

Oviposition site selection by the bromeliad-dweller harvestman *Bourguyia hamata* (Arachnida: Opiliones)

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Abstract *Bourguyia hamata* females oviposit almost exclusively inside the rosette formed by the curled leaves of the epiphytic bromeliad *Aechmea nudicaulis*. We investigated whether the architecture of the individual bromeliads influences oviposition site selection by this harvestman species. We collected data on the presence of clutches inside bromeliads, rosette length, rosette slope in relation to tree trunks, and the amount of debris inside the rosette. Additionally, we measured the water volume inside the rosettes as well as the variation in the humidity inside and outside bromeliads with long and short rosettes. Longer rosettes were preferred as oviposition site possibly because they accumulate more water and maintain lower internal humidity variation than the external environment. Although the slope of the rosettes did not influence the occurrence of oviposition, the probability of debris accumulation inside the rosettes increased with their slope, and the frequency of clutches was greater in bromeliads with small amounts of debris. A field experiment showed that bromeliads with water inside the rosette were more frequently used as

oviposition sites than bromeliads without water. In conclusion, females oviposit predominantly in bromeliads that accumulate more water and have small amounts of debris inside the rosettes, probably because these characteristics promote a more adequate microhabitat for egg development.

Keywords Animal–plant interaction · Bromeliaceae · Gonyleptidae · Habitat selection · Maternal care · Microhabitat · Plant architecture

Introduction

Oviposition site selection by parents is crucial for offspring survival because the habitat may provide access to shelters with good thermal, hydric, and structural conditions for the eggs and young (Huey 1991; Martin 2001). In addition, these conditions are likely to affect offspring fitness by increasing the chances of finding food and sexual partners, while decreasing the chances of meeting competitors and predators (Resetarits and Wilbur 1989; Bernardo 1996; Schoonhoven et al. 1998; Martin 2001; Romero and Vasconcellos-Neto 2005b). In species with parental care, the nest-site selected must have appropriate conditions for the offspring as well as for the parental individuals (Morse 1985) because an inadequate place may expose both to a wide range of unfavorable factors (Wilson 1971; Clutton-Brock 1991). Therefore, nest-site selection is one of the most important decisions made by arthropods that lay eggs, and many species exhibit precise selection for oviposition sites (e.g., Fritz and Morse 1985; Morse 1990, 1992; Figueira and Vasconcellos-Neto 1993; Morse and Stephens 1996; Judd 1998; Goldsborough et al. 2003).

In tropical areas, many terrestrial vertebrate and invertebrate species can be found inside tank bromeliads, and

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this is especially common during the dry season when these plants may be the only water reservoir available in the environment (Neill 1951). In fact, some arthropods and amphibians are dependent on tank bromeliads for their reproduction and for the development of their offspring (e.g., Diesel 1989; Giaretta 1996; Judd 1998; Bourne et al. 2001). Females of the spider *Psecas chapoda* (Salticidae), for instance, reproduce strictly on *Bromelia balansae* and evaluate the micro-habitat architecture, selecting bromeliads without inflorescence or dry leaves inside the rosettes (Romero and Vasconcellos-Neto 2005a, b). A study with the crab *Metopaulias depressus* (Decapoda) showed that females breed in tank bromeliads and are capable of accessing not only the physical characteristics of the bromeliads, but also the chemical conditions of the phytotelma, i.e., the water reservoir accumulated in the plant axils (*sensu* Varga 1928). Parental females of this crab remove the leaf litter and organic matter from the bromeliad axils and buffer the phytotelma with snail shells in order to increase the pH as well as the oxygen and Ca^{2+} concentrations (Diesel and Schuh 1993; Diesel 1997).

The bromeliad-dweller harvestman *Bourguyia hamata* (Gonyleptidae) is a large-bodied species (≈ 7 mm of body length), which can be frequently found at night foraging on vegetation. Machado and Oliveira (2002) showed that *B. hamata* females oviposit almost exclusively inside the epiphytic bromeliad *Aechmea nudicaulis* at Cardoso Island, southeastern Brazil—even though this species represents only approximately 10% of the epiphytic bromeliads in the study area. *Aechmea nudicaulis* is a bromeliad with long curled leaves forming a tubular rosette that accumulates water (Wanderley and Mollo 1992; see also Fig. 1a in Machado and Oliveira 2002). Females of *B. hamata* lay their eggs inside the rosette and guard the clutch until the hatching and dispersal of all nymphs, which lasts from 35 to 43 days. Maternal care has a crucial protective role for egg survival, because unprotected clutches can be entirely consumed by ants and/or conspecifics in a few hours (Machado and Oliveira 2002).

