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To cite this version:
Etienne Waleckx, Sébastien Gourbière, Eric Dumonteil. Intrusive versus domiciliated triatomines and the challenge of adapting vector control practices against Chagas disease. Memórias do Instituto Oswaldo Cruz, 2015, 110 (3), p. 324-338. 10.1590/0074-02760140409 . hal-01240420

HAL Id: hal-01240420
https://univ-perp.hal.science/hal-01240420
Submitted on 9 Dec 2015

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Intrusive versus domiciliated triatomines and the challenge of adapting vector control practices against Chagas disease

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Chagas disease prevention remains mostly based on triatomine vector control to reduce or eliminate house infestation with these bugs. The level of adaptation of triatomines to human housing is a key part of vector competence and needs to be precisely evaluated to allow for the design of effective vector control strategies. In this review, we examine how the domiciliation/intrusion level of different triatomine species/populations has been defined and measured and discuss how these concepts may be improved for a better understanding of their ecology and evolution, as well as for the design of more effective control strategies against a large variety of triatomine species. We suggest that a major limitation of current criteria for classifying triatomines into sylvatic, intrusive, domiciliary and domestic species is that these are essentially qualitative and do not rely on quantitative variables measuring population sustainability and fitness in their different habitats. However, such assessments may be derived from further analysis and modelling of field data. Such approaches can shed new light on the domiciliation process of triatomines and may represent a key tool for decision-making and the design of vector control interventions.

Key words: triatomine - domiciliation - intrusion - vector control - ecohealth - integrated vector management

Chagas disease is a major public health problem in the Americas, where it affects seven-eight million people (WHO 2014). The pathogenic agent is a protozoan parasite, Trypanosoma cruzi, mainly transmitted to humans and other mammals through the contaminated faeces of blood-sucking insects called triatomines (Hemiptera: Reduviidae), also known as “kissing bugs”. Control of Chagas disease relies on the treatment of infected patients and prevention of transmission is based mainly on vector control.

Currently, more than 140 species of triatomines are recognised. Over half of them have been shown to be naturally or experimentally infected with T. cruzi, but all are suspected to be able to transmit the parasite (or “serve as vectors”) (Bargues et al. 2010). Nevertheless, not all the triatomine species are considered important vectors of T. cruzi. Vector competence varies considerably between the different species/populations of triatomines and depends on multiple criterions. Among these, the level of domiciliation, which is understood as the level of adaptation to human and its domestic environment, is one of the most important, as it defines the level of human-vector contacts (Dujardin et al. 2002). Indeed, species highly adapted to and able to colonise human dwellings are more likely to actively contribute to the transmission of T. cruzi to humans than species that are only found in sylvatic environment. While the domiciliation of triatomine species/populations is clearly a gradual evolutionary process (Schofield et al. 1999), it has important implications for the design and efficacy of vector control interventions. To date, vector control is mainly achieved through indoor residual insecticide spraying, initially designed to target triatomine species living inside human dwellings and highly adapted to the domestic environment (i.e. domiciliated or domesticated). However, it is becoming increasingly clear that triatomine species presenting lower levels of domiciliation are also playing an important role in T. cruzi transmission to humans and thus need to be taken into account by vector control programs in many regions. The efficacy of conventional insecticide spraying may indeed be directly affected by the level of domiciliation of triatomines and alternative control strategies thus need to be considered against nondomiciliated species/populations. These populations are a potential source of continuous house infestation and post-spraying re-infestation, making the control by insecticide spraying unsustainable, even in areas where transmission is primarily due to highly domiciliated vectors. The level of domiciliation/intrusion of triatomine species thus needs to be clearly defined in operative terms to allow for its precise evaluation and the design of effective vector control interventions.

In this review, we examine how the domiciliation/intrusion level of different triatomine species/populations has been defined and measured and discuss how these concepts may be improved for a better understanding of their ecology and evolution, as well as for the design of more effective control strategies against a large variety of triatomine species.

Level of domiciliation of triatomine species

Triatomine species have for a long time been classified according to their adaptation to human dwellings. According to Lent and Wygodzinsky (1979), the hab-

doi: 10.1590/0074-0276014040409
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Received 31 October 2014
Accepted 9 March 2015

online | memorias.ioc.fiocruz.br
its of the various species of triatomines allow to divide them into sylvatic and domestic species, with an intermediate category of peridomestic species, which are occasionally attracted into houses, but do not effectively colonise them, and which thus feed on man only occasionally. Dujardin et al. (2002) and Noireau and Dujardin (2010) later refined these definitions and proposed four different categories: sylvatic, intrusive, domiciliary and domestic species (Table I). These definitions have been the most widely accepted and used in the literature for the classification of many triatomine species. In Table II, we summarise how some triatomine species have been classified and the type of data and observations that helped defining their potential association with human habitat. These species/populations were selected based on their epidemiological significance and contribution to *T. cruzi* transmission to human. As can be observed in Table II, their level of domiciliation appears highly variable depending on the type of data collected by the authors, their own interpretation and the study area. Field collections by manual searches and/or community participation are the most common type of studies, allowing to establish conventional entomological indexes including infestation index (percentage of houses with triatomines), colonisation index (percentage of infested houses with evidence of reproductive cycle: presence of nymphs, but also eggs and/or exuviae), density index (number of triatomines per house) and dispersion index (percentage of localities infested) as the most commonly used (WHO 1991). Infestation and density index have often been considered as indicators of the level of intrusion of a species into the domestic habitat, while the colonisation index can be viewed as a measure of its domiciliation/domestication. More recently, a visitation index has been proposed (percentage of houses visited exclusively by adult triatomines) to evaluate intrusion by adult bugs (Úbeda 2003). As indicated in Table I, the peridomestic, but many adult specimens are reported inside human dwellings, probably attracted there by light or introduced by passive carriage (marsupials, for instance). In this situation, there is no evidence of colonisation (eggs, nymphs and exuviae).

**Domestic species** - Characterised by the presence inside houses or peridomiciles of adults and nymphs, eggs and exuviae, which means that the complete cycle of the insect was occurring in domestic environment. The resulting colonies are not very abundant and represent merely a tentative adaptation to houses. It is not necessarily a permanent situation and a domiciliary species can progressively disappear from the houses without any control intervention.

**Domestic species** - The definition includes the aforementioned observations for domiciliary species, with an additional criterion related to the type of geographic extension. It is no more a local, geographically restricted observation, but rather concerns a more widely extended territory with obvious arguments supporting migration by passive carriage. It is, for instance, a discontinuous geographic extension, with gaps apparently unexplained unless the human intervention is admitted. Importantly, sylvatic populations/loci can also exist for the species considered as domestic, as it is well documented even for the highly domesticated emblematic species, *Triatoma infestans* (Dujardin et al. 2002, Noireau & Dujardin 2010).
TABLE II
Main triatomine species and their level of domiciliation

