

## Ecological patterns of blood-feeding by kissing-bugs (Hemiptera: Reduviidae: Triatominae)

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*Host use by vectors is important in understanding the transmission of zoonotic diseases, which can affect humans, wildlife and domestic animals. Here, a synthesis of host exploitation patterns by kissing-bugs, vectors of Chagas disease, is presented. For this synthesis, an extensive literature review restricted to feeding sources analysed by precipitin tests was conducted. Modern tools from community ecology and multivariate statistics were used to determine patterns of segregation in host use. Rather than innate preferences for host species, host use by kissing-bugs is influenced by the habitats they colonise. One of the major limitations of studies on kissing-bug foraging has been the exclusive focus on the dominant vector species. We propose that expanding foraging studies to consider the community of vectors will substantially increase the understanding of Chagas disease transmission ecology. Our results indicate that host accessibility is a major factor that shapes the blood-foraging patterns of kissing-bugs. Therefore, from an applied perspective, measures that are directed at disrupting the contact between humans and kissing-bugs, such as housing improvement, are among the most desirable strategies for Chagas disease control.*

Key words: foraging - null models - diet analysis - multivariate statistics - Chagas disease - niche breadth

The biology of kissing-bugs (Triatominae: Reduviidae), which are vectors of Chagas disease, has been relatively well studied. Although the amount of knowledge is scarce when compared with other vectors, such as ticks or mosquitoes, a valuable body of knowledge on the physiology, behaviour, genetics, life history, geographical distribution, habitat use and feeding patterns and preferences has been accumulated in the century following Dr Carlos Chagas' groundbreaking discovery of the role of kissing-bugs as vectors of *Trypanosoma cruzi* (Chagas 1909). For kissing-bugs, hematophagy is a source of energy and nutrients. Unlike other blood-sucking insect vectors such as mosquitoes and sandflies, whose larvae rely on resources other than blood, kissing-bugs are strictly hematophagous (in a wide sense, including feeding on invertebrate haemolymph) during their entire life cycle (Lehane 2005). Earlier studies on kissing-bugs described the importance and wide range of their diet (Brumpt 1927). The process of triatomine feeding has been studied from at least three different perspectives: (i) physiological and behavioural, (ii) fitness (effects on survival and reproduction) and (iii) patterns of host use in the field and in laboratory-based tools, including those applied to other vectors, such as mosquitoes and sandflies (Añez et al. 1994, Hamer et al.

2009). The following is a summary of the research on kissing-bug haematophagy presented from these three perspectives as opposed to an exhaustive review.

*The physiological approach to the study of kissing-bugs* - The physiological approach is likely the best developed and the following presents the variety of topics that are particularly well studied in kissing-bugs: extreme starvation and recovery (Wigglesworth 1982), action of digestive cells (Rocha et al. 2010), changes in haemolymph serotonin levels (Lange et al. 1989), intestinal erythrocyte agglutination (Araujo et al. 2009), nutritionally essential amino acids (Pickett & Friend 1965), metabolic pathways for dietary lipids (Canavoso et al. 2004), salivary secretion during feeding (Friend & Smith 1971, Ribeiro & Garcia 1980, 1981, Barbosa et al. 1999, Faudry et al. 1999, Sant'Anna et al. 2001, Andersen et al. 2005, Soares et al. 2006), release of CO<sub>2</sub> following feeding (Bradley et al. 2003), temperature-induced responses, CO<sub>2</sub> and other compounds in host search (Smith & Friend 1972, Taneja & Guerin 1997, Canals et al. 1999, Otálora-Luna et al. 2004, Barrozo & Lazzari 2006), the effect of gorging stimulation on different compounds (Friend 1965, Friend & Smith 1971, 1982, Smith & Friend 1976) and humoral factors transmitted to the brain (Mulye & Davey 1995), the effects of diet composition on ecdysis (Azambuja et al. 1993), the influence of nutrition on immune responses (Feder et al. 1997), fat body reserves (Canavoso & Rubiolo 1998) and haemolymph (Paz et al. 1988), pressures produced in the pharyngeal pump (Bennet-Clark 1963a), proteolytic enzymes in the midgut (Garcia & Guimarães 1979), and the relationship between feeding and respiration (Cirano & Zeledón 1964).

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Several aspects of feeding-related behaviour in triatomines have also been well studied. Such aspects include feeding preferences (Quintal & Polanco 1977), avoidance of excessive warming during feeding (Lazzari et al. 2009), importance of nutritional status in flight initiation and dispersal (Lehane & Schofield 1982, Lehane et al. 1992, Noireau & Dujardin 2001, Emmanuelle-Machado et al. 2002, Ceballos et al. 2005), avoidance of predators during feeding (Bodin et al. 2009a, b), frequency and size of the blood intake (Maddrell 1963, Wood 1976, Montenegro & Pasina 1984, Maifrino et al. 1986, Pietrovsky et al. 1996, Pereira et al. 1998), control of meal size (Bennet-Clark 1963b) and the relationship between feeding and defecation patterns as well as other aspects of feeding with epidemiological importance (Wood 1951, Dias 1956, Zeledón et al. 1970, 1977, Da Rocha e Silva et al. 1979, Crocco & Catalá 1996, Kollien & Schaub 1998, Zabala & D' Antonio 1988, Braga & Lima 1999, Aldana et al. 2001, Emmanuelle-Machado et al. 2002, Nattero et al. 2002, Almeida et al. 2003, Arévalo et al. 2007, Rodriguez et al. 2008, Klotz et al. 2009).

Studies have been conducted on the relationship between the impacts of the triatomine feeding process and demographic parameters (Davies 1990, Malo et al. 1993, Emmanuelle-Machado et al. 2002), mortality and fecundity (Goodchild 1955, Hays 1965, Regis 1977, Patterson 1979, Catalá de Montenegro 1989, Braga et al. 1998, Braga & Lima 2001, Davey 2007), development time (Martinez-Ibarra et al. 2003, Martinez-Ibarra & Novello-López 2004), resistance to starvation (Gajardo Tobar 1952, Pellegrino 1952, Dias 1965, Pratt & Davey 1972, Costa & Paranhos Perondini 1973, Friend & Smith 1975, Costa et al. 1987, Costa & Jurberg 1989, Gonçalves et al. 1989, Galvão et al. 1996, Canavoso & Rubiolo 1998, Cortéz & Gonçalves 1998, Costa & Marchon-Silva 1998, Lorosa et al. 1999, Cabello 2001, Moreira & Spata 2002, Gomes Dias-Lima & Sherlock 2002), mating frequency, mating speed and duration of copulation (Lima et al. 1986). *T. cruzi* infections have also been related to nutritional indicators (Petersen et al. 2001), principally cleptohaematophagy, in some triatomine species (Sandoval et al. 2000). Only a few studies have focused on the quantitative estimation of feeding under natural conditions (Rabinovich et al. 1979, Lopez et al. 1999).