The main objective of this study was to determine whether architectural features of the individuals of the bromeliad *A. nudicaulis* may influence the oviposition site choice by females of the harvestman *B. hamata*. Specifically, the following hypotheses were tested: (1) bromeliads with longer rosettes should be preferred as oviposition site because these plants can accumulate more water and maintain high levels of humidity inside the leaf-tube; (2) females should oviposit in bromeliads in which the slope of the rosette related to the tree trunk permits the accumulation of water inside the leaf-tube; (3) bromeliads that accumulate debris inside the rosette should be avoided by ovipositing females because it could block the entrance of the leaf-tube.

Materials and methods

Study area

This study was carried out in a sandy coastal area at Cardoso Island (25°03'S; 47°53'W), south coast of São Paulo state, southeastern Brazil. The sandy coastal forest (locally known as “restinga”) is part of the Atlantic Forest domain and frequently adjoins coastal rainforests (Oliveira-Filho and Fontes 2000). The vegetation grows on poor sandy soils and is composed of small trees (6 m high) and an understory dominated by terrestrial bromeliads, herbs, and a few shrubs (Barros et al. 1991). The cold season lasts from June to September and is characterized by infrequent rainfall (≈ 500 mm) and a mean temperature of 17.4°C. From October to May there is a warm season when rainfall is abundant (1,800 mm) and the mean temperature is 25.5°C (Pfeifer et al. 1989).

Oviposition site selection

This part of the study was conducted from February 2005 to January 2006. All clumps of the epiphytic bromeliad *Aechmea nudicaulis* ($N = 46$) found at the margins of a 700-m-long transect (≈ 1 m wide) received an individual number, and each bromeliad in these clumps was individually marked ($N = 227$). The following data were recorded for each bromeliad: (1) rosette length, from the bromeliad base to the leaf-tube opening; (2) slope of the rosette related to the tree trunk (assuming all trunks are mostly vertical)—this slope varied from 0°, when the leaf-tube opening was pointing to the ground, to 180°, when the opening was pointing to the canopy; (3) amount of debris (mainly dry leaves fallen from the canopy) inside the rosette, a categorical measure that varied from 0 to 3 according to the following criteria: (0) with no debris; (1) small amount of debris, so that an adult individual of *B. hamata* could enter the leaf-tube freely; (2) moderate amount of debris, in which the quantity of debris inside the leaf-tube was higher than the previous category, but did not block its opening, and (3) great amount of debris, when the accumulated debris blocked the passage of an adult individual of *B. hamata* (which is unable to remove debris from the leaf-tube).

All bromeliads in the transect were inspected monthly (at 25–35-day intervals) to search for *B. hamata* females, recording the clump number and the bromeliad number where they were found. Each female found inside the individuals of *A. nudicaulis* was captured and classified according to her reproductive condition as non-reproductive, ovigerous (recognized through the enlarged abdomen with distended intersegmental membranes), or guarding (when taking care of eggs or nymphs). Each female

received an individual mark with enamel paint and was released at the same bromeliad where she was found (following Machado and Oliveira 2002).

To assess which factors affect the probability of a female to oviposit inside bromeliads, oviposition probabilities were modeled as a function of rosette length and slope using generalized linear models with binomial error structure and logit link function (McCullagh and Nelder 1989). Models constraining oviposition probabilities as a function of the following effects were fitted to the data on the presence/absence of clutches inside bromeliads: (1) rosette length; (2) rosette slope; (3) additive effects of rosette length and slope; (4) interaction between rosette length and slope. The fully parameterized model, including the interaction between rosette length and slope, fitted well to the data ($\chi^2 = 220.83$, $df = 223$, $P = 0.53$). However, using a model selection approach based on the bias-corrected version of the Akaike Information Criterion (Burnham and Anderson 1998; Johnson and Omland 2004), the model including only the rosette length effect was selected as the best model to describe oviposition probabilities ($AIC_c = 259.01$, ΔAIC_c to second best model = 0.91, $w_i = 0.50$, number of parameters = 2). Because the best model to describe oviposition probabilities does not include the slope of the rosettes, the following analysis of oviposition site preference considered only rosette length.

