

Phenotypic Diversity of *Triatoma infestans* at the Microgeographic Level in the Gran Chaco of Argentina and the Andean Valleys of Bolivia

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ABSTRACT *Triatoma infestans* (Klug) is the main vector of *Trypanosoma cruzi*, etiologic agent of Chagas disease. The phenotype of the species varies at different geographic scales. The objective of this study was to compare the antennal phenotype of spatially close *T. infestans* populations and to evaluate its usefulness as a marker of exchange of individuals between populations. The antennal phenotype of 190 *T. infestans* from Argentina and Bolivia was analyzed using uni- and multivariate techniques. This study shows heterogeneity of the antennal phenotypes of closely related *T. infestans* populations living in different habitats. Specimens collected in a goat corral and a rabbit cage in La Rioja (Argentina) were dissimilar to the specimens collected in the nearby intradomestic environment. Similarly, specimens from peridomestic corrals in Cochabamba (Bolivia) were different from the intradomestic and sylvatic specimens, indicating some degree of isolation between these populations. In contrast, *T. infestans* collected in chicken coops and the intradomestic environment were similar, in all studied regions, suggesting a frequent exchange of individuals between the two habitats and/or because of the similarity of the habitat due to the presence of chickens in the intradomestic environment. We propose that each habitat affects in a particular mode the insect morphology and these changes could be used to identify recolonizing *T. infestans*. These results support the hypothesis of different degrees of isolation between intradomestic and peridomestic habitats. Within this context, special attention should be given to chicken coops and other close peridomestic structures in relation to the recolonization process of domestic habitats by *T. infestans*.

KEY WORDS *Triatoma infestans*, Chagas disease, habitat, antennal sensilla, phenotype

Triatoma infestans (Klug) is the main vector of *Trypanosoma cruzi*, the etiologic agent of Chagas disease. At its highest expansion, the species occupied extensive areas of seven countries of the Southern Cone of South America. Between 1999 and 2005, Uruguay, Chile, and Brazil have certified interruption of vectorial transmission of the disease due to *T. infestans* (Schofield et al. 2006), but this species is still present in parts of Bolivia, southern Peru, Paraguay, and Argentina, inhabiting domestic habitats, although sylvatic populations also have been reported in the Andean Valleys of Bolivia and the Gran Chaco of Bolivia and Argentina (Dujardin et al. 1987; Noireau et al. 2002, 2005).

The occurrence of populations of *T. infestans* in peridomestic habitats (chicken coops, store rooms, and goat corrals) poses some problems for the elimination of the species from domestic habitats, because they show strong resilience to traditional control interventions with pyrethroid insecticides. Reinfestation of domestic and peridomestic structures is frequent (Gürtler et al. 2004, Cecere et al. 2006, Catalá et al. 2007). Populations moving from the peridomestic

structures and residual populations surviving the effect of the insecticide within the house are the two candidate sources identified to play a role in domestic reinfestation (Dujardin et al. 1996, 1997, 1999; Schachter-Broide et al. 2004).

Estimation of the exchange rate of individuals between subpopulations and the exploration of markers of population structure has particular interest for vector control interventions. The study of phenetic changes promoted by environmental influence during the development of the individuals is also important in understanding the adaptive processes of the species. The objective of this study was to compare the antennal phenotype of spatially close *T. infestans* populations living in different ecotopes, and to analyze possibilities for its application as a marker for the exchange of individuals between habitats.

Materials and Methods

The Insects. We examined the antennae of 94 females and 96 males of *T. infestans* collected from two regions of Argentina (La Rioja and Chaco provinces) and two of Bolivia (Tarija and Cochabamba departments) (Fig. 1). In La Rioja, specimens were collected

