GEOGRAPHIC DISTRIBUTION OF TRIATOMA DIMIDIATA AND TRANSMISSION DYNAMICS OF TRYpanosoma CRUZI IN THE YUCATAN PENINSULA OF MEXICO

ERIC DUMONTEIL, SEBASTIEN GOURBIÈRE, MARIO BARRERA-PÉREZ, EUGENIA RODRIGUEZ-FÉLIX, HUGO RUÍZ-PINA, OTHÓN BÁÑOS-LOPEZ, MARÍA JESÚS RAMIREZ-SIERRA, FRÉDÉRIC MENU, AND JÖRGE E. RABINOVICH

Laboratorio de Parasitología, Centro de Investigaciones Regionales Dr. Hideyo Noguchi, Universidad Autónoma de Yucatán, Mérida, Yucatán, Mexico; Laboratoire de Biométrie et Biologie Evolutive, Université de Lyon, Villeurbanne, France; Centro de Estudios Parasitológicos y de Vectores, Universidad Nacional de La Plata, La Plata, Argentina

Abstract. Chagas disease represents a major public health concern in most of Latin America, and its control is currently based on vector control and blood bank screening. We investigated the geographic distribution and seasonal variations in triatome populations in the Yucatan peninsula of Mexico to obtain entomologic data for the optimization of potential control programs. We collected domiciliated and peri-domiciliated Triatoma dimidiata from 115 houses in 23 villages distributed throughout most of the peninsula. A high abundance of bugs was observed in the northern part of the peninsula, indicating a priority area for vector control. Part of this distribution could be attributed to the type of vegetation. We also documented strong seasonal variations in T. dimidiata populations, with a higher abundance during the hot and dry season in April–June. These variations, associated with reduced year-round colonization of houses and the analysis of developmental stage structure, suggest that flying adults seasonally invading houses may play a larger role than domiciliated bugs in transmission of Trypanosoma cruzi to humans. The importance of this transmission dynamics may not be limited to the Yucatan peninsula, but may be a general mechanism contributing to natural transmission that should be taken into account in other regions for the design and optimization of control strategies.

INTRODUCTION

Chagas’ disease, or American trypanosomiasis, is caused by the protozoan parasite Trypanosoma cruzi. This disease represents a major public health problem in Latin America, where the World Health Organization (WHO) estimates that approximately 100 million people are at risk of infection, and between 16 million and 18 million are infected. In Mexico, Chagas’ disease is endemic in various regions, but little is known about the epidemiology of the disease. In the Yucatan peninsula, epidemiologic studies have reported the presence of infected vectors and reservoirs, as well as a significant prevalence of infection and disease in humans, so that American trypanosomiasis is an important health concern in this region.

Because of difficulties associated with current therapeutic treatment, and the elusive development of an effective vaccine, control of Chagas’ disease remains based on vector control by insecticides and housing improvement and on blood bank screening to prevent transfusion-associated transmission. Hematophagous bugs from the Triatominae subfamily serve as vectors of T. cruzi parasites. Depending on their association with human dwellings, triatome populations have classically been divided into domiciliated, peri-domestic (patios, courtyards, and livestock quarters), and sylvatic populations. Vector control programs in South America have focused on the interruption of natural transmission by attacking domiciliated vector populations, and they have been very successful in several countries. It is thus expected that natural transmission will be interrupted in the coming years in some southern cone countries (Argentina, Brazil, Bolivia, and Chile). The success of domestic triatome population control in reducing human T. cruzi infection confirmed that these populations were responsible for most of the natural transmission of the parasite in these regions. However, potential limitations of such programs are the recolonization of treated areas and the development of insecticide resistance. Indeed, colonization of houses by migrating insects (from the same or other species) from sylvatic/peri-domestic environments has been documented, as well as the reemergence of population from residual individuals. In addition, entomologic surveillance following control programs showed that adults flying from potential sylvatic areas could also contribute significantly to transmission, even in the absence of colonization of houses. In fact, the relationships between triatome sub-populations from different environments are not always clearly understood, even though this has considerable implications for parasite transmission.