To test the null hypothesis that females were selecting host plants at random, all bromeliads in the transect were divided into length classes ranging from 0 to 50 cm (10-cm intervals). Thereafter, a modified G-test recommended by Manly et al. (1993) to investigate resource selection was applied:

$$\chi^2 = 2 \sum_{i=1}^n \left[u_i \ln \left(\frac{u_i}{Up_i} \right) \right],$$

where χ^2 is the chi-square value for $(n - 1)$ degrees of freedom; u_i is the number of bromeliads in the length class i that was used as oviposition site; U is the total number of bromeliads used as oviposition site in the transect ($\sum u_i$); n is the number of length classes ($n = 5$), and p_i is the proportion of bromeliads in the length class i available in the transect (following Krebs 1998).

A similar procedure was used to test whether females were also selecting bromeliads according to the amount of debris inside the rosettes. The main difference, however, was that we used the categories of amount of debris accumulated inside the rosette instead of classes. Thus u_i is the number of bromeliads in the category i that was used as oviposition site, and p_i is the proportion of bromeliads in the category i available in the transect. To identify in which classes or categories the frequency of use differed from the

availability in the transect, a partition chi-square was performed using the program BioEstat 3.0 (Ayres et al. 2003).

Water and debris accumulation

Data on bromeliad length and slope, as well as air humidity and amount of water accumulated inside the rosettes were collected at the study area in March 2001 (end of wet season). To measure the water volume inside the rosettes, 60 bromeliads were cut at the base (preventing water leakage) and the entire volume of each phytotelma was transferred to a graduated cylinder (ml). For all these bromeliads, rosette length and their slope in relation to the tree trunk were measured as previously described.

General linear models were used to model the volume of water accumulated inside bromeliads as a function of rosette length and slope (Dobson 2002). Models including the following effects were fitted to the log-transformed data on the volume of water accumulated inside bromeliads: (1) rosette length; (2) rosette slope; (3) additive effects of rosette length and slope; (4) interaction between rosette length and slope. A model selection approach based on the bias-corrected version of the Akaike Information Criterion (Burnham and Anderson 1998; Johnson and Omland 2004) was used to select the best model to describe the volume of water accumulated inside bromeliads. Additionally, a logistic regression was used to test whether rosette slope affected the presence of dry leaves accumulated inside the bromeliads. For this analysis, the category 0 was considered as debris absence (0) and the categories 1–3 were considered as debris present (1).

Data about relative air humidity variation along the day were collected 10 cm inside and 1 m outside each rosette ($N = 22$). Measurements were taken with a digital hygrometer in three periods of the day (0800, 1400, and 2000 hours), during 2 non-consecutive days, inside 11 small bromeliads (18–20 cm of rosette length) and 11 large bromeliads (30–32 cm of rosette length), all of them, with slopes ranging from 120° to 160°. To test if larger bromeliads are more effective in maintaining humidity inside their rosettes when compared with smaller bromeliads, the humidity inside each bromeliad was subtracted from the humidity outside the rosette. Thus, positive values indicate that the humidity inside the rosettes was higher than that in the external environment, while negative values indicate the opposite pattern. Values close to zero indicate that the humidity inside and outside the rosettes is nearly the same. The data obtained were used as the dependent variable in a repeated measures ANOVA, in which the time of the day (0800, 1400, and 2000 hours) was the repetition factor and the size of the bromeliads (small and large) was the independent variable.