| Species                  | Country, region                          | Evidence                                                                 | Classification                           | Seroprevalence (%) | References                                                                 |
|--------------------------|------------------------------------------|--------------------------------------------------------------------------|------------------------------------------|--------------------|---------------------------------------------------------------------------|
| *Triatoma infestans*     | Brazil, Argentina, Bolivia, Chile, Paraguay, southern Peru, Uruguay | Domestic and peridomestic collections of nymphs (and adults) showing high colonisation. | Domestic (with some sylvatic foci/populations) | > 80 in Bolivia    | Torrico (1946), Schofield (1988), Bermudez et al. (1993), Norreau et al. (1997b), Brenière et al. (1998, 2013), Panzera et al. (2004), Ceballos et al. (2009), Bacigalupo et al. (2010), Buitrago et al. (2010), Rolón et al. (2011), Waleckx et al. (2011, 2012) |
| *Triatoma longipennis*   | Mexico (Jalisco and Morelos)             | High peridomestic infestation (16-60%) and colonisation (75-93%).       | Peridomestic with domestic intrusion     | 1.8                | Ramsey et al. (2003), Brenière et al. (2004, 2007, 2010, 2012)          |
| *Triatoma barberi*       | Mexico (Jalisco and Morelos)             | High peridomestic infestation (16-60%) and colonisation (75-93%).       | Peridomestic with domestic intrusion     | 1.8                | Ramsey et al. (2003), Brenière et al. (2004, 2007, 2010, 2012)          |
| *Rhodnius pallescens*    | Costa Rica, Nicaragua, Panama, Colombia  | Infestation by adults (30%), rare colonisation.                          | Sylvic (palm trees) with some domestic intrusion | 0.2-6.7e           | Christensen and de Vasquez (1981), Lopez and Moreno (1995), Vasquez et al. (2004), Calzada et al. (2006), Zeledón et al. (2006), Pineda et al. (2008) |
| *Rhodnius prolixus*      | Guatemala, El Salvador                   | Significant colonisation of houses.                                      | Domiciliated (introduced)                | 38.8               | Paz-Bailey et al. (2002), Nakagawa et al. (2003a), Sasaki et al. (2003), Cedillos et al. (2012), Hashimoto et al. (2012) |
| Species               | Country, region          | Evidence                                                                 | Classification                                                                 | Seroprevalence (%) | References                                                                 |
|-----------------------|--------------------------|---------------------------------------------------------------------------|--------------------------------------------------------------------------------|--------------------|---------------------------------------------------------------------------|
| *R. prolixus*         | Colombia, Venezuela      | High colonisation of houses (domestic habitat) and in palm trees (sylvatic habitat). Population genetics data with variable results: absence of gene flow in Colombia, significant gene flow in Venezuela. Frequent blood meals on humans from domestic populations (53%). | Domiciliated and sylvatic populations                                           |                    | Rabinovich et al. (1979), Lopez and Moreno (1995), Feliciangeli et al. (2004, 2007), Fitzpatrick et al. (2008), Angulo et al. (2012) |
| *Panstrongylus geniculatus* | Brazil, Venezuela, Peru, Colombia, Bolivia, Argentina, Ecuador | Peridomestic and domestic infestation by adults with some seasonality. High levels of intrusion by adult bugs. Rare findings of nymphs and of complete colonies. Housing quality and type not associated with infestation. Risk factors include reduced vegetation cover, reduced presence of animals in the peridomicile combined to increased presence inside dwellings, distance to forest and artificial light. Frequent contact with human and frequent human blood meals reported (up to 60% in adult bugs collected inside dwellings). Reduction of the sexual dimorphism of the isometric size and smaller size of adult specimens collected inside homes in Caracas (Venezuela) suggesting an adaptation to domiciles. | Sylvic with domestic intrusion Species with potential for domestication | > 15.5 in Venezuela<sup>a</sup> > 14.2 in Ecuador<sup>c</sup> > 1.3 in Bolivia<sup>d</sup> | Chico et al. (1997), Naïff et al. (1998), Valente et al. (1998), Reyes-Lugo and Rodriguez-Acosta (2000), Damborsky et al. (2001), Cáceres et al. (2002), Feliciangeli et al. (2004), Carrasco et al. (2005), Rodríguez-Bonfante et al. (2007), Serrano et al. (2008), Fe et al. (2009), Reyes-Lugo (2009), Aldana et al. (2011), Depickère et al. (2011, 2012) |
| *Triatoma brasiliensis* | Brazil                   | Colonies found in peridomestic and sylvatic environments. Colonisation index of 20-59% intradomiciliary and 33-62% peridomiciliary. | Domesticated                                                                |                    | Lent and Wygodzinsky (1979), Costa et al. (2003)                           |
| *Triatoma sordida*<sup>e</sup> | Brazil, Argentina, Bolivia, Paraguay | Peridomestic collections showing large infestation and colonisation of the peridomiciles. Intrusion (with some seasonality) of adult bugs inside dwellings with anecdotic colonisation. Implicated in re-infestation post-spraying against *T. infestans*. Population dynamic model supporting insect presence as the outcome both of a local scale “near-to-near” dispersal and infestation from the wild. | Sylvic with an advanced process of adaptation to human habitat Predominantly peridomestic, without significant colonisation inside dwellings. | > 29.6<sup>f</sup> | Forattini et al. (1983), Bar et al. (1993, 2002, 2010), Wisnivesky-Colli et al. (1993), Gurtler et al. (1999), Noireau et al. (1999a), Pires et al. (1999), Canale et al. (2000), Falavigna-Guilherme et al. (2004), da Silva et al. (2004), Dias et al. (2005), Cominetti et al. (2011), Roux et al. (2011), Maeda et al. (2012) |
| Species          | Country, region       | Evidence                                                                 | Classification               | Seroprevalence (%) | References                                                                 |
|------------------|-----------------------|---------------------------------------------------------------------------|-------------------------------|-------------------|-----------------------------------------------------------------------------|
| *T. sordida*     | Eastern Bolivia       | Small colonies (3.1 insects/colony) are frequently found inside dwellings (infestation index > 80% and colonisation index > 90%). Up to 70.4% of human blood meals in *T. sordida* found inside dwellings. Wider panmictic unit than *T. infestans*. | Domiciliated                 | > 4               | Noireau et al. (1995, 1997a, 1999b)                                        |
| *Rhodnius ecuadoriensis* | Ecuador (costal region) | Domestic/peridomestic collections showing infestation and colonisation. Association of domestic infestation with sylvatic infestation. Morphometric analysis indicates flow between sylvatic and domestic habitats. Rapid reinfestation following insecticide spraying. | Sylvatic with capability for domiciliation | 3.6               | Grijalva et al. (2005, 2011, 2012), Black et al. (2009), Villacís et al. (2010) |
| *Triatoma dimidiata* | Mexico (Yucatan) | Domestic collections showing seasonal infestation by adults (> 85%). Population dynamics models. Gene flow between sylvatic and domestic habitats from population genetics. Housing quality and type and socioeconomic factors not associated with infestation. Risk factors for infestation include domestic animals, proximity of bushes, light. Rapid re-infestation following insecticide spraying. Colonisation of peridomiciles. | Nondomiciliated               | 1-5               | Dumonteil et al. (2002, 2004, 2007, 2013), Gourbière et al. (2008), Pacheco-Tucuch et al. (2012) |
| *T. dimidiata*   | Belize                | Domestic collections showing seasonal infestation by adults.              | Nondomiciliated               | 1                | Polonio et al. (2009), Ramos-Lionio (2010), Torres-Monterio et al. (2012)  |
| *T. dimidiata*   | Mexico (Veracruz)     | Domestic collections showing seasonal infestation by adults with some colonisation. Blood meal analysis showing dispersal among habitats. | Nondomiciliated with domiciliation in process | 16.8              |                                                                                  |
| *T. dimidiata*   | Guatemala, Costa Rica | Domestic collections of nymphs (and adults) showing high colonisation. Some seasonal variations. Blood meal from domestic hosts only. Housing quality and type and low socioeconomic level associated with infestation. | Domestic                     | 8.9               | Paz-Bailey et al. (2002), Dorn (2003), Monroy et al. (2003a, b), Nakagawa et al. (2003a, b) |
| *Triatoma mexicana* | Mexico               | Domestic collections showing seasonal infestation by adults. Housing quality and type not associated with infestation. | Intrusive                     | -                 | Schettino et al. (2007)                                                   |
may have important implications for an effective vector control. Indeed, while very few species have been able to reach domestication [estimated at less than 5% of all species following Noireau and Dujardin (2010)], most show very variable capability to invade human housing. It is clear that more objective (and quantitative) criteria are needed to describe this process. We next focus on three triatomine species that have been extensively studied to evaluate additional criteria which may be helpful for a better understanding of infestation.

Case studies

**Triatoma dimidiata** - *T. dimidiata* is one of the most important vector of *T. cruzi*, distributed from central Mexico throughout Central America, to Colombia, Venezuela, Ecuador and Peru (Dorn et al. 2007) (Figure). It is actually a species complex, although the exact number of taxonomic groups to be considered is still debated (Bargues et al. 2008, Dorn et al. 2009, Herrera-Aguilar et al. 2009, Monteiro et al. 2013). This species complex presents highly variable levels of adaptation to humans housing, depending of the geographic region, but possibly also depending on the taxonomic group.

In Guatemala, populations are well domesticated as evidenced by bug collections throughout the country showing high infestation and colonisation indexes (Monroy et al. 2003a, b, Nakagawa et al. 2005). Housing quality and type are key factors affecting domestic colonisation/infestation and in particular poor wall plastering, which may offer a favourable habitat for bugs (Bustamante et al. 2009). Population genetics studies showed some conflicting results, with limited gene flow in agreement with domestication in some cases, but also significant gene flow between sylvatic and domestic populations, suggesting dispersal (Calderon et al. 2004). The analysis of the genetic structure of the population in a single house further showed a great genetic heterogeneity suggesting polyandry and/or high levels of migration of the vector (Melgar et al. 2007).

Vector control with insecticide spraying has been relatively effective in Guatemala, although some re-infestation has been occurring (Nakagawa et al. 2003b, Hashimoto et al. 2006). Dispersing sylvatic bugs may contribute to re-inestation (Monroy et al. 2003b), as well as to the seasonal variations in infestation that have been observed, but the importance of sylvatic populations in domestic infestation is still unclear. More recent studies suggest that integrated and community-based interventions may provide a better and more sustainable control of *T. dimidiata* in this region (Monroy et al. 2012, Pellecer et al. 2013, Bustamante et al. 2014, de Urioste-Stone et al. 2015).