Describing kissing-bug blood-feeding patterns across vertebrate hosts is important for a better understanding of the epidemiology of *T. cruzi* and how it circulates among mammalian hosts. Ecological niche theory is applicable to the study of kissing-bug feeding patterns. By definition, the niche is the manner in which organisms or a population responds to the distribution of resources and other species (competitors, predators, parasites and pathogens). Niches have two components: position and breadth. Niche position characterises which resources are used by a particular species, i.e., presence/absence of certain hosts as a food source (for example, if the blood of a certain species of host is found in individuals of a given kissing-bug species), whereas niche breadth characterises the number of resources, i.e., the number or proportion of different host species in the diet of a given

kissing-bug species (Brandle et al. 2002). In this sense, blood-feeding profiles can be used to estimate the niche breadth of kissing-bugs because studying field-caught bug species can quantify host use. Both niche position and niche breadth may be affected by climatic variability, habitat type and other constraints such as life history traits and phylogenetic conservatism (Sherry 1984).

Feeding patterns of kissing-bugs are typically studied in habitats of epidemiological importance: the domicile, the peridomicile and the wild (often called "sylvatic"). Habitat type can play a major role in kissing-bug feeding choices because preferences could be limited by host availability, as observed in mosquito vectors (Lefevre et al. 2009). In addition, species distributions tend to be nested, that is, species inhabiting a certain habitat may be a subset of species from another habitat (Kolasa 1996). Nestedness is a commonly observed pattern in nature in which small communities form proper subsets of large communities (Ulrich & Gotelli 2007a, b, Ulrich et al. 2009). Thus, diet overlap across kissing-bug species could be limited by host species overlap across habitats, i.e., the degree of nestedness in host community composition could be reflected in the diet of kissing-bugs.

In this article, we present a study of the variation in niche breadth across kissing-bug species and their patterns of host co-feeding. We analysed the feeding profiles of kissing-bugs under natural conditions using data obtained exclusively by the precipitin test. We restricted our analysis to precipitin tests because this test has been the technique most widely used with kissing-bugs, given its relatively low cost and appropriate resolution to study host use at the level of families and orders. The precipitin test has been widely used for the identification of triatomine blood-meals since the 1960s (Rodriguez 1966) and its powerful sensitivity has been reported by several researchers (Wisnivesky-Colli et al. 1982, Lorosa et al. 1999, 2003). In addition, the precipitin test has the power to detect multiple meals, unlike more recent techniques based on DNA polymerase chain reaction (Hamer et al. 2009, Chaves et al. 2010), which have been used in a few instances to study kissing-bug blood-feeding patterns (Mota et al. 2007, Pizarro & Stevens 2008). In our analysis, several analytical techniques were used to provide qualitatively different insights regarding the blood-feeding niche breadth of kissing-bugs. The null model test of host use (i.e., the null hypothesis that observed patterns result from random processes is assumed) was used to determine patterns of segregation, aggregation or randomness in host exploitation, i.e., whether kissing-bug species have strong preferences for certain host categories (segregation), if all kissing-bug species feed in the same host categories (aggregation), or if there are no patterns (random). However, such an analysis does not take full advantage of the compositional information from the relative abundance of different blood-sources to describe similarities in blood-feeding. To further exploit information on relative host use, multivariate analysis tools of ordination and clustering were used. The patterns of host co-feeding at the host class level and order/family level within mammals in areas in which Chagas

disease is zoonotic in 30 species of kissing-bugs were studied. The variability in the blood-feeding patterns of eight selected kissing-bug species that have major epidemiological importance for the transmission of *T. cruzi*, and for which samples were collected in several locations, was also studied. Additionally, the patterns of nestedness and clustering in habitat use by kissing-bug species were investigated, largely because such patterns could partially explain the patterns of blood-feeding choices. Finally, the results were evaluated in light of the eco-epidemiology of Chagas disease transmission.

## MATERIALS AND METHODS

**Data** - The primary information for analysis was extracted from a unique and extensive triatomine database on the geographical distribution, life-history, diet and habitat of 116 triatomine species reported in the literature (Carcavallo et al. 1999). Over 500 bibliographic references were surveyed, of which 61 presented data on blood-feeding profiles. From these references, a subset 159 cases, representing 30 species, with reliable precipitin blood-feeding profiles from bugs sampled under natural conditions was obtained.

The extracted data were compiled in a Table (Supplementary data). For each of the 159 cases, the following was recorded: the triatomine species name, country of study, region of triatomine collection, number of individual insects analysed with the precipitin test, number of insects positive to each of the tested host antiserum and corresponding bibliographic source. The habitat type was categorised epidemiologically as domiciliary, peridomestic or sylvatic (wild).

Data were entered as the absolute number of collected insects that had been identified as feeding in one or more of the hosts. When a certain number of triatomine individuals showed the same mixed (multiple) feeds (e.g., four triatomines being positive to dogs, cats and humans), they were distributed to the corresponding individual feeding category in the same proportion as that in which the individual feeding categories were found (e.g., if individual feeds had been 25% on dogs, 25% on cats and 50% on humans, those 4 mixed feedings were distributed as follows: 1 to dogs, 1 to cats and 2 to humans). If the resulting numbers were not integers, they were rounded up.

From the data compilation, five matrices were constructed: 1: the full data matrix, as described in the Supplementary data; 2: the species-dominant habitat matrix (pooling the habitats collected in each study for each species and identifying the habitat with the higher per cent of use as the dominant habitat); 3: the host class species feeding profile matrix, in which the diet profile of each species was pooled, and the host groups were represented only at the host class level (Mammalia, Aves, Amphibia, Reptilia and Insecta); 4: the mammal feeding profile matrix, which is similar to 3 but with the host groups represented exclusively at the family and order level within the class Mammalia, with 13 families [Chiroptera, Hominidae (Human), Felidae, Canidae, Leporidae, Rodentia, Bovidae, Dasypodidae, Didelphidae, Equidae, Suidae, Myrmecophagidae, Bradypodi-

dae, Hominidae (non human) and Mephitidae] and the order Rodentia; 5: the selected species feeding profile matrix, composed of eight kissing-bug species at the individual study level and 15 groups of hosts (the classes Aves, Reptilia and Amphibia and the 12 families of the class Mammalia). The eight kissing-bug species, *Panstrongylus geniculatus*, *Panstrongylus megistus*, *Rhodnius neglectus*, *Rhodnius prolixus*, *Triatoma brasiliensis*, *Triatoma dimidiata*, *Triatoma infestans* and *Triatoma sordida*. *R. prolixus*, *T. brasiliensis*, *T. dimidiata* and *T. infestans* were selected because they are the dominant vector species of *T. cruzi* transmission to humans. The other four kissing-bug species were added because they are abundant in diet profile studies (more than 6 cases) and are epidemiologically significant (they are usually considered in the secondary transmission of Chagas disease). *P. geniculatus* is of additional interest because, of all kissing-bug species, it has the largest geographical range (with a range area of approximately 12 million km<sup>2</sup> in the New World). Matrices 2, 3, 4 and 5 were used for the different analyses described next.

