Active dispersal of *Triatoma infestans* and other triatomines in the Argentinean arid Chaco before and after vector control interventions

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ABSTRACT: Peridomestic structures are considered the main sites where *Triatoma infestans* (Hemiptera: Reduviidae) remain and disperse, representing the first risk factor for intradomestic invasion, even after vector control activities. This study analyzed *T. infestans* dispersal during vector control interventions in six rural houses of the arid Chaco (La Rioja, Argentina). Flying and walking dispersers were captured during five months of two consecutive warm seasons after insecticide spraying of intra- and peridomiciles. These data were compared with previous published data in the same scenario but without insecticide spraying in peridomiciles. Recorded climatic conditions were favorable for active dispersion during the study. Total number of *T. infestans* dispersers moving among domestic habitats decreased after insecticide spraying. Sylvatic triatomines *T. guasayana, T. eratyrusiformis*, *T. garciabesi,* and *T. platensis,* not targeted by insecticide spraying, were captured simultaneously within peridomestic areas and showed higher invasion pressure than *T. infestans.* Adult *T. infestans* peridomestic populations showed high nutritional status, indicating low dispersion probability. Some peridomiciles remained infested at the end of the study. However, no intradomiciles were recolonized. These results suggest that there is a low probability of intradomestic recolonization by active dispersion from peridomiciles during 15 months post-spraying. ***Journal of Vector Ecology* 41 (1): 90-96. 2016.**

Keyword Index: Chagas disease, dispersion, peridomestic populations, reinfestation, triatomines, vector control.

INTRODUCTION

The control of *Triatoma infestan*s, the main vector of Chagas disease in the Southern Cone countries, is based primarily on entomological surveillance and application of pyrethroid insecticides in houses of endemic areas (Schofield et al. 2006). In the region of the Gran Chaco, peridomestic sites are the first to be recolonized by *T. infestans* after control interventions, maintaining more abundant populations than domestic sites (Cecere et al. 2004, Gorla et al. 2009, Porcasi et al. 2007). Pyrethroid insecticide application had low efficacy in peridomiciles, leaving residual vector populations that recover after one to two years (Gürtler et al. 2004, Porcasi et al. 2007).

Houses from the arid region of Los Llanos (La Rioja, Argentina, south of the Gran Chaco) showed high intra- and peridomestic infestation by *T. infestans* (46.8%) in 2004 (Porcasi et al. 2007). Rural populations in this region are subject to economic, social, and cultural conditions that favor the presence of this insect and require strengthened surveillance and vectorial control interventions. The reinfestation of treated sites, especially intradomiciles, is attributed mainly to the active dispersal of *T. infestans* from peridomestic residual foci and/or the recovery of residual populations. The dispersion of *T. infestans* is poorly understood due to ethical concerns related to field experiments and to the difficulty of carrying out field or laboratory experiments that replicate natural conditions (Schofield and Matthews 1985).

The analysis of domestic triatomine dispersion is important for understanding the epidemiology of Chagas disease (Schofield 1994). There have been a number of studies that reported on the dispersal of *Triatoma dimidiata* (Pacheco-Tucuch et al. 2012) and *Rhodnius* species (Sanchez-Martin et al. 2006). Other studies showed the results of the use of new tools to quantify triatomine dispersal by combining field surveys of vector populations and spatially explicit population dynamic models (Barbu et al. 2013, Zu Dohna et al. 2009). These studies estimate dispersal parameters by fitting models to observed changes in the spatial distribution of triatomines. Although powerful, these studies provide only indirect measures of dispersion.

The dispersion by flight used light traps to capture *T. infestans* in Argentina (Abrahan et al. 2011, Vazquez-Prokopec et al. 2004, 2006) and Bolivia (Noireau et al. 2000). The terrestrial dispersion of *T. infestans* has been less explored. Abrahan et al. (2008) manually collected an adult of *T. infestans* walking between two peridomestic habitats separated by a few meters. Vazquez-Prokopec et al. (2004, 2006) collected 5th instar nymphs in light traps placed to capture flight dispersers from peridomestic sites. Recently, Abrahan et al. (2011) have demonstrated that the terrestrial dispersion of adults and nymphs of *T. infestans* using sticky ground traps on peridomestic sites is possible. These authors have also demonstrated that *T. infestans* females use this type of dispersion when they are heavier, carrying numerous eggs within the oviducts and blood reserves in the midgut to ensure successful colonization of a new habitat.