On the other hand, in the Yucatan Peninsula, Mexico, *T. dimidiata* populations are one of the best-characterised examples of a nondomiciliated but intrusive vector. Initial observations indicated that adult *T. dimidiata* transiently infests houses on a seasonal basis during the months of March-July (Dumontel et al. 2002, 2009, Guzman-Tapia et al. 2007, Payet et al. 2009). This infestation is responsible for a seroprevalence of *T. cruzi* infection in humans of about 1-5% (Guzman-Bracho et al. 1998, Sosa-Estani et al. 2008, Gamboa-León et al. 2014). Population genet-
ics and mathematical models describing the population stage-structure as well as the dispersal of *T. dimidiata* indicate that house infestation is caused by the seasonal dispersal of bugs from peridomestic and sylvatic habitats surrounding the villages, while triatomine reproduction in the domestic habitat (i.e., domiciliation) plays a negligible role (Dumonteil et al. 2007, Gourbière et al. 2008, Barbu et al. 2009). Indeed, while nymphs may occasionally be found in houses (Dumonteil et al. 2002), the low colonisation index (< 20%) rather suggests unsuccessful attempts at colonising the domestic habitat by intruding bugs, possibly because of insufficient feeding (Payet et al. 2009). Such poor feeding in the domestic habitat may be associated with sleeping habits in the region, as hammocks were found to complicate bug access to a host and particularly for nymphs (E Waleckx et al., unpublished observations).

Further modelling and field investigations of the spatiotemporal infestation patterns indicated that houses located in the periphery of the villages are significantly more infested than those located in the village centre (Slimi et al. 2009, Barbu et al. 2010, 2011, Ramirez-Sierra et al. 2010). Attraction by public lights also contributes significantly to transient infestation (Pacheco-Tucuch et al. 2012), together with the presence of domestic animals such as dogs and chickens, while housing type and quality or socioeconomic level do not play a significant role (Dumonteil et al. 2013). Inhabitants are rather familiar with this seasonal invasive behaviour of *T. dimidiata* (Rosecrans et al. 2014).

In this situation, effective insecticide spraying would require yearly applications within a narrow time window of less than two months, which would be difficult to implement and clearly unsustainable, while insect screens may offer a sustainable and effective alternative (Dumonteil et al. 2004, Barbu et al. 2009, 2011, Ferral et al. 2010). Environmental management of the peridomiciles, i.e., the elimination of peridomestic colonies by cleaning and insecticide spraying, was found to partially but durably reduce house infestation and may thus be an important component of vector control interventions (Ferral et al. 2010). Spatially targeted interventions may allow for further optimisation of vector control (Barbu et al. 2011). Based on this, an ecohealth approach has recently been tested at a small scale, based on a community-based installation of window insect screens in bedrooms, with or without education for improved peridomestic animal management (Waleckx et al. 2015). Such integrated control strategy seems very promising for the sustainable control of this intrusive vector in the Yucatan Peninsula.

Analysis of the genetic structure of *T. dimidiata* in Boyaca, Colombia, also indicated a low level of genetic differentiation and a high level of exchanges of bugs among domestic, peridomestic and sylvatic habitats (Ramírez et al. 2005), suggesting that the situation observed in the Yucatan Peninsula and Belize (Polonio et al. 2009) may also be occurring in parts of Colombia.

*Panstrongylus geniculatus* - *P. geniculatus* is one of the most widely distributed species of triatomine in South and Central America (Leite et al. 2007) (Figure). It is commonly considered as a sylvatic species frequently flying to human habitations, probably attracted by light (Lent & Wygodzinsky 1979). The intrusion of adult bugs is well documented and collections of only adult specimens inside dwellings have been reported in different areas (particularly in the Amazon Basin, but not only) in Venezuela (Serrano et al. 2008, Reyes-Lugo 2009, Colombia (Angulo et al. 2012), Brazil (Naiff et al. 1998, Fe et al. 2009, Maeda et al. 2012), Peru (Cáceres et al. 2002, Torres & Cabrera 2010), Bolivia (Depickère et al. 2011, 2012) and Argentina (Damborsky et al. 2001). The main factors that cause *P. geniculatus* to increasingly invade human dwellings seem to be the devastation of the primary forests (for example for the construction of human dwellings), overhunting and burning of forests, all of which destroying the triatomines’ natural habitat and causing them to seek alternative shelter and hosts (Valente 1999). Although the intrusion of adult bugs and the absence of colonisation seem to be the most common behaviours of this species, some events of domicile colonisation have also been reported. Indeed, there are some reports of nymphal stages and colonies of *P. geniculatus* found in peridomicles and/or inside dwellings in Venezuela (Reyes-Lugo & Rodríguez-Acosta 2000, Feliciangeli et al. 2004, Rodríguez-Bonfante et al. 2007), Brazil (Valente et al. 1998), Ecuador (Chico et al. 1997), Bolivia (Depickère et al. 2011) and Colombia (Maestre-Serrano & Eyes-Escalante 2012). Consequently, the species is now increasingly considered as a species in the process of domiciliation/domestication.

Interestingly, Aldana et al. (2011) found that the sexual dimorphism of the isometric size of adults of *P. geniculatus* was reduced in bugs collected in domestic environment compared to bugs collected in sylvatic environments in Venezuela. In this study, the authors considered that this may be an indicator of domiciliation, as proposed by Dujardin et al. (1999).

Additionally, there are reports of people being attacked by this bug species inside their homes (Valente et al. 1998, Reyes-Lugo & Rodríguez-Acosta 2000, Carrasco et al. 2005, Reyes-Lugo 2009), which has been
confirmed by blood meal analyses (Feliciangeli et al. 2004, Carrasco et al. 2005). *P. geniculatus* has also been increasingly identified as the likely responsible vector in some acute cases of Chagas disease (Vega et al. 2006, Valente et al. 2009, Cabrera et al. 2010, Rios et al. 2011) in South America. Consequently, it is given more consideration as a major vector of Chagas disease by vector control programs, but no strategy has been specifically defined against this vector and current data indicate that a more precise evaluation of its level of intrusion inside houses and of its potential for domiciliation/domestication is clearly needed so that these aspects may be taken into account for the design of effective and sustainable vector control interventions against *P. geniculatus*.

*Rhodnius ecuadoriensis* – *R. ecuadoriensis* is distributed from southern Colombia throughout eastern Ecuador and in northern Peru, where it is considered an important vector of *T. cruzi* (Figure). However, studies on its ecology and vectorial role have been limited and report somewhat conflicting results. The species was initially described infesting and colonising domiciles in Peru and Ecuador and this was quickly extended to the peridomestic habitat and *R. ecuadoriensis* was labelled as a synanthropic species (Abad-Franch et al. 2002, Cuba Cuba et al. 2002, 2003, Grijalva et al. 2005), in the sense that it was domiciliated/domesticated. Frequent blood feeding on humans from these bug populations was also reported (Abad-Franch et al. 2002). However, further studies showed that *R. ecuadoriensis* was also abundant in sylvatic habitats, principally associated with palm trees, as most *Rhodnius* species (Abad-Franch et al. 2000, 2005, Grijalva & Villacic 2009, Suarez-Davalos et al. 2010, Grijalva et al. 2012), raising the question of the relationship between its sylvatic and domestic/peridomestic populations. The initial hypothesis was that synanthropic populations were relatively isolated from sylvatic ones, at least in southern Ecuador and northern Peru, raising the possibility that synanthropic populations may be eliminated by insecticide spraying interventions (Abad-Franch et al. 2001, Cuba Cuba et al. 2002). However, such interventions were met with limited success, as a significant re-infestation was observed following spraying (Grijalva et al. 2011), indicating that vector control may result much more challenging.

Morphometric analysis of wing size and shape supported the presence of extensive exchanges of bugs among habitats in coastal Ecuador, but conversely suggested a significant population structuring in southern Ecuador, with a low dispersal and exchange of bugs among habitats (Villacic et al. 2010). Such variability may be due to ecological differences in these regions, but may also reflect intrinsic differences in behaviour linked to genetic differences within the species. Indeed, two phylogenetic clades have been described in *R. ecuadoriensis* based on the cytochrome B mitochondrial marker (Abad-Franch & Monteiro 2005) and significant morphometric differences have been observed as well (Villacic et al. 2010). The level of domiciliation of *R. ecuadoriensis* may thus be variable, being more domiciliated in southern Ecuador and northern Peru and more sylvatic and intrusive in eastern Ecuador, although the factors underlying these differences remain unclear.

As evidenced by the difficulties in controlling this vector with indoor insecticide spraying (Grijalva et al. 2011), defining the exact level of domiciliation/intrusion of the different populations of *R. ecuadoriensis* is still needed to define effective vector control interventions in the different regions where this species is present.

**Revisiting the domiciliation process: toward operational definitions for vector control**

The classification of triatomine species/populations into sylvatic, intrusive, domiciliary and domestic proposed earlier (Noireau & Dujardin 2010) is useful from a general evolutionary perspective. However, as evidenced in Table II and the examples detailed above, these theoretical concepts may be challenged by the realities of vector control.

