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

Etienne Waleckx¹, Sébastien Gourbière², Eric Dumonteil^{1/+}

¹Laboratorio de Parasitología, Centro de Investigaciones Regionales Dr Hideyo Noguchi, Universidad Autónoma de Yucatán, Mérida, Yucatán, Mexico ²Institut de Modélisation et d'Analyses en Géo-Environnement et Santé, Université de Perpignan Via Domitia, Perpignan, France

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 criteria. 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 spe-

cies/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-

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+ Corresponding author: edumonte@tulane.edu

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TABLE I
Classification of triatomine species according to their relationship with human housing

Sylvatic species - Strictly found in sylvatic environment.

Intrusive species - Mostly sylvatic, 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).

Domiciliary 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/foci 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).

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 (Zeledón 2003). As indicated in Table I, the peridomi-

cile is considered as part of the domicile by Dujardin et al. (2002) and Noireau and Dujardin (2010), so that species adapted to peridomestic areas, but not found inside houses, are considered domiciliated/domesticated. However, some of these species have also been classified as peridomestic (e.g., *Tritoma sordida*) or synanthropic by other authors to differentiate them from those that are also extensively found inside houses.

Population genetics studies based on morphometric and molecular markers are also commonly used. Phylogeographic studies have been used to understand the general distribution of species over wide geographic areas and finer scale studies have focused on evaluating the relationships among populations from different habitats (Gourbière et al. 2012). A high gene flow between populations found inside dwellings and sylvatic environment (and the concomitant lack of population genetic structure - i.e., panmixia) is indicative of an elevated dispersal of bugs between habitats, hence a strongly intrusive behaviour. Conversely, a low gene flow resulting in the genetic differentiation of domestic and sylvatic populations suggests a significant domiciliation/domestication of a population. These approaches have been extensively used to assess the population genetic structure of several species (Table II).

Interestingly, based on the observation of a reduced sexual dimorphism in domesticated populations compared to sylvatic ones, Dujardin et al. (1999) proposed that morphometry may be used as an indicator of the level of adaptation of a species to domestic habitat. However, these observations were not associated with a clear measure of adaptation or fitness of the populations to the domestic habitat.

The data presented in Table II indicate that the classification of triatomine association with human habitat according to current definitions (Table I) is sometimes subjective, depending on the type of data available to establish the nature of the infestation process and this

TABLE II
Main triatomine species and their level of domiciliation

Species	Country, region	Evidence	Classification	Seroprevalence (%)	References
<i>Triatoma infestans</i>	Brazil, Argentina, Bolivia, Chile, Paraguay, southern Peru, Uruguay	Domestic and peridomestic collections of nymphs (and adults) showing high colonisation. Sylvatic foci/populations in the Andean valleys of Bolivia, in the Argentinean, Bolivian and Paraguayan Chaco and in Chile. Very low gene flow and high population genetic structure. Marked reduction of the geographic extension after residual insecticide spraying of dwellings in South America. Domiciliation appears to have been linked to human activities. Dispersal of the species appears to have been associated with human economic migrations. The species was apparently imported by human migrations in northern Uruguay at the beginning of the XX century and in the Northeast Region of Brazil in the 1970s.	Domestic (with some sylvatic foci/populations)	> 80 in Bolivia	Torrico (1946), Schofield (1988), Bermudez et al. (1993), Noireau 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)
<i>Triatoma longipennis</i> and <i>Triatoma barberi</i>	Mexico (Jalisco and Morelos)	High peridomestic infestation (16-60%) and colonisation (75-93%). Domestic intrusion by adults (> 70%). Feeding on humans. Population genetics shows high structuring at the peridomestic level, but high dispersal at larger scale. Significant reinfestation following insecticide spraying.	Peridomestic with domestic intrusion	1.8	Ramsey et al. (2003), Brenière et al. (2004, 2007, 2010, 2012)
<i>Rhodnius pallescens</i>	Costa Rica, Nicaragua, Panama, Colombia	Infestation by adults (30%), rare colonisation. Possible attraction to houses by light. Frequent blood feeding on humans when inside houses (25-50%). Population genetics shows gene flow between sylvatic and domestic populations.	Sylvatic (palm trees) with some domestic intrusion	0.2-6.7 ^a	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)
<i>Rhodnius prolixus</i>	Guatemala, El Salvador	Significant colonisation of houses. Effective control with indoor insecticide spraying. Frequent blood meals on humans (28%).	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
<i>R. prolixus</i>	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)
<i>Panstrongylus geniculatus</i>	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.	Sylvatic with domestic intrusion Species with potential for domestication	> 15.5 in Venezuela ^b > 14.2 in Ecuador ^c > 1.3 in Bolivia ^d	Chico et al. (1997), Naiff 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), Rodriguez-Bonfante et al. (2007), Serrano et al. (2008), Fe et al. (2009), Reyes-Lugo (2009), Aldana et al. (2011), Depickère et al. (2011, 2012)
<i>Triatoma brasiliensis</i>	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)
<i>Triatoma sordida</i> ^e	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 <i>T. infestans</i> . Population dynamic model supporting insect presence as the outcome both of a local scale "near-to-near" dispersal and infestation from the wild.	Sylvatic with an advanced process of adaptation to human habitat Predominantly peridomestic, without significant colonisation inside dwellings.	> 29.6 ^f	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
<i>T. sordida</i>	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 <i>T. sordida</i> found inside dwellings. Wider panmictic unit than <i>T. infestans</i> . 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.	Domiciliated	> 4	Noireau et al. (1995, 1997a, 1999b)
<i>Rhodnius ecuadoriensis</i>	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), Villacis et al. (2010)
<i>Triatoma dimidiata</i> ^s	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)
<i>T. dimidiata</i> ^s	Belize	Domestic collections showing seasonal infestation by adults.	Nondomiciliated	1	Polonio et al. (2009),
<i>T. dimidiata</i> ^s	Mexico (Veracruz)	Domestic collections showing seasonal infestation by adults with some colonisation. Blood meal analysis showing dispersal among habitats. 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.	Nondomiciliated with domiciliation in process Domestic	16.8 8.9	Ramos-Ligonio (2010), Torres-Montero et al. (2012) Paz-Bailey et al. (2002), Dorn (2003), Monroy et al. (2003a, b), Nakagawa et al. (2003a, b)
<i>Triatoma mexicana</i>	Mexico	Domestic collections showing seasonal infestation by adults. Housing quality and type not associated with infestation.	Intrusive	-	Schettino et al. (2007)



