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RESEARCH ARTICLE



## Food, shelter or competitors? Overlapping of life stages and host plant selection in a Neotropical stink bug species

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### ABSTRACT

Phytophagous insects may choose host plants based on conditions that enhance offspring performance. However, some insect species may also select plants based on attributes that enhance their own performance regardless of the consequences for offspring survival. An approach evaluating both hypotheses could provide a more comprehensive understanding of the host plant selection by phytophagous insects. In this study, we described the life stages of a Neotropical stink bug, *Edessa contermina*, co-occurring on *Byrsonima verbascifolia* plants in a conservation area of the Brazilian Savannah. We also empirically evaluated how food supply, shelter availability and competitors' density on the host plants affected the densities of nymphs, adults and mating pairs. We identified and described five life stages of *E. contermina*. The amount of plant resources did not explain the nymph, adult and mating pairs' density. However, adults and mating pairs chose plants with a low density of nymphs, probably because egg laying on the host plants with a high density of competitors may negatively affect offspring performance.

### ARTICLE HISTORY

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### KEYWORDS

Oviposition choice; foraging choice; competition; plant–insect interaction

### Introduction

Host selection by phytophagous insects is often explained by the optimal oviposition theory, that is, the preference–performance hypothesis, originally proposed by Jaenike (1978). This hypothesis states that females should select hosts plants based on their capacity to provide suitable resources for offspring development, such as food and shelter (Levins and MacArthur 1969; Jaenike 1978; Thompson 1988; Mayhew 1997; reviewed by Gripenberg et al. 2010). Indeed, several studies have presented empirical and theoretical evidences supporting this hypothesis (reviewed by Thompson 1988; Courtney and Kibota 1990; Jaenike 1990; Mayhew 1997; Craig and Itami 2008). For example, the limited mobility of immature stages is an important factor conducting female choice by host plants that provide suitable conditions to enhance offspring performance (Thompson 1988; Craig and Itami 2008).

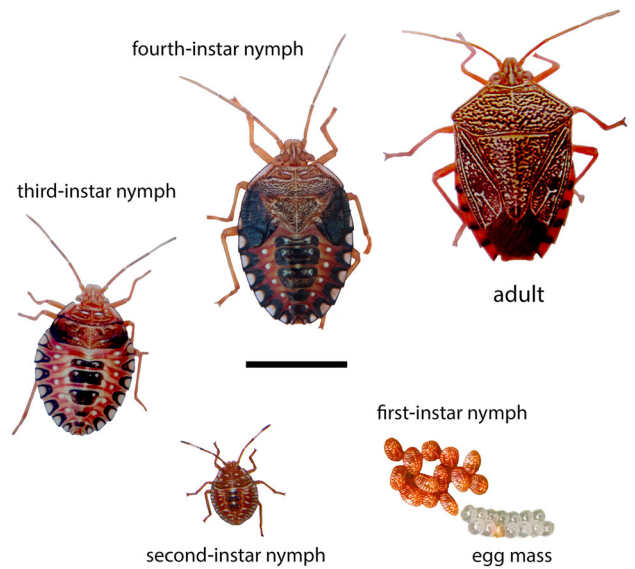
Contrary to expectations of the preference–performance hypothesis, some studies found a weak correlation between female preference and offspring performance on the host plants (e.g. Rausher 1979; Valladares and Lawton 1991; Underwood 1994; Fritz et al. 2000; Faria and Fernandes 2001; reviewed by Scheirs and De Bruyn 2002; Gripenberg et al. 2010). Consequently, recent studies have proposed an integration of optimal foraging and optimal oviposition theory in plant–insect interactions to explain these findings (Scheirs and De Bruyn 2002). The optimal foraging theory predicts that foraging behaviors should be based on energetic balance between the costs and benefits of location and acquisition of resources (MacArthur and Pianka 1966; Pyke 1984; Perry and Pianka 1997; Moura et al. 2016). According to this approach, phytophagous insects may choose oviposition sites that enhance their own performance regardless of the

consequences for offspring survival (Mayhew 1997, 2001; Scheirs and De Bruyn 2002). Females of the grass miner *Chromatomyia nigra* (Meigen) (Diptera: Agromyzidae), for example, choose plants based on the food supply favoring their own performance (realized fecundity and survival) to the detriment of offspring benefits (Scheirs et al. 2000, 2003). Thus, optimal foraging theory may also provide a suitable framework to understand host plants' selection by phytophagous insects.