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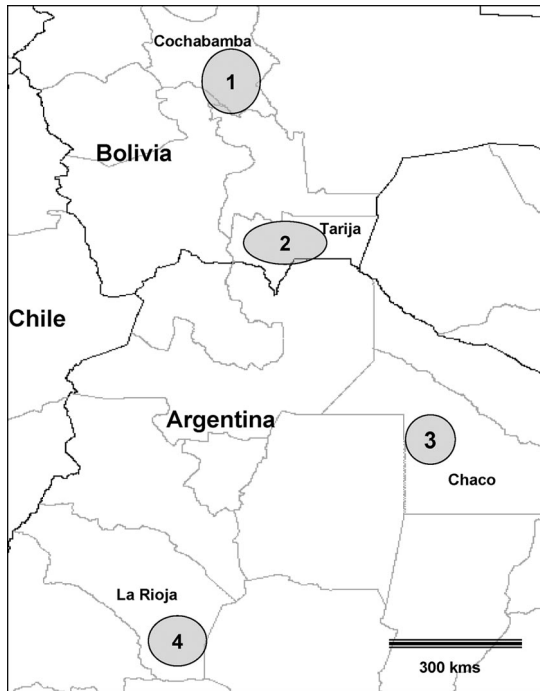


Fig. 1. Regions where *T. infestans* were collected. 1, Cochabamba; 2, Tarija; 3, Chaco; and 4, La Rioja. Localities within each region are listed in Table 1.

in one goat corral, one rabbit cage, one chicken coop, and seven intradomestic habitats. In Chaco and Tarija, the insects were collected from various chicken coops and intradomestic habitats. The specimens of Cochabamba came from sylvatic, peridomestic, and intradomestic habitats (Table 1).

Habitat Description. Houses in the studied regions are usually built with adobe walls and thatched roofs, with one or two rooms and a veranda at the front. Other building materials are also used, such as wood (in the warm chaco region) and stone (in the Andean valleys). Chicken coops are spatially close to the

houses and show a variety of structures. In some regions, these are wired compounds with roofs of a variety of materials (wood, tin, cardboard, plastic, fabric, adobe or straw). In other regions, brooding hens are kept in small structures or store rooms built with adobe bricks and thatched roofs. One group of specimens was collected in a rabbit cage in La Rioja (Argentina), built with cement blocks and tin and cardboard roof. This habitat was 10 m from a chicken coop (same owner), where another collection of *T. infestans* was carried out.

Goat corrals of north western Argentina and Bolivian valleys are complex structures. In general, they have a wall made from interwoven sticks of natural vegetation, with a small roofed area made with sticks of natural vegetation and mud, where calves are protected. In Cochabamba (Bolivia), corrals have goats, sheep, and sometimes hens.

T. infestans specimens of sylvatic habitats were collected in natural habitats constituted of rock piles with burrows occupied by small mammals (*Galea musteloides*) (Rojas Cortez et al. 2007).

Antennae Analysis. Antennae were cut from the head by using fine forceps, stored in 70% ethanol before diaphanization in 4% NaOH, and then neutralized with 5% glacial acetic acid. After clearing, they were individually slide mounted in glycerin and examined by stereomicroscope at 400×. Only one antenna was examined from each specimen, and the ventral side of the three distal segments of the antennae was drawn. Sensilla were counted along the entire length of the pedicel (P) and the two flagellar segments (F1 and F2); and classified according to Catalá and Schofield (1994) as bristles (BR), thin-walled trichoids (TH), thick walled trichoids (TK), and basiconica (BA).

Data Analysis. Means and standard deviations of sensilla number by type and antennal segment were calculated. Levene test was used to determine homoscedasticity. Variables with homogeneous variances were analyzed using analysis of variance (ANOVA). Univariate analysis was used to show which sensilla type had greater differences among

Table 1. Geographic origin of *T. infestans* specimens (country, province, habitat); cytotype, and number of specimens of *T. infestans* collected during 2005

	Locality	Cytotype ^a	Habitat	No. specimens	
				Female	Male
Argentina	Alto Bayo	Non-Andean	Goats corrals	10	10
			Chicken coop	9	10
La Rioja	San Antonio		Rabbit cage	9	8
			Intradomestic	9	8
Argentina Chaco	Pampa Avila	Non-Andean	Chicken coop	10	8
			Intradomestic	5	8
Bolivia Tarija	Palmar Chico, Quebrada Busuy,	Intermediate	Chicken coop	8	7
	Yaguacua, El Barrial		Intradomestic	13	16
Bolivia	Cotapachi	Andean	Sylvatic (rodents nests)	10	5
Cochabamba	Mataral-Bandormiyoc,		Corrals: goats + ewes,	6	11
			goats + chickens		
	Jamach'uma		Intradomestic	5	5
Total				94	96

^a Cytotypes according to Panzera et al. (2004).