**Null model test - Co-occurrence of host feedings:**  
**C-score** - The patterns of blood-feeding in kissing-bugs were studied using null model analysis, a technique that has been used in other disease vectors such as mosquitoes (Chaves et al. 2010). The C-score was used, which is an index that, in the context of this study, quantifies the overlap of host-use relative to the maximum possible overlap in a host community (Stone & Roberts 1990). With the estimated C-score, the null hypothesis that kissing-bug species are equally likely to forage on a given host was tested. The C-score of the original data matrix (kissing-bug species as rows and host as columns) was compared to the output of simulated matrices and inferences were made depending on the relationship of the C-score of the original data to that of the simulations. When the original C-score was larger than that of the simulations for a given significance level, segregated feeding was inferred, i.e., a pattern of strict host-specific feeding. When the original C-score was smaller than that of the simulations, the inference was made that all the kissing-bugs share at least one of the host-species in their blood-meals. When the original C-score was equal to the simulated C-score, host-use patterns were inferred to be random. The analysis was implemented by making simulated matrices of species (columns)-blood meal feeding profile (rows). The matrices were made with constant row sums, which assume a constant number of host types on which the kissing-bugs can feed, and equiprobable columns, which indicates an equal probability to feed on any of the host types. The fixed-equiprobable algorithm was chosen because it provides a robust predictor (Gotelli 2000) and although not the most powerful tool, it allows the testing of the null hypothesis of equal preference among host species. Simulations were conducted using the software Ecosim 7.0 (Gotelli 2000) and 5,000 randomisations were used for the tests.

**Null model test - Nestedness in epidemiological habitat-use** - Whether epidemiological habitat-use was nested was determined with the null model testing of a matrix

of kissing-bug species (columns) vs. habitat (rows), using  $NODF_{col}$ , a nestedness index based on overlap and decreasing fills of columns (Ulrich et al. 2009). The nestedness measure based on overlap and decreasing fills (NODF) is a method that aims to quantify independently whether (i) a community in a depauperate assemblage constitutes subsets of progressively richer communities and (ii) the less frequent species are found in subsets of the sites in which the percentage of occurrences in the right columns and the species in the inferior rows overlap with those found in left columns and upper rows with higher marginal totals for all pairs of columns and rows, respectively, most commonly occur (Almeida-Neto et al. 2008). A fixed-equiprobable algorithm was chosen, which tests whether the diversity of kissing-bug species observed in less species-rich epidemiological habitats is a subset of the species-richest habitat, i.e., with the highest number of species per habitat. Whether the nestedness pattern was non-random was tested using a standardised effect size test, in which a resulting absolute value of standardised nestedness above 2 (using the mean and standard deviation of the simulated matrices) indicates a significant pattern of nestedness (Ulrich et al. 2009).

*Niche breadth* - Niche width is a measure of the breadth or diversity of resources used by an individual or species (Magurran 1988). The Shannon diversity index is typically used for calculating niche width by simply replacing the number of resource categories observed (e.g., food types eaten) with the number of species in a community. Hutcheson (1970) and Bowman et al. (1971) suggested the following estimation formula for the Shannon index:

$$H' = - \sum p_i \ln p_i - \frac{S-1}{N} + \frac{1 - \sum p_i^{-1}}{12N^2} + \frac{\sum (p_i^{-1} - p_i^{-2})}{12N^3}$$

where  $p_i$  is the relative abundance of each blood-source species calculated as the proportion of individuals of a given species to the total number of individuals tested ( $n_i/N$ ).  $n_i$  is the number of individuals of species  $i$ , i.e., the frequency of species  $i$  in the diet  $S$  is the number of taxonomic categories (or blood-source taxonomic categories richness) and  $N$  is the total number of triatomine individuals tested.

However, Magurran (1988) suggested that, as shown by Peet (1974), the contribution of all of the terms of the series after the second are very small, so the following simplified version of the Shannon index was used:

$$H' = - \sum p_i \ln p_i - \frac{S-1}{N}$$

where all symbols remain as described.

For the calculation of the Shannon diversity index and their 95% confidence intervals, the software PAST (Hammer et al. 2001) was used.

*The issue of compositional data* - Although the numbers of a kissing-bug species' feeding profile do not have any significant relevance, the relative abundance or composition can be compared across species, so that the distortion of raw numbers from the multivariate

statistics may be avoided. However, using proportions as simple standardisation may distort the results of the multidimensional analysis (Jackson 1997). To avoid this problem, the matrices containing data on blood-feeding frequencies of kissing-bugs on certain host categories were transformed into compositional (relative quantity) data (Aitchison 1986). A composition analysis was performed on the D-1 dimensional simplex, in which the positive elements of a vector of dimension  $D$  sum to 1,  $D$  is the number of hosts on which kissing-bug species can feed and compositions are the ratios in the data. This approach was preferred over the more conventional Aitchison log-ratio metric, given the limitation of logarithmic transformations in datasets with several proportions that are zero (Rehder & Zier 2001), resulting from the absence of food sources across kissing-bugs species.

*Principal component analysis* - Principal component analysis is an ordination technique that allows for a summary of variability patterns in multidimensional datasets (Venables & Ripley 2002). A principal component analysis on the matrices was performed by transforming them and obtaining compositional data, which are called "composition matrices". Here, the principal components were estimated from the matrix of variance-covariance computed from the composited matrices (Venables & Ripley 2002).

*Cluster analysis* - Cluster analysis is a type of analysis in which elements in a dataset are arranged in groups or subsets based on their characteristics. In this study, the subsets (groups of species) are formed based on the similarity of host or habitat-use. A partition technique, partitions around medoids (PAM), was used in which a number of clusters is proposed *a priori* and can be selected based on the silhouette value, a measurement of the average similarity between any element (in our study, a kissing-bug species) in a given cluster when compared with the rest of the cluster elements (Kaufman & Rousseeuw 1990). Results were confirmed by using an agglomerative hierarchical cluster technique in which elements (i.e., kissing-bug species) were iteratively joined with the most similar elements during iterative steps of a joining algorithm. For the clustering, a complete linkage algorithm was used that aimed to find very similar clusters (Kaufman & Rousseeuw 1990).

*Multiple correspondence analysis* - The pattern of association of the two clustering methods and the dominant habitat of a kissing-bug species was studied using a multiple correspondence analysis. This type of analysis is a multivariate analysis performed on more than two categorical variables and can be used to determine patterns of association between the studied variables. The outcome of this analysis is a set of coordinates that indicate the association between the different categories and the different elements (in this study, elements are kissing-bug species). The closer that two coordinates are in space, the more associated that the categories or elements are that they represent. Here, multiple correspondence analysis was implemented using a singular value decomposition of a Burt matrix with an adjustment of inertias (Nenadic & Greenacre 2007).

**RESULTS**

The bibliographic compilation on feeding sources of triatomines resulted in 30 species, representing seven genera (13 of *Triatoma*, 6 of *Panstrongylus* and *Rhodnius*, 2 of the genus *Belminus* and 1 of the genera *Cavernicola*, *Mepraia* and *Psammolestes*).