Based on optimal foraging theory, host selection may also depend on bottom-up and top-down forces (Stephens and Krebs 1986; Scheirs and De Bruyn 2002). For example, food supply, shelter availability and competition may have strong bottom-up effects constraining host selection (Stephens and Krebs 1986). In the beetle *Altica carduorum* (Guer.) (Coleoptera: Chrysomelidae), individuals chose host plants that favor their own fecundity and survival (Scheirs and De Bruyn 2002). In other species, a conflict of interest among different life stages was also proposed as one of the possible forces constraining adult choice of suitable plants (Reavey and Lawton 1991; Nylin and Janz 1996; Mayhew 1997). However, due to high interspecific variation, there is still no consensus on the relevance of those conditions to the host plant selection, and some groups of phytophagous insects are still poorly studied. Furthermore, most studies evaluated only female choice based on the food provided by host plants (see Gripenberg et al. 2010 and references therein). Other plant attributes, however, may have adaptive consequences for adult and offspring performance, such as shelter availability. Leaves, for example, may act as shelter protecting individuals against harmful abiotic factors and natural enemies.

The Neotropical stink bug *Edessa contermina* Walker 1867 (Hemiptera: Pentatomidae) is a phytophagous insect that

feeds on host plants of *Byrsonima verbascifolia* (L.) Rich. ex. Juss. (Malpighiaceae) (Figure 1). Like other phytophagous stink bugs (Silva and Oliveira 2010), nymphs and adults may feed on plant sap of stems of leaves, inflorescences, fruits and seeds (Figure 1C, D). They do not feed on leaves, but rather they use those structures as shelter when resting or as protection against insolation, rainfall or natural enemies (see Silva and Oliveira 2010; R. R. Moura, pers. obs.). Furthermore, some life stages of *E. contermina* co-occur on *B. verbascifolia* (Figure 2). The overlapping of developmental stages may constrain the host plant choice by adults because they have high mobility due to the developed wing, while immature stages have limited mobility and usually stay sedentary on the plant on which they were hatched, at least until they reach maturity, similar to other *Pentatomidae* species (e.g. Lee et al. 2014). Therefore, *E. contermina* adults may select plants with a low density of nymphs and, consequently, minimize the exploitation competition. Mating pairs may also avoid plants with high competitor density to oviposit because this strategy should minimize competition between nymphs and their own offspring.



**Figure 2.** Life stages of *E. contermina* that co-occurred and feed on plant sap of *B. verbascifolia* plants. Scale: 5 mm.



**Figure 1.** (A) Study area of cerrado stricto sensu in the PESCAN, GO, Brazil; (B) *Byrsonima verbascifolia* (L.) DC. (Malpighiaceae); (C) life stages of *Edessa contermina* Walker 1867 (Pentatomidae) co-occurring on a *B. verbascifolia* plant; (D) adults feeding on plant sap of stems of inflorescences. Scales of figures A and B correspond to 1 m; while scales of C and D correspond to 10 mm.

Stink bugs are usually studied because of their economic interest. They may act as crop pests (Delabie 2001) or can be used as agents of biological control (Grazia et al. 1999). Therefore, most studies were performed in agricultural environments (Panizzi et al. 2000 and references therein, Grazia et al. 2015). Consequently, little information is available about their interaction with native host plants in the wild (e.g. Silva and Oliveira 2010). In this study, we described the life stages of *E. contermina* that occur simultaneously on *B. verbascifolia* plants in a conservation area of the Brazilian Savannah. We also hypothesized that the food supply, shelter availability and competition between life stages may constrain (1) foraging, (2) oviposition and (3) mating choice of this Neotropical stink bug by the host plants. Thus, we predicted that (1) adult, (2) nymph and (3) mating pairs' densities will depend on food supply, shelter availability and the density of competitors. We did not consider effects of competition on nymph density because nymphs are not able to move to another host plant regardless of the number of competitors.

