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ASSOCIATION OF THE STILT BUG *JALYSUS OSSESAE* HENRY (HEMIPTERA: HETEROPTERA: BERYTIDAE) WITH MYRMECOPHYTIC PLANTS OF THE GENUS *MAIETA* (MELASTOMATACEAE) IN AN UPLAND FOREST AREA IN CENTRAL AMAZON, BRAZIL

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Abstract.—*Maieta guianensis* Aubl. and *M. poeppigii* Mart. ex. Triana (Melastomataceae) are among the most common myrmecophytic plants in the Amazonian forest understory. These myrmecophytes are colonized exclusively by the ants *Pheidole minutula* Mayr or *Crematogaster* sp. and usually host two other arthropods, the spider *Faiditus subflavus* Exline and Levi and the recently described stilt bug *Jalysus ossesae* Henry. In this study, the association between *J. ossesae* and the myrmecophytic plants *M. guianensis* and *M. poeppigii* in an upland forest area in central Amazon, Brazil, is described. The presence of the stilt bugs on *M. guianensis* and *M. poeppigii* and on plants around these myrmecophytes was recorded in five transects. The number and position of the stilt bugs on the leaf surface (upper or lower) and leaf type (with or without domatia) of these myrmecophytes, as well as their behavioral acts, were recorded. *Jalysus ossesae* was found only on the myrmecophytic plants *M. guianensis* and *M. poeppigii*. The stilt bug occurred at similar frequencies on *M. guianensis* and *M. poeppigii*, and the number of leaves significantly influenced the presence and number of stilt bugs on these myrmecophytes. Feeding, agonistic interaction between males, and mating were observed. Our data indicate that *J. ossesae* uses the myrmecophytes *M. guinanensis* and *M. poeppigii* as reproductive and foraging sites.

Key Words: Hemiptera, animal-plant interaction, host plants, *Maieta guianensis*, *Maieta poeppigii*, trichomes, ant-plants

Myrmecophytes are tropical plants that have specialized structures known as domatia (e.g., hollow stems, leaf pouches, swollen petioles) where ants nest (Beattie 1985; Benson 1985; Davidson and McKey 1993a, b; Heil and McKey 2003). Traditionally, studies on myrmecophytic plants have focused on their mutualistic association with ants and, therefore, have been of paramount importance for our understanding of ant-myrmecophyte mutualisms and mutualistic associations in general (Bronstein 1998). However, myrmecophytes are frequently inhabited by other arthropods (Fowler and Venticinque 1996, Gastreich 1999), and studies have suggested that a better description of ant-myrmecophyte mutualisms should consider the influence of other animals associated with myrmecophytic plants (Price et al. 1986, Jolivet 1991, Letourneau and Dyer 1998, Gastreich 1999).

Myrmecophytic plants are a conspicuous element of central Amazonian forests, where about 16 species are found at relatively high densities (Fonseca and Ganade 1996). Of the many myrmecophytic species studied, *Maieta guianensis* Aubl. and *M. poeppigii* Mart. ex. Triana (Melastomataceae) are among the most common in the Amazonian forest understory (Benson 1985; Vasconcelos 1991, 1993; Christianini and Machado 2004). These myrmecophytes have pubescent (high trichome density on upper leaf surfaces; F. Osses, personal observation), opposite and dimorphic leaves, with the larger leaf of each pair bearing domatia–leaf pouches–inside which ants nest (Vasconcelos 1991, Ribeiro et al. 1999). Both *M. guianensis* and *M. poeppigii* are colonized exclusively by the ants *Pheidole minutula* Mayr or *Crematogaster* sp. (Vasconcelos 1991, 1993; Lapola et al. 2003; Christianini and Machado 2004). Two other arthropods typically are found associated with these plants, namely, the spider *Faiditus subflavus* Exline and Levi (Theridiidae) (Fowler and Venticinque 1996) and the recently discovered stilt bug *Jalysus ossesae* Henry (Berytidae; Henry 2007).

In this study, we describe the association between *J. ossesae* and the myrmecophytic plants *M. guianensis* and *M. poeppigii* in an upland forest of the central Amazon, Brazil. The main questions we address are: 1) Are the stilt bugs strictly associated with *M. guianensis* and *M. poeppigii*? 2) What is the relationship of the stilt bug to these myrmecophytes? 3) What is the relationship of the stilt bug to the ants associated with *M. guianensis* and *M. poeppigii*?

