Behavioral Plasticity of Triatominae Related to Habitat Selection in Northeast Brazil

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ABSTRACT *Triatoma pseudomaculata* Corrêa and Espínola, 1964 and *Triatoma juazeirensis* Costa and Felix, 2007 (=*T. brasiliensis* Neiva, 1911 [part]), are sylvatic vectors of *Trypanosoma cruzi* (Chagas, 1909), the causative agent of Chagas disease, in northeast Brazil—especially in the caatinga region. In an area of caatinga in the State of Bahia, we compared the wild and peridomestic habitats of these two species of Triatominae to assess their behavioral plasticity in relation to habitat selection in different environments. In the sylvatic environment, the habitat of these two species is never shared. *T. pseudomaculata* is found in trees and bird nests, but without apparent preference for any particular tree species. In contrast, *T. juazeirensis* is exclusively rupicolous (found among rocks). Both species invade peridomestic structures but do not display a significant ability to colonize human dwellings. In the peridomestic area, they are highly adaptable to different habitats and can occupy substrates that they do not colonize in the sylvatic environment. This behavioral plasticity seems to be more striking in *T. juazeirensis*—rupicolous in sylvatic environments but colonizing wooden structures in the peridomicile in >80% of cases.

KEY WORDS *Triatoma pseudomaculata*, *Triatoma juazeirensis*, sylvatic environment, peridomicile, Brazil

In many Southern Cone regions, autochthonous species of Triatominae, originally restricted to a wild environment, are increasingly reported to invade human dwellings and peridomestic structures where they might act as vectors of *Trypanosoma cruzi,* the causative agent of Chagas disease. This is the case for *Triatoma pseudomaculata* Corrêa and Espínola, 1964, and *Triatoma brasiliensis* Neiva, 1911, both native of xerophitic ecosystems in northeastern Brazil. Their geographical ranges overlap in the State of Bahia, and both are reported to invade and colonize artificial structures, mainly the peridomicile (Silveira and Vinhaes 1998, Dias et al. 2000).

Triatoma pseudomaculata often invades peridomestic structures but does not display a significant ability to colonize human dwellings, even though large domestic colonies have been reported in urban areas of Sobral, Ceará (Souza et al. 1999) and Berilo, Minas Gerais (Assis et al. 2006). Reports on its sylvatic habitat are scarce. According to Barretto (1967), *T. pseudomaculata* occurs in hollow trees and rock cavities, where it feeds on rodents and marsupials.

In contrast, *T. brasiliensis* seems to represent at least four forms constituting the *T. brasiliensis* species complex (Costa 1999, Monteiro et al. 2004). One of these, found in the State of Bahia, was recently described as *T. juazeirensis* Costa and Felix, 2007. However, Costa (1999) and Costa et al. (2003) suggested that the northern population (*brasiliensis* s.s.) would be most important epidemiologically because of its widespread distribution (Ceará, Maranhão, Paraíba, Piauí, and Rio Grande do Norte), highest *T. cruzi* infection rate (15%), and the ability to colonize domestic ecotopes.

The objective of this study was to compare the wild and peridomestic habitats of *T. pseudomaculata* and *T. juazeirensis*, to assess their behavioral plasticity as related to habitat selection in different environments, and to understand their natural ecology in relation to their process of domestication.

Materials and Methods

Study Area. Curaçá (287 miles above sea level [masl]; 08°58′ S, 39°53′ W) is a rural district of Bahia State, Brazil. It is located near the São Francisco River, in a region of caatinga, a set of xerophytic formations