## Materials and methods

### Study area

We performed field observations during October and November 2016 in the Parque Estadual da Serra de Caldas Novas – PESCAN (17°46'03.0"S; 48°39'37.4"W), located between the cities of Caldas Novas and Rio Quente, southwest Goiás State, Brazil. The study area consists of a cerrado *sensu stricto*, a type of vegetation occurring in the Brazilian Savannah (i.e. Cerrado) (Silva et al. 2002; see Batalha et al. 2001). The altitude ranges from 700 to 720 m above sea level. According to the Köppen–Geiger classification, the climate of this region is Aw (Peel et al. 2007). The dry season is from April to October and rainy season is from November to March with average temperature of 26°C and average annual precipitation of 1049 mm (Aquino et al. 2007). Cerrado *sensu stricto* has an intermediary diversity, richness and basal area compared to other Cerrado vegetation (Batalha et al. 2001) and is often regulated by natural fire regimes (Miranda et al. 2002).

### Insect–plant interaction

The fourth largest family in Heteroptera is Pentatomidae, usually called stink bugs. This family has 800 genera and 4700 described species are included in nine subfamilies. Of these, seven subfamilies with 230 genera and 1400 species are found only in the Neotropical Region (Schuh and Slater 1995; Grazia et al. 2015). Most of these species belong to the subfamily Edessinae (Panizzi and Grazia 2015). Edessinae are plant feeder bugs and two species are pests of plants with economic importance, such as *Edessa meditabunda* (F.) and *Edessa rufomarginata* (De Geer) (Panizzi et al. 2000); however, there is little information about the interactions of those species with native plants (Silva and Oliveira 2010; Grazia et al. 2015).

*Edessa contermina* Walker 1867 (Heteroptera: Pentatomidae) is a Neotropical stink bug that feeds on *Byrsonima verbascifolia* (L.) Rich. ex. Juss. (Malpighiaceae) in the Brazilian Savannah (i.e. Cerrado) (Grazia et al. 2015). Some life stages also feed on the plant sap of stems in the

*B. verbascifolia* (Figure 1C, D). Its inflorescence stems are racemes, and each one may have different stages of floral buds, open flowers, fruits and seeds in a single plant, but some plants of similar size may not still have racemes. Plants of *B. verbascifolia* are typically found in areas of cerrado *sensu stricto* (Figure 1A, B; Silva et al. 2002). They have tortuous trunks and reach, on average, 2.1 m of height (Souza 2015).

### Data collection

We evaluated effects of plant resources and competitors on host plant selection by stink bugs between 7:30 and 12:00 a.m. of 26 October 2016. We chose this sampling day to test predictions of our hypothesis because we found higher numbers of adults mating on the host plants. Other records and measures of eggs and nymphs were conducted during daylight between 23 October and 6 November 2016, totalizing 67h30 min of field observations. We selected the first 15 plants of *B. verbascifolia* observed with stink bugs in the study area. They were distributed near to a trail of PESCAN in an area of cerrado *sensu stricto* with approximately 100 m in length and 10 m in width. We counted the number of inflorescences and leaves and measured the length of inflorescences and height on each plant to provide a general description of plant traits that stink bugs may explore as resources and to evaluate host plant selection. We also recorded the number of nymphs, adults and mating pairs and photographed each one with a known scale in the background. After that, we released all individuals on plants. From photos, we estimated the length  $l$  (i.e. from the anterior tip of the head to the posterior tip of the abdomen) and width  $w$  (i.e. at the widest part of the abdomen) of each individual using the ImageJ program (National Institutes of Health). Finally, we calculated the dorsal body area of individuals as an ellipse ( $S = 3.14 \times 0.25 \times l \times w$ ). The voucher specimens were deposited in the Instituto de Ciências Biológicas, Universidade Federal do Pará (curator J. A. M. Fernandes), Pará, Brazil.

We classified the life stages of *E. contermina* occurring simultaneously on *B. verbascifolia* based on morphological characters, field observations and the description of instars of *E. rufomarginata* by Silva and Oliveira (2010). We analyzed size distribution using a histogram and performed an ANOVA and Tukey's post hoc test to distinguish their body dorsal areas (response variable) between instars of *E. contermina* (predictor variable). We log transformed body dorsal area to improve homogeneity of residual variance. To evaluate host plant selection by stink bugs, we measured the following three predictors of plant resources: (1) the number of inflorescences, (2) the sum of inflorescence lengths of each and (3) the number of leaves. Predictors (1) and (2) were considered as proxies for food supply, whereas (3) is considered as a proxy for shelter availability. Then, we performed Spearman's correlations between these predictor variables to test for collinearity. We used the sum of inflorescence lengths and the number of leaves in the analyses because they presented stronger correlations (higher correlation coefficient values) with nymph, adult and mating pair density compared with the number of inflorescences (see Results). We also used the numbers of second-, third-, and fourth-instar by plant as a proxy for competitors' density in the analysis of adult counts. We did not include first-instar nymphs in the analysis because they were found only on one plant and did not feed on plant sap in this stage (see Results).