Blood-meal sources of our 29 triatomine species include five taxonomic classes (Mammalia, Aves, Amphibia, Reptilia and Insecta). Mammals were differentiated using the precipitin tests in 14 families [Chiroptera, Hominidae (Human), Felidae, Canidae, Leporidae, Bovidae, Dasypodidae, Didelphidae, Equidae, Suidae, Myrmecophagidae, Bradypodidae, Hominidae (non human) and Mephitidae] and the order Rodentia. In total, 19 taxonomic host categories were used to identify blood-source.

The 159 cases provided data from a total of 39,520 feeds that were grouped into three habitats (and their

combinations): sylvatic (wild), domiciliary and peridomiciliary. Table I shows the grouping of each of the 30 kissing-bug species by dominant habitat-use. In the nestedness analysis of epidemiological habitat-use, a NOD- $F_{col}$  of 64.23 was estimated and because the simulation average was 56.02 with a standard deviation of 10.58, it was concluded that the nestedness of habitat-use is random ( $Z = 0.78, p > 0.05$ ).

Table II shows the patterns of co-feeding using the C-score method for the different dominant habitats and the blood-feeding data grouped at the five taxonomic classes. Estimated C-score values were calculated from the data and the mean  $\pm$  variance values were the results from the simulations. With the exception of the “peridomicile and/or sylvatic” habitat for which results were random, all habitat-use patterns were aggregated when hosts were analysed at the class level.

TABLE I  
Dominant habitat types used by the 30 kissing-bug species analyzed

Kissing-bug species	Dominant habitat					
	SYL	PER	DOM	SYL-PER	PER-DOM	SYL-PER-DOM
<i>Cavernicola pilosa</i>	X					
<i>Panstrongylus lignarius</i>	X					
<i>Panstrongylus geniculatus</i>	X					
<i>Rhodnius neglectus</i>	X					
<i>Rhodnius pictipes</i>	X					
<i>Triatoma longipennis</i>		X				
<i>Triatoma maculata</i>		X				
<i>Belminus ferroae</i>			X			
<i>Belminus herreri</i>			X			
<i>Panstrongylus herreri</i>			X			
<i>Panstrongylus lutzi</i>			X			
<i>Triatoma pallidipennis</i>			X			
<i>Triatoma vitticeps</i>			X			
<i>Mepraia spinolai</i>				X		
<i>Panstrongylus megistus</i>					X	
<i>Triatoma costalimai</i>					X	
<i>Rhodnius pallescens</i>					X	
<i>Triatoma barberi</i>					X	
<i>Triatoma dimidiata</i>					X	
<i>Triatoma brasiliensis</i>					X	
<i>Triatoma infestans</i>					X	
<i>Triatoma pseudomaculata</i>					X	
<i>Triatoma rubrofasciata</i>					X	
<i>Triatoma sordida</i>					X	
<i>Rhodnius ecuadoriensis</i>					X	
<i>Rhodnius nasutus</i>						X
<i>Panstrongylus tupynambai</i>						X
<i>Psammolestes tertius</i>						X
<i>Rhodnius prolixus</i>						X
<i>Triatoma rubrovaria</i>						X

DOM: domiciliary; PER: peridomiciliary; SYL: sylvatic.

TABLE II  
Patterns of host class co-feeding

Habitats	Number of species	C-score	Mean ± variance	p < exp	p > exp	Pattern
All	30	0.258	1.457 ± 0.004	1	0	Aggregated
Domicile and/or peridomicile	11	0.527	1.238 ± 0.040	1	0	Aggregated
Peridomicile and/or sylvatic	4	0.167	0.082 ± 0.007	1	0.49	Random
Domicile, peridomicile and sylvatic	15	0.029	1.491 ± 0.020	1	0	Aggregated

habitat indicates the different habitats where bugs were sampled. Estimated C-score values are calculated from the data. Mean ± variance is the results from the simulations. The values of p < exp and p > exp indicate the probability that the C-score value is significantly smaller (indicating aggregated pattern) or larger (segregated pattern) than that expected (exp) by random, respectively. p value < 0.05 indicates statistical significance and so the pattern is random. Pattern indicates the interpretation of the pattern.

TABLE III  
Patterns of mammal host co-feeding

Habitats	Number of bug species	C-score	Mean ± variance	p < exp	p > exp	Pattern
All	28 <sup>a</sup>	2.788	9.683 ± 0.092	1	0	Aggregated
Domicile and/or peridomicile	9	1.444	5.800 ± 0.430	1	0	Aggregated
Peridomicile and/or sylvatic	4	4.333	3.756 ± 0.196	0.98	0.10	Random
Domicile, peridomicile and sylvatic	15	3.220	10.739 ± 0.390	1	0	Aggregated

<sup>a</sup>: the number of kissing-bug species is reduced to 28 because samples from *Belminus herreri* and *Panstrongylus lignarius* fed only on insects and birds, respectively. This Table is similar to Table II, but with the analysis restricted to mammal families and the order Rodentia. Columns and identification of results are the same as for Table II.

Table III is similar to Table II but with the analysis restricted to mammal families (and to the order Rodentia) to establish the patterns of host co-feeding. Again, as with the host class level, with the exception of the “peridomicile and/or sylvatic” habitat for which results were random, all habitat-use patterns were aggregated when hosts were analysed at the mammal family (and order Rodentia) level.

The results of the various multivariate analyses of blood-feeding patterns at the host class level are shown in Fig. 1. In general, results robustly show three main host types that kissing-bugs more frequently feed on: insects, birds and mammals. The first two components explain more than 99% of the variability. The x axis presents the first component, which explains 66.77% of the variability. On this axis, positive values represent more frequent feedings on mammal hosts, while negative values represent more frequent feedings on avian hosts. The y axis presents the second component, which explains 32.83% of the variability, with positive values representing feedings on insects. Fig. 1B shows the PAM clusters. A clustering in three groups had the best fit, with an average silhouette (*h*) of 0.71 (with 1 as the possible maximum). This clustering separates kissing-bugs species into three main groups: those that primarily feed on other insects (*Belminus herreri* and *Belminus ferroae*), those that primarily feed on birds (*Panstrongylus lignarius*, *Psammolestes tertius*, *Rhodnius ecuadoriensis*, *Rhodnius nasutus*, *R.*

*neglectus*, *T. brasiliensis*, *Triatoma longipennis*, *Triatoma maculata*, *Triatoma pseudomaculata* and *T. sordida*) and those that primarily feed on mammals (*Cavernicola pilosa*, *Mepraia spinolai*, *P. geniculatus*, *Panstrongylus herreri*, *Panstrongylus lutzi*, *Panstrongylus megistus*, *Panstrongylus tupynambai*, *Rhodnius pallescens*, *Rhodnius pictipes*, *R. prolixus*, *Triatoma barberi*, *Triatoma costalimai*, *T. dimidiata*, *T. infestans*, *Triatoma pallidipennis*, *Triatoma rubrofasciata*, *Triatoma rubrovaria* and *Triatoma vitticeps*). Fig. 1C shows the results of the agglomerative hierarchical cluster analysis. This clustering technique also produced three clear clusters (at a height of 0.6) in which species correspond to those identified with the partitions around medoids. It is worth noticing that there is no habitat overlap because the different dominant habitats overlap in the different clusters. Fig. 1D shows the results of the multiple correspondence analysis; the two axis represent 93.5% of the variability (61% by axis x and 32.5% by axis y). The domiciliary habitat is most associated with feeding on insects (Fig. 1A) and is separated from the peridomiciliary habitat along the x axis. Both of these habitats are separated from the sylvatic species along the y axis. The peridomiciliary habitat is associated with more frequent feeding on birds (Fig. 1B) and species that colonise all habitats (sylvatic, peridomiciliary and domiciliary) are associated with more frequent feeding on mammals (Fig. 1C). Species with other patterns of