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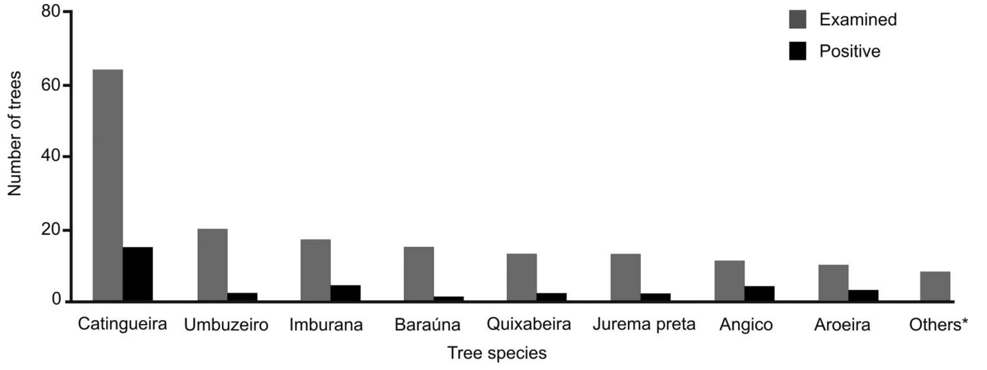

Fig. 1. *Triatoma pseudomaculata* infestation according to tree species. *Pereira (*Aspidosperma pyrifolium*) and Faveleira (*Cnidoscolus phyllacanthus*).

located in northeast Brazil and characterized by the fall of leaves during the dry season and the abundance of cacti and bromeliads (Forattini 1980, Emperaire 1989). The climate is semiarid and presents two seasons: dry from April to October and rainy from November to March. Mean temperatures range between 24 and 29°C, and the mean annual precipitation is 300 mm. The sylvatic environment studied displayed a diversity of flora associated with the range of human intervention. It is covered by scattered or dense vegetation (elevation, 3–6 m) dominated by *Caesalpinia pyramidalis* Tul, locally known as "catingueira." Thorn shrubs, cacti, and bromeliads predominate at the lowest strata. In places, the plain overlaps with large rocky formations consisting of quartzite, and the elevation is generally <100 m. Rural houses tend to be isolated but sometimes are grouped in small settlements. Houses are made of brick or mud. The peridomestic structures are often extensive and usually include various animal enclosures fenced in with sticks, shelters for chickens, material for building (tiles and bricks), and woodpiles. Some trees, in which chickens frequently roost, are located in the peridomestic area. Natural rockpiles are often close to the houses. The main activity of the human population is livestock farming (principally goats and sheep); during the dry season, livestock are usually allowed to roam throughout the surrounding areas, but during the wet season, they are kept in enclosures at night.

Collection of Triatomines in Sylvatic Environments. Insect collections were carried out from 2001 to 2004 during the dry and rainy seasons. Various potential habitats were searched for the presence of Triatominae in sylvatic areas in the Curaçá district. Mouse-baited Noireau traps (Noireau et al. 1999) were used to capture insects living in hollow trees and rocks. Some bird nests, built principally by Dendrocolaptidae and Furnariidae and located in cactus "mandacaru" (*Cereus jamacaru* DC) or any tree, were also dissected.

Collection of Triatomines in Peridomestic-domestic Environments. In June and July 2003, 58 domiciliary units (DUs; constituted by the intradomicile and the peridomicile) were studied. They were randomly selected from a wider sample of 136 houses previously mapped and studied (Walter et al. 2005). All potential vector habitats were located on a map and described according to a standardized questionnaire. A 2- to 3-h search for bugs was conducted in and around the domicile by two inspectors. The peridomestic area was defined as all natural or artificial structures used more or less daily by farmers or domestic animals, without the limitation of distance from the house. Inside this area, all potential habitats for Triatominae were examined. They were classified according to substrate: baked clay for construction material (tile and brick) and wood, including stick fences, trees, and bird-nests. Animals present in domiciliary units were noted.

Processing of Insects. Triatominae were placed in labeled plastic bags according to the capture site and transported to the laboratory. Species were identified according to Lent and Wygodzinsky (1979) and, for *T. brasiliensis*, according to the chromatic patterns described by Costa et al. (1997).

