to February 2009 (Fig. 1D, E); although the percentage of *C. brasiliense* shrubs producing fruits was low compared with 1986–1987 (Figs. 1B, E).

E. rufomarginata adults were observed on *C. brasiliense* shrubs from August to December 1986 (Fig. 1C). Egg masses and nymphs were observed from October 1986 to January 1987. Increased abundance of *E. rufomarginata* egg masses and nymphs was clearly associated with the host plant's reproductive phase. The same phenological patterns were observed for *E. rufomarginata* during 2008–2009 (Figs. 1D–F), except that no egg was found during December and January (Fig. 1F).

Oviposition Behavior, Egg-Masses, and Nymph Gregariousness. Two oviposition events were observed in the field. As the eggs are sequentially deposited on the host plant, the female touches them repeatedly with the last tarsomere of one of the hind legs. The whole oviposition process lasts 20–25 min, after which the females fly away and abandon the eggs.

Twenty three egg masses were observed on *C. brasiliense* shrubs, none of which were guarded by females. The egg masses usually contained 14 bluish-green eggs, divided in two rows of seven eggs each. This pattern varied only twice: two egg-masses had each one and 10 eggs. The average number of eggs laid by females was 13.26 (SD = 2.7 eggs; $n = 23$). The height of the egg-masses above ground level varied from 21 to 112 cm ($\overline{X} = 63.4$ cm; $n = 23$; SD = 27.72 cm). Three darkened egg-masses were found in the field, and no hatching was observed after 3 wk.

No mating was observed under laboratory conditions, indicating that females were already fertilized in the field. Seventeen egg masses were obtained. Seven of them were laid in the morning and nine in the afternoon. No egg was laid at night. Egg masses normally had 14 eggs, but two egg-masses had each 11 and 27 eggs. The average number of eggs laid per females was 14.53 (SD = 3.2 eggs; $n = 17$). Nearly 74% of the eggs laid were fertilized, whereas 26% had no embryo. Nymphs hatched from 82% of the fertilized eggs, 7–10 d after oviposition ($\overline{X} = 8.7$ d; $n = 17$; SD = 1.0 d).

After hatching, first-instar nymphs remained grouped at the oviposition site consuming the liquid from inside the eggshells. Occasionally, they also consumed the contents from the unviable eggs. On one occasion, first-instar nymphs also consumed the contents of all eggs from an adjacent egg mass of which no nymph hatched. No first-instar nymphs were recorded consuming plant sap. After molting, second-instar nymphs no longer aggregate near eggshells (but still present some gregariousness), increase locomotion within the host plant, and feed on plant sap. From the third-instar onwards, nymphs become entirely solitary. Nymphs of different instars hatching from distinct egg batches are occasionally seen together on *C. brasiliense* shrubs.

Host Plant Use by *E. rufomarginata*. Eighteen egg-masses were observed on mature stems of *C. brasiliense*, five were observed on young stems, and none occurred on leaves. Mature stems were used more frequently as oviposition sites by females compared with young stems and leaves ($\chi^2 = 14.695$; d.f. = 1; $P < 0.01$). In fact, two egg-masses deposited on young stems fell from the plant. Sixteen egg-masses were recorded on plants that did not develop floral buds/fruits during the reproductive season, while seven were found on plants with reproductive structures ($\chi^2 = 1.935$; d.f. = 1; $P = 0.164$). Egg-masses were more frequently observed on plants with increased quantity of leaves ($\chi^2 = 13.791$; d.f. = 1; $P < 0.01$; Fig. 2).