Field experiment

The role of the accumulated water inside the rosette of *A. nudicaulis* in the choice of oviposition sites by females of *B. hamata* was evaluated through a field experiment done from March to May 2006. Two experimental groups containing 30 bromeliads each were randomly designated by the flip of a coin as treatment or control. In the treatment group, a square hole of 1 cm² was made at the base of the leaf-tube in order to remove all the water inside the rosette. This hole also prevented the accumulation of water inside these bromeliads during all the experiment period. In the control group, a similar hole was made in the apex of the leaf-tube, so that the phytotelma was preserved. All experimental bromeliads were inspected once a month searching for clutches. Regarding this experiment, it is important to stress that: (1) all bromeliads selected for both experimental groups were used at least once as oviposition site during the reproductive season of 2005; (2) there was no difference in the rosette length in the treatment (mean \pm DP = 30.5 \pm 6.8 cm) and control (mean \pm DP = 31.4 \pm 6.8 cm) groups (Student's *t* test, *t* = 0.536, *df* = 58, *P* = 0.594); (3) there was no difference in the rosette slope in the treatment (mean \pm DP = 136.3 \pm 21.7°) and control (mean \pm DP = 136.3 \pm 21.9°) groups (Student's *t* test, *t* = 0.006, *df* = 58, *P* = 0.995); (4) the rosettes in both experimental groups were maintained free of debris throughout the study period by removing dry leaves once a month. The frequency of bromeliads used or not as oviposition site in each experimental group was compared using a Fisher's exact test.

Results

Oviposition pattern

From February 2005 to January 2006, 133 clutches of *Bourguyia hamata* were found in 64 individuals of the bromeliad *Aechmea nudicaulis*. Among these bromeliads, 23 were used as oviposition site only once, 23 were used twice, 12 were used three times, five were used four times, and just one was used eight times. Most of the bromeliads (94%) had just one clutch and one guarding female inside the rosette, but on five occasions bromeliads had two clutches and two guarding females inside the same rosette. On 14 occasions one adult male was found close (2–5 cm) to a guarding female.

The oviposition activity of *B. hamata* began in February and finished in October (Fig. 1). The flowering season of *A. nudicaulis* started in November, concomitant with the end of the reproductive season of *B. hamata* (Fig. 1). During the study season, 119 females were marked in the popu-

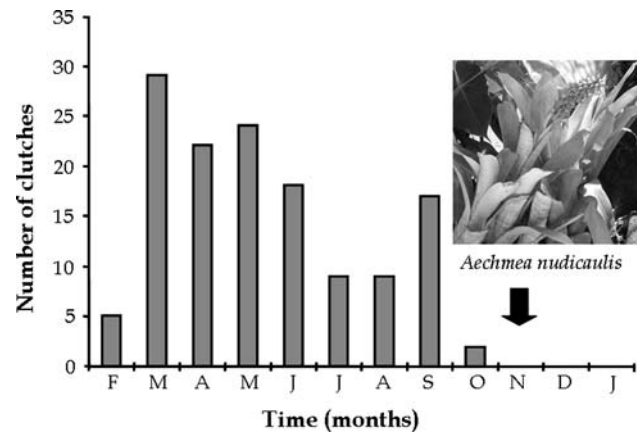


Fig. 1 Number of clutches of the bromeliad-dweller harvestman *Bourguyia hamata* found along a 700-m-long transect at Cardoso Island, southeastern Brazil, between February 2005 and January 2006. The arrow indicates the beginning of flowering season of the host plant, the epiphytic bromeliad *Aechmea nudicaulis*, which is coincident with the end of the reproductive season of *B. hamata*

lation, and among them, 56% produced only one clutch, 18% produced two and only 6% produced three. On only one occasion a guarding female was not close to her clutch, and in this case there was a katydid (Orthoptera: Tettigoniidae) eating the unattended eggs. In all the other occasions, the guarding females were close (0–5 cm) to their respective clutches.

Fifty-five females (out of 119) were captured more than once during the study period. Among these females, 69% were re-captured at the same clump of bromeliads and 29% were recaptured exactly at the same bromeliad where they were previously found. Among the 29 females with two or three reproductive events, 69% oviposited at the same clump, and among them, 45% oviposited or came back at least once to the same bromeliad where they previously laid their eggs. Only 15 females moved between distant bromeliads. Among them, 12 covered distances less than 50 m and only 3 females covered distances higher than 100 m. The greatest distance one female traveled was 210 m between February and March 2005.