In the Yucatan peninsula, the main vector of Chagas’ disease is Triatoma dimidiata. However, little is known about the distribution of this vector species within the peninsula, even though this information would be of major importance to identify areas with risks of vector-borne transmission, and ensure the cost-effectiveness of potential control programs in the region. Also, T. dimidiata is not strictly domiciliated like Triatoma infestans, and can be found in a variety of environments, including domestic, peri-domestic and sylvatic environments, with all these sub-populations potentially participating in transmission. Initial data on the control of domiciliary T. dimidiata in Central America suggest that domestic populations can be significantly reduced for four months up to a year with insecticides, but no longer term data are available. In addition, anecdotal evidence from local inhabitants in the Yucatan peninsula, as well as some preliminary data (Ruiz H, unpublished data), led us to suspect possible seasonal variations in the infestation of houses by flying T. dimidiata adults, with major infestation occurring during the hot and dry months of the year. However, the relevance and magnitude of this phenomenon remains poorly understood.

Because such entomologic data are strongly needed for the optimization/adaptation of control programs aimed at reducing the risks of natural transmission, our objective was to document the geographic distribution of T. dimidiata in the...
Yucatan peninsula. We thus collected triatomines from several sites in the peninsula to identify potential risk areas in the region. In addition, we also investigated the seasonal variations in domiciliated and peri-domestic populations, and the possible role of these variations on the dynamics of *T. cruzi* natural transmission.

**MATERIALS AND METHODS**

**Study area.** Field work was carried out from October 1999 to September 2000 in the Yucatan peninsula, which is located in southeastern Mexico between latitudes 87° and 92° west and longitudes 17° and 22° north. It includes the Mexican states of Campeche, Yucatan, and Quintana Roo. We selected 23 rural villages to cover most of the peninsula for insect collection (Figure 1).

**Collection of triatomines.** In each village, we randomly selected five houses (i.e., a total of 115 houses), and insect collection was carried out by households as previously described. Briefly, we conducted an initial interview with each household, displaying dried triatomines, which all participants were able to positively identify. After informed consent was obtained, we then provided them with plastic vials labeled for domicile and peri-domestic areas and requested that any triatomine found in each area be collected in their respective vials. Households were then visited every three months during one year to collect the insects captured during the previous three-month period, and provide them with new vials. A major concern was to achieve a capture effort that would be constant during the whole year, and as homogenous as possible between villages. Indeed, an increased or decreased interest by the households could induce a bias in the observed bug densities and their seasonal variations. However, since participating households were chosen randomly in each village, we believe that even if the capture effort was heterogenous between families, it would be mostly homogenous and constant among villages. In fact, interviews carried out at each visit and collection data confirmed that household participation was variable, but their random distribution in all the villages resulted in a rather homogenous capture effort among villages and during the year. In addition to the collection of insects, a sensor box (14 × 25 × 9 cm) was placed inside each house to monitor insect presence and domiciliation. These sensor boxes, designed as artificial shelters, detect mostly domiciliated insect populations through the presence of larvae, exuviae, eggs, or feces, although they may occasionally indicate the transient presence of non-domiciliated adult insects. The sensors were examined every three months during each visit to households.

**Diagnosis of *T. cruzi* infection.** The presence of *T. cruzi* in triatomine feces was detected by direct microscopic observation for live insects. We also used polymerase chain reaction (PCR) amplification of *T. cruzi* kinetoplast DNA in dead insects. The abdomen of insects was washed with 0.5 mL of sterile water with an insulin syringe. The wash fluid was then boiled for 10 minutes, centrifuged for two minutes at 13,000 × g, and 10 μL of the supernatant was used for the PCR. The reaction was carried out as described previously, and PCR products were visualized after electrophoresis on 1% agarose gels stained with ethidium bromide (0.5 μg/mL). Great care was taken to ensure contamination-free reactions, including the use of separate and closed areas for sample and reaction preparation and analysis of PCR products, respectively. Positive and negative controls were included for each PCR.