A major limitation of current criteria defining the association of triatomine with human habitat is that these are essentially qualitative (Table I) and do not rely on quantitative variables, leaving much to the subjective interpretation of the data. This and the apparent regional variability of domiciliation level of the different populations of a same species may be the main reasons why some species/populations are classified differently by authors as shown in Table II. For most species, a quantification of the ability of species/population to reproduce and adapt in human habitat is needed for effective vector control. Indeed, indoor residual insecticide spraying has been very effective in only two settings: domestic *Triatoma infestans* in most of the Southern Cone countries and domestic *R. prolixus* in Central America. Thus, several Southern Cone countries and regions have been certified (or are in the process) as free of *T. infestans* vectorial transmission and similarly in Central America with *R. prolixus* (Schofield et al. 2006). This success is largely due to the fact that these *T. infestans* and *R. prolixus* populations were exclusively domesticated and introduced in these countries (i.e., with no sylvatic populations), which considerably limited the possibilities for re-infestation following spraying. On the other hand, the control of most other triatomine species/populations has been more challenging, mostly because domestic populations remain connected to sylvatic populations, which can then contribute to re-infestation. The same fact mostly explains why, in areas where *T. infestans* sylvatic foci exist, the elimination of house infestation is jeopardised. Indeed, while *T. infestans* has been described as one of the most domesticated triatomine species, the persistence and re-infestation of houses by this species in the Andean region can be attributed, at least in part, to the dispersal of bugs from sylvatic populations (Noireau et al. 2005, Ceballos et al. 2011, Brenière et al. 2013). In the Andes, these have been found to be well established in sylvatic habitats over an extensive region (Buitrago et al. 2010, Waleckx et al. 2011, Bremond et al. 2014) and to feed on humans relatively frequently (Buitrago et al. 2013). Dispersal of these sylvatic bugs towards houses for re-infestation will thus need to be taken into account for an effective control, even in the case of this emblematic highly domesticated species.
From the perspective of vector control, it is thus of major importance to determine precisely three aspects of the relationship of triatomines with humans: (i) the presence of sylvatic populations of triatomines, (ii) the level of intrusion of these sylvatic populations in peridomiciles and inside houses and (iii) the level of domiciliation or domestication in peridomiciles and inside houses. Indeed, this information should guide vector control program in their decision-making over the design of evidence-based interventions to ensure their effectiveness. A significant domiciliation or domestication inside dwellings would suggest that indoor insecticide spraying and/or housing-improvement interventions aimed at reducing the suitability of the domestic habitat would be effective in reducing/eliminating house infestation as was the case with *T. infestans* (Schofield et al. 2006). On the other hand, a high level of intrusion inside dwellings would rule out indoor insecticide spraying as a key component of vector control, which would rather need to focus on limiting triatomin entry inside houses. Interventions based on window insect screens or insecticide-impregnated curtains (Herber & Kroeger 2003, Barbu et al. 2009, 2011, Ferral et al. 2010, Waleckx et al. 2015) would thus be recommended. In any case, community education should also be considered as part of all vector interventions to strengthen their sustainability. Importantly, long-term entomological surveillance should be implemented to detect potential changes in vector population dynamics due to the adaptation or replacement of vector species, as well as the emergence of insecticide resistance.

Analysis of Table II and of the cases studies presented provides clues to the type of empirical and theoretical data needed to appreciate the levels of intrusion and domiciliation of triatomin species. As can be seen, the primary source of evidences comes from field studies based on timed-manuals collections, traps and sensors and/or community participation to document infestation patterns in different habitats. However, such studies may be misleading if too limited in scope, geographic coverage and sample size, as seen with the initial studies of *R. ecuadoriensis*, which suggested that it was synanthropic. Additionally to the collections in the domestic habitat, exhaustive searches in peridomestic and sylvatic habitats are needed for a complete description of triatominine distribution. Infestation data at different geographic scales is critical, with in depth studies limited to a small number of villages providing precise data on population structure and demography, complemented with larger scale studies including many villages, to allow for generalisation over large regions. The establishment of the level of domiciliation/intrusion of triatomines in the different habitats should be properly done at the same geographic scale as that of vector control intervention, since species can present regional differences in their level of domiciliation. In addition, while most studies are based on a single time-point, longitudinal studies clearly provide a more complete description of the infestation dynamics and its potential seasonal variations (Dumonteil et al. 2002, Schettino et al. 2007, Payet et al. 2009).

The definitions in Table I are rather subjective and lack clear “thresholds” between the different domiciliation levels to objectively classify the triatomin populations in any of the categories. The classical entomological indexes mentioned above may be seen as attempts to provide a quantitative evaluation of the domiciliation status of triatomines. However, they do not provide a clear description of the level of adaptation to human habitat. For example, while the colonisation index is often taken as indicative of the domiciliation/domestication of a species/population, it actually falls short of demonstrating the occurrence of the complete reproductive cycle of the bugs, nor of its sustainability over time. Also, nymphs may reach houses by walking or may have emerged from eggs released by a visiting female. Similarly, the visitation index does not take into account seasonal intrusion or may be biased by a low detection of nymphs.

Population genetics analysis leading to the characterisation of population genetic structure, population assignment and assessment of gene flow can also shed some light on bug dispersal among habitat and on domiciliation (Gourbière et al. 2012). However, these studies remain costly and technically challenging and more appropriate for basic research than for vector control programs. It is also worth noting that the genetic structure strictly depends on the molecular clock of the genetic markers used and these needs to be carefully selected to provide reliable information. Indeed, conflicting results may be obtained depending on the methods used to infer gene flow among populations, as observed for *T. infestans* (Brenière et al. 1998). Similarly, other types of molecular studies, such as the identification of blood feeding sources and profiles are central to further evaluate and quantify the risks of transmission of *T. cruzi* to humans (Dumonteil et al. 2013, Waleckx et al. 2014), but may be limited to a research setting. On the other hand, the analysis of infestation risk factors may be useful and can be applied to entomological data from very large number of houses from surveillance program (Campbell-Lendrum et al. 2007), but the evidence provided is very indirect, so often insufficient to determine the level of intrusion/domiciliation.

Finally, the modelling of vector population dynamics and *T. cruzi* transmission provides a very powerful way of analysing field collection data, as it allows quantifying the effects of bug dispersal (i.e., intrusion) and demography (i.e., domiciliation) on the infestation process and transmission of *T. cruzi*, as well as anticipating the potential efficacy of control strategies when empirical approaches are difficult for practical, financial or ethical reasons. An interesting example in the field is the modelling of *T. dimidiata* source-sink dynamics in the Yucatan Peninsula, that provided quantitative evidences that although nymph stages were occasionally detected inside houses, such limited colonisation was not compatible with an effective domiciliation, as domestic populations were not self-sustainable, but rather strictly depended on seasonal intrusion of adult bugs (Gourbière et al. 2008, Barbu et al. 2009, 2010, 2011). Such models can easily be adjusted to a variety of bug collection data from field
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studies [see Nouvellet et al. (2015) for a review] and sensitivity analysis can provide (theoretical) thresholds for both intrusion/domiciliation of bugs populations, as well as for the transmission of *T. cruzi* to humans (Rascalou et al. 2012, Nouvellet et al. 2013). Setting up more (“Leslie” or “LevKovitch”) (Caswell 2001) matrix models of triatomine’s life history and population dynamics would also lay the foundations for micro-evolutionary studies. In fisherian optimality approaches (RoT 2010), this type of modelling indeed allows identifying the fitness value of a given strategy according to the complete life history it corresponds to. Direct comparisons between the fitness values of alternative strategies then provide an objective and quantitative way to predict the evolutionary “optimal” strategy. More elaborated description of the meta-population dynamics (Gourbière & Gourbière 2002), the nonlinear ecological (e.g., competitive) interactions and/or the genetic deterministic of the strategies can be accounted in identifying evolutionary dynamics (Meszena et al. 2001, Dieckmann et al. 2002), potentially leading to more complex insect life-history evolutionary dynamics according to frequency and density-dependent fitness values (Gourbière & Menu 2009). These approaches are barely used to understand triatomine’s evolution [but see Menu et al. (2010) and Pelosse et al. (2013)], while they could provide critical quantitative insights into the domiciliation of triatomine or their adaptive response to control interventions, two issues that are critical to our understanding of the ecolgy, evolution and control of Chagas disease.

Concluding remarks

While domiciliation is clearly a gradual evolutionary process, we argued here that more precise evaluations of the level of adaptation of triatomine species to human habitats are needed for the optimisation of vector control. While only a few species have been able to effectively adapt to human housing, most remain connected to sylvatic populations and show variable levels of intrusion. Such behaviour requires the design of specific vector control interventions targeting this intrusion process, rather than insecticide spraying which only targets domesticated triatomine populations. Most current approaches used to assess triatomine association with human habitat, based on field and laboratory studies, provide insufficient information on the level of domestic adaptation of triatomines. Further analysis and modelling of field data can provide quantitative estimates of population persistence and fitness, shed new light on the domiciliation process of triatomine and may represent a key tool for decision-making and the design of vector control interventions.

REFERENCES

Abad-Franch F, Aguilar VHM, Paucar CA, Lorosa ES, Noireau F 2002. Observations on the domestic ecology of *Rhodnius ecutadoriensis* (Triatominae). *Mem Inst Oswaldo Cruz* 97: 199-202.

Abad-Franch F, Monteiro FA 2005. Molecular research and the control of Chagas disease vectors. *An Acad Bras Cienc* 77: 437-454.

Abad-Franch F, Noireau F, Paucar A, Aguilar HM, Carpio C, Racines J 2000. The use of live-bait traps for the study of sylvatic *Rhodnius populations* (Hemiptera: Reduviidae) in palm trees. *Trans R Soc Trop Med Hyg* 94: 629-630.