Oviposition site selection

Bourguyia hamata females preferentially used bromeliads with rosettes longer than 31 cm ($\chi^2 = 23.07$, *df* = 4, *P* < 0.001, Fig. 2a). Moreover, the frequency of clutches was significantly greater in bromeliads with smaller amount of debris in the rosette, i.e., in the categories 0 and 1 ($\chi^2 = 27.08$, *df* = 3, *P* < 0.001, Fig. 2b). Bromeliads in category 3, i.e., those with the leaf-tube completely blocked by debris, were not used at all.

Nearly 96% of the clutches were found in bromeliads with the rosette slope between 91° and 180°, i.e., those with

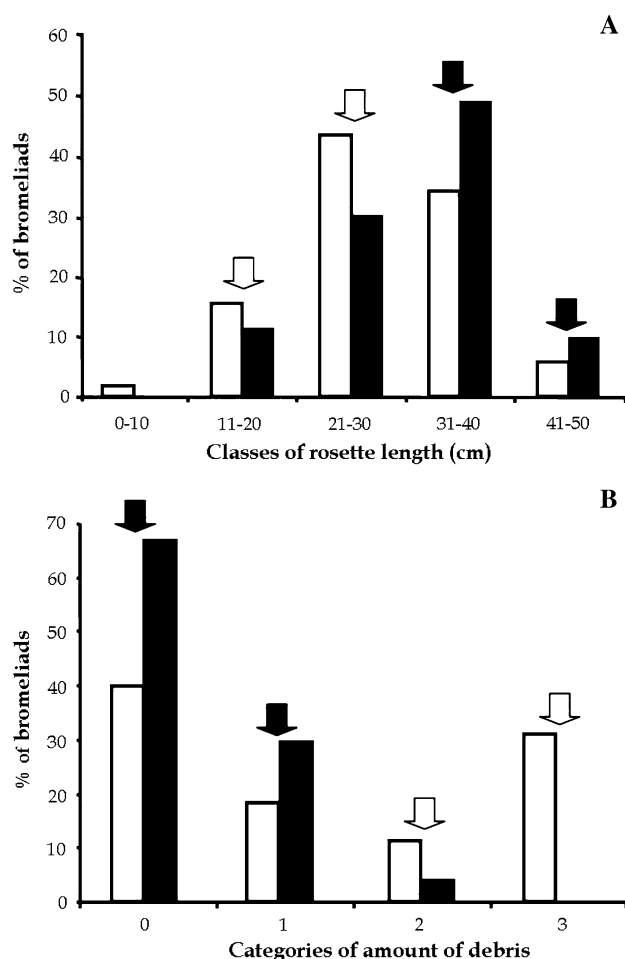


Fig. 2 Percentage of individuals of the epiphytic bromeliad *Aechmea nudicaulis* used as oviposition site by the harvestman *Bourguigia hamata* (black bars) compared to the percent of individuals available in the transect (white bars) according to the classes of **a** rosette length and **b** amount of debris found inside the rosettes (see text for definition of the categories). Black arrows indicate classes in which there was significant female preference ($P < 0.05$) and white arrows, classes in which there was significant female avoidance ($P < 0.05$)

the opening of the leaf-tube pointing to the canopy. Only two bromeliads with slopes lower than 90° were used as oviposition sites; one of these bromeliads was nearly parallel to the ground (89°) and was used four times, whereas the other one, with a slope of 62° , was used just once.

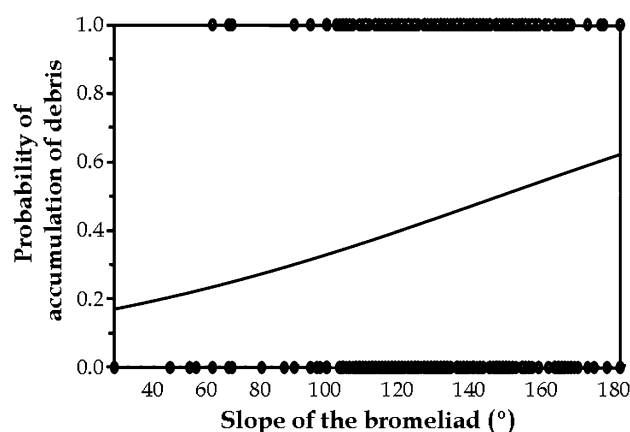


Fig. 3 Probability of accumulation of debris inside the rosette of the epiphytic bromeliad *Aechmea nudicaulis* according to the slope of the rosette in relation to the tree trunk (in 0° the leaf-tube opening is pointing to the ground, and at 180° the opening is pointing to the canopy). The equation that describes the logistic curve is $y = \exp(-1.921247 + (0.0134976)x) / (1 + \exp(-1.921247 + (0.0134976)x))$