We fitted generalized linear models (GLMs) with Poisson error distributions to evaluate the effects of the sum of inflorescence lengths and the number of leaves on the host plant (as predictor variables) on adult density (foraging choice) and nymph density (oviposition choice), as response variables. We also included nymph density as a predictor in the foraging choice model because only adults can move between host plants. We also used two models of multiple logistic regression to test the effects of host plant resources and competitor density (predictor variables) on the probability of finding a mating pair (response variable). In the first model, we used only nymphs to estimate competitor density, whereas we also included non-copulating adults in the second model. We used these approaches to evaluate if mating pairs were selecting the host plants with lower number of nymphs to avoid competition with their progeny, or if they selected *B. verbascifolia* plants on the basis of competition for food or shelter that influence their own performance.

We tested the models for significant effects using chi-squared tests (Hastie and Pregibon 1992). We conducted all data analysis in R software version 3.3.2 (R Development Core Team 2017). We performed overdispersion tests using package ‘AER’ (Kleiber and Zeileis 2008) and built a jitter plot using the package ‘ggplot2’ (Wickham 2009). We made a plot with partial values of a multiple regression using the method of Cook and Weisberg (1999) of the package ‘car’ (Fox and Weisberg 2011).

## Results

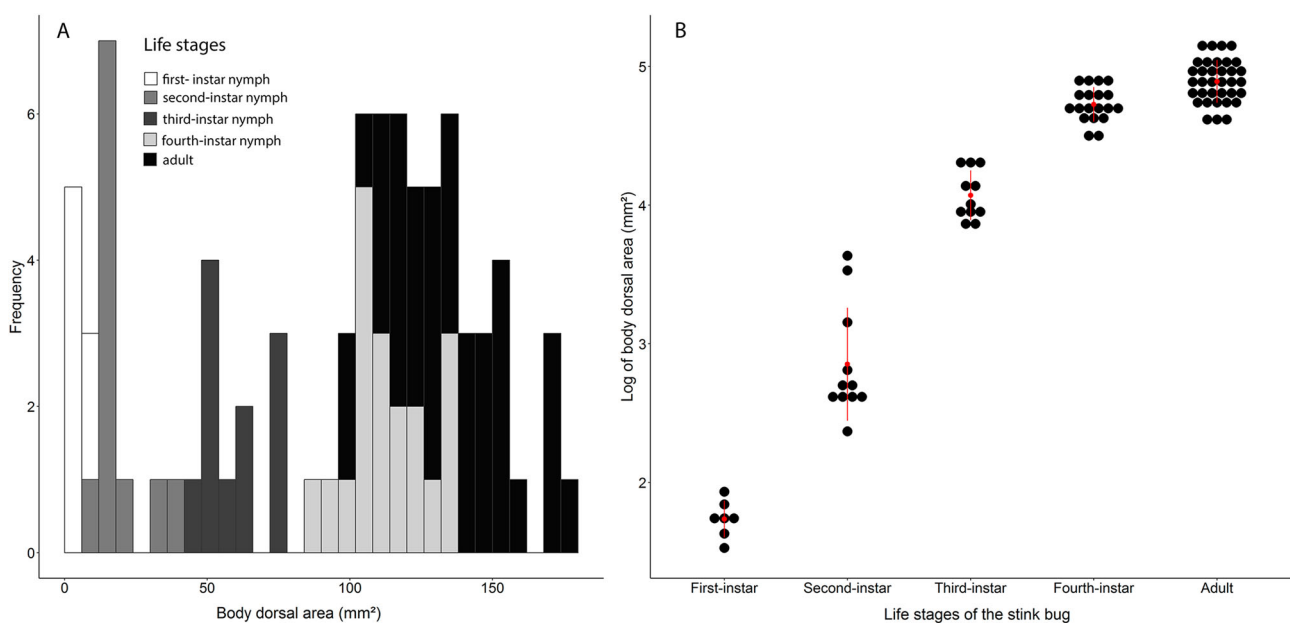
In the study area, *E. contermina* occurred only on *B. verbascifolia* plants. Most stink bugs were observed feeding on inflorescence sap, except for one female, which was feeding on a stem with young leaves. We found a total of 83 individuals on the 15 *B. verbascifolia* plants: 7 first nymphs on one plant, 11 second nymphs on two plants, 11 third nymphs on four plants, 19 fourth nymphs on nine plants and 35 adults on nine plants. We also found seven mating pairs on four plants. We observed three sets of eggs laid on inflorescences