**Environmental data.** The type of housing was recorded for 80 houses and classified either as stone/block/concrete houses or adobe/sticks/thatched roof houses. Bioclimatic data, including vegetation type and annual cumulative rainfall, were obtained from digital map images (1:15,000,000) from Environmental Systems Research Institute (ESRI) on-line Web site (http://www.esri.com).

**Data analysis.** Entomologic indexes defined by the WHO were calculated as previously described (infection = percentage of *T. cruzi*-infected bugs; infestation = percentage of triatomine-positive houses; colonization = percentage of bug-positive houses with larval stages; and dispersion = percentage of triatomine-positive villages). Dispersion of *T. dimidiata* populations between villages was estimated using the classic variance/mean ratio of the number of bugs per village. To test the relationship between bug abundance and environmental variables, we first classified all the villages according to the observed cumulative number of bugs for all five houses and all four seasons. We used four categories of densities: 0, 1–10, 11–20 and more than 20 insects collected. The relationship between bug abundance and the type of housing, the type of vegetation, and rainfall was analyzed with contingency tables, using Fisher’s exact test to account for the small theoretical number of villages expected for several abundance-environment categories. Variations in bug abundance and *T. cruzi* infection rates between villages were assessed by chi-square tests, using only villages where at least 10 insects had been collected during the whole one-year study period. Variations in bug abundance and infection rates during the four seasons were also assessed by chi-square tests using the pooled data for all villages. For the correlation between abundance of *T. dimidiata* and infection rate by *T. cruzi*, we again only considered villages where more than 10 insects were collected, and Spearman test of correlation ranks was used to detect a possible non-linear relationship.

![Figure 1](image-url)  
**Figure 1.** The study area. The smaller map shows the location of the Yucatan peninsula in Mexico. The larger map shows the Yucatan peninsula, with the states of Campeche, Yucatan, and Quintana Roo. Circles indicate the location of the villages where bug collection was carried out.
RESULTS

Geographic distribution of *T. dimidiata*. The general distribution of triatomines in the Yucatan peninsula was investigated by collecting insects from a total of 23 villages, covering most of the peninsula. A total of 508 triatomines were collected, all of them were identified as *T. dimidiata*. The majority were adults (480 of 508, 94.5%), approximately 40% were males and 60% females. Table 1 shows the cumulative number of insects collected in all five houses of each village, and for each season. In only four villages (Bacalar, Haro, Pino Suárez, and Revolución) no triatomines were collected at any time of the year, indicating a wide distribution of *T. dimidiata* in the peninsula. Overall, there were approximately 4.3 more insects in domestic areas than peri-domestic areas, ranging from a minimum of 2.1 in the January-March period, to a maximum of 5.1 in the April-June. We calculated entomologic indexes for comparison with a previous study realized in 1990, in which manual collection of bugs by research personnel was performed, and found no major differences. Indeed, the presence of *T. dimidiata* in most of our collecting sites confirmed the high dispersion index of this species (83% in this study versus 95% in 1990). Similarly, we also confirmed the rather elevated house infestation index (47% in this study versus 61% in 1990) associated with a low colonization index (18% in this study versus 25% in 1990). Sensor boxes were always negative and showed no sign of established domiciliated triatomine population inside the houses, in spite of bugs being manually collected. Overall, there was a great heterogeneity in the number of insects collected from the different villages as indicated by a CV index of 56.09 (as calculated from the total column on the right side of Table 1, and adding the value 0 for the four villages where no insects were collected). The geographic distribution of insect collection data shown in Figure 2A confirmed some clustering of the sites with high and low number of collected insects. Indeed, villages with no or few collected triatomines were mostly found in the southern part of the peninsula, whereas villages with large number of insects were mostly located in the northern part.