Table 2. Mean number (SD) of antennal sensilla according to sex and region (only variables with significant differences are shown)

Region	Sex	Sensilla	Habitat				
			Sylvatic	Corrals	Intradomestic	Rabbit cage	Chicken coop
Bolivia Cochabamba	Female	PTH	59.1 (16.42) ^a	81.17 (16.24) ^a			
		F1TH	66.9 (11.08) ^a	80.83 (9.06) ^{a,b}	53.44 (17.47) ^b		
		F2TK	186.9 (25.26) ^{a,c}	219.83 (17.93) ^a	213 (9.85) ^c		
	Male	F1TH	79.40 (11.04) ^a	95.27 (10.63) ^{a,b}	69.6 (13.28) ^b		
		F1TK	203.2 (29.75) ^a	300.27 (62.4) ^a			
		F2TK	189.6 (20.62) ^{a,c}	227.91 (14.1) ^a	218 (13.76) ^c		
Bolivia Tarija	Female	F2TH			23.91 (6.88) ^d		30.13 (4.49) ^d
Argentina Chaco	Female	F1TH			81.4 (20.4) ^d		98.1 (8.67) ^d
Argentina La Rioja	Female	PBR		135.5 (12.02) ^{e,f}	141.56 (15.13) ^{d,g}	163.33 (23.57) ^{e,g}	164.11 (23.5) ^{d,f}
		PTH		116.6 (26.19) ^e	98.56 (34.99) ^{d,g}	171.56 (22.57) ^{e,g,h}	138.44 (36.46) ^{d,h}
		F1TH		62 (12.11) ^{e,f}	73.33 (19.36) ^g	90.56 (19.26) ^{e,g}	80.67 (12.36) ^f
		F1TK		355.6 (35.31) ^{e,f}	387.89 (93.96) ^{d,g}	472 (49.89) ^{e,g}	458.33 (27.29) ^{e,f}
		F2TH		23.9 (3.9) ^{b,e,f}	31.22 (6.99) ^b	37 (6.78) ^e	33.67 (7.12) ^f
		F2TK		220 (24.73) ^{b,e,f}	266.33 (35.59) ^b	267.22 (33.8) ^e	259.56 (36.31) ^f
	Male	PBR		124.7 (15.89) ^{e,f}		163.12 (31.96) ^e	153.7 (19.3) ^f
		F1TH		90 (18.04) ^{e,f}	84.81 (14.73) ^g	113.87 (23.97) ^{e,g}	98.1 (14.97) ^f
		F1TK		381.5 (54.41) ^{b,e,f}	454.73 (38.84) ^b	460 (76.67) ^e	439.6 (48.63) ^f
		F2BR		7.5 (1.18) ^f	7.09 (1.14) ^d		8.6 (1.17) ^{d,f}
		F2TH		35.1 (8.48) ^e	32.18 (6.18) ^g	44 (10.08) ^{e,g}	
		F2TK		231.7 (22.36) ^{b,e,f}	257.45 (20.11) ^b	298.62 (61.32) ^e	279.2 (24.63) ^f

PBR, bristles on pedicel; PTH, thin walled trichoids on pedicel; F1TH, thin-walled trichoids on first flagellar segment; F1TK, thick walled trichoids on first flagellar segment; F2BR, bristles on second flagellar segment; F2TH, thin-walled trichoids on second flagellar segment; F2TK, thick walled trichoids on second flagellar segment.

^a Difference between corrals and sylvatic habitat.

^b Difference between corrals and intradomestic habitat.

^c Difference between sylvatic and intradomestic habitats.

^d Difference between chicken coop and intradomestic habitat.

^e Difference between rabbit cage and corrals.

^f Difference between chicken coop and corrals.

^g Difference between rabbit cage and intradomestic habitat.

^h Difference between rabbit cage and chicken coop.

habitats. Variables showing heteroscedasticity were analyzed using the nonparametric Kruskal-Wallis test (STATISTICA, StatSoft 2005).