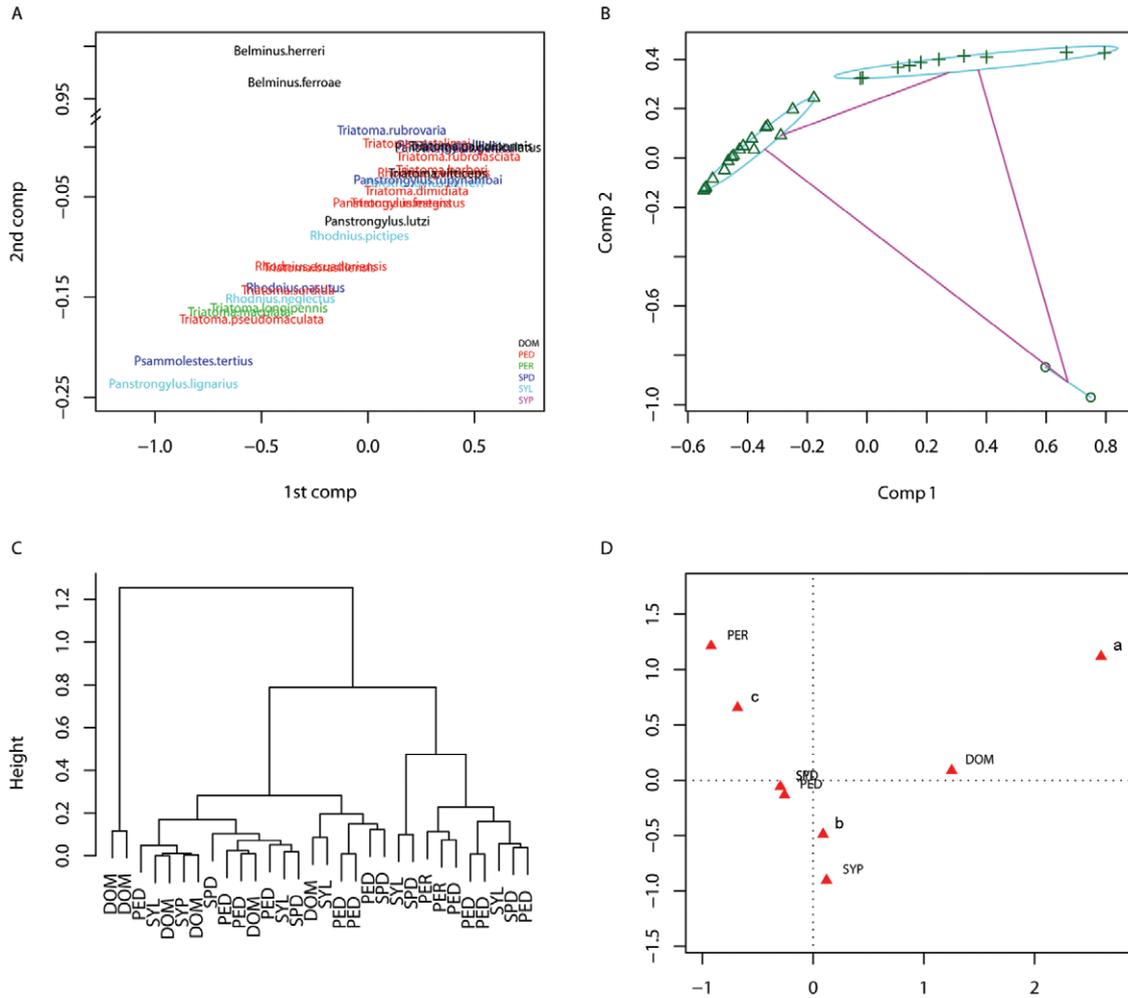


Fig. 1: multivariate analysis of kissing-bug species blood-feeding patterns at the class level (Aves, Mammalia, Amphibia, Reptilia and Insecta). A: principal component (comp) analysis. On the x axis positive values represent more frequent feedings on mammal hosts, while negative values represent more frequent feedings on avian hosts. On the y axis positive values represent feedings on insects. Colours indicate the habitats where kissing-bugs were sampled; B: partitions around medoids clusters. o: species that primarily feed on other insects (*Belminus herrerri* and *Belminus ferroae*); +: species that primarily feed on mammals (see text for the listing of the species); C: agglomerative hierarchical cluster analysis. Three clear clusters can be seen at a height of 0.6; D: multiple correspondence analysis {a: species most associated with feeding on insects [in the domiciliary (DOM) habitat]; b: species most associated with more frequent feeding on birds [in the peridomiciliary (PER) habitat]; c: species most associated with more frequent feeding on mammals (and that colonize all habitats)}. PED: PER + DOM; SPD: sylvatic (SYL) + PER + DOM; SYP: SYL + PER.

habitat-use do not seem to be specifically associated with any class of blood-source because they are close to the origin (coordinates  $x = 0$  and  $y = 0$  in the plot).

Fig. 2 shows results similar to Fig. 1 but in relation to the blood-feeding patterns on mammals. In general, the major divisions were between humans, canids and rodents vs. didelphids (i.e., opossums and related organisms). In Fig. 2A, the first two components explain approximately 53% of the variability; the x axis (the 1st component) explains 30.78% of the variability, with positive values representing more feedings on humans, dogs and rodents hosts, while negative values represent more frequent feedings on didelphids. The y axis (the 2nd component) explains 22.02% of the variability, with positive values representing feeding on rodents and didelphids. Fig. 2B shows the PAM clusters; a cluster with four medoids had

the best fit, with an  $h$  of 0.52 (being 1 the maximum possible). With this method, kissing-bug species are separated into four main groups: those that primarily feed on didelphids (*Ps. tertius*, *R. nasutus*, *R. neglectus* and *R. pictipes*), those with a more diverse diet that included some rodents; those that feed primarily on humans and rodents (*P. megistus*, *R. pallescens*, *R. prolixus*, *T. brasiliensis*, *T. infestans*, *T. pallidipennis* and *T. pseudomaculata*) and those that feed primarily on rodents and didelphids (*M. spinolai*, *P. herrerri*, *P. lutzi*, *P. tupynambai*, *R. ecuadoriensis*, *T. barberi*, *T. costalimai*, *T. dimidiata*, *T. maculata*, *T. rubrofasciata* and *T. sordida*). Fig. 2C shows the results of the agglomerative hierarchical cluster analysis; this clustering technique also produced four clear clusters (at a height of about 0.4) in which species correspond to those identified with the partitions around medoids.