and leaves of three plants: one had 14 hatched eggs, one had 10 eggs unhatched and another had 14 eggs with 13 first nymphs nearby (Figure 2). All sets of eggs were organized in two parallel rows. We did not find adults close to the egg mass. One host plant presented 17 nymphs and no adult, while eight plants hosted  $3 \pm 0.79$  nymphs (mean  $\pm$  standard error), ranging from one to seven nymphs, and six plants had no nymphs.

*Byrsonima verbascifolia* plants presented some different traits compared to descriptions in the literature (see Batista et al. 2005). Plants had  $5 \pm 1.24$  inflorescences (mean  $\pm$  standard error), ranging from zero to 15, and  $60.87 \pm 7.86$  leaves, ranging from 21 to 122. Sum of inflorescences was  $58.93 \pm 17.03$  m, ranging from 0 to 218 m, and height was  $73.33 \pm 5.06$  cm, ranging from 48 to 116 cm.

We identified five life stages of *E. contermina* co-occurring on *B. verbascifolia* plants (Figure 2). Most life stages presented different sizes ( $F_{4,78} = 518.14$ ,  $p < .0001$ , Figure 3). First-instar nymphs recently hatched from eggs and were often located close to them, but they were not feeding on plant sap. These nymphs were the smallest individuals and were, on average, 3.3 times smaller than second-instar nymphs ( $p < .0001$ ). Other nymph stages were feeding on inflorescence sap. However, second-instar nymphs were, on average, 6.03 times smaller than fourth-instar nymphs and 3.15 times smaller than third-instar nymphs ( $p < .0001$ ). Fourth-instar nymphs, in turn, moved more actively on the host plant than on other nymphs, but they did not move between the host plants. These nymphs presented incompletely developed wings and were not able to fly. They were, on average, 1.91 times larger than third-instar nymphs and 1.18 times smaller than adults ( $p = .0414$ ).

The number of inflorescences was correlated with the sum of inflorescence lengths ( $r_s = 0.955$ ,  $p < .001$ ) and the number of leaves ( $r_s = 0.515$ ,  $p = .049$ ). Therefore, we included the sum of inflorescence lengths (adult density:  $r_s = 0.332$ , nymph density:  $r_s = -0.047$ ) and the number of leaves (adult density:  $r_s = 0.290$ , nymph density:  $r_s = -0.017$ ) in the analyses instead of number of inflorescences (adult den-



**Figure 3.** (A) Histogram of size distribution of life stages of *E. contermina*; (B) comparisons of logarithm of body dorsal area (response variable) between life stages of *E. contermina* (predictor variable). Black points correspond to each measure; red point and line represent mean and standard error, respectively.

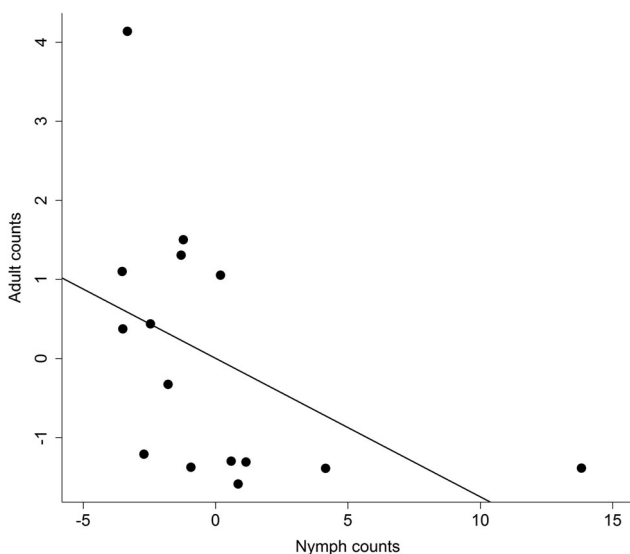
**Table 1.** Results of multiple regression models (Poisson error distributions) using adult and nymph density as response variables and plant resources and competitor density as predictors.