Considering the variables that showed significant differences by univariate analysis, two discriminant analyses were carried out: one analysis between three habitats of Cochabamba, and the other analysis between four habitats of La Rioja. For these multivariate analyses, the software PAD version 80 was used to estimate functions that identify the studied groups. PAD (Dujardin 2004, <http://www.mpl.ird.fr/morphometrics>) is a software performing classical discriminant analyses, but estimating statistical significance (Wilks and Mahalanobis distances) by a permutation tests (1,000 permutations), and a reclassification test.

Because the *T. infestans* antennal phenotype shows a strong relationship with the chromosomal cytotype (Catalá et al. 2007), *T. infestans* populations were compared by region.

Results

Phenotypic Similarity of *T. infestans* from Chickens Coops and Intradomestic Environments. Chicken coops near rural houses, both infested by *T. infestans*, were present in three of the four studied regions: Tarija, Chaco, and La Rioja. In all three regions, the antennal phenotype of the intradomestic and chicken coop specimens was very similar. Males collected in both habitats from Tarija (Bolivia) and Chaco (Ar-

gentina) showed no significant differences in the number of different sensilla types. Females collected within the rural houses (intradomestic) showed a marginally significant ($P = 0.04$) lower number of the flagellar TH compared with the females collected from chicken coops (Table 2).

Males collected in chicken coop of La Rioja showed antennal phenotypes similar to the ones collected within houses, but females showed more sensilla of two types (pedicel BR and TH and F1 [first flagellar segment] TH) in chicken coop specimens compared with intradomestic specimens.

Microgeographic Variation of *T. infestans* Populations in Different Habitats. Region of La Rioja. Females *T. infestans* collected in the rabbit cage showed a significantly higher number of sensilla PBR, PTH, F1TH, and F1TK than intradomestic and goat corral females. The latter showed significantly fewer F2TH and F2TK than specimens collected in the other habitats. Male specimens showed a similar pattern of variation, although with less significant differences between phenotypes (Table 2). The six variables mentioned above were used in discriminant analysis of the antennal phenotype that produced a first function explaining 61% of the total variation in the females and 55% in the males. The second function explained 33% in females and 44% in males. Mahalanobis distances calculated during the analysis showed that specimens of both sexes collected in the chicken coop were not significantly different from those collected in intrado-

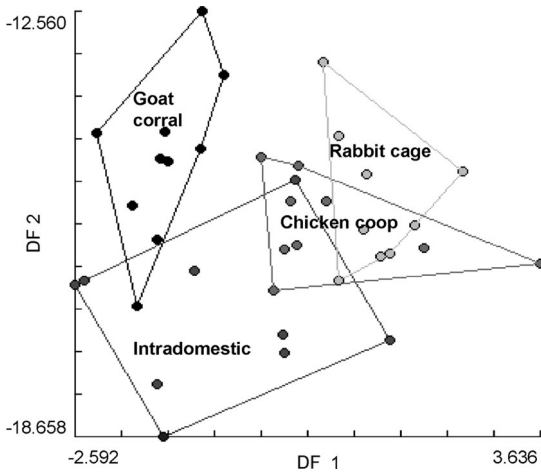


Fig. 2. Discriminant analysis of *T. infestans* females collected in different habitats within La Rioja, Argentina. DF1 and DF2 discriminant function 1 and 2, respectively. Mahalanobis distances: chicken coop–rabbit cage, 1.16; chicken coop–intradomestic, 2.18; chicken coop–goat corral, 2.51; rabbit cage–intradomestic, 2.76; rabbit cage–goat corral, 2.91; goat corral–intradomestic, 2.41.

domestic habitats and in the rabbit cage. However, specimens collected in the rabbit cage were significantly different to those from the goat corral ($P < 0.01$). Significant difference also was found between goat corral and intradomestic individuals ($P < 0.017$) (Fig. 2).

In the reclassification test, the highest fraction of correctly classified individuals corresponded to females and males of goat corrals (90% and 80%, respectively) and to intradomestic males (81%). The cross classification showed 80 and 60% for females and males of goat corrals and 63% for intradomestic males. Specimens collected in the rabbit cage and chicken coop showed low values of correct classification, with specimen mixture between the two habitats. The intradomestic specimens that did not classify correctly were assigned to the chicken coop habitat.