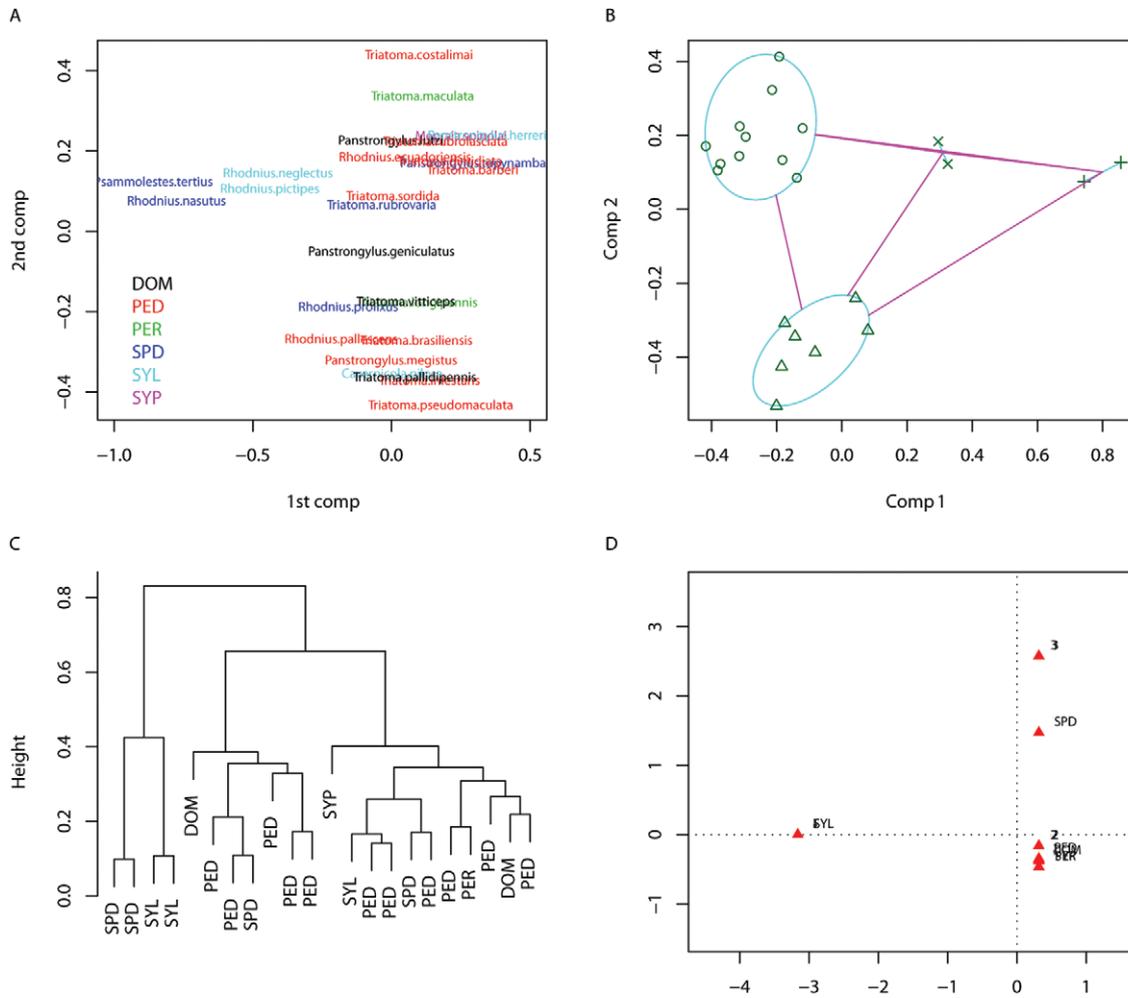


Fig. 2: multivariate analysis of kissing-bug species blood-feeding patterns related to mammals (family level and order Rodentia). A: principal component (comp) analysis. The first two components explain about 53% of the variability. Colours indicate the habitats where bugs were sampled; B: partitions around medoids clusters; C: agglomerative hierarchical cluster analysis, with four clear clusters (at a height of about 0.4); D: multiple correspondence analysis. The sylvatic habitat is strongly related to the feeding on didelphids (identified as 4) and the use of all habitats. In 3 are the species associated with feeding on humans and rodents. DOM: domiciliary; PED: peridomiciliary (PER) + DOM; SPD: sylvatic (SYL) + PER + DOM; SYP: SYL + PER.

Fig. 2D shows the results of the multiple correspondence analysis. The two axes represent 80.1% of the variability (49.5% by the x axis and 30.5% by the y axis). Most species with other patterns of habitat-use do not seem to be particularly associated with any category of blood-source because they are close to the origin (coordinates  $x = 0$  and  $y = 0$ ) (Fig. 2D). In summary, there is a clear habitat segregation because the different dominant habitats overlap in the different clusters. Most feeding choices were not associated with a particular habitat, but kissing-bugs colonising all epidemiological habitats (domiciliary, peridomiciliary and sylvatic) tended to feed on humans, while the sylvatic kissing-bugs fed on didelphids. For the feeding patterns on mammals, the following species were not considered: *C. pilosa*, *P. geniculatus*, *T. longipennis*, *T. rubrovaria* and *T. vitticeps*. These species had a relatively small sample size and behaved as outliers that distorted the multivariate analysis. It is worth noticing that

*C. pilosa* is a kissing-bug species that inhabits caves and feeds exclusively on bats, while the other species have a very diverse and even resource use.

Fig. 3 shows the results for eight selected species that have epidemiological importance and were most widely sampled for their feeding source. Fig. 3A shows the results of the principal component analysis. The first two components explain slightly above 71% of the variability; 51% was explained by the x axis (positive values represent more frequent feeding on rodents and didelphids, while negative values represent a more frequent feeding on humans, bovinds and canids) and 20% of the variability was explained by the y axis (positive values represent feedings on humans and didelphids). Fig. 3B shows the results of the partitions around the medoids clusters method; a clustering of three groups had the best fit, with an  $h$  of 0.5 (with 1 as the possible maximum). Fig. 3C shows the results of the agglomerative hierarchical cluster analysis; this tech-