Materials and Methods

Study area.—This study was conducted in July 2004 at the Reserva Florestal do Km 41 (2°24′S, 59°44′W), an area of "terra firme" (upland forest) belonging to the Biological Dynamics of Forest Fragments Project (BDFFP), ca. 70 km north of Manaus, central Amazon, Brazil. The altitude of the area ranges between 100 and 150 m and the average total rainfall is 2186 mm. See Lovejoy and Bierregard (1990) for details of the study area.

Data collection.—To verify whether *J. ossesae* is strictly associated with *M. guianensis* and *M. poeppigii* plants, we surveyed four 5 × 100 m transects to inspect 61 myrmecophytes (39 individuals of *M. guianensis* and 22 of *M. poeppigii*) and each herbaceous plant or shrub within 1 m from each myrmecophyte (n = 244). We also inspected another common pubescent myrmecophytic species in the study area, *Hirtella myrmecophila* (Chrysobalanaceae) (n = 30). We inspected *H. myrmecophila* on four other transects because this plant was absent on transects used to inspect the *Maieta* plants.

For each of the 61 individuals of *Maieta*, we recorded the number of leaves. We also recorded the presence/absence and counted the number of *J. ossesae* on each myrmecophyte in the morning (0800–1100), afternoon (1400–1700), and at night (1900–2200) for two consecutive days. In addition, we recorded the position of the stilt bugs on the leaf surface (upper or lower) and the leaf type (domatia present or absent). All behavioral acts of the stilt bugs were observed and recorded.

Statistical analyses.—To compare the frequency of occurrence of *J. ossesae* between *M. guianensis* and *M. poeppigii*, we used the chi-square test. Logistic

Table 1. Mean (± 1 SD) number of stilt bugs, *Jalysus ossesae*, found on the myrmecophytes *Maieta guianensis* and *M. poeppigii*. Means shown for each period are averages of the total number of stilt bugs found on each myrmecophyte in two days. Means shown for each leaf type and leaf surface are averages of the total number of stilt bugs found on each myrmecophyte across all the periods of the day for two days.

	Period			Leaf surface		Leaf type	
Myrmecophyte	Morning	Afternoon	Night	Upper	Lower	With domatia	Without domatia
M. guianensis	10.0 ± 1.4	6.0 ± 0.0	8.0 ± 1.4	8.7 ±0.3	1.7 ± 0.5	8.0 ± 1.8	1.0 ± 1.0
M. poeppigii	3.0 ± 0.0	4.5 ± 0.7	4.5 ± 0.7	4.2 ± 1.2	0.3 ± 0.5	4.0 ± 0.9	0.5 ± 0.5