Adults and nymphs of *E. rufomarginata* spent considerable time feeding on particular plant parts. Both stages were frequently observed feeding on mature
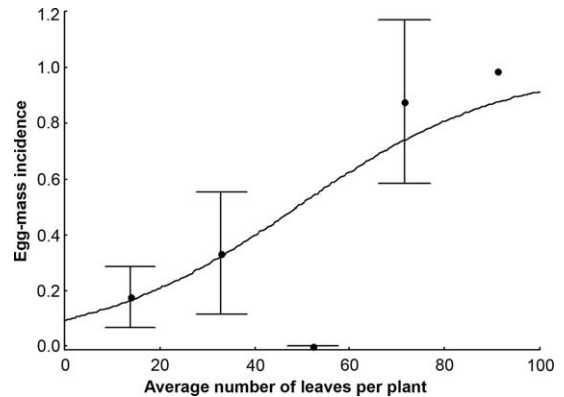

Fig. 2. Preference of oviposition site by *E. rufomarginata* on *C. brasiliense*, according to host plant size. The curve indicates the predicted probability of egg mass incidence, and filled squares with vertical lines designate the mean ± 95% confidence interval of egg mass occurrence according to each leaf quantity class ($n = 75$ plants).

and young stems, whereas floral buds and fruits were rarely used as feeding resources by *E. rufomarginata*. The pentatomids did not feed on leaves, but rather used these structures as resting and protection sites against natural enemies. Snapshot observations revealed that both adults and nymphs tended to be more abundant on mature stems compared with other plant locations (adults: $F_{2,30} = 3.518$; d.f. = 2; $P = 0.042$; nymphs: $F_{2,30} = 4.703$; d.f. = 2; $P = 0.017$; Fig. 3).

Interactions Between *E. rufomarginata* and Other Organisms. When disturbed, adults and nymphs of *E. rufomarginata* vibrated their antennae vigorously and usually fled to protected sites among the foliage. They could also jump off the plant and hide among the leaf litter. Adults occasionally flew off to neighboring plants. Disturbed adults and nymphs frequently secreted volatile substances from their metathoracic (adults) or dorso-abdominal (nymphs) scent glands.

Pheidole sp. ants (Hymenoptera: Formicidae: Myrmicinae) were once observed preying upon *E. rufomarginata* eggs (Fig. 4A). A large worker of *Pachycondyla villosa* (Hymenoptera: Formicidae: Ponerinae) was observed preying upon a third-instar nymph. Nymphs and adults of predacious reduviids *Heniartes* sp. (Hemiptera: Reduviidae) were observed sucking up the body contents of both adults and nymphs of *E. rufomarginata* (Fig. 4B; $n = 6$). No vertebrate species was observed preying upon *E. rufomarginata*.

Other interactions involving ants and stink bugs were observed at the study site. *Camponotus* ants (Hymenoptera: Formicidae: Formicinae) were frequently seen tapping the abdomen of third to fifth-instar nymphs of *E. rufomarginata* on *C. brasiliense* host plants. On two such occasions, the nymphs secreted droplets of honeydew that were promptly collected by the ants. Adult individuals were also seen producing such droplets but no ants were observed consuming it. Nymphs and adults of *E. rufomarginata* do not flick away their accumulated honeydew droplets, as re-
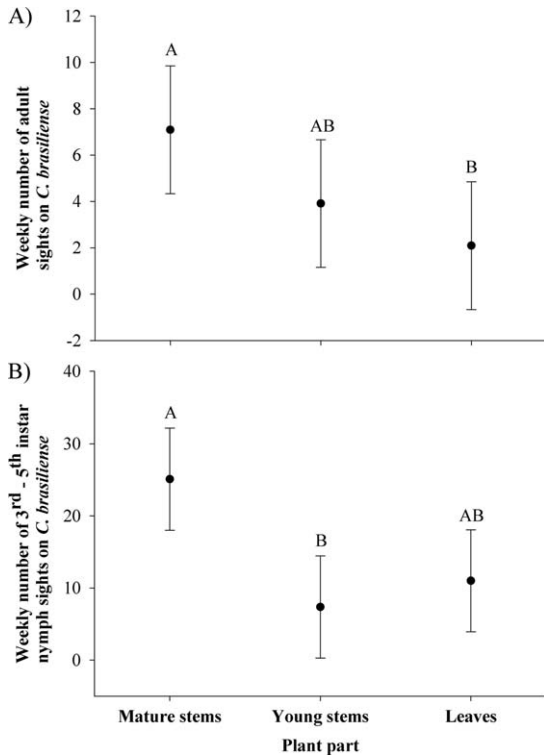
Fig. 3. Occurrence of adults (A) and nymphs (B) of *E. rufomarginata* individuals on different *C. brasiliense* plant parts. Vertical lines represent 95% confidence intervals; equal letters designate means that are not statistically different according to *posthoc* Tukey test, $\alpha = 0.05$. Nymph abundance was analyzed using log+1 transformed values, but the graph presents untransformed data.