Statistical Analysis. A χ^2 test with Yates correction was used to compare distributions between several categories. A Mann–Whitney nonparametric test was used to compare median values from different categories.

Results

Wild Environments. From a total of 599 trees studied, 129 (21.5%) were infested with Triatominae. *T. pseudomaculata* was the only species collected and was mainly represented by nymphs (95.0% of 222 Triatominae collected). Triatomine burden per positive tree was very low (medians equal to 1 or 2). Some of the studied trees were taxonomically identified. Infestation rate of *T. pseudomaculata* according to the tree species is shown in Fig. 1. All tree species were found infested when several (≥10) were studied, and their infestation rates were not significantly different (χ^2 test, df = 8, $P = 0.38$). In *C. pyramidalis*, the most common species in the region, the *T. pseudomaculata* infestation rate detected by trapping was 23.3%.

We also searched for Triatominae in nests or shelters of small mammals located between or under the

Table 1. Comparative distribution and abundance of *T. juazeirensis* and *T. pseudomaculata* in peridomestic ecotopes

Ecotopes	*N* examined	*T. juazeirensis* No. (%) positive ecotopes	*T. juazeirensis* Median catch (first and third quartiles) per positive ecotope	*T. pseudomaculata* No. (%) positive ecotopes	*T. pseudomaculata* Median catch (first and third quartiles) per positive ecotope	*P* value (χ^2 test)[a]	*P* value (M-W test)[b]
Corral[c]	109	26 (23.9)	3.0 (1–7)	21 (19.3)	1.0 (1–2)	0.62	0.01[f]
Roofed corral	32	6 (18.8)	7.5 (1–15)	2 (6.3)	8.5 (1–16)	0.34	0.86
Stick fence[d]	30	2 (6.7)	11.5 (1–22)	1 (3.3)	6.0	0.57	—
Pile of wood	49	2 (4.1)	1.0 (1–1)	4 (8.2)	3.5 (2–4.5)	0.71	—
Artificial chicken coop	29	3 (10.3)	2.0 (1–2)	5 (17.2)	5.0 (2–7)	0.77	0.14
Fowl tree[e]	44	2 (4.5)	10.0 (9–11)	8 (18.2)	1.0 (1–2.5)	0.14	0.04
Bird nest	47	0	—	9 (19.1)	2.0 (1–5)	—	—
Pile of tiles	38	5 (13.2)	2.0 (1–17)	1 (2.6)	12.0	0.25	—
Pile of bricks	31	1 (3.2)	22.0	1 (3.2)	1.0	1.00	—
Other structures	80	6 (7.5)	2.5 (1–8)	3 (3.8)	2.0 (1–3)	0.53	0.71
Total	489	53 (10.8)	3.5 (2–6)	55 (11.2)	2.5 (1–8)	0.94	0.97

[a] χ^2 test (with Yates correction when necessary) to compare the no. of positive ecotopes for *T. juazeirensis* and *T. pseudomaculata.*
[b] Mann-Whitney test (M-W) to compare the median catches for each species.
[c] Enclosure made of vertical wood posts.
[d] Fence made of vertical, horizontal, or oblique trunks.
[e] Trees where chickens roost.
[f] Significant difference with $P < 0.05$.

rocks. From a total of 307 traps placed in rocky ecotopes, 59 (19.2%) collected Triatominae. Except for one adult *Panstrongylus lutzi* (Neiva and Pinto 1923), *T. juazeirensis* was the only species collected from among rocks, and, as with *T. pseudomaculata,* most were nymphal stages (100/103).