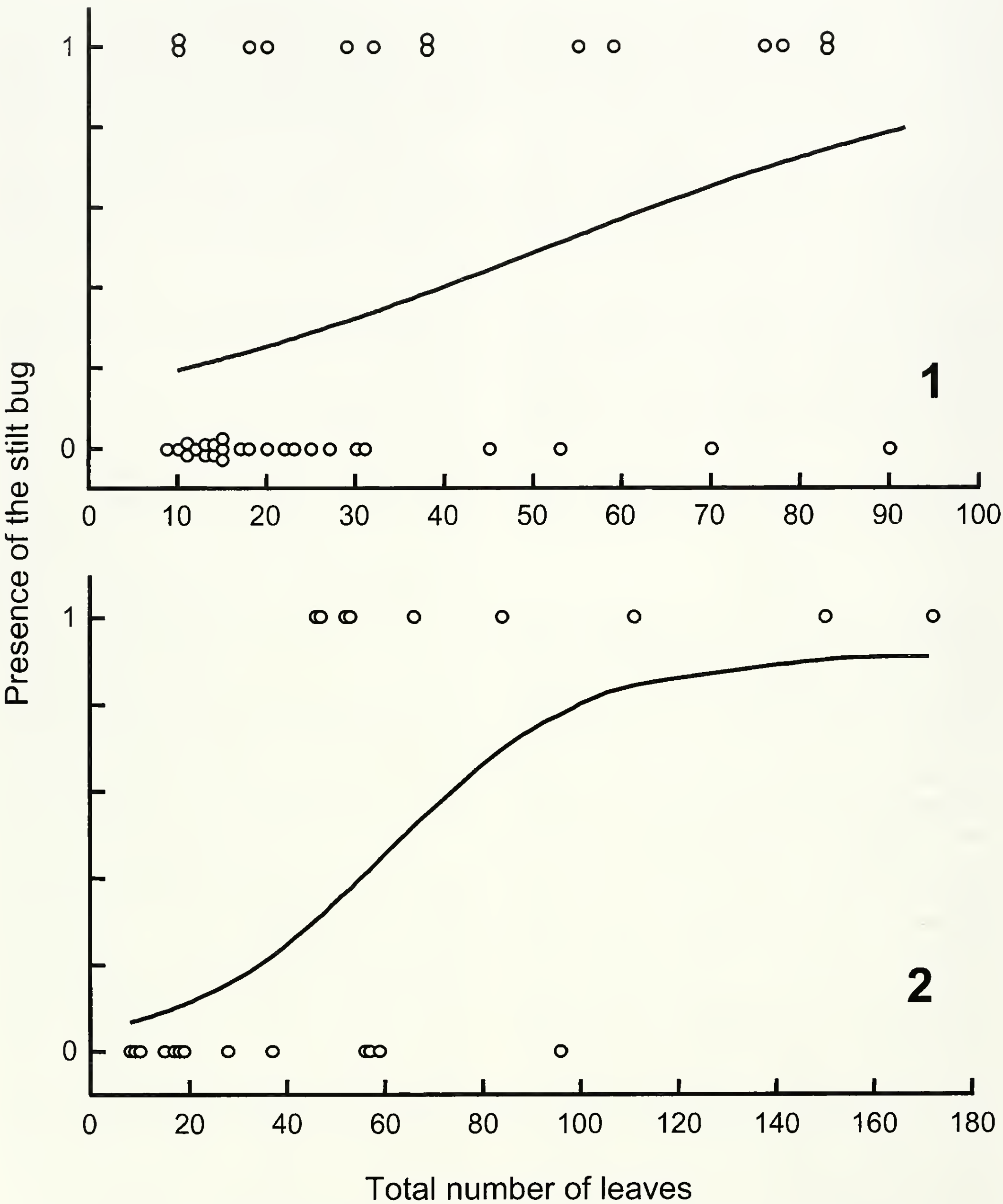
regressions were used to evaluate the influence of the number of leaves on the presence of the stilt bugs, and simple linear regressions were used to evaluate the relation between the number of leaves on the plants and the mean number of stilt bugs on each plant across all the periods of the day for two days.

Results

Jalysus ossesae was found only on the myrmecophytic plants *M. guianensis* and *M. poeppigii*. Stilt bugs were recorded on 14 and 11 individuals of *M. guianensis* and *M. poeppigii*, respectively. These frequencies of occurrence of stilt bugs on the myrmecophytes were not significantly different between the two plants ($\chi^2 = 1.11$; df = 1; $P = 0.29$). The mean number of stilt bugs found on *M. guianensis* and *M. poeppigii* was nearly constant throughout periods of the day (Table 1). On both *M. guianensis* and *M. poeppigii*, the mean number of stilt bugs on the upper surface of leaves tended to be greater than that on the lower surface (Table 1). The mean number of stilt bugs on leaves with domatia also tended to be greater than that on leaves without domatia (Table 1). However, since the leaves bearing domatia of *M. guianensis* and *M. poeppigii* are 7–10 fold larger than those without domatia (mean surface area in mm^2 ± 1 SD; *M. guianensis*: domatia present: 5200.5 ± 359.1; domatia absent: 554.2 ± 69.3; *M. poeppigii*: domatia present: 7438.6 ± 1219.4; domatia absent: 1132.9 ± 384.3; *t*-test: $t = 4.9$, $P < 0.001$), there is no strong support for the tendency of the stilt bugs to occur more frequently on leaves with domatia.