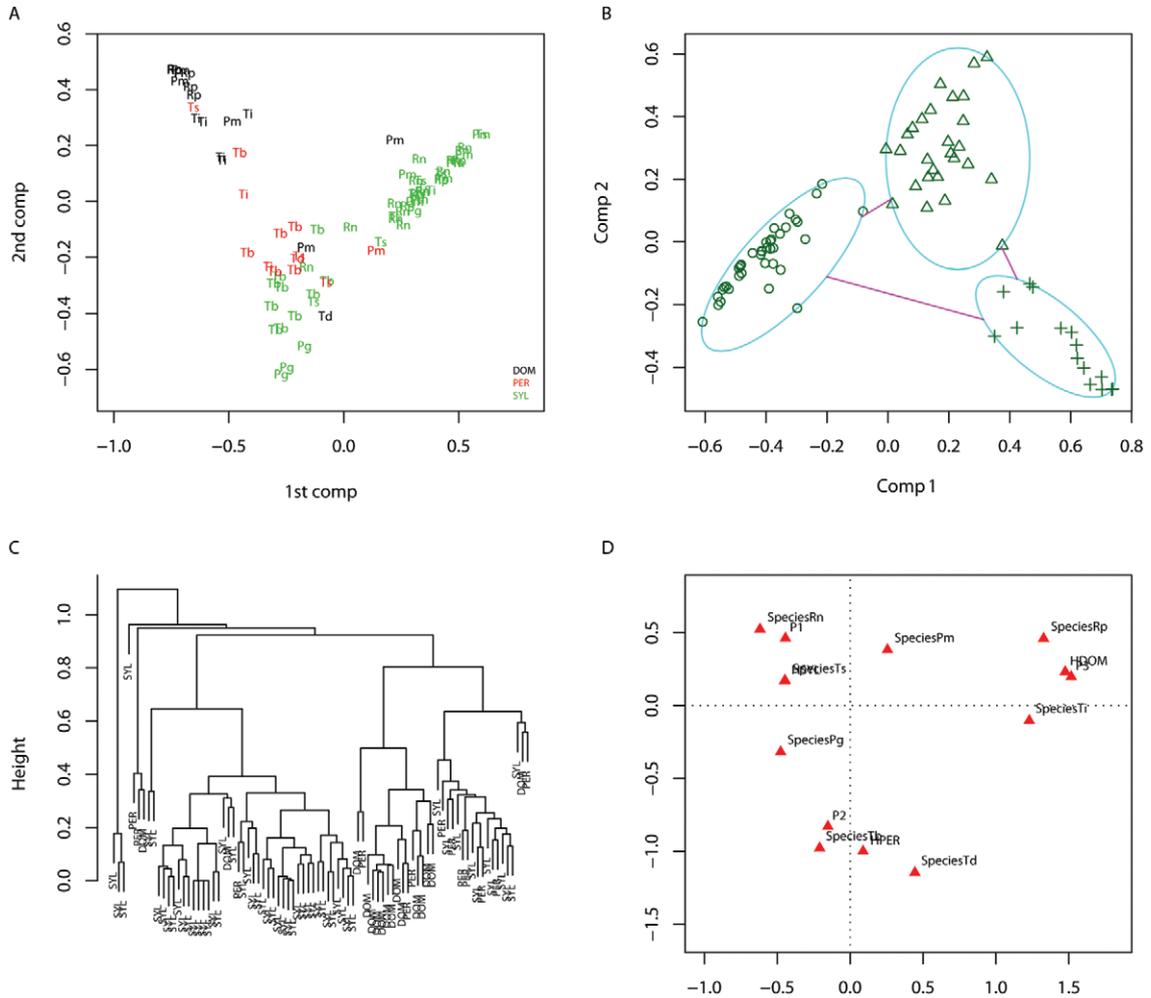


Fig. 3: multivariate analysis of eight selected kissing-bug species blood-feeding patterns related to mammals (family level and order Rodentia). The selected species are: *Rhodnius prolixus* (Rp), *Triatoma dimidiata* (Td), *Triatoma infestans* (Ti), *Triatoma brasiliensis* (Tb), *Panstrongylus geniculatus* (Pg), *Rhodnius neglectus* (Rn), *Panstrongylus megistus* (Pm) and *Triatoma sordida* (Ts). See Materials and Methods for the criteria of selection. A: principal component (comp) analysis. The first two components explain slightly above 71% of the variability, with colours indicating the dominant habitats where bugs were sampled in a given study (DOM: domiciliary; PER: peridomiciliary; SYL: sylvatic); B: partitions around medoids clusters. A clustering of three groups had the best fit, with an average silhouette (*h*) of 0.5; C: agglomerative hierarchical cluster analysis. There are three clear clusters (at a height of 0.8); D: multiple correspondence analysis. The two axes represent 94% of the variability.

nique also produced three clear clusters (at a height of 0.8) in which species correspond to those identified with the partitions around medoids. There is a clear habitat segregation; outliers can be present in any habitat, but one group is clearly present in more sylvatic habitats, while the rightmost cluster is primarily present in domiciliary and peridomiciliary environments. Fig. 3D shows the results of the multiple correspondence analysis; the two axes represent 94% of the variability (60% by the x axis and 34% by the y axis). The sylvatic habitat is strongly related to the feeding on didelphids (identified as P1) and the species *T. sordida* and *R. neglectus*. The domiciliary habitat is strongly related to the feeding on humans and canids and *T. infestans* and *R. prolixus*. The peridomiciliary habitat is related to more frequent feeding on rodents and canids and *T. dimidiata* and *T. brasiliensis*. *P. megistus* and *P. geniculatus* do not seem to be strongly associated with any habitat nor feeding source because they are

close to the origin (coordinates  $x = 0$  and  $y = 0$ ). In summary, for these eight selected species of epidemiological importance, the clusters around habitats indicate that colonised habitats could be a template for feeding. Domiciliary bugs tended to feed primarily on humans and canids (i.e., dogs), while peridomiciliary bugs fed on rodents and dogs. The most important vector species were primarily associated with the domiciliary habitat (*R. prolixus* and *T. infestans*) or peridomiciliary habitat (*T. dimidiata* and *T. brasiliensis*).

Table IV ranks, in increasing order, the niche breadth of the 30 kissing-bug species for the Shannon diversity index. In the Shannon index, the following eight species were in the lower quartile of feeding diversity: *C. pilosa*, *P. lignarius*, *P. tertius*, *B. ferroae*, *B. herreri*, *P. geniculatus*, *T. longipennis* and *R. nasutus*, while another eight species were found to be in the upper quartile of feeding diversity: *T. barberi*, *P. megistus*, *R. prolixus*, *T. infestans*, *P. lutzi*, *T. dimidiata*, *T. vitticeps* and *T. rubrovaria*.

TABLE IV

Niche breadth estimates based on the Shannon diversity index for the 30 species of kissing-bugs from all habitats pooled, ranked from smallest to largest