Water and debris accumulation

The fully parameterized model, including the interaction of rosette length and slope, fitted well to the data on the volume of water accumulated inside bromeliads ($\chi^2 = 12.20$, $df = 56$, $P = 1.00$). However, the model including additive effects of rosette length and slope was the best model to describe the volume of water accumulated inside bromeliads ($AIC_c = 74.68$; ΔAIC_c to second best model = 2.30; $w_i = 0.76$; number of parameters = 3). Thus, larger bromeliads with higher slopes held more water inside the rosette. Additionally, the probability of accumulation of debris inside the rosettes increased with the increase in the rosette slope ($\chi^2 = 14.16$, $df = 1$, $P < 0.001$, Fig. 3).

Bromeliad size affects the difference between air humidity inside and outside the rosette throughout the day (Table 1; Fig. 4). Bromeliads with longer rosettes maintained higher humidity inside them when compared with the external environment (Fig. 4). This pattern is especially clear at 14 h, the hottest period of the day (Fig. 4). In contrast, air humidity inside bromeliads with short rosettes was nearly the same as the external environment throughout the day (Fig. 4).

Table 1 Results of the repeated measures ANOVA performed to compare the difference in the relative air humidity inside and outside large (30–32 cm of rosette length) and small (18–20 cm of rosette length) individuals of the bromeliad *Aechmea nudicaulis* during the day

Factors	df effect	MS effect	df error	MS error	F	P -level
Size of the bromeliad (small and large)	1	132	42	2.737	48.2214	<0.001
Time (morning, afternoon and night)	2	85.144	84	1.424	59.76678	<0.001
Size \times time	2	79.023	84	1.425	55.46999	<0.001

Morning samples ($N = 22$) were taken at 0800 hours, afternoon samples ($N = 22$) were taken at 1400 hours, and night samples ($N = 22$) were taken at 2000 hours

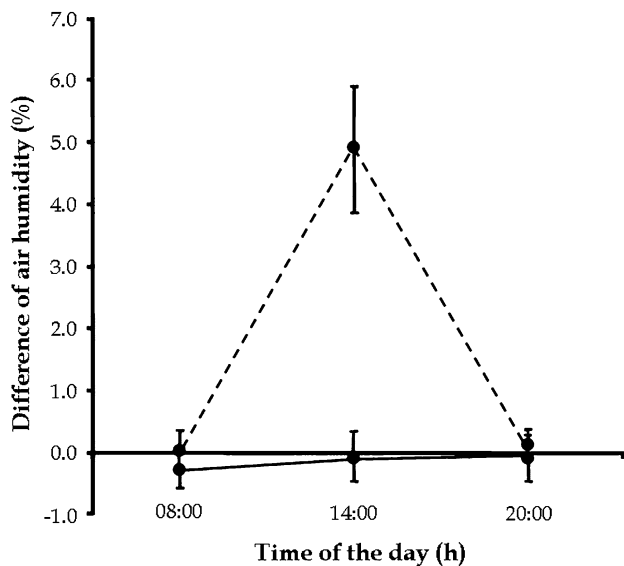


Fig. 4 Comparison of relative air humidity difference during the day inside and outside the rosettes of large (30–32 cm; dashed line) and small (18–20 cm; solid line) individuals of the epiphytic bromeliad *Aechmea nudicaulis*. Positive values indicate that the humidity inside the rosettes was higher than that in the external environment, while values close to zero indicate that the humidity inside and outside the rosettes was nearly the same. Large bromeliads buffer the variation of humidity maintaining a wetter micro-climate inside the rosette during the hottest period of the day, i.e., at 14 h. Note that humidity inside the rosette of small bromeliads is nearly the same as that of the external environment during all day. Error bars represent standard error

Field experiment

Twelve bromeliads with water inside the rosette (control group, $N = 30$) were used as oviposition sites, whereas, only three bromeliads without water inside the rosette (treatment group, $N = 30$) were used by the females (Fisher exact test, $P = 0.008$). Four bromeliads in the control group were used twice as oviposition site during the 3 months of the experiment, and no bromeliad was used more than once in the treatment group.