Abad-Franch F, Palomeque FS, Aguilar HM, Miles MA 2005. Field ecology of sylvatic *Rhodnius* populations (Heteroptera, Triatominae): risk factors for palm tree infestation in western Ecuador. *Trop Med Int Health* 10: 1258-1266.

Abad-Franch F, Paucar CA, Carpio CC, Cuba Cuba CA, Aguilar VHM, Miles MA 2001. Biogeography of Triatominiae (Hemiptera: Reduviidae) in Ecuador: implications for the design of control strategies. *Mem Inst Oswaldo Cruz* 96: 611-620.

Aldana E, Heredia-Coronado E, Avendano-Rangel F, Lizzo E, Concepcion JL, Bonfante-Cabarcas R, Rodriguez-Bonfante C, Pulido MM 2011. Morphometric analysis of *Panstrongylus geniculatus* (Heteroptera: Reduviidae) from Caracas city, Venezuela. *Biomedica* 31: 108-117.

Angulo VM, Esteban L, Luna KP 2012. *Attalea butyrateca* palms adjacent to housing as a source of infestation by *Rhodnius prolirus* (Hemiptera: Reduviidae). *Biomedica* 32: 277-285.

Bacigalupo A, Torres-Pérez F, Segovia V, García A, Correa JP, Moreno L, Arroyo P, Catton PE 2010. Sylvatic foci of the Chagas disease vector *Triatoma infestans* in Chile: description of a new focus and challenges for control programs. *Mem Inst Oswaldo Cruz* 105: 633-641.

Bar ME, Damborsky MP, Oscherov EB, Milano AMF, Avalos G, Wisnivesky-Colli C 2002. Triatomines involved in domestic and wild *Trypanosoma cruzi* transmission in Concepcion, Corrientes, Argentina. *Mem Inst Oswaldo Cruz* 97: 43-46.

Bar ME, Oscherov EB, Damborsky MP 1993. Presence of *Triatoma sordida* Stål, 1859 in Corrientes city urban ecotopes. *Rev Saude Publica* 27: 117-122.

Bar ME, Oscherov EB, Damborsky MP, Borda M 2010. Epidemiology of American trypanosomiasis in the north of Corrientes province, Argentina. *Medicina (B Aires)* 70: 133-138.

Barbu C, Dumonteil E, Gourbière S 2009. *Optimization of control strategies for non-domiciliated Triatoma dimidiata*, Chagas disease vector in the Yucatan Peninsula, Mexico. *PLoS Negl Trop Dis* 3: e416.

Barbu C, Dumonteil E, Gourbière S 2010. *Characterization of the dispersal of non-domiciliated Triatoma dimidiata* through the selection of spatially explicit models. *PLoS Negl Trop Dis* 4: e777.

Barbu C, Dumonteil E, Gourbière S 2011. *Evaluation of spatially targeted strategies to control non-domiciliated Triatoma dimidiata* vector of Chagas disease. *PLoS Negl Trop Dis* 5: e1045.

Bargues MD, Klisioiwicz DR, Gonzalez-Candelas F, Ramsey J, Monroy C, Ponce C, Salazar-Schettino PM, Panzera F, Abad F, Sousa OF, Schofield C, Dujardin JP, Guhl F, Mas-Coma S 2008. Phylogeography and genetic variations of *Triatoma dimidiata*, the main Chagas disease vector in Central America and its position within the genus *Triatoma*. *PLoS Negl Trop Dis* 2: e253.

Bargues MD, Schofield CJ, Dujardin JP 2010. Classification and phylogeny of the Triatominae. In J Telleria, M Tibayrenc (eds.), *American trypanosomiasis Chagas disease - One hundred years of research*, Elsevier, Burlington, p. 117-147.

Bermudez H, Balderrama F, Torrico F 1993. *Identification and characterization of sylvatic foci of Chagas infestations in Central Bolivia. Am J Trop Med Hyg* 49 (Suppl.): 371.

Black CL, Ocanas-Mayorga S, Riner DK, Costales JA, Lascano MS, Arcos-Teran L, Preissler JS, Seed JR, Grijalva MJ 2009. *Seroreivalence of Trypanosoma cruzi* in rural Ecuador and clustering of seropositivity within households. *Am J Trop Med Hyg* 81: 1035-1040.

Bremond P, Salas R, Waleckx E, Buitrago R, Aliaga C, Barnabé C, Depickere S, Dangles O, Brenière SF 2014. Variations in time and space of an Andean wild population of *T. infestans* at a microgeographic scale. *Parasit Vectors* 7: 164.
Brenière SF, Bosseno MF, Gualtram-Estelam, Gutierrez MMS, Monges MJK, Salas JHB, Paredes JIR, Kasten EJL 2010. Community participation and domiciliary occurrence of infected Meccus longipennis in two Mexican villages in Jalisco state. *Am J Trop Med Hyg* 83: 382-387.

Brenière SF, Bosseno MF, Magallon-Gastelum E, Ruvalcaba EGC, Gutierrez MS, Luna ECM, Basulto JT, Marfil-Mauve D, Walter A, Lozano-Kasten F 2007. Periodic domination of *Triatoma longipennis* (Hemiptera, Reduviidae) and *Triatoma barberi* (Hemiptera, Reduviidae) in a rural community with active transmission of *Trypanosoma cruzi* in Jalisco state, Mexico. *Acta Trop* 101: 249-257.

Brenière SF, Bosseno MF, Vargas F, Yaksic N, Noireau F, Noel S, Dujardin JP, Tabinrren M 1998. Smallness of the panmictic unit of *Triatoma infestans* (Hemiptera: Reduviidae) in peridomestic habitats of a rural community in Jalisco state, Mexico. *J Med Entomol* 41: 1015-1020.

Brenière SF, Salas R, Buitrago R, Bremond P, Sosa V, Bosseno MF, Waleckx E, Depickère S, Barnabé C 2013. Wild populations of *Triatoma infestans* are highly connected to intra-peridomestic conspecific populations in the Bolivian Andes. *PLoS ONE* 8: e80786.

Brenière SF, Waleckx E, Magallon-Gastelum E, Bosseno MF, Hardy X, Ndo C, Lozano-Kasten F, Barnabé C, Kengne P 2012. Population genetic structure of *Meccus longipennis* (Hemiptera, Reduviidae, Triatominae), vector of Chagas disease in west Mexico. *Insect Genet Evol* 12: 254-262.

Buitrago R, Bosseno MF, Waleckx E, Bremond P, Vidaurre P, Zoveda F, Brenière SF 2013. Risk of transmission of *Trypanosoma cruzi* by wild *Triatoma infestans* (Hemiptera: Reduviidae) in Bolivia supported by the detection of human blood meals. *Insect Genet Evol* 19: 141-144.

Buitrago R, Waleckx E, Bosseno MF, Zoveda F, Vidaurre P, Salas R, Mamani E, Noireau F, Brenière SF 2010. First report of widespread wild populations of *Triatoma infestans* (Reduviidae, Triatominae) in the valleys of La Paz, Bolivia. *Am J Trop Med Hyg* 82: 574-579.

Bustamante DM, de Urioste-Stone SM, Juarez JG, Pennington PM 2014. Ecological, social and biological risk factors for continued *Trypanosoma cruzi* transmission by *Triatoma dimidiata* in Guatemala. *PLoS ONE* 9: e94599.

Bustamante DM, Monroy C, Pineda S, Rodas A, Castro X, Ayala V, Quinones J, Moguel B, Trampe R 2009. Risk factors for intradomiciliary infection by the Chagas disease vector *Triatoma dimidiata* in Jutiapa, Guatemala. *Cad Saude Publica* 25 (Suppl. 1): 83-92.

Cabrera R, Vega S, Caceres AG, Ramal AC, Alvarez C, Ladera P, Pinedo R, Chuquimpondo G 2010. Epidemiological investigation of an acute case of Chagas disease in an area of active transmission in Peruvian Amazon Region. *Rev Inst Med Trop Sao Paulo* 52: 269-272.

Caceres AG, Troyes L, Gonzáles-Pérez A, Llontop E, Bonilla C, Murius E, Heredia N, Velásquez C, Yáñez C 2002. Enfermedad de Chagas by random amplification of polymorphic DNA-polymerase chain reaction. *Rev Inst Med Trop Sao Paulo* 44: 173-211.

Calzada JE, Pineda V, Montalvo E, Alvarez D, Santamaría AM, Samudio F, Bayvard V, Caceres L, Saldana A 2006. Human trypanosome infection and the presence of intradomicile Rhodnius pallescens in the western border of the Panama Canal, Panama. *Am J Trop Med Hyg* 74: 762-765.

Campbell-Lendrum D, Angulo VM, Esteban L, Tarazona Z, Parra GJ, Restrepo M, Restrepo BN, Guel F, Pinto N, Aguillera G, Wilkinson P, Davies CR 2007. House-level risk factors for triatomine infestation in Colombia. *Int J Epidemiol* 36: 866-872.