corded in other sap-feeding hemipteran species in the cerrado savanna (see Del-Claro and Oliveira 1996).

Discussion

Phenological Relationships. The phenological pattern of *C. brasiliense* observed at Itirapina corresponded with that recorded for *C. brasiliense* and other tree species in cerrado that concentrate the production of new vegetative and reproductive tissues in the transition from the dry to the wet season

Fig. 4. (A) *Pheidole* sp. workers attacking an egg mass of *E. rufomarginata* (photo by D. P. Silva). (B) *Heniartes* sp. adult feeding on *E. rufomarginata* (photo by S. F. Sendoya).

(Batalha and Martins 2004, Leite et al. 2006). This phenological pattern of plants is an important physiological mechanism to save water and nutrients during the dry season in the cerrado savanna (Oliveira et al. 2005).

The phenology of *E. rufomarginata* matched that of its host plant reproductive activity, and the development of immature stink bugs occurred along the wet season simultaneously with the production of new vegetative and reproductive plant tissue. However, when *C. brasiliense* shrubs dry out at the end of the wet season (March–April), *E. rufomarginata* adults may respond in two different ways: (1) they may start a reproductive diapause, as do other pentatomid species (Jones and Sullivan 1981), or (2) they may search for alternative host plants (Panizzi 1997, 2000). Because no bug was seen feeding or reproducing on plant species other than *C. brasiliense,* it is possible that dormant or quiescent individuals overwinter under bark or within the leaf litter. Further field studies are needed before we can properly assess the fate of *E. rufomarginata* during the dry/cold season in cerrado.

Oviposition Behavior, Egg-Masses, and Nymph Gregariousness. Panizzi (2006) hypothesized that egg-laying females of *Nezara viridula* L. (Pentatomidae) may provide better egg positioning and attachment to the substrate when they arrange the eggs with the hind legs during oviposition, as reported here for ovipositing *E. rufomarginata.* Although Panizzi (2006) did not relate egg attachment to nymph hatchability or survival, eggs weakly attached to the oviposition substrate seem more prone to fall off the plant, which indeed occurred twice with two egg masses oviposited on *C. brasiliense* young stems.

Our laboratory data on egg production per *E. rufomarginata* female, egg viability, and egg development time were similar to those found by Rizzo and Saini (1987). Egg parasitoids are probably the cause of the darkened egg masses found in the field on *C. brasiliense* shrubs. Although we were not able to identify egg parasitoids of *E. rufomarginata*, three Scelionidae species are known to parasitize egg-masses of this species: *Telenomus edessae* Bréthes, *T. schrottky* Bréthes, and *Dissolcus paraguayensis* Bréthes (Silva et al. 1968).