Discussion

Oviposition pattern

Many arthropods in tropical areas show a reproductive peak during the warm and wet season (Wolda 1988), and most harvestman species seem to follow this same pattern (e.g., Gnaspini 1995; Machado and Oliveira 1998; Willemart and Gnaspini 2004). In contrast, the reproductive peak of the bromeliad-dweller harvestman *Bourguyia hamata* is at the beginning of the cold season, and there is no reproductive activity during the warmest and the most humid months of

the year. The reproductive season of *B. hamata* ends at the beginning of the flowering season of the bromeliad *Aechmea nudicaulis*, the exclusive oviposition site of this species at Cardoso Island (Machado and Oliveira 2002; Fig. 1). During the flowering season of *A. nudicaulis*, the inflorescence stalk occupies the leaf-tube, so that the oviposition sites are not available for ovigerous females. Moreover, with the inflorescence growth, the stalks could drag the eggs out of the rosette. Therefore, it is possible that *B. hamata* females adjust their phenology according to the availability of appropriate oviposition sites, as previously suggested by Machado and Oliveira (2002).

Bourguyia hamata females seem to be highly phylopatric and might have a restricted home range because most of them were recaptured at the same clump of bromeliads where they were first found. Probably, as a consequence of phylopatry, almost 70% of the females that reproduced two or more times used bromeliads of the same clump as oviposition site. Males, on the other hand, were rarely recaptured in our transect traveling longer distances when compared to females (F. Osses, unpublished data). Apparently, males do not monopolize the clumps or individual bromeliads, probably because this reproductive resource is abundant in the studied site. The few instances in which a male was found together with a guarding female inside the same bromeliad probably corresponded to cases of mate guarding, a common behavioral strategy in harvestmen, including *B. hamata* (review in Machado and Macías-Ordóñez 2007).

Oviposition site selection

The family Bromeliaceae, with a predominantly tropical distribution, includes nearly 1,000 species of plants that commonly accumulate water in the leaf axils (Fish 1983). In some tropical forests where the leaf litter can dry fast, even in a few days of no rain, bromeliads might be a source of water, shelter, and nutrients for several animal groups (Richardson 1999). Indeed, the water reservoirs accumulated inside bromeliads are used in many ways by a wide range of terrestrial organisms, including insects (Corbet 1983; Fish 1983; Naeem 1990; Judd 1998; Greeney 2001), annelids (Fragoso and Rojas-Fernández 1996; Sota and Mogi 1996), crabs (Diesel 1989, 1997; Diesel and Schuh 1993), and anurans (Caldwell 1993; Summers 1992; Giarretta 1996; Bourne et al. 2001). Several harvestman species have already been recorded inside bromeliads, but few seem to be closely associated with this habitat (review in Curtis and Machado 2007). *Bourguyia hamata*, however, is strictly associated with the bromeliad *A. nudicaulis*, using it as oviposition substrate, and seems to select not only the host plant species, but also architectural features of individual plants. Figure 5 shows a diagram that summarizes

some of these architectural features and their possible influences (positive and negative) on the oviposition site selected by females.

In this study we showed that *B. hamata* females prefer bromeliads with longer rosettes (Fig. 2a). This preference for larger bromeliads has also been observed in the crab *Metopaulius depressus* (Diesel 1989), the ant *Gnamptogenys moelleri* (Cogni and Oliveira 2004), and the jumping spider *Psecas chapoda* (Romero and Vasconcellos-Neto 2005a, b). Larger individuals of *A. nudicaulis* may intercept and accumulate a higher volume of water inside the rosette, which can lead to a decrease in moisture loss inside the leaf-tube, especially during the drier hours of the day (Fig. 4). Because harvestman eggs are extremely sensitive to dehydration (Edgar 1971; Machado and Oliveira 1998), attenuation of moisture loss could be important for offspring development (Fig. 5). Furthermore, a higher volume of water could confer additional protection to the parental individuals (Fig. 5) because disturbed females drop into the phytotelma (personal observation)—a defensive behavior also recorded for young crabs of *M. depressus* (Diesel 1989) and for the jumping spiders *Coryphasia* sp., *Psecas* sp., and *Eustiromastix nativo* (Romero 2005). Even though it could be proposed that large-sized bromeliad themselves may maintain high moisture inside their leaf-tubes protecting guarding females against predators, our field experiment demonstrates that bromeliads that could not accumulate water inside the rosette were avoided by