The search for new habitats while looking for mates and food would be the main determinants of active dispersal of *T. infestans* and other triatomines. Schofield (1985) has proposed that active dispersal of these vectors is related to the regulation of population density and metabolism activated by particular climatic conditions. Flight dispersal of *T. infestans* is associated with low nutritional status and is favored during the warm season characterized by high temperatures and low relative humidity (Abrahan et al. 2011, Curto de Casas and Carcavallo 1995, Lehane and Schofield 1982, McEwen and Lehane 1993, Schofield et al. 1992, Vazquez-Prokopec et al. 2004).

This work is part of a more comprehensive project on the arid Chaco, aiming to understand the *T. infestans* reinfestation process of intradomiciles after the vector control activities of La Rioja Chagas Program (PPCh). In 2004, after 15 years without systematic interventions in the province, the first evaluation of the rural areas of the province showed the highest rates of intradomestic (45.1%) and peridomestic (57.3%) infestation in the Independencia department (Porcasi et al. 2007). In October 2006, the PPCh carried out the first systematic control intervention in the Independencia department, where only intradomicilies were sprayed. After two years (2008), we showed the occurrence of flying and walking triatomines, including *T. infestans,* moving among domestic habitats in six domiciliary units (DU) of the Independencia department (Abrahan et al. 2011).

The latest intervention of the PPCh in 2009 included peridomestic and intradomestic insecticide spraying, so we decided to determine the number of flying and walking insects within the same six DU during two consecutive warm seasons, six and 15 months after the blanket spraying. These results were compared with those obtained previously (Abrahan et al. 2011) in order to estimate whether the total spraying (including peridomicile) affected the *T. infestans* dispersion activity. We believe that the effective number of walking and flying *T. infestans* is an excellent epidemiological indicator, as it is directly related to the house invasion and colonization risk, independent of the factors contributing to these vector movements. To complement the study we added an estimation of "probable fliers" (*T. infestans* adults with nutritional status <8 mg/mm) in peridomestic populations at the end of the dispersion study.

MATERIALS AND METHODS

Study area

The study was carried out in the Independencia Department (La Rioja, Argentina), located at the southern end of the Gran Chaco, in the region of Los Llanos, one of the poorest and most arid areas of Argentina. Rural communities in Los Llanos exploit available natural resources in a lifestyle based on economic subsistence. The breeding of domestic animals, mainly goats and chickens, led to the presence of complex peridomiciles, which provide shelter for *T. infestans* a few meters away from houses (Gorla et al. 2013, Porcasi et al. 2007).

The capture of dispersers was carried out in six DU as described in Abrahan et al. (2011). Three DU are located in Patquia Viejo, two DU in Salinas de Busto, and one DU in La Torre. Patquia Viejo is approximately 85 km from Salinas de Busto and La Torre, which are 5 km apart from each other (Figure 1). The DUs were selected by the availability and authorization of the owners to allow triatomine searches in their houses.

Vector control activities by PPCh and *T. infestans* sampling

Figure 2 shows a timeline of PPCh and our research activities, including those of the first study (Abrahan et al. 2011). PPCh made an insecticide spraying in all peridomestic and intradomestic

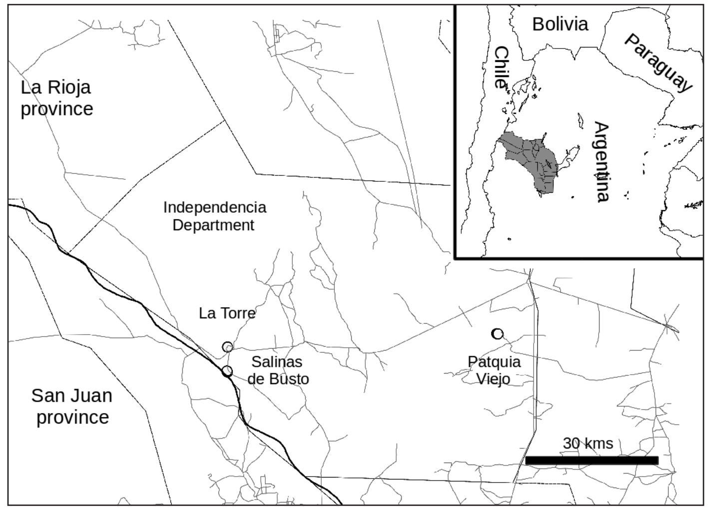

Figure 1. Study area of the Independencia department of La Rioja, Argentina. Circles indicate localities: Patquia Viejo, La Torre, and Salinas de Busto.