Variable	d.f.	$\chi^2$ -value	<i>p</i> -value
<i>Adult density</i>			
Sum of inflorescence lengths	1	1.744	.187
No. of leaves	1	1.777	.183
No. of nymphs	1	18.499	<.001
<i>Nymph density</i>			
Sum of inflorescence lengths	1	0.626	.429
No. of leaves	1	2.307	.129

sity:  $r_s = 0.241$ , nymph density:  $r_s = 0.002$ ). Adult density increased with decreasing density of nymphs on the *B. verbascifolia* plants, but was not related to the sum of inflorescence lengths and the number of leaves (Table 1, Figure 4). Likewise, the host plant resources did not explain nymph density on *B. verbascifolia* plants (Table 2). Mating pairs avoided plants with higher nymph density, as did adults (Table 2, Figure 5). When we added the number of non-copulating adults to nymph density, however, there was no relationship (Table 2).

## Discussion

In this study, we presented information about the field biology and host plant selection of a Neotropical stink bug species that interact with *B. verbascifolia* plants in a conservation area of the Brazilian Savannah. These plants housed five *E. contermina* life stages and varied in food supply and shelter availability. This variation in plant resources associated with the overlapping of life stages may affect host plant selection by stink bugs, as occurs in other phytophagous insects (Reavey and Lawton 1991; Nylin and Janz 1996; Mayhew 1997; Scheirs and De Bruyn 2002; reviewed by Gripenberg et al. 2010). Adults and mating pairs selected plants with lower nymph density regardless of host plant resources (i.e. number of leaves and inflorescences). We proposed that individuals may select host plants with lower nymph density to avoid competition between these nymphs and their own progeny. Thus, our findings supported the oviposition choice hypothesis. We also discuss similarities and differences between the



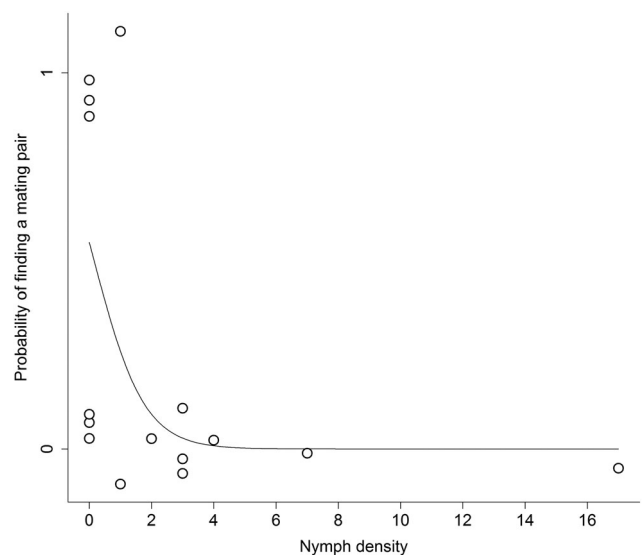
**Figure 4.** Partial values of a multiple regression (Poisson error distribution) to the relationship between adult density (response variable) and nymph density (one of the predictors).

**Table 2.** Results of multinomial logistic regressions using plant resources and competitor density as predictors and nymph and non-copulating individuals (nymphs and adults) density as response variables in Model 1 and Model 2, respectively.

Variable	d.f.	$\chi^2$ -value	<i>p</i> -value
<i>Model 1</i>			
Sum of inflorescence lengths	1	0.538	.463
No. of leaves	1	1.276	.259
No. of nymphs	1	5.284	.022
<i>Model 2</i>			
Sum of inflorescence lengths	1	0.538	.463
No. of leaves	1	1.276	.259
No. of non-copulating individuals	1	2.235	.135

interaction examined in this study and that between *E. rufomarginata* and *Caryocar brasiliense* and propose hypotheses to explain why females did not preferentially lay eggs on plants offering more resources.