Region of Cochabamba. Males and females collected in the peridomestic corrals in this region showed a significantly higher number of TH and TK trichoid sensilla compared with specimens collected in the intradomestic and sylvatic habitats (Table 2). Discriminant analysis (with three variables) of the antennal phenotype of the specimens collected in this area, produced a first function that explained 55% of the total variation in the females and 75% in the males, whereas the second function explained 45 and 25%, respectively. Mahalanobis distances were significant for peridomestic specimens compared with sylvatic and intradomestic, both for females and for males ($P < 0.0083$) (Fig. 3).

In the reclassification test, the highest fraction of correctly classified individuals corresponded to those collected in peridomestic structures (100% females and 90% males). Sylvatic and intradomestic *T. infestans* showed 80% of correctly classified individuals for both sexes. The cross-classification showed 100 and 81% for

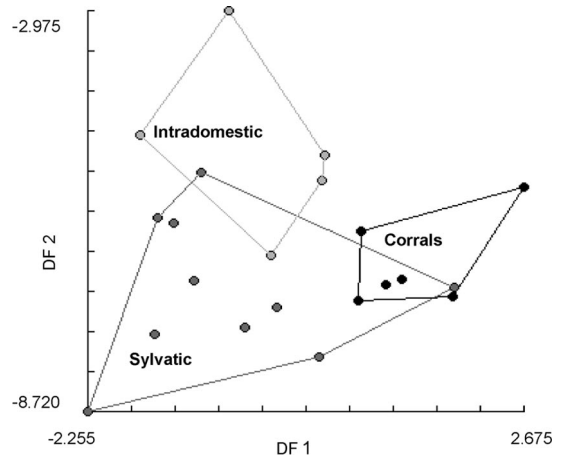


Fig. 3. Discriminant analysis of *T. infestans* females collected in different habitats within Cochabamba, Bolivia. DF1 and DF2 discriminant function 1 and 2, respectively. Mahalanobis distances: peridomestic corrals–intradomestic, 2.43; peridomestic corrals–sylvatic, 2.16; sylvatic–intradomestic, 2.10.

females and males of peridomestic structures; and 80 and 60% for intradomestic females and males, respectively. Two of the three intradomestic individuals that did not classify correctly, were assigned as sylvatic.

Both in Cochabamba and La Rioja, specimens from goat corrals showed the largest Mahalanobis distances from specimens from the other habitats.

Discussion

Recolonization of domestic structures by *T. infestans* in the Gran Chaco region is currently driving many studies because of its implications for the interruption of vectorial transmission of Chagas disease. Morphometric and genetic studies support the hypothesis of a strong geographic structuring of *T. infestans* populations, either at the macro (Panzer et al. 2004; Bargues et al. 2006; Catalá et al. 2007; Pérez de Rosas et al. 2007; Hernández et al. 2008) or the microgeographic scales (Dujardin et al. 1997; Schachter-Broide et al. 2004), suggesting a low exchange rate of individuals between the vector populations. If this hypothesis is true and the flux of individuals between intra- and peridomestic populations is low, vector control intervention should focus mainly on the efficient elimination of intradomestic populations, which are mainly responsible for vectorial transmission of the disease to humans.

T. infestans has low mobility during nymphal development, and it seems that the species disperses mainly by active flight of adults (Vazquez-Prokopec et al. 2004). The low mobility obliges the nymphs to be closely associated with the niche occupied. The quality of this niche could be reflected in the antennal phenotype of the adult, as a consequence of the higher or lower stress the individual endured during its development. So, if each habitat imposes a specific sig-

nature over the antennal phenotype in *T. infestans*, it could be possible to identify the origin of the adults recolonizing empty habitats, as was shown for *Triatoma dimidiata* (Latreille) in Colombia (Arroyo et al. 2007).