Canale DM, Cecere MC, Chuit R, Gurtler RE 2000. Periodic distribution of *Triatoma garciables* and *Triatoma guasayana* in north-west Argentina. *Med Vet Entomol* 14: 383-390.

Carrasco HJ, Torrellas A, Garcia C, Segovia M, Feliciangeli MD 2005. Risk of *Trypanosoma cruzi* 1 (Kineto plastida: Trypanosomatiidae) transmission by *Panstrongylus geniculatus* (Hemiptera: Reduviidae) in Caracas (metropolitan district) and neighboring states, Venezuela. *Int J Parasitol* 35: 1379-1384.

Caswell H 2001. Matrix population models: construction, analysis and interpretation, 2nd ed., Sinauer Associates Inc, Sunderland, 722 pp.

Ceballos LA, Piccinali RV, Berkinsky I, Kitron U, Gurtler RE 2009. First finding of melanotic *Triatoma infestans* (Hemiptera: Reduviidae) colonies in the Argentine Chaco. *J Med Entomol* 46: 1195-1202.

Ceballos LA, Piccinali RV, Marcet PL, Vazquez-Prokopec GM, Cardinal MV, Schachtier-Broide J, Dujardin JP, Dotson EM, Kitron U, Gurtler RE 2011. Hidden sylvatic foci of the main vector of Chagas disease *Triatoma infestans*: threats to the vector elimination campaign? *PLoS Negl Trop Dis* 5: e1365.

Cedillos RA, Romero JE, Sasagawa E 2012. Elimination of *Rhodnius prolixus* in El Salvador, Central America. *Mem Inst Oswaldo Cruz* 107: 1068-1069.

Chico HM, Sandoval C, Guevara EA, Calvopiña HM, Cooper PJ, Reed SG, Guderman RH 1997. Chagas disease in Ecuador: evidence for disease transmission in an indigenous population in the Amazon Region. *Mem Inst Oswaldo Cruz* 92: 317-320.

Christensen HA, de Vasquez AM 1981. Host feeding profiles of *Rhodnius pallescens* (Hemiptera: Reduviidae) in rural villages of central Panama. *Am J Trop Med Hyg* 30: 278-283.

Cominetti MC, Andreotti R, Oshiro ET, Dorval MEMC 2011. Epidemiological factors related to the transmission risk of *Trypanosoma cruzi* in a Quilombola community, state of Mato Grosso do Sul, Brazil. *Rev Soc Bras Med Trop* 44: 576-581.

Costa JA, Almeida CE, Dottone EM, Lins A, Vinhaes M, Silveira AC, Beard CB 2003. The epidemiologic importance of *Triatoma brasiliensis* as a Chagas disease vector in Brazil: a revision of domiciliary captures during 1993-1999. *Mem Inst Oswaldo Cruz* 98: 443-449.

Cuba Cuba CA, Abad-Franch F, Rodriguez JR, Vásquez FV, Velásquez LF, Miles MA 2002. The triatomines of northern Peru with emphasis on the ecology and infection by trypanosomes of *Rhodnius ecuadoriensis* (Triatominae). *Mem Inst Oswaldo Cruz* 97: 175-183.

Cuba Cuba CA, Vargas F, Roldan J, Ampuero C 2003. Domestic *Rhodnius ecuadoriensis* (Hemiptera, Reduviidae) infestation in northern Peru: a comparative trial of detection methods during a six-month follow-up. *Rev Inst Med Trop Sao Paulo* 45: 85-90.

diva SA, Sampaio SMP, Poloni M, Koyanagui PH, de Carvalho CB 2004. Pesquisa sistemática positiva e House-level risk factors for triatomine infestation in peridomestic habitats of a rural community in Jalisco state, Mexico. *J Med Entomol* 41: 1015-1020.
De Urioste-Stone SM, Pennington PM, Pellecer E, Aguilar TM, Samayoa G, Perdomo HD, Enríquez H, Juárez JG 2015. Development of a community-based intervention for the control of Chagas disease based on peridomestic animal management: an eco-social perspective. *Trans R Soc Trop Med Hyg* 109: 159-167.

Depickère S, Durán P, López R, Chávez T 2011. Presence of intra-domicile colonies of the triatomine bug *Panstrongylus rufotuberculatus* in Muñecas, La Paz, Bolivia. *Acta Trop* 117: 97-100.

Depickère S, Durán P, Lopez R, Martinez E, Chavez T 2012. After five years of chemical control: colonies of the triatomine *Eratyulus mucronatus* are still present in Bolivia. *Acta Trop* 123: 234-238.

Dias JCP, Vieira EP, Tadashi H, Azeredo BVM 2005. Nota sobre o uso de bio-sensores “Maria” nas ações de vigilância entomológica contra a doença de Chagas ao norte de Minas Gerais. *Rev Soc Bras Med Trop* 38: 377-382.

Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K 2002. *Adaptive dynamics of infectious diseases: in pursuit of virulence management*, Cambridge University Press, Cambridge, 463 pp.

Dorn PL, Calderon C, Melgar S, Moguel R, Solorzano E, Dumonteil E, Rodas A, de la Rua N, Garnica R, Monroy C 2009. Two distinct *Triatoma dimidiata* (Latreille, 1811) taxa are found in sympathy in Guatemala and Mexico. *PLoS Negl Trop Dis* 3: e393.

Dorn PL, Melgar S, Rouzier V, Gutierrez A, Combe C, Rosales R, Rodas A, Kott S, Salvia D, Monroy CM 2003. The Chagas vector, *Triatoma dimidiata* (Hemiptera: Reduviidae), is panmictic within and among adjacent villages in Guatemala. *J Med Entomol* 40: 436-438.

Dorn PL., Monroy C, Curtis A 2007. *Triatoma dimidiata* (Latreille, 1811): a review of its diversity across its geographic range and the relationship among populations. *Infect Genet Evol* 7: 343-352.

Dujardin JP, Schofield CJ, Panzera F 2002. *Los vectores de la enfermedad de Chagas*, Académie Royale des Sciences d’Outre-Mer, Bruxelles, 189 pp.

Dujardin JP, Steindel M, Chavez T, Machane M, Schofield CJ 1999. Changes in the sexual dimorphism of triatominae in the transition from natural to artificial habitats. *Mem Inst Oswaldo Cruz* 94: 565-569.

Dumonteil E, Ferral J, Euan-Garcia M, Ramirez-Sierra MJ, Najera-Vasquez MR, Dumonteil E 2010. Comparative field trial of alternative vector control strategies for non-domiciliated *Triatoma dimidiata* in the Yucatan Peninsula, Mexico. *Am J Trop Med Hyg* 82: 60-66.

Fitzpatrick S, Feliciangeli MD, Sanchez-Martin M, Monteiro FA, Miles MA 2008. Molecular genetics reveal that silvatic *Rhodnius prolixus* do colonise rural houses. *PLoS Negl Trop Dis* 2: e210.

Forattini OP, Ferreira OA, Rabello EX, Barata JMS, Santos JLF 1983. Ecological aspects of South American trypanosomiasis. 17. The domiciliation development of local Triatominae populations in the *Triatoma sordida* endemic center. *Rev Saúde Pública* 17: 159-199.

Gajate PP, Bottazzi MV, Pietrokovsky SM, Wisnivesky-Colli C 1996. Potential colonization of the peridomicaly by *Triatoma guasayana* (Hemiptera: Reduviidae) in Santiago del Estero, Argentina. *J Med Entomol* 33: 635-639.

Gamboa-León R, Ramirez-Gonzalez C, Pacheco-Tucuch F, O’Shea M, Rosecrans K, Pippitt J, Dumonteil E, Buekens P 2014. Chagas disease among mothers and children in rural Mayan communities. *Am J Trop Med Hyg* 91: 348-353.

Garcia MN, Aguilar D, Gorchakov R, Rossmann SN, Montgomery SP, Rivera H, Woc-Colburn L, Hotez P, Murray KO 2015. Evidence of autochthonous Chagas disease in southern Texas. *Am J Trop Med Hyg* 92: 325-330.

Gourbière S, Dumonteil E 2012. *Genetics and evolution of triatomines*: from phylogeny to vector control. *Hereditas* 108: 190-202.

Gourbière S, Dumonteil E, Rabinovich J, Minkoue R, Menu F 2008. Demographic and dispersal constraints for domestic infestation by non-domiciliated *Triatoma dimidiata* in the Yucatan Peninsula, Mexico. *Trans R Soc Trop Med Hyg* 52: 17.

Gourbière S, Gourbière F 2002. Competition between unit-restricted fungi: a metapopulation model. *J Theor Biol* 217: 351-368.

Gourbière S, Menu F 2009. Adaptive dynamics of dormancy duration variability: evolutionary trade-off and priority effect lead to suboptimal adaptation. *Evolution* 63: 1879-1892.

Grijalva MJ, Palomeque-Rodriguez FS, Costales JA, Davila S, Arcos-Teran L 2005. *High household infestation rates by non-domiciliated Chagas disease vectors in the Yucatan Peninsula of Mexico*. *J Med Entomol* 42: 68-74.