Gregariousness in *E. rufomarginata* first-instar nymphs may provide them with a more humid environment, preventing them from desiccation. Indeed previous studies with other pentatomid species have already stressed out the importance of a humid microenvironment during nymphal development, especially during their first instar (Lockwood and Story 1986, Hirose et al. 2006). Gregariousness in first-instar nymphs may also facilitate the acquisition of endosymbionts. Pentatomids harbor several strains of mutualistic endosymbionts that are very important throughout the insect's life cycle, and females of many species infect egg-masses with these bacteria during oviposition (Abe et al. 1995), thus permitting first-instar nymphs to acquire them through direct contact with eggshells (Fukatsu and Hosokawa 2002).
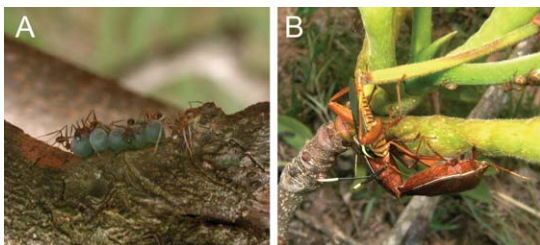
Host Plant Use by *E. rufomarginata*. Egg attachment on mature and young stems may vary because of different physical characteristics of these plant locations (lignified or soft bark, presence/absence of cracks, and holes), and *E. rufomarginata* females may distinguish such traits and prefer mature stems as oviposition sites (Oliveira 1997, Oliveira and Freitas 2004). Among species from several insect groups, plant characteristics such as tissue toughness, age of plant organ, presence/absence of plant structural defenses, and plant nutritious quality are very important during host plant selection, serving as cues for egg-laying females during oviposition. This is especially true for species of Lepidoptera (Thompson and Pellmyr 1991, Oliveira and Freitas 2004), beetles (Réu and Del-Claro 2005), gall-inducing insects (Stein and Price 1995), and Hemiptera (Romani et al. 2005).

Although plants with developing reproductive structures provide phytophagous insects with a high quality sap (Salisbury and Ross 1992), our data showed that females preferably oviposit on plants with increased numbers of leaves, indicating that plant architecture and structure may be also important for *E. rufomarginata* in cerrado. Plants with more leaves may provide enhanced microhabitat conditions for insects (Raghu et al. 2004), protecting adults and especially immatures from desiccation. Bigger plants may also provide more protection against natural enemies (Price et al. 1980, Jeffries and Lawton 1984), and better feeding sites (Heisswolf et al. 2005) compared with smaller plants. In addition, in accordance with the "plant vigor hypothesis" (Price 1991), bigger *C. brasiliense* shrubs (with more leaves) may be more nutritious than smaller ones and consequently may allow better performance for *E. rufomarginata* nymphs (Jaenike 1978, Thompson 1988; but see also Forrister et al. 2009).

Finally, *E. rufomarginata* nymphs and adults were more abundant on *C. brasiliense* mature stems compared with young ones. Because ant traffic on young stems is usually more intense because of offer of extrafloral nectar at flower buds and new leaves of *C. brasiliense*, interference from ants is expected to be strongest at these plant parts. Indeed predation by ant visitors increases toward the apex of the branches (Oliveira 1997), and adults and nymphs of *E. rufomarginata* conspicuously avoid ants on such locations of *C. brasiliense* host plants.

Interactions Between *E. rufomarginata* and Other Organisms. Many predaceous reduviids were already successfully used in Integrated Pest Management Programs (Nishi et al. 2004, Grundy 2007) and our field observations confirm that *Heniartes* sp. could potentially act as biological control agents against *Edessa* species on crop plants. Similarly, *Pheidole* and *Pachycondyla* ants may also contribute to suppress *Edessa* not only on foliage as documented in this study, but also possibly on the ground by attacking overwintering adults (see Fernandes et al. 1994).

The honeydew secreted by *E. rufomarginata* nymphs probably contains important nutrients, such as sugars and proteins (Blüthgen et al. 2004) that may appease the ants and decrease their willingness to attack (Stadler and Dixon 2008). These substances are commonly found in the honeydew produced by several groups of ant-tended herbivorous insects, such as riodinid and lycaenid butterflies (Pierce et al. 2002), and many auchenorrhynchous and sternorrhynchous hemipterans (Delabie 2001). Honeydew production by *E. rufomarginata* probably plays an important defensive role against attacks by aggressive ants that commonly visit the extrafloral nectaries of *C. brasiliense* (Oliveira and Freitas 2004, Sendoya et al. 2009). The trade-offs faced by trophobiont insects while maintaining myrmecophilous interactions on foliage have been extensively assessed elsewhere (reviewed by Stadler and Dixon 2005). Because such mutualistic interactions with ants are poorly known among heteropterans (Waldkircher et al. 2004), further studies concerning *E. rufomarginata* and cerrado ants are certainly needed to better understand the adaptive nature of myrmecophily in this species of stink bug.