This study shows heterogeneity of the antennal phenotypes of closely related *T. infestans* populations, living in different habitats. Lorenzo et al. (2000) suggest that each single habitat within a human rural house has specific characteristics in terms of type and number of hosts, microenvironmental conditions, and available refuges. We propose that each environment affects in a particular mode the insect morphology and these changes could be used to identify recolonizing *T. infestans*. Our results also support the hypothesis of different degrees of isolation between intradomestic and peridomestic habitats. The phenotypic variation due to the main genetic variation (genotypes) and the genetic drift between regions, would not affect the analysis, because each region was considered separately (Catalá et al. 2007). Other results indicate that insects from similar habitats (chicken coop) 150 km apart did not differ in their antennal phenotype. However, when chicken coop were 350 km apart some phenotypic differences were detected, presumably due to isolation and genetic drift (L.A. et al., unpublished data).

For studies of the exchange of individuals between populations, it is important to know whether the phenotype of the antenna changes quickly under environmental change. It is known that the antennal phenotype in hematophagous insects reflects an ancestral pattern that is modified according to current requirements (McIver 1987). Significant changes can occur after relatively few generations in laboratory culture, that may be correlated with bloodmeal availability (feeding frequency) (Catalá et al. 2004b). Hernández et al. (2008) demonstrated a close association between macroenvironmental conditions, chromosome cytotypes, and antennal phenotypes of *T. infestans*, proposing that genetic and environmental features act modulating the insect morphology. The importance of these selective forces upon the antenna is not surprising, because this organ constitutes the primary sensory link of the insect with its environment.

A remarkable finding of this study is that phenotypes of *T. infestans* collected in chicken coops and intradomestic environments were similar in each region, suggesting frequent exchange of individuals and/or phenotypic similarity due to the presence of chickens within the coops and intradomestic environment. Chickens are one of the main food source for *T. infestans* and chicken coops tend to be the closest peridomestic habitats to the house (Wisnivesky-Colli 1982, 1987; López et al. 1999). Chickens frequently enter into the house and sleep below the beds, allowing the growth of abundant populations of *T. infestans* (Catalá et al. 2004a; Cecere et al. 1997; Gürtler et al. 1996, 1997). López et al. (1999) showed presence of human blood in the intestine of 30% of *T. infestans* collected in chicken coops up to 6 m from houses. Our phenotypical analyses of *T. infestans* indicate that

chicken coops might represent an important link for the colonization process of the intradomestic environment.

The movement of triatomines between very close habitats is also indicated by the phenotypic similarity of populations collected in a rabbit cage and a chicken coop a few meters apart. In this particular case, one *T. infestans* adult was captured while walking between both habitats, confirming dispersal and mixture between the populations. We propose that habitats very close (several meters) function as a single system, and the bug populations will show a mixed phenotypic pattern.

Populations collected in the peridomestic corrals of Cochabamba were significantly different from the sylvatic and intradomestic corrals, suggesting a low exchange rate between them. Among the sylvatic habitats, the phenotypes were characterized by low number of TK sensilla, compared with the intradomestic specimens, as already shown by Catalá and Dujardin (2001). Sylvatic specimens showed higher phenotypic similarity with the intradomestic specimens than with those from peridomestic corrals. However, Richer et al. (2007) showed genetic differences, by using microsatellite markers, between sylvatic and domestic populations in the Cochabamba Department, suggesting restricted gene flow between these populations.

The numerical difference in the abundance of antennal sensilla in specimens from different habitats seems to be related with known functions of these receptors. The sensilla most involved in discrimination between populations were the BR and TH. The BR sensilla receive tactile information associated with the nearby environment, including vibrations, variations of the air currents, and contact stimuli (McIver and Siemicki 1984). The higher number of these receptors in the specimens collected in the rabbit cage and the chicken coop compared with the specimens from intradomestic habitats could be attributed to the higher density of *T. infestans* in these habitats, as suggested by Catalá et al. (2004b), where an increase of BR sensilla in the pedicel was shown in specimens bred at high density under laboratory conditions. The TH multiporous sensilla are associated with olfaction and receive compounds linked with the perception of host odor and the environment (Bernard 1974), suggesting they might represent good markers of host-specific features of the habitat.

The results found in this study show the utility of the antennal phenotypes as morphological markers and open ways for further studies exploring phenotypic relationships of *T. infestans* specimens in the context of vector control interventions. The results reinforce the idea that special attention should be given to chicken coops and other very close peridomestic structures in the recolonization process by *T. infestans*.

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