We then looked for environmental factors that could explain some of this heterogeneous geographic distribution of *T. dimidiata* populations. We tested for possible relationships between the number of insects collected and the type of housing, the type of vegetation, and the cumulative rainfall. The type of housing (stone/block/concrete versus adobe/sticks/thatched roof) had no statistically significant effect on *T. dimidiata* house infestation (Table 2; Fisher’s exact test FI = 5.479, *P* = 0.1316). Conversely, bug abundance was significantly associated with the type of vegetation (Figure 2B, Fisher’s exact test FI = 16.34, *P* = 0.0012), with high bug abundance usually associated with the sclerophilous vegetation typical of the northern part of the peninsula. Bug abundance also seemed to be somewhat related to rainfall, but this did not reach statistical significance (Figure 2C, Fisher’s exact test FI = 7.649, *P* = 0.0539).

Seasonal variations of *T. dimidiata* populations. Seasonal variations of triatomine populations were investigated by collecting bugs during four periods of the year. As observed in the bottom row of Table 1, the number of insects collected from all villages varied significantly during the year, both in domestic (χ² = 372.9, degrees of freedom [df] = 3, *P* < 0.0001) and in peri-domestic areas (χ² = 50.4, df = 3, *P* < 0.0001). Figure 3 shows the seasonal variations of the number of collected bugs for all the villages in which we collected at least 10 bugs. Very few bugs were found between October and March, and a strong increase in the number of collected bugs was repeatedly observed during the period of April-June in all of these villages (a 3–52-fold increase as compared with the January-March period). Bug collection then progressively decreased to return to basal low levels in July-September.

These data indicate a strong seasonality of domestic and peri-domestic *T. dimidiata* populations. The near absence of year-round insect populations in the domestic and peri-

<table>
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<tr>
<th>Village</th>
<th>Oct-Dec</th>
<th>Jan-Mar</th>
<th>Apr-June</th>
<th>July-Sept</th>
</tr>
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<tr>
<td></td>
<td>Dom</td>
<td>Peri</td>
<td>Total</td>
<td>Dom</td>
</tr>
<tr>
<td>Dzilzilché</td>
<td>Not done</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Eknakán</td>
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<td>5</td>
<td>16</td>
<td>6</td>
</tr>
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<td>8</td>
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<tr>
<td>Tetiz</td>
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<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Tres Reyes</td>
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<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Buctzotz</td>
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<td>0</td>
</tr>
<tr>
<td>Baca</td>
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<td>3</td>
<td>6</td>
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<tr>
<td>Chacsinkin</td>
<td>4</td>
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<td>0</td>
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<tr>
<td>Loche</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
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<tr>
<td>Temozón</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
<td>Presumida</td>
<td>Not done</td>
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</tr>
<tr>
<td>Dzilzilché</td>
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<td>Valle Hermoso</td>
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</tr>
<tr>
<td>Andrés Q Roo</td>
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<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>8</td>
<td>33</td>
<td>23</td>
</tr>
</tbody>
</table>

*Values are the total number of bugs collected in all five houses from each village and for each season. Dom = in the domestic area; Peri = in the peri-domical area (patio/courtyard).
domestic areas suggested a seasonal invasion of houses. To clarify this point, we looked at the developmental stage structure of *T. dimidiata* populations. Because of the low number of larval stages collected, the data were pooled for all villages. Figure 4 shows the pooled number of adults and different larval stages collected during each season. A strong seasonal variation in the number of collected adults is again observed, with an approximately 10-fold increase in April-June, followed by a decrease. Conversely, larval populations were very small between October and June, and increased markedly in July-September, immediately after the maximum number of adults. In addition, the increase in larval populations during this period was mostly due to the appearance of younger developmental stages (stages 1 and 2).