References Cited

Abe, Y., K. Mishiro, and M. Takanashi. 1995. Symbiont of brown-winged green bug *Plautia stali* Scott. Jpn. J. Appl. Entomol. Zool. 39: 109–115.

Batalha, M. A., and F. R. Martins. 2004. Reproductive phenology of the Cerrado plant community in Emas National Park. Aust. J. Bot. 52: 149–161.

Blüthgen, N., G. Gottsberger, and K. Fiedler. 2004. Sugar and amino acid composition of ant-attended nectar and honeydew sources from an Australian rainforest. Aust. Ecol. 29: 418–429.

Delabie, J.H.C. 2001. Trophobiosis Between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an overview. Neotrop. Entomol. 30: 501–516.

Del-Claro, K., and P. S. Oliveira. 1996. Honeydew flicking by treehoppers provides cues to potential tending ants. Anim. Behav. 51: 1071–1075.

Del-Claro, K., and H. M. Torezan-Silingardi. 2009. Insect-plant interactions: new pathways to a better comprehension of ecological communities in Neotropical savannas. Neotrop. Entomol. 38: 159–164.

Fernandes, J.A.M., and P. H. van Doesburg. 2000a. The *E. dolichocera*-group of *Edessa* Fabricius, 1803 (Heterop-

tera: Pentatomidae: Edessinae). Zool. Meded. 73: 305–315.

Fernandes, J.A.M., and P. H. van Doesburg. 2000b. The *E. beckeri*-group of *Edessa* Fabricius, 1803 (Heteroptera: Pentatomidae: Edessinae). Zool. Meded. 74: 143–150.

Fernandes, W. D., P. S. Oliveira, S. L. Carvalho, and M.E.M. Habib. 1994. *Pheidole* ants as potential biological control agents of the boll weevil, *Anthonomus grandis* (Coleoptera: Curculionidae), in Southeast Brazil. J. Appl. Entomol. 118: 437–441.

Forrister, M. L., C. C. Nice, J. A. Fordyce, and Z. Gompert. 2009. Host range evolution is not driven by the optimization of larval performance: the case of *Lycaeides melissa* (Lepidoptera: Lycaenidae) and the colonization of alfalfa. Oecologia 160: 551–561.

Fukatsu, T., and T. Hosokawa. 2002. Capsule-transmitted gut symbiotic bacterium of the Japanese common plataspid stinkbug, *Megacopta punctatissima.* App. Environ. Microbiol. 68: 389–396.

Grazia, J., and C. F. Schwertner. 2008. Pentatomidae e Cyrtocoridae, pp. 223–234. *In* L.E. Claps, G. Debandi, and S. Roig-Juñent (eds.), Biodiversidad de Artrópodos Argentinos, vol. 2. Sociedad Entomológica Argentina, Mendoza, Argentina.

Grazia, J., N.D.F. De Fortes, and L. A. Campos. 1999. Heteroptera, Infraordem Pentatomoidea, pp. 101–112. *In* C.R.F. Brandão and E. M. Cancello (eds.), Biodiversidade do Estado de São Paulo, Brasil: síntese do conhecimento ao final do século XX, vol. 5: invertebrados terrestres. FAPESP, São Paulo, Brasil.

Grimaldi, D., and M. S. Engel. 2005. Evolution of the Insects, 1st ed. Cambridge University Press, Cambridge, MA.