Grijalva MJ, Suarez-Davalos V, Villacis AG, Ocana-Mayorga S, Dangles O 2012. Ecological factors related to the widespread distribution of sylvatic *Rhodnius ecuadoriensis* populations in southern Ecuador. *Parasit Vectors* 5: 17.
Grijalva MJ, Villacís AG 2009. Presence of Rhodinus eucadoriensis in sylvatic habitats in the southern highlands (Loja province) of Ecuador. J Med Entomol 46: 708-711.

Grijalva MJ, Villacís AG, Ocana-Mayorga S, Yumiseva CA, Baus EG 2011. Limitations of selective deltamethrin application for triatomine control in central coastal Ecuador. Parasit Vectors 4: 20.

Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 1999. Monitoring house reinfestation by vectors of Chagas disease: a comparative trial of detection methods during a four-year follow-up. Acta Trop 72: 213-234.

Guzman-Braico C, García-García L, Floriani-Verdugo J, Guerrero-Martínez S, Torres-Cosme M, Ramirez-Melgar C, Velasco-Castrejon O 1998. Riesgo de transmisión de Trypanosoma cruzi por transmisión de sangre en México. Rev Panam Salud Publica 4: 94-99.

Guzman-Tapia Y, Ramirez-Sierra MJ, Dumontelle E 2007. Urban infestation by Triatoma dimidiata in the city of Mérida, Yucatan, Mexico. Vector Borne Zoonotic Dis 7: 597-606.

Hashimoto K, Álvarez H, Nakagawa J, Juarez J, Monroy C, Cordon-Rosas C, Gil E 2012. Vector control intervention towards interruption of transmission of Chagas disease by Rhodinus prolirus, main vector in Guatemala. Mem Inst Oswaldo Cruz 107: 877-887.

Hashimoto K, Cordon-Rosas C, Trampe R, Kawabata M 2006. Impact of single and multiple residual sprays of pyrethroid insecticides against Triatoma dimidiata (Reduviidae; Triatominae), the principal vector of Chagas disease in Jutiapa, Guatemala. Am J Trop Med Hyg 75: 226-230.

Herber O, Kroeger A 2003. Pyrethroid-impregnated curtains for Chagas disease control in Venezuela. Acta Trop 88: 33-38.

Herrera-Aguilar M, Be-Barragán LA, Ramirez-Sierra MJ, Tripet F, Grijalva MJ, Villacís AG 2009. Revision of the Triatominae (Hemiptera, Reduviidae). In J Telleria, M Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 2007. Human-rodent interface; Chagas disease control efforts? Trends Parasitol 23: 212-218.

Herrera-Aguilar M, Be-Barragán LA, Ramirez-Sierra MJ, Tripet F, Grijalva MJ, Villacís AG 2009. Revision of the Triatominae (Hemiptera, Reduviidae). In J Telleria, M Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 2007. Human-rodent interface; Chagas disease control efforts? Trends Parasitol 23: 212-218.

Herrera-Aguilar M, Be-Barragán LA, Ramirez-Sierra MJ, Tripet F, Grijalva MJ, Villacís AG 2009. Revision of the Triatominae (Hemiptera, Reduviidae). In J Telleria, M Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 2007. Human-rodent interface; Chagas disease control efforts? Trends Parasitol 23: 212-218.

Herrera-Aguilar M, Be-Barragán LA, Ramirez-Sierra MJ, Tripet F, Grijalva MJ, Villacís AG 2009. Revision of the Triatominae (Hemiptera, Reduviidae). In J Telleria, M Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 2007. Human-rodent interface; Chagas disease control efforts? Trends Parasitol 23: 212-218.

Herrera-Aguilar M, Be-Barragán LA, Ramirez-Sierra MJ, Tripet F, Grijalva MJ, Villacís AG 2009. Revision of the Triatominae (Hemiptera, Reduviidae). In J Telleria, M Gurtler RE, Cecere MC, Canale DM, Castanera MB, Chuit R, Cohen JE 2007. Human-rodent interface; Chagas disease control efforts? Trends Parasitol 23: 212-218.
Nouvèillet P, Cucunubá ZM, Gourbière S 2015. Ecology, evolution and control of Chagas disease: a century of neglected modelling and a promising future. Adv Parasitol 87: 135-191.

Nouvèillet P, Dumonteil E, Gourbière S 2013. The improbable transmission of Trypanosoma cruzi to human: the missing link in the dynamics and control of Chagas disease. PLoS Negl Trop Dis 7: e2505.

Pacheco-Tueuch FS, Ramírez-Sierra MJ, Gourbière S, Dumonteil E 2012. Public street lights increase house infestation by the Chagas disease vector Triatoma dimidiata. PLoS ONE 7: e36207.

Panzena F, Dujardin JP, Nicolini P, Caraccio MN, Rose V, Tellez T, Bermudez H, Bargues MD, Mas-Coma S, O’Connor JE, Perez R 2004. Genomic changes of Chagas disease vector, South America. Emerg Infect Dis 10: 438-446.

Payet V, Ramírez-Sierra MJ, Rabinovich J, Menu F, Dumonteil E 2009. Variations in sex-ratio, feeding and fecundity of Triatoma dimidiata between habitats in the Yucatan Peninsula, Mexico. Vector Borne Zoonotic Dis 9: 243-251.

Paz-Bailey G, Monroy C, Rodas A, Rosales R, Tabaru R, Davies C, Lines J 2002. Incidence of Trypanosoma cruzi infection in two Guatemalan communities. Trans R Soc Trop Med Hyg 96: 48-52.

Pellecer MJ, Dorn PL, Bustamante DM, Rodas A, Monroy MC 2013. Vector blood meals are an early indicator of the effectiveness of the ecohealth approach in halting Chagas transmission in Guatemala. Am J Trop Med Hyg 88: 638-644.

Pelosse P, Kribis-Zaleta CM, Ginoux M, Rabinovich JE, Gourbière S, Menu F 2013. Influence of vectors’ risk-spreading strategies and environmental stochasticity on the epidemiology and evolution of vector-borne diseases: the example of Chagas disease. PLoS ONE 8: e70830.

Pineda V, Montalvo E, Álvarez D, Santamaria AM, Calzada JE, Saldana A 2008. Feeding sources and trypanosome infection index of Rhodnius pallescens in a Chagas disease endemic area of Amapá State, Brazil. Rev Inst Med Trop Sao Paulo 50: 116.

Pires HHR, Borges EC, de Andrade RE, Lorosa ES, Diotaïuti L 1999. Peridomiciliary infestation with Triatoma sordida Stål, 1859 in the county of Serra do Ramalho, Bahia, Brazil. Mem Inst Oswaldo Cruz 94: 147-149.

Polonio R, Ramírez-Sierra MJ, Dumonteil E 2009. Dynamics and distribution of house infestation by Triatoma dimidiata in central and southern Belize. Vector Borne Zoonotic Dis 9: 19-24.

Rabinovich JE, Leal JA, de Piñero DF 1979. Domiciliary biting frequency and blood ingestion of the Chagas disease vector Rhodnius prolixus Stål (Hemiptera: Reduviidae) in Venezuela. Trans R Soc Trop Med Hyg 73: 272-283.

Ramírez CJ, Jaramillo CA, Delgado MP, Pinto NA, Aguilera G, Guhl F 2005. Genetic structure of sylvatic, peridomestic and domestic populations of Triatoma dimidiata (Hemiptera: Reduviidae) from an endemic zone of Boyaca, Colombia. Acta Trop 93: 23-29.

Ramírez-Sierra MJ, Herrera-Aguilar M, Gourbière S, Dumonteil E 2010. Patterns of house infestation dynamics by non-domiciliated Triatoma dimidiata reveal a spatial gradient of infestation in rural villages and potential insect manipulation by Trypanosoma cruzi. Trop Med Int Health 15: 77-86.

Ramos-Lignon A, López-Monteron A, Gázman-Gómez D, Rosales-Encina JL, Limón-Flores Y, Dumonteil E 2010. Identification of a hyperendemic area for Trypanosoma cruzi infection in central Veracruz, Mexico. Am J Trop Med Hyg 83: 164-170.

Ramsey JM, Cruz-Celis A, Salgado L, Espinosa L, Ordoñez R, Lopez R, Schofield CJ 2003. Efficacy of pyrethroid insecticides against domestic and peridomestic populations of Triatoma pallidipennis and Triatoma barberi (Reduviidae: Triatominae) vectors of Chagas disease in Mexico. J Med Entomol 40: 912-920.

Rascalu G, Pontier D, Menu F, Gourbière S 2012. Emergence and prevalence of human vector-borne diseases in sink vector populations. PLoS ONE 7: e36858.

Reyes-Lugo M 2009. Panstrongylus geniculatus Latreille 1811 (Hemiptera: Reduviidae, Triatominae), vector de la enfermedad de Chagas en el ambiente domiciliario del centro-norte de Venezuela. Rev Bioméd 20: 180-205.

Reyes-Lugo M, Rodríguez-Acosta A 2000. Domiciliation of the sylvatic Chagas disease vector Panstrongylus geniculatus Latreille, 1811 (Triatominae: Reduviidae) in Venezuela. Trans R Soc Trop Med Hyg 94: 508.