Infection of *T. dimidiata* by *T. cruzi*. Infection by *T. cruzi* of collected bugs was investigated because it is an important factor to consider in the evaluation of transmission. Infection rates for the different villages and each season are shown in Table 3. The overall infection rate was of 34%, which was significantly higher than what had been previously reported (34% versus 16% in 1990, $\chi^2 = 12.08$, df = 1, $P < 0.001$). However, analysis of the year-round total percentage of infected bugs indicates that there was a statistically significant difference in infection rates among villages (Table 3 right column and Figure 2D, $\chi^2 = 68.29$, df = 10, $P < 0.001$ using only the 11 villages with at least 10 bugs). We also tested for a correlation between infection rates and bug densities, but found no significant correlation (Spearman test of correlation ranks $\rho = -1.527$, $P = 0.13$). Finally, infection rates for all villages pooled varied significantly according to seasons (Table 3 bottom row, $\chi^2 = 21.55$, df = 3, $P < 0.001$), with again a maximum during April-June, strengthening the existence of a higher transmission risk during this period.

**Table 2**

<table>
<thead>
<tr>
<th>Type of house</th>
<th>Stone/block/concrete</th>
<th>Adobe/thatched roof</th>
</tr>
</thead>
<tbody>
<tr>
<td>Houses without bugs</td>
<td>11 (34.3%)</td>
<td>26 (54.2%)</td>
</tr>
<tr>
<td>Houses with 1–10 bugs</td>
<td>15 (47.0%)</td>
<td>17 (35.4%)</td>
</tr>
<tr>
<td>Houses with 11–20 bugs</td>
<td>2 (6.2%)</td>
<td>4 (8.3%)</td>
</tr>
<tr>
<td>Houses with &gt; 20 bugs</td>
<td>4 (12.5%)</td>
<td>1 (2.1%)</td>
</tr>
<tr>
<td>Total number of houses</td>
<td>32</td>
<td>48</td>
</tr>
</tbody>
</table>

*The number of houses corresponding to each *T. dimidiata* abundance category is shown. There was no significant differences in bug abundance according to the type of construction (Fisher’s exact test $F1 = 5.479$, $P = 0.13$).
DISCUSSION

Since the main control measure against Chagas’ disease is currently based on vector control, an important pre-requisite for a successful program is to know the relative distribution and infection rates of vector populations to define potential priority areas. We thus report here data on *T. dimidiata* micro-distribution in the Yucatan peninsula. Our data confirmed previous work showing that this species is the main, if not only, vector of *T. cruzi* in the Yucatan peninsula, since we did not collect any other triatomine species. Overall, our entomologic data are consistent with previous indexes from the State of Yucatan obtained using manual collection of bugs, confirming that bug collection by households was homogenous between villages and did not generate any specific bias. Thus, our data clearly confirm that natural transmission of Chagas’ disease may occur in most of the Yucatan peninsula.

However, we found that vector populations were distributed very heterogeneously, and we could identify the northern part of the peninsula as the area with the highest bug abundance. Some sites from this area also presented high infection rates, even though there was no statistically significant correlation between bug abundance and infection rates. This would imply a greater risk of natural transmission in these areas, which should be considered as priority for potential vector control programs. Part of this heterogeneous distribution could be explained by bioclimatic factors such as the type of vegetation and possibly slightly by rainfall. This is in agreement with previous work in the state of Oaxaca where it was found that factors such as altitude and rainfall were major determinants for habitat partitioning and the existence of micro-regions limiting triatomine species distribution. On the

**FIGURE 3.** Seasonal variations of the total population of *Triatoma dimidiata* in villages in the Yucatan peninsula. The total number of collected insects (domicile + peri-domicile) for each three-month period was plotted for all houses in each village. Only villages with 10 or more collected insects were included.