We dissected 66 bird nests located in "mandacaru" cactus or in trees. In these, *Rhodnius neglectus* Lent, 1954 ($n = 66$) was more frequently found than *T. pseudomaculata* ($n = 38$) in nests built in mandacaru (19 and 38% of the 21 nests were positive for each species, respectively). The 45 bird nests in trees showed similar infestation rates with *T. pseudomaculata* and *Psammolestes tertius* Lent and Jurberg, 1965 (13.3 versus 11.1%, respectively). None of these Triatominae captured in sylvatic environments were infected with *T. cruzi.*

Peridomestic Environments. From a total of 576 triatomine bugs collected in peridomestic structures, 408 were *T. juazeirensis* (155 adults and 253 nymphs) and 168 were *T. pseudomaculata* (42 adults and 126 nymphs). Some specimens of *P. tertius* ($n = 33$) and *R. neglectus* ($n = 6$) were also collected in bird nests from trees located in the peridomestic area. None of the collected Triatominae were infected with *T. cruzi.* From 58 peridomiciles studied, 42 (72.4%) were positive for triatomine bugs. *T. juazeirensis* was found in 30 (51.7%), *T. pseudomaculata* in 31 (53.4%), *P. tertius* in 8 (13.8%), and *R. neglectus* in 5 (8.6%) of the peridomestic areas. From a total of 489 potential peridomestic habitats studied, 108 (22.1%) were positive for Triatominae. Fifteen positive ecotopes (2 chicken coops and 13 corrals) contained both species (13.8%). The comparative distribution and abundance of *T. juazeirensis* and *T. pseudomaculata* in peridomestic ecotopes are shown in Table 1. *T. juazeirensis* and *T. pseudomaculata* showed similar infestation rates in all ecotopes surveyed (χ^2 test, df = 1, $P > 0.05$). Both species were found in all ecotopes except for bird nests, where *T. juazeirensis* was absent. A dismember χ^2 test applied to *T. juazeirensis* showed two groups of ecotopes with significantly different proportions of infestation ($P < 0.05$): corrals and roofed corrals versus the remaining ecotopes. For *T. pseudomaculata,* two groups of ecotopes were significantly different: corrals, artificial chicken coops, fowl trees, and bird nests versus the remaining ones ($P < 0.05$). Concerning the median catches for each species, the only significant difference between species was found for corrals, where the *T. juazeirensis* colonies were larger (Mann–Whitney test, df = 1, $P = 0.01$). Stick fences, fowl trees, and piles of bricks were the ecotopes with the largest *T. juazeirensis* colonies, whereas only the pile of tiles had a high apparent density of *T. pseudomaculata.*

A total of 348 ecotopes associated with domestic animals were surveyed. The comparative distribution and abundance of *T. juazeirensis* and *T. pseudomaculata* as related to the animal host are shown in Table 2. Both species showed similar qualitative and quantitative association with all animals except goats. Colonies of *T. juazeirensis* were larger than those of the other vector in ecotopes related to goats (Mann–Whitney test, df = 1, $P = 0.01$). A dismember χ^2 test applied to *T. juazeirensis* showed two groups of animals according to their association with the vector: pigs, cows, and goats versus the remaining animals ($P < 0.05$; Table 2). However, no animal or group of animals was significantly more associated with *T. pseudomaculata.* The relationship between the presence of both triatomine species and the material forming the peridomestic structures is shown in Table 3. Three types of material were considered: wood, baked clay (tiles and bricks), and a mixture of both. *T. juazeirensis* and *T. pseudomaculata* showed similar infestation rates regardless of the material (χ^2 test, df = 1, $P >$ 0.05). In contrast, colonies of *T. juazeirensis* were

Table 2. Relationship between triatomine species and synantropic animals in the peridomicile