ovipositing females. This finding highlights the importance of phytotelma as a key factor used by females to select oviposition sites in *B. hamata*.

Although the slope of the rosettes did not affect the probability of the females ovipositing inside the bromeliads, we demonstrated that this architectural feature influences the accumulation of water and debris inside the rosette. Bromeliads with slopes lower than 90° , i.e., with the opening of the leaf-tube pointing to the ground, do not accumulate debris. However, they also do not accumulate water inside them, which is probably harmful for the development of the eggs, as explained above. Bromeliads pointing up (with slopes higher than 90°) may accumulate water inside the rosettes, but above some slopes they may retain larger amounts of dry leaves that fall from the canopy (Fig. 3). Debris can block the rosette entrance and hamper the use of this microhabitat by ovigerous females (Fig. 5). In fact, bromeliads with small amounts of debris inside the rosette were preferred by ovipositing females, whereas bromeliads with great amounts of debris were clearly avoided or not used at all (Fig. 2b). A similar pattern was recorded in studies with the jumping spider *Psecas chapoda*, whose females do not produce egg-sacs in bromeliads with leaf litter because it blocks the axils of the bromeliad, which are used as shelter by nymphs and adults (Romero and Vasconcellos-Neto 2005a, b). Also, *M. depressus* females selected bromeliads with less leaf litter and removed leaves, twigs and other material dropped from the canopy into the axils, as well as decaying organic matter from the reservoir base throughout the entire breeding season (Diesel 1989).

To the best of our knowledge, this study is the first to demonstrate that harvestman females are able to assess architectural features of the plants used for oviposition, or at least key factors that relate to such features that could be directly related to their reproductive success, such as water and debris content. *Bourguyia hamata* females oviposit almost exclusively inside the leaf-tube of the epiphytic bromeliad *A. nudicaulis* and additionally prefer individuals with longer rosettes, which accumulate more water and have small amounts of debris inside them. These features probably promote a more adequate microhabitat for egg development and consequently may increase offspring survival.

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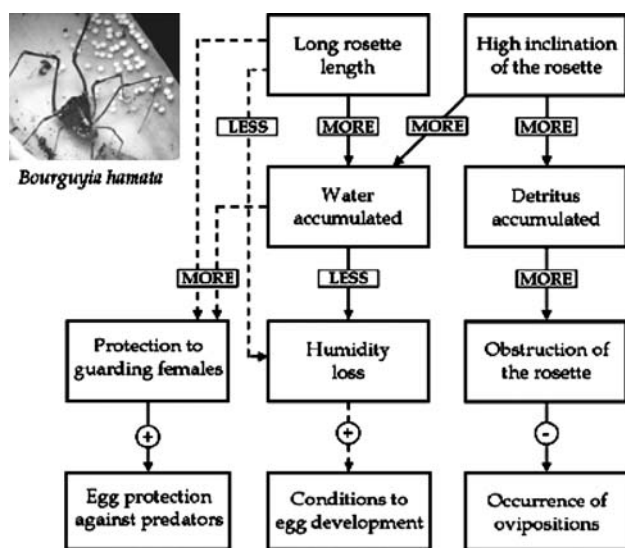


Fig. 5 Schematic diagram showing how the architectural features of the bromeliad *Aechmea nudicaulis* may influence the oviposition site selection by females of the harvestman *Bourguyia hamata*. Positive influences are indicated by the sign plus, and negative influences are indicated by the sign minus. Solid lines indicate relationships that have already been demonstrated, while dashed lines indicate putative relationships that still lack demonstration. See text for details

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