**FIGURE 4.** Seasonal variations of the age structure of *Triatoma dimidiata* in the Yucatan peninsula. The total number of collected adult and distinct larval stages were pooled for all houses and villages, and plotted for each three-month period.
other hand, we found no clear association with the type of housing, in spite of Chagas' disease being classically associated with poorer housing conditions, i.e., houses made of adobe/sticks/thatched roof. Indeed, housing improvement has been repeatedly shown to greatly contribute to the control of natural transmission of T. cruzi. The collection of a majority of adults (and few larval stages), independently of the kind of construction, associated with negative sensor boxes, suggest a poor domiciliation of the kind of construction, associated with negative sensor boxes. A detailed analysis of the stage structure of bug populations can help us discriminate between these explanations. Indeed, we do observe an increase in reproduction, as shown by a larger larval population, specifically younger stages, in July-September. Because development times for T. dimidiata are around 30 days for each stage 1 and 2, their presence indicates a recent reproduction cycle (i.e. 2–3 months earlier). This increase in larval population can be explained by the increase in adult population of April–June, but the reverse is not true: the small number of fourth and fifth larval nymphs in the January–March period would not possibly explain the sudden increase of adults in the next three-month period. Thus, our results are more in agreement with a seasonal invasion of houses by flying adults (possibly from sylvatic environment). Invading adults would then oviposit inside the houses, resulting in increased larval populations in the following period (July–September). However, colonization of the domestic environment does not appear to be successful because adult and larval populations then decrease until a next invasion the following year (in the April-June period). This conclusion is in agreement with T. cruzi strain typing studies showing that isolates from Mexico (including Yucatan and strains isolated from patients) all belong to T. cruzi lineage I, which is classically associated with a sylvatic transmission cycle in South America, as opposed to T. cruzi lineage II, which is more associated with domestic transmission. A detailed analysis of T. dimidiata populations and gene fluxes between habitats using DNA markers is currently under way to verify and further characterize T. dimidiata migration within habitats in the Yucatan peninsula. Such a behavior of T. dimidiata is very similar to what has been suggested in Belize, where there has been no evidence of house colonization by this species, but a strong dispersal of sylvatic bugs during the hot and dry season. Similarly, several sylvatic species such as Rhodnius brethesi, R. pictipes and R. neglectus are thought to efficiently transmit T. cruzi to humans with reduced or even completely absent colonization of domiciles. Thus, the importance of this transmission dynamics may not be limited to the Yucatan peninsula or the Amazon basin, but may be a more general contributing mechanism of natural transmission that should be taken into account in other regions for the design and optimization of control strategies.

Indeed, there are important implications of this behavior for T. cruzi transmission. On one hand, natural transmission would be markedly seasonal, coinciding with the invasion of houses by flying adult bugs with high infection rates, suggest-
ing an overall lower transmission risk than when domiciliated triatomine populations are well established. On the other hand, because transmission would not be exclusively associated with poor rural housing, the population at risk would be much larger. In fact, *T. dimidiata* is regularly found in wealthier urban environments in the city of Merida (Dumonteil E, unpublished data). Finally, current control strategies based on insecticide spraying in domestic areas would likely not be very effective given such transmission dynamics. Available data on the control of domiciliated *T. dimidiata* in Guatemala and Nicaragua suggest that control is effective for four months up to one year, respectively, but unfortunately these studies did not address longer-term efficacy. Preliminary data from an ongoing study in Yucatan suggest that house reinfestation by *T. dimidiata* occurs 4–6 months after insecticide spraying. Thus, an effective control of seasonal invasion would require frequent spraying campaigns, which would have prohibitive operating costs. Thus, alternative strategies would have to be defined, such as window/door screens and/or mosquito nets, that can physically reduce domestic migration of bugs and may prove to be more cost-effective.

In conclusion, our study shows that natural transmission of *T. cruzi* by *T. dimidiata* is widely distributed in the Yucatan peninsula, but that a higher risk of transmission is present the northern part of the peninsula. In addition, we report strong seasonal variations in *T. dimidiata* populations and *T. cruzi* infection rates that are more likely to be due to seasonal invasion of houses by adults flying from the surroundings, rather than the existence of large domiciliated bug populations. These observations imply that vector control strategies should be redesigned according to this observed dynamics of transmission. Also, we suggest that this type of transmission associated with non-domiciliated triatomines may be a general mechanism accounting for significant transmission in other regions, and should thus be taken into account.

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