Animal	No. associated ecotopes	*T. juazeirensis*		*T. pseudomaculata*		*P* value (χ^2 test)[a]	*P* value (M-W test)[b]
		No. (%) positive ecotopes	Median catch (first and third quartiles) per positive ecotope	No. (%) positive ecotopes	Median catch (first and third quartiles) per positive ecotope		
Goat	133	27 (20.3)	5.0 (1–15)	20 (15.0)	1.0 (1–2.5)	0.43	0.01[d]
Sheep	16	2 (12.5)	11.5 (2–21)	2 (12.5)	2.0 (1–3)	—	—
Cow	25	7 (28.0)	3.0 (1–4)	4 (16.0)	1.5 (1–2.5)	0.63	0.32
Pig	7	2 (28.6)	13.5 (8–19)	1 (14.3)	3.0	—	—
Dog	25	1 (4.0)	22.0	1 (4.0)	6.0	—	—
Chicken	121	10 (8.3)	2.0 (2–9)	17 (14.0)	2.0 (1–3)	0.28	0.44
Others[c]	21	1 (4.8)	1.0	—	—	—	—
Total	348	50 (14.4)	3.0 (2–10)	45 (12.9)	2.0 (1–6)	0.71	0.70

[a] χ^2 test (with Yates correction when necessary) to compare the no. of positive ecotopes for *T. juazeirensis* and *T. pseudomaculata.*
[b] Mann-Whitney test (M-W) to compare the median catches for each species.
[c] Other animals: donkey, horse, pigeon, chicken, peacock, cat, monkey, and armadillo.
[d] Significant difference with $P < 0.05$.

larger in wood than those of *T. pseudomaculata* (Mann–Whitney test, df = 1, $P = 0.04$).

Table 4 shows comparative habitat associations of *T. juazeirensis* and *T. pseudomaculata* in the different environments. In peridomestic environments, *T. juazeirensis* was mainly associated with wood ecotopes, whereas in a sylvatic environment, it was never found associated with such ecotopes. Conversely, *T. pseudomaculata* was less associated with wood in the peridomestic environments (χ^2 test, df = 1, $P < 0.001$).

Domestic Environments. Sixteen of the 58 houses (27.6%) contained indoor Triatominae. From a total of 17 triatomine bugs collected indoors, 14 were *T. juazeirensis* (all adults), whereas the remaining 2 were *T. pseudomaculata* (1 adult) and *P. lutzi* (1 adult). None of the collected triatomines were infected with *T. cruzi.*

Discussion

Triatoma juazeirensis and *T. pseudomaculata* are native species of the caatinga. Both species are considered to be Chagas disease vectors of regional importance (Silveira and Vinhaes 1998, Dias et al. 2000, Diotaiuti et al. 2000, Costa et al. 2003).

Our observations on the occurrence and abundance of *T. juazeirensis* and *T. pseudomaculata* in sylvatic environments were based on trapping. The baited trap used has been proven to be effective for detecting Triatominae in terrestrial and arboreal habitats (Noireau et al. 2002). Nevertheless, because the trapping system is likely to attract and capture starved bugs, it presents a quantitative and qualitative bias. Therefore, the detection of triatomines depends on the occurrence/abundance of blood resources. Moreover, the observed stage structure of the population may be biased. In contrast to nymphal instars, adults are able to disperse by flight until they find a blood source. This probably explains the small number of adults captured by our trapping system. Nevertheless, our results clearly show isolation between *T. juazeirensis* and *T. pseudomaculata* in sylvatic environments. *T. juazeirensis,* as well as the other melanic forms of the *T. brasiliensis* complex, is exclusively found in rocky habitats (Costa et al. 1998, Dias-Lima et al. 2003). However, *T. pseudomaculata* is an arboricolous species, found in hollow trees and bird nests (Carcavallo et al. 1998). With regard to this species, our results disagree with previous work that also reported the occurrence of *T. pseudomaculata* in rock cavities (Barretto 1967). In relation to its propensity for colonizing a particular tree, *T. pseudomaculata* does not exhibit a restricted association with one (or some) tree species. It can be found in any tree of the caatinga, including the predominant species *C. pyramidalis. T. pseudomaculata, P. tertius,* and *R. neglectus* were the three species col-

Table 3. Relationship between triatomine species and material of construction for the peridomicile