Grundy, P. R. 2007. Utilizing the assassin bug, Pristhesancus plagipennis (Hemiptera: Reduviidae) as a biological control agent within an integrated pest management programme for *Helicoverpa* spp. (Lepidoptera: Noctuidae) and *Creontiades* spp. (Hemiptera: Miridae) in cotton. Bull. Entomol. Res. 97: 281–290.

Heisswolf, A., E. Obermaier, and H. J. Poethke. 2005. Selection of large host plants for oviposition by a monophagous leaf beetle: nutritional quality or enemy-free space? Ecol. Entomol. 30: 299–306.

Hirose, E., A. R. Panizzi, and A. J. Cattelan. 2006. Effect of relative humidity on emergence and on dispersal and regrouping of First Instar *Nezara viridula* (L.) (Hemiptera: Pentatomidae). Neotrop. Entomol. 35: 757–761.

Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. Theor. Popul. Biol. 14: 350–356.

Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. Biol. J. Linn. Soc. 23: 269–286.

Jones, W. A., and M. J. Sullivan. 1981. Overwintering habitats, spring emergence patterns, and winter mortality of some South Carolina Hemiptera. Environ. Entomol. 10: 409–414.

Leite, G.L.D., R.V.S. Veloso, J. C. Zanúncio, L. A. Fernandes, and C.I.M. Almeida. 2006. Phenology of *Caryocar brasiliense* in the Brazilian cerrado region. For. Ecol. Manage. 236: 286–294.

Lockwood, J. A., and R. N. Story. 1986. Adaptive functions of nymphal aggregation in the southern green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae). Environ. Entomol. 15: 739–749.

Nishi, A., T. Imamura, A. Miyanoshita, S. Morimoto, K. Takahashi, P. Visarathanonth, R. Kengkanpanich, M.E.H. Shazali, and K. Sata. 2004. Predatory abilities of *Amphi-*

bolus venator (Klug) (Hemiptera: Reduviidae), a predator of stored-product insect pests. Appl. Entomol. Zool. 39: 321–326.

Oliveira, P. S. 1988. On the interaction between ants and *Caryocar brasiliense* Camb. (Caryocaraceae) in cerrado vegetation: the ecological function of extrafloral nectaries. PhD dissertation, Universidade Estadual de Campinas, São Paulo, Brazil.

Oliveira, P. S. 1997. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). Funct. Ecol. 11: 323–330.

Oliveira, P. S., and C.R.F. Brandão. 1991. The ant community associated with extrafloral nectaries in the Brazilian Cerrados, pp. 198–212. *In* C. R. Huxley and D. F. Cutler (eds.), Ant-Plant Interactions. Oxford University Press, Oxford, United Kingdom.

Oliveira, P. S., and A.V.L. Freitas. 2004. Ant-plant-herbivore interactions in the neotropical Cerrado savanna. Naturwissenschaften 91: 557–570.

Oliveira, R. S., L. Bezerra, E. A. Davidson, F. Pinto, C. A. Klink, D. C. Nepstad, and A. Moreira. 2005. Deep root function in soil water dynamics in cerrado savannas of central Brazil. Funct. Ecol. 19: 574–581.

Oliveira-Filho, A.T., and J.A. Ratter. 2002. Vegetation physiognomies and woody flora of the Cerrado biome, pp. 91–120. *In* P. S. Oliveira and R. J. Marquis (eds.), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Panizzi, A. R. 1997. Wild hosts of pentatomids: ecological significance and role in their pest status on crops. Annu. Rev. Entomol. 42: 99–122.

Panizzi, A. R. 2000. Suboptimal nutrition and feeding behavior of hemipterans on less preferred plant food sources. An. Soc. Entomol. Brasil. 29: 1–12.

Panizzi, A. R. 2006. Possible egg positioning and gluing behavior by ovipositing southern green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae). Neotrop. Entomol. 35: 149–151.