*Edessa contermina* individuals interacted only with *B. verbascifolia* plants in the study area, despite the high floristic diversity of cerrado *sensu stricto*, which included another plant species of the same genus, *B. coccolobifolia* (see Silva et al. 2002). This interaction presented some similarities with the interaction between *E. rufomarginata* and *C. brasiliense* (Caryocaraceae) (Silva and Oliveira 2010). During October–November, flowers of *C. brasiliense* were open, and there was overlapping of life stages of *E. rufomarginata*. Consequently, there was a positive correlation between reproductive phase of the host plants and stink bug reproduction, as we observed in the *E. contermina*–*B. verbascifolia* interaction. Females of *E. rufomarginata* laid approximately 14 eggs divided into two rows, similar to *E. contermina* females. However, egg masses of *E. contermina* were laid on stems of inflorescences and leaves, whereas eggs of *E. rufomarginata* were found on mature stems of *C. brasiliense*. Feeding behavior was also different: *E. rufomarginata* individuals preferentially feed on mature and young stems. Otherwise, the most attractive part of the host plants as a food supply for *E. contermina* was inflorescence stems probably because they act as drain of nutrients (see Salisbury and Ross 1992). In addition, Silva and Oliveira (2010) found five instars of *E. rufomarginata* nymphs, while we only distinguished four instars. Both stink bug species showed some developmental and



**Figure 5.** Relationship between predicted probability of finding a mating pair and nymph density of *E. contermina* ( $n = 15$ ).

behavioral similarities, but *E. contermina*'s preference for stems of inflorescences of *B. verbascifolia* may imply variations in host plant selection behaviors.

Phytophagous insects may choose host plants based on conditions that enhance their own performance regardless of the consequences for offspring survival (Scheirs et al. 2000, 2003; Scheirs and De Bruyn 2002). Although *E. contermina* nymphs and adults occupy host plants regardless of their offering of resources, adults avoided host plants with higher densities of nymphs. This decision could be a foraging strategy to avoid competition for the food supply and increase adult reproductive performance. If this hypothesis was true, mating pairs would select plants with a low density of nymphs and non-copulating adults (i.e. potential competitors). However, the density of non-copulating individuals was not a limiting factor in the host plant selection. On the other hand, mating pairs chose plants with low nymph density, probably to avoid competition between these nymphs and their own progeny. Therefore, avoidance of competition by adults and mating pairs seems more reasonable as a strategy of oviposition choice instead of foraging choice. Females may also gain additional benefits from using the strategy of oviposition on several plants instead of a single one, because to do so may spread the risk of predation and parasitism and, consequently, increase offspring survival (Mangel 1987; Hopper 1999).

The lack of evidence supporting the hypothesis that females may oviposit on plants offering more resources must be due to restrictions in the stink bug perception. Females may fail in the selection of suitable plants for offspring development because these plants may exhibit temporal variation in resource offering, such as food and shelter availability (Gripenberg et al. 2010). This variation would have stronger effects on female perception when they oviposit on herbaceous or shrubby plants because these plants may change resource offerings more quickly during the growing season than woody plants (Salminen et al. 2004; Gripenberg et al. 2007; Craig and Itami 2008). Therefore, *E. contermina* females may have selected *B. verbascifolia* plants with larger food supply and greater shelter availability during oviposition, but these plants may have lost some leaves and had shorter flowering period due to their growing period. Supporting this hypothesis, *B. verbascifolia* plants usually have 2.1 m of height, while plants in the study area were smaller (73.33 cm). In addition, *B. verbascifolia* produce, on average, 7.92 inflorescences by plant, whereas plants at study area presented, on average, five inflorescences by plant. Therefore, the great variation in weather and rainfall inconstancy of the cerrado *sensu stricto* (Batalha and Mantovani 2000) may affect the timing of the flowering period during plant growth (Batalha et al. 2001), hampering the evaluation of females. To test this hypothesis, further studies may evaluate plant phenology and its effects on the selection of stink bugs.

In conclusion, we identified five life stages of *E. contermina* co-occurring and feeding on *B. verbascifolia* plants. We also found evidence that adults and mating pairs avoid host plants with a high density of nymphs, whereas plant resource offerings did not constrain adult and nymph distributions. We suggested that *E. contermina* individuals use this strategy to increase offspring performance by avoiding competition between their own progeny and other nymphs. Furthermore, stink bugs may also gain benefits from spreading their progeny between different plants because to do so may reduce

the risk of predation and parasitism. In addition, some specific conditions of the cerrado *sensu stricto*, such as the timing of rainfall and the natural fires and its consequences for the phenology of *B. verbascifolia*, may hamper female evaluation of host plant resources. Finally, future studies may investigate the consequences of risk-spreading strategy and the relationship between *B. verbascifolia* phenology and oviposition choice of *E. contermina*.

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