Rios JF, Arboleda M, Montoya AN, Alarcon EP, Parra-Henao GJ 2011. Probable outbreak of oral transmission of Chagas disease in Turbo, Antioquia. Biomedica 31: 185-195.

Rodríguez-Bonfante C, Amaro A, Garcia M, Wohlert LEM, Guillen P, Garcia RA, Alvarez N, Diaz M, Cárdenas E, Castillo S, Bonfante-Garrido R, Bonfante-Cabarcas R 2007. Epidemiology of Chagas disease in Andres Eloy Blanco, Lara, Venezuela: triatomin infestation and human seroprevalence. Cad Saude Publica 23: 1133-1140.

Roff DA 2010. Modeling evolution: an introduction to numerical methods, Oxford University Press, Oxford, 352 pp.

Rolón M, Vega MC, Román F, Gómez A, de Arias AR 2011. First report of colonies of sylvatic Triatoma infestans (Hemiptera: Reduviidae) in the Paraguayan Chaco, using a trained dog. PLoS Negl Trop Dis 5: e1026.

Rosecrans K, Cruz-Martin G, King A, Dumonteil E 2014. Opportunities for improved Chagas disease vector control based on knowledge, attitudes and practices of communities in the Yucatan Peninsula, Mexico. PLoS Negl Trop Dis 8: e2763.

Roux E, Venancio AF, Girres J-F, Romana CA 2011. Spatial patterns and eco-epidemiological systems - Part I: multi-scale spatial modelling of the occurrence of Chagas disease insect vectors. Geospatial Health 6: 41-51.

Sasaki H, Rosales R, Tabaru Y 2003. Host feeding profiles of Rhodnius prolixus and Triatoma dimidiata in Guatemala (Hemiptera: Reduviidae: Triatominae). Med Entomol Zool 54: 283-289.

Schiettino PMS, Piña JSH, Wastavino GR, Bravo MC, Blanco MV, Cárdenas JL 2007. Triatoma mexicana (Hemiptera: Reduviidae) in Guanajuato, Mexico: house infestation and seasonal variation. Mem Inst Oswaldo Cruz 102: 803-807.

Schofield CJ 1988. Biosystematics of the Triatominae. In MW Servín (ed) The biology of vectors. Academic Press, London, 315 pp.

Schofield CJ, Diotaïuti L, Dujardin JP 1999. The process of domestication in Triatominae. Mem Inst Oswaldo Cruz 94(Suppl. 1): 375-378.

Schofield CJ, Jannin J, Salvatella R 2006. The future of Chagas disease control. Trends Parasitol 22: 583-588.

Serrano O, Mendoza F, Suarez B, Soto A 2008. Seroepidemiology of Chagas disease in two rural populations in the municipality of Costa de Oro, at Aragua state, northern Venezuela. J Med Entomol Zool 31: 283-289.

Shapiro CA, Esquivel M, Hernández FC, followed by 500 patients in the town of San Juan, San Pedro Sula, Honduras, who had been treated for Chagas disease with nifurtimox. Am J Trop Med Hyg 45: 246-250.

Sosa-Estani S, Gamboa-Leon MR, Del Cid-Lemus J, Althabe F, Alberga J, Almendares O, Cañabate ML, Chipaupa JP, Dumonteil E, Gibbons L, Padilla-Raygoza N, Schneider D, Belizan JM, Buckens
P 2008. Use of a rapid test on umbilical cord blood to screen for Trypanosoma cruzi infection in pregnant women in Argentina, Bolivia, Honduras and Mexico. *Am J Trop Med Hyg* 79: 755-759.

Suárez-Duvalos V, Dangles O, Villacis AG, Grijalva MJ 2010. Microdistribution of sylvatic triatomine populations in central-coastal Ecuador. *J Med Entomol* 47: 80-88.

Torres DB, Cabrera R 2010. Geographical distribution and intra-domicaly capture of sylvatic triatomines in La Convención province, Cusco, Peru. *Rev Inst Med Trop Sao Paulo* 52: 157-160.

Torres-Montero J, López-Monleon A, Dumontell E, Ramos-Ligonio A 2012. House infestation dynamics and feeding sources of *Triatoma dimidiata* in central Veracruz, Mexico. *Am J Trop Med Hyg* 86: 677-682.

Torrico RA 1994. Hallazgo de *Eratyrus mucronatus*, infestación natural de vinchuca de cerro y *Etiatria sordida* en Cochabamba. *An Lab Central Cochabamba* 1: 19-23.

Valente SAS, Valente VC, Pinto AYN, César MJB, dos Santos MP, Miranda COS, Cuervo P, Fernandes O 2009. Analysis of an acute Chagas disease outbreak in the Brazilian Amazon: human cases, triatomines, reservoir mammals and parasites. *Trans R Soc Trop Med Hyg* 103: 291-297.

Valente VC 1999. Potential for domestication of *Panstrongylus geniculatus* (Linnaeus, 1758) (Hemiptera, Reduviidae, Triatominae) in the municipality of Muana, Marajó Island, Pará state, Brazil. *Rev Soc Bras Med Trop* 32: 595-597.

Valente VC, Valente SAS, Noireau F, Carrasco HJ, Miles MA 1998. Chagas disease in the Amazon Basin: association of *Panstrongylus geniculatus* (Hemiptera: Reduviidae) with domestic pigs. *J Med Entomol* 35: 99-103.

Vasquez AM, Samudio FE, Saldana A, Paz HM, Calzada JE 2004. Eco-epidemiological aspects of *Trypanosoma cruzi*, *Trypanosoma rangeli* and their vector (*Rhodius pallescens*) in Panama. *Rev Inst Med Trop Sao Paulo* 46: 217-222.

Vazquez-Prokopec GM, Cecere MC, Canale DM, Gurtler RE, Kitron U 2005. Spatiotemporal patterns of reinfestation by *Triatoma guasayana* (Hemiptera: Reduviidae) in a rural community of northernwestern Argentina. *J Med Entomol* 42: 571-581.

Vega S, Mendoza A, Cabrera R, Cáceres AG, Campos E, Ancua J, Pinto J, Torres S, Cabrera D, Yale G, Cevallos R, Náquira C 2006. Primer caso de enfermedad de Chagas aguda en el Sevna Central del Perú: investigación de coloniales, vectores y reservorios. *Rev Peru Med Exp Salud Publica* 23: 288-292.

Waleckx E, Camara-Mejia J, Ramirez-Sierra MJ, Cruz-Chan V, Rosado-Vallado M, Vazquez-Narvaez S, Najera-Vazquez R, Gourbière S, Dumontell E 2015. An innovative ecohealth intervention for Chagas disease vector control in Yucatan, Mexico. *Trans R Soc Trop Med Hyg* 109: 143-149.

Waleckx E, Depickère S, Salas R, Aliaga C, Monje M, Calle H, Buitrago R, Noireau F, Brenière SF 2012. New discoveries of sylvatic *Triatoma infestans* (Hemiptera: Reduviidae) throughout the Bolivian Chaco. *Am J Trop Med Hyg* 86: 455-458.

Waleckx E, Salas R, Huamán N, Buitrago R, Bosseno MF, Aliaga C, Barnabé C, Rodríguez R, Zoveda F, Monje M, Baune M, Quisberth S, Villena E, Kengne P, Noireau F, Brenière SF 2011. New insights on the Chagas disease main vector *Triatoma infestans* (Reduviidae, Triatominae) brought by the genetic analysis of Bolivian sylvatic populations. *Infect Genet Evol* 11: 1045-1057.

Waleckx E, Suarez J, Richards B, Dorn PL 2014. *Triatoma sanguisuga* blood meals and potential of Chagas disease transmission in Louisiana, United States. *Emerg Infect Dis* 20: 2141-2143.

WHO - World Health Organization 1991. *Control of Chagas disease: report of a WHO expert committee*. Available from: whqlibdoc.who.int/trs/WHO_TRS_811.pdf.

WHO - World Health Organization 2014. Chagas disease (American trypanosomiasis). Available from: who.int/mediacentre/factsheets/fs340/en/.

Wisnivesky-Colli C, Gürtler RE, Solarz ND, Schweigmann NJ, Petrokovsky SM, Alberti A, Flo J 1993. Dispersive flight and house invasion by *Triatoma guasayana* and *Triatoma sordida* in Argentina. *Mem Inst Oswaldo Cruz* 88: 27-32.

Zeledón R 2003. A new entomological indicator useful in epidemiological studies and in control campaigns against Chagas disease. *Entomol Vect* 10: 269-276.

Zeledón R, Berad B, Dias JCP, Leiby DA, Dorn PL, Coura JR 2012. *An appraisal of the status of Chagas disease in the United States*. Elsevier, Amsterdam, 102 pp.

Zeledón R, Marín F, Calvo N, Lugo E, Valle S 2006. Distribution and ecological aspects of *Rhodius pallescens* in Costa Rica and Nicaragua and their epidemiological implications. *Mem Inst Oswaldo Cruz* 101: 75-79.