Species	n	S	Shannon	Lower	Upper
<i>Belminus herreri</i>	76	1	0	0	0
<i>Cavernicola pilosa</i>	17	1	0	0	0
<i>Panstrongylus lignarius</i>	6	1	0	0	0
<i>Psammolestes tertius</i>	51	3	0.319	0.096	0.522
<i>Belminus ferroae</i>	121	4	0.363	0.179	0.522
<i>Panstrongylus geniculatus</i>	178	5	0.659	0.504	0.785
<i>Triatoma longipennis</i>	113	3	0.694	0.559	0.783
<i>Rhodnius nasutus</i>	278	4	0.810	0.727	0.881
<i>Triatoma pseudomaculata</i>	3,789	10	0.859	0.823	0.892
<i>Triatoma maculata</i>	435	10	0.976	0.854	1.079
<i>Rhodnius neglectus</i>	4,982	9	1.059	1.033	1.084
<i>Panstrongylus herreri</i>	77	5	1.202	0.996	1.326
<i>Rhodnius ecuadoriensis</i>	8	4	1.213	0.376	1.321
<i>Panstrongylus tupynambai</i>	7	4	1.277	0.410	1.352
<i>Mepraia spinolai</i>	109	7	1.388	1.194	1.514
<i>Rhodnius pictipes</i>	106	8	1.419	1.196	1.557
<i>Triatoma sordida</i>	8,764	13	1.424	1.396	1.450
<i>Triatoma costalimai</i>	321	7	1.439	1.331	1.518
<i>Rhodnius pallescens</i>	1,683	13	1.444	1.392	1.488
<i>Triatoma rubrofasciata</i>	548	7	1.475	1.400	1.537
<i>Triatoma pallidipennis</i>	18	7	1.519	0.854	1.721
<i>Triatoma brasiliensis</i>	1,430	10	1.566	1.509	1.620
<i>Triatoma barberi</i>	958	12	1.574	1.506	1.629
<i>Panstrongylus megistus</i>	6,872	11	1.584	1.561	1.606
<i>Rhodnius prolixus</i>	1,071	10	1.587	1.526	1.634
<i>Triatoma infestans</i>	5,282	11	1.596	1.572	1.617
<i>Panstrongylus lutzi</i>	79	8	1.696	1.474	1.819
<i>Triatoma dimidiata</i>	751	14	1.705	1.625	1.765
<i>Triatoma vitticeps</i>	79	9	1.980	1.754	2.071
<i>Triatoma rubrovaria</i>	847	11	2.221	2.178	2.251

n: number of insects used for the precipitin method; S: number of taxa used as food-source for each triatomine species; lower and upper: refer to the 95% confidence limits by bootstrap.

## DISCUSSION

Although experimental trials have shown that some kissing-bug species can have strong preferences for a particular host when given a choice (Gurtler et al. 2009, Guerenstein & Lazzari 2009), it is clear that outcomes are dependent on the ecological context of foraging. The analysis here supports a scenario of high plasticity in the patterns of host-use by kissing-bugs, which, in the ecological context of blood-foraging and primarily defined by the availability of hosts in the environments colonized by these vectors, could explain the patterns of host use. This pattern has been very well-studied for some species, with the most comprehensive studies having been conducted with *T. infestans* in which both

surveys and experiments have shown that the density of bugs and hosts plays a major role on the patterns of host-use (Wisnivesky-Colli et al. 1982, Gurtler et al. 1997, 2009). But the pattern is common to other species, such as *T. longipennis*, which in Mexico has been shown to diversify its food sources and disperse following habitat modifications (Breniere et al. 2004, Bosseno et al. 2009). The catholic host-use is a pre-condition for the emergence of vector-borne zoonotic diseases (Levins et al. 1994, Chaves et al. 2010). This observation in kissing-bugs is important because plans to control Chagas disease transmission via the suppression of dominant vector species could prove inefficient in the long-term and because other kissing-bug species that have similar feeding profiles could, in principle, transmit *T. cruzi*. The importance of the possible feeding source and mixed feedings in triatomines in terms of fecundity and fertility has been shown by Aldana et al. (2009) with *R. prolixus*.

This study also shows the urgent need to expand the focus of kissing-bug blood-foraging studies from that centred around the dominant vector species to the entire community of kissing-bug species. This expansion is necessary for several reasons: it can provide insights into the vectorial potential of species that are not currently considered as important vectors (Canale et al. 2000); it can increase knowledge on the diversity of the subfamily Triatominae (Hutchinson 1941, 1959, Colwell & Coddington 1994, Colwell & Hurtt 1994); and it can provide insights about the ecological determinants of kissing-bug blood-foraging. For example: are patterns driven by inter-specific interactions or by habitat colonisation (Chaves & Añez 2004)? Do species share hosts at the local habitat scale or do the preferences translate into patterns of segregation in host-use (Chaves et al. 2010)? The type of multivariate analysis conducted in this study can be very useful to study feeding patterns in kissing-bugs and other vectors at the population and community levels.

Although the analysis was restricted to the epidemiologically important habitat categories [the domicile, peridomicile and sylvatic (i.e., wild) habitat that encompasses all other habitats], there are other relevant criteria to include in future studies, including the details of the feeding profile within the sylvatic ecotopes. For example, it is known that virtually all species of the genus *Rhodnius* are primarily associated with palms, the genus *Panstrongylus* with burrows and tree cavities and the genus *Triatoma* with terrestrial rocky habitats or rodent burrows (Gaunt & Miles 2000). Considering the rapid adaptation to new environments and the accelerated process of domiciliation by many kissing-bug species (Noireau et al. 2005), future studies will need to define "sylvatic" habitats using more ecologically sound criteria because, from the kissing-bug perspective, some of these habitats could be considered more peridomiciliary than sylvatic. Ecologically based categories for peridomiciliary habitat classification are also necessary because, for some kissing-bug species, the peridomicile could be considered sylvatic because species are not colonizing new habitats; however, humans are becoming part of the kissing-bug species natural habitat.

In the early 1960s, it was commonly assumed that only some kissing-bug species were able to transmit parasites across certain habitats and host-species (Barretto et al. 1966, Barretto 1968). This perception was reinforced by the association of some hosts with *T. cruzi* discrete typing units (Zingales et al. 2009) and the untested assumption that these patterns are shaped by feeding preferences, which in some cases are assumed to be genetically determined due to fitness differences associated with feeding sources (Piesman et al. 1983, Acuña-Retamar et al. 2009). However, one of the evolutionary expectations for organisms living in changing environments is the absence of specialisation when, for example, resources are not constant or differences in quality are small from the perspective of the consumer (Levins 1968). Thus, uncertainty in resource-use, or the lack of major differences in nutritional blood quality from different hosts could explain the apparent lack of host-specialisation in kissing-bugs, which might be further supported by the monophyly of the Triatominae as a sub-family and the evolutionary time since their divergence (Gaunt & Miles 2000, Patterson & Gaunt 2010). Future studies in which phylogenetic and ecological information are considered together should be further explored (Vamosi et al. 2009).

The analysis of kissing-bug species feeding profiles and phylogenetic information will also allow the testing of a hypothesis suggested by Aragão (1983) that colonisation of new habitats by kissing-bug species is driven by the vertebrate classes inhabiting such habitats. Aragão (1983) proposed this hypothesis based on the observation that blood-meals in kissing-bugs species collected in different habitats were correlated with the abundance and ubiquity of host-species across the colonised habitats. In this sense, these results are encouraging because some species, for example *B. herreri* and *P. lignarius*, have restricted sets of host-species, indicating a potentially very specialised niche, but also limited sampling in the studies we analysed (Teixeira et al. 2001, Sandoval et al. 2004). Gaunt and Miles (2000) suggested that these types of species (as well as *Microtriatoma trinidadensis*, *Eratyrus mucronatus* and *Triatoma tibiamaculata*) remained in a relatively primitive feeding stage and did not follow the “recent dramatic spread of a few eclectic, domiciliated triatomine species”.

Finally, given the positive association between kissing-bug habitat colonisation and host use, our results imply that control measurements directed at disrupting the contact between humans and kissing-bugs, especially housing improvement (Briceño-León 1990), are among the most desirable strategies for Chagas disease control.

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