Species	Country, region	Evidence	Classification	Seroprevalence (%)	References
<i>Triatoma guasayana</i>	Bolivian and Argentinean Chaco	Peridomestic collections of adults and nymphs. Intrusion of adult bugs inside dwellings without evidence of colonisation. Bugs collected inside dwellings feed on human. Implicated in re-infestation post-spraying against <i>T. infestans</i> .	Sylvatic - Peridomestic, with intrusion of adult bugs inside human dwellings	-	Wisnivesky-Colli et al. (1993), Gajate et al. (1996), Gurtler et al. (1999), Noireau et al. (1999a), Canale et al. (2000), Vazquez-Prokopec et al. (2005)
<i>Triatoma sanguisuga</i>	Southern United States of America	Adults occasionally visiting houses. Mainly adults collected inside houses, but some nymphs have also been found in several occasions. Reports of insect bites from <i>T. sanguisuga</i> . Frequent human blood meals.	Essentially sylvatic, with Adults visiting human dwellings	Suspected or incriminated vector for several autochthonous cases of vectorial transmission	Dorn et al. (2007), Zeledón et al. (2012), Waleckx et al. (2014), Garcia et al. (2015)

a: higher seroprevalence may also be attributed to *T. dimidiata* present in this region; *b*: seroprevalence may also be attributed to *R. prolixus* present in the same area (mixed colonies) as reported by Feliciangeli et al. (2004); *c*: seroprevalence may also be attributed to *Rhodnius pictipes* and *Rhodnius robustus* present in the same area as reported by Chico et al. (1997); *d*: seroprevalence may also be attributed to *Rhodnius rufotuberculatus* present in the same area as reported by Depickère et al. (2011); *e*: species complex with two recognised cryptic species, *T. sordida* and *Triatoma garciabeci* (*T. sordida* group 2); *f*: seroprevalence may also be attributed to *T. infestans* present in the same area as reported by Bar et al. (2002); *g*: species complex.

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.

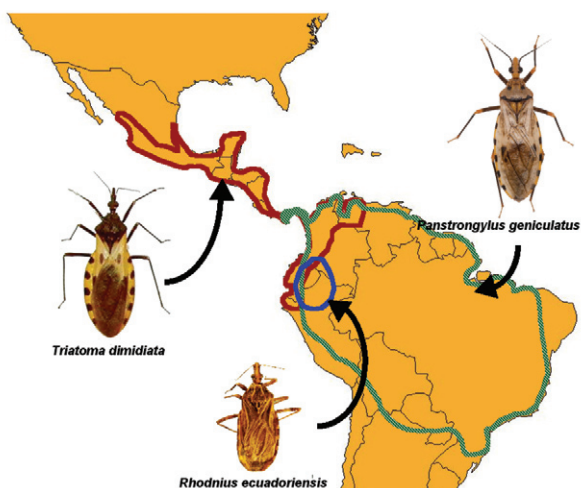
Case studies

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-infestation (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 nondomesticated but intrusive vector. Initial observations indicated that adult *T. dimidiata* transiently infests houses on a seasonal basis during the months of March-July (Dumonteil 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-



Geographic distribution of *T. dimidiata*, *P. geniculatus* and *R. ecuadoriensis*.

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 (Ramirez 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 peridomiciles 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 (Felicangeli 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 & Villacis 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 (Villacis 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 (Villacis 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 peridomestic and inside domiciles and (iii) the level of domiciliation or domestication in peridomestic 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 triatomine 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 triatomine 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 triatomine 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 triatomine populations in any of the categories. The classical entomologic 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

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 “Lefkovitch”) (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 (Roff 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 determinism 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 ecology, 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.

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