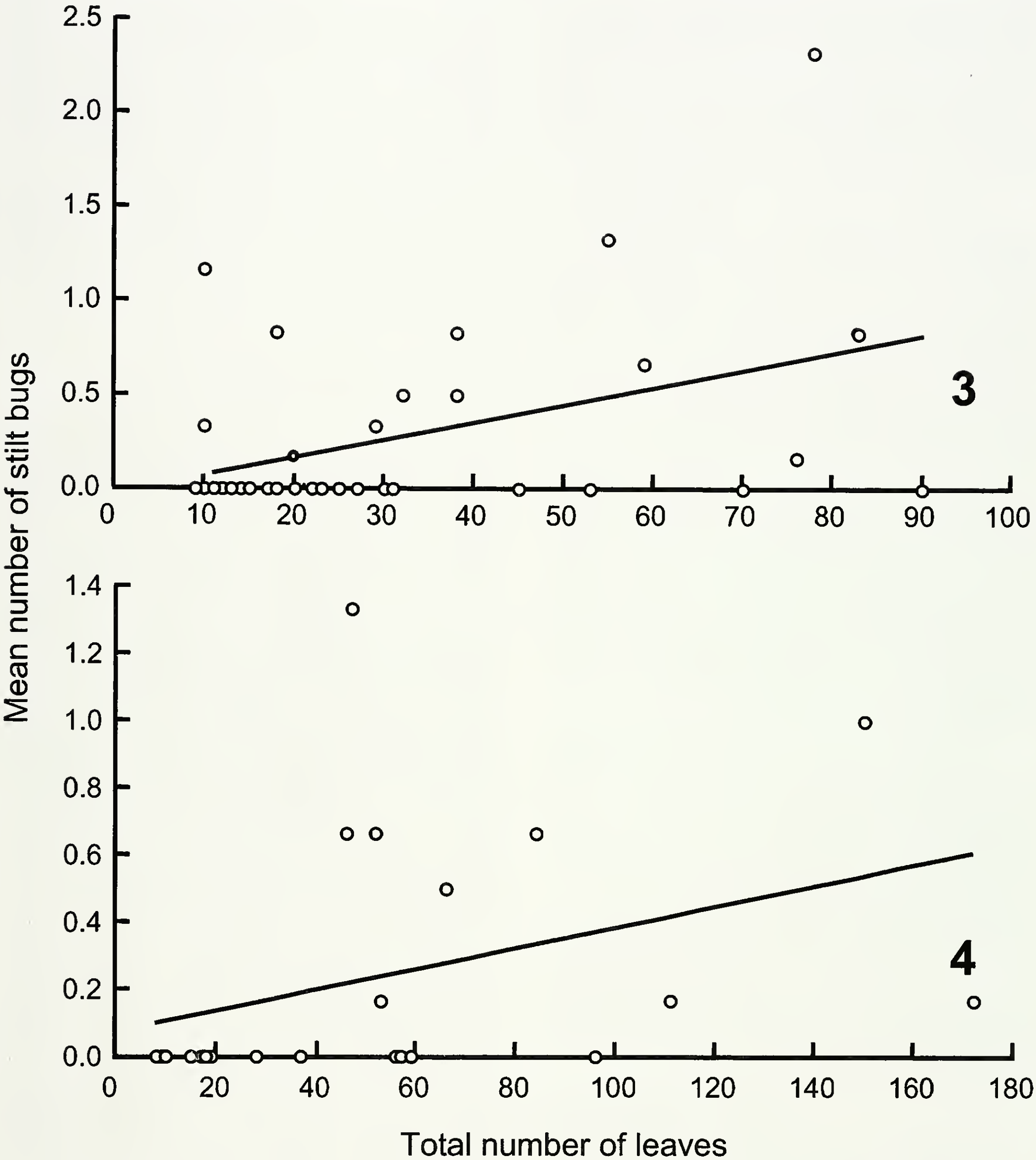
The presence of stilt bugs on the myrmecophytes was significantly influenced by the number of leaves on both *M. guianensis* (logistic regression: $\chi^2 = 6.14$, df = 1, $P = 0.01$, $n = 39$, Fig. 1) and *M. poeppigii* (logistic regression: $\chi^2 = 10.07$, df = 1, $P < 0.01$, $n = 22$, Fig. 2). In general, *M. guianensis* and *M. poeppigii* with fewer leaves had no stilt bugs, whereas the probability of finding a stilt bug on plants with about 95 leaves increased to about 80% (Figs. 1–2). The mean number of stilt bugs on these plants ranged from 0 to 2.3 and from 0 to 1.3 in *M. guianensis* and *M. poeppigii*, respectively, and was positively related to the number of leaves in *M. guianensis* ($r^2 = 0.20$, $F_{1,37} = 9.16$, $P < 0.01$, $n = 39$, Fig. 3) and not related to the number of leaves in *M. poeppigii* ($r^2 = 0.13$, $F_{1,20} = 2.93$, $P = 0.10$, $n = 22$, Fig. 4).