Material	No. ecotopes	*T. juazeirensis*		*T. pseudomaculata*		*P* value (χ^2 test)[a]	*P* value (M-W test)[b]
		No. (%) positive ecotope	Median catch (first and thirdquartiles) per positive ecotope	No. (%) positive ecotope	Median catch (first and third quartiles) per positive ecotope		
Wood	327	40 (12.2)	3.0 (1–10)	42 (12.8)	2.0 (1–3)	0.55	0.04[e]
Backed clay[c]	84	8 (9.5)	2.0 (1–19.5)	3 (3.6)	1.0 (1–12)	0.25	0.50
Mixture[d]	21	5 (23.8)	7.0 (5–8)	1 (4.8)	16.0	0.27	—
Total	432	53 (12.3)	3.0 (2–7)	46 (10.6)	2.0 (1–16)	0.57	0.70

[a] χ^2 test (with Yates correction when necessary) to compare the no. of positive ecotopes for *T. juazeirensis* and *T. pseudomaculata.*
[b] Mann-Whitney test (M-W) to compare the median catches for each species.
[c] Tiles and bricks.
[d] Wood and baked clay.
[e] Significant difference with $P < 0.05$.

Table 4. Habitat associations of *Triatoma juazeirensis* and *T. pseudomaculata* according to the environment

	No. positive ecotopes for *T. juazeirensis*		No. positive ecotopes for *T. pseudomaculata*	
	Sylvatic	Peridomestic	Sylvatic	Peridomestic
Wood	0	45	129	43
Other substrate	72	13	0	4
P value (χ^2 test)	$P < 0.001$		$P < 0.001$	

lected in bird nests. As pointed out by Dias-Lima et al. (2003) and Emperaire and Romaña (2006), an association exists between the cactus *C. jamacaru* in peridomestic environments and the occurrence of bird nests infested with *R. neglectus.*

Study of the dispersal flight of *T. juazeirensis* and *T. pseudomaculata* showed that light affects the orientation of bugs, which can actively invade human dwelling containing a light source (Carbajal de la Fuente et al. 2007). Once in the peridomicile, both species invade and colonize different ecotopes, with the exception of bird nests mainly occupied by Furnariidae, where *T. juazeirensis* is never found. However, both species showed a marked preference for structures made of wood. This observation differs from Sarquis et al. (2004), who suggested that, in Ceará, *T. brasiliensis* and *T. pseudomaculata* tend to colonize peridomestic ecotopes similar to their original habitat. We found a significant association between the structures frequented by goats (principally corrals) and the occurrence of *T. juazeirensis.* Walter et al. (2005) had previously pointed out such an association. The fact that goats climb and rest on the rocky formations, which provide hiding places for *T. juazeirensis,* suggests a close association with goats in the sylvatic environment and suggests a possible mechanism for passive transportation of *T.juazeirensis* to peridomestic structures.

Our results also suggest behavioral plasticity both in *T. juazeirensis* and *T. pseudomaculata,* which allows occupation of peridomestic materials that they do not colonize in sylvatic environments. This plasticity seems more marked in *T. juazeirensis,* which leaves a rupicolous habitat in sylvatic environments for colonizing, in the peridomicile, which is wood material in >80% of cases.

Records based on domiciliary captures of *T. brasiliensis* s.l. in the different states of northeast Brazil emphasize that Ceará, Paraíba, and Piauí are the states where indexes of colonization are the highest (Costa et al. 2003). However, the form found in these three states is *T. brasiliensis* s.s. (Costa et al. 2002, Monteiro et al. 2004). In contrast, the epidemiological role of *T. juazeirensis,* which occurs in a more restricted ecological zone than *T. brasiliensis* s.s. (), is questionable. Our survey shows that this species, as well as *T. pseudomaculata,* is not commonly found entering human dwellings and is not infected with *T. cruzi.* Nevertheless, considering their high prevalence in peridomestic premises and high potential to repopulate treated habitats from neighboring sylvatic populations, both triatomine species must be considered as vector candidates and targets for continuing vigilance (Diotaiuti et al. 2000).

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