Panizzi, A. R., J. E. McPherson, D. G. James, M. Javahery, and R. M. McPherson. 2000. Economic importance of stink bug (Pentatomidae), pp. 421–474. *In* C. W. Schaefer and A. R. Panizzi (eds.), Heteroptera of Economic Importance. CRC, Boca Raton, FL.

Pierce, N. E., M. F. Brady, A. Heath, D. J. Lohman, J. Mathew, D. B. Rand, and M. A. Travassos. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu. Rev. Entomol. 47: 733–771.

Prance, G. T., and M. Freitas da Silva. 1973. Caryocaraceae. Fl. Neotrop. Monogr. 12: 1–75.

Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. Oikos 62: 244–251.

Price, P. W., C. E. Bouton, P. Gross, B. A. Mcpheron, N. J. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect, herbivores, and natural enemies. Annu. Rev. Ecol. Syst. 11: 41–65.

Raghu, S., R.A.I. Drew, and A. R. Clarke. 2004. Influence of host plant structure and microclimate on the abundance and behavior of a tephritid fly. J. Insect Behav. 17: 179–190.

Réu, W. F., and K. Del-Claro. 2005. Natural history and biology of *Chlamisus minax* Lacordaire (Chrysomelidae: Chlamisinae). Neotrop. Entomol. 34: 357–362.

Rizzo, H. F., and E. D. Saini. 1987. Aspectos morfologicos y biologicos de *Edessa rufomarginata* (De Geer) (Hemiptera: Pentatomidae). Rev. Fac. Agron. 8: 51–63.

Romani, R., G. Salermo, F. Frati, E. Conti, N. Isidoro, and F. Bin. 2005. Oviposition behaviour in *Lygus rugulipennis:* a morpho-functional study. Entomol. Exp. Appl. 115: 17–25.

Salisbury, F. B., and C. W. Ross. 1992. Plant physiology, 1st ed. Wadsworth Publishing Company, Belmont, CA.

Schuh, R. T., and J. A. Slater. 1995. True bugs of the world (Hemiptera: Heteroptera): classification and natural history, 1st ed. Cornell University Press, Ithaca, NY.

Sendoya, S. F., A.V.L. Freitas, and P. S. Oliveira. 2009. Egg-laying butterflies distinguish predaceous ants by sight. Am. Nat. 174: 134–140.

Silva, A.G.D'.A., C. R. Gonçalves, D. M. Galvão, A.J.L. Gonçalves, J. Gomes, M. N. Silva, and L. Simoni. 1968. Quarto Catálogo dos Insetos que Vivem nas Plantas do Brasil - seus Parasitas e Predadores, 1st ed. Ministério da Agricultura, Rio de Janeiro, Brazil.

Silva, E.J.E., J.A.M. Fernandes, and J. Grazia. 2004. Variações morfológicas em *Edessa rufomarginata* e revalidação de *E. albomarginata* e *E. marginalis* (Heteroptera, Pentatomidae, Edessinae). Iheringia 94: 261–268.

Stadler, B., and A.F.G. Dixon. 2005. Ecology and evolution of aphid-ant interactions. Annu. Rev. Ecol. Evol. Syst. 36: 345–372.

Stadler, B., and A.F.G. Dixon. 2008. Mutualism: ants and their insect partners, 1st ed. Cambridge University Press, Cambridge, MA.

Stein, S. J., and P. W. Price. 1995. Relative effects of plant resistance and natural enemies by plant developmental age on sawfly (Hymenoptera: Tenthredinidae) preference and performance. Environ. Entomol. 24: 909–916.

Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47: 3–14.

Thompson, J. N., and O. Pellmyr. 1991. Evolution of oviposition behavior and host plant preference in Lepidoptera. Annu. Rev. Entomol. 36: 65–89.

Waldkircher, G., M. D. Webb, and U. Maschwitz. 2004. Description of a new shieldbug (Heteroptera: Plataspidae) and its close association with a species of ant (Hymenoptera: Formicidae) in Southeast Asia. Tijdschr. Entomol. 147: 21–28.