We observed three mating events, all of them in the morning. In all events, the male held the female with its hind legs, positioned the end of its abdomen below that of the female and introduced its copulatory organ. Two feeding events also were observed, one in the morning and one in the afternoon. In both cases, *J. ossesae* was found on leaves with domatia, but one individual was on the upper surface of the leaf and the other on the lower surface. Food items could not be determined because feeding was not observed from the beginning and, when



Figs. 1–2. Relationships between the total number of leaves and the presence/absence of the stilt bug *Jalysus ossesae* on myrmecophytes. 1, *Maieta guianensis*. 2, *Maieta poeppigii*. The presence and absence of stilt bugs are indicated as 1 and 0 on the *y* axis, respectively. Dots are displaced vertically to avoid overlapping.

it was discovered, the food items were too small to be identified. Only one agonistic interaction between two males was observed. In the afternoon, one male moved to a leaf where another male was present. When the intruder reached the middle of the leaf, the resident placed itself in front of the intruder until it was



Figs. 3–4. Relationships between the total number of leaves and the mean number of stilt bugs, *Jalysus ossesae*, found on myrmecophytes. 3, *Maieta guianensis*. 4, *Maieta poeppiggii*.

displaced from the leaf. The agonistic interaction lasted three minutes.

Discussion

We observed *J. ossesae* feeding only on *M. guinanensis* and *M. poeppigii*, suggesting that it is using *Maieta* spp. as a food source. The trichomes in these myrmecophylous plants are apparently important in helping segregate *J. ossesae* from ants; thus, avoiding contact between them and preventing ants from detecting the stilt bugs. Additionally, *J. ossesae* uses these plants as reproductive sites. Other species of *Jalysus* also use pubescent plants as breeding hosts (Wheeler and Henry 1981, Wheeler and Schaefer 1982). In addition to our observations on mating and agonistic interactions between males, we observed fourth- and fifth-instar nymphs, providing further evidence that *J. ossesae* uses *M. guianensis* and *M. poeppigii* as its main host plants in the study area.

Although species of *Jalysus* feed on sap and reproductive parts of their host plants, they also may require some animal food source for proper development and fecundity (Elsey and Stinner 1971). Because other species of *Jalysus* feed on arthropods associated with their host plants (Elsey and Stinner 1971, Gilmore 1938, Kulash 1949, Wheeler and Henry 1981, Henry 2000), *J. ossesae* might scavenge on prey captured by the ants or even occasionally prey on ants that are, perhaps, injured or dying. Thus, the association between *J. ossesae* and *M. guianensis* and *M. poeppigii* is likely affected by the presence of ants on these plants.

The above contention is supported by our results showing that the probability of occurrence and the number of stilt bugs on *M. guianensis* and *M. poeppigii* increases with increasing number of leaves because the number of ants is greater on plants with large numbers of leaves bearing domatia (Christianini and Machado 2004). Consequently, the stilt bugs would be expected to remain on the pubescent surface of these leaves to avoid detection by the ants, as was observed for first-instar lepidopteran caterpillars on *M. guianensis* (Vasconcelos 1991). As expected, our results showed that *J. ossesae* occurs more frequently on the upper surface of leaves, which is densely covered by trichomes, than on the lower surface (low trichome density).

Because we could not identify the food items found with *J. ossesae*, further observations are necessary to evaluate the contention that the stilt bug might occasionally prey on injured or dying ants associated with *M. guianensis* and *M. poeppigii*. Furthermore, future investigations should focus on the influence, if any, of *J. ossesae* on this ant-myrmecophyte system. Additional data on feeding behavior, egg laying and beneficial or harmful interaction of this stilt bug-ant-myrmecophyte system could be useful for understanding the evolution of the specificity of *J. ossesae* on *M. guianensis* and *M. poeppigii*.

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