structures in August, 2009 and the dispersion study was carried out between November, 2009 and March, 2010, two to six months post-spraying, and between November, 2010 and March, 2011, 11-15 months post-spraying. Traps were installed in the peridomestic area of the selected DU. Flying insects were captured using light traps (LT) and walking specimens were captured using dispersal barriers (DB), a double-side adhesive tape attached to the ground by hooks, both described in Abrahan et al. (2011).

For the capture of flying *T. infestans,* three light traps were installed in each DU each night, between 10-30 m from the nearest habitat and up to 50 m from the farthest. Light trapping was performed from 19:30 to 07:00. Each LT was positioned with a GPS to maintain the same location along the time study. Total capture effort was 270 trap-nights, except during the last period (11-15 months post-spraying) when the capture effort was 234 trap-nights.

To capture walking *T. infestans,* dispersal barriers were placed surrounding the chicken coops (n=5) and calf-protecting structures (n=5). The total trapping effort was 375 m of adhesive tape for chicken coops and 862 m for goat corrals during 30 nights. No capture of walking dispersers was carried out during

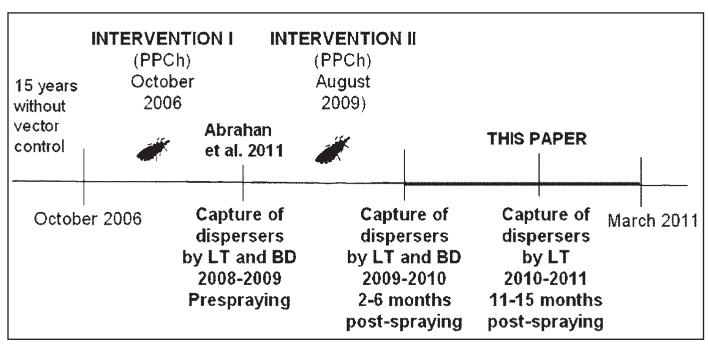

Figure 2. Timeline of dispersers capture by light traps (LT) and/ or dispersal barriers (DB) and vector control activities in the study area. Intervention 1: Indoor residual spraying and treatment of domestic animals with pour-on veterinary formulations. Intervention 2: Insecticide spray in peridomestic and intradomestic structures.

the last sampling period (11-15 months post-spraying) due to the impossibility of using the same sticky tape in dispersion barriers.

All specimens collected were maintained in labeled plastic jars identifying house of origin, habitat, locality, date, and capture method used. Insects were kept alive at 10° C in a portable refrigerator and once in the laboratory, species and developmental stages were identified (Brewer et al. 1981, 1983; Lent and Wygodzinsky 1979). The individuals were quantified by sex, stage, habitat, DU, capture method, and date.

Nutritional status was estimated for adult dispersers of *T. infestans* as body weight/length (W/L) (Lehane and Schofield 1982). Flight muscle ratio (TR) was estimated as flight muscle weight/body weight (Abrahan et al. 2011, Gurevitz et al. 2006). In order to record the reproductive status of females, the state of the spermatheca (empty: virgin female, full: fertilized) and the number of chorionated eggs present in the oviducts were examined. In males, the state of the seminal vesicles, efferent duct, and accessory glands were recorded. Reproductive status indicates the potential of dispersers as colonizers.

In March, 2011, the nutritional status was estimated as W/L in adults of peridomestic populations collected by PPCh. Furthermore, the percentage of probable fliers in peridomestic populations was estimated based on a low nutritional status. The number of adults with W/L < 8 mg/mm was divided by the total number of adults x 100. Likewise, an evaluation of infestation in the six domestic units was carried out by the PPCh at the end of the study in March, 2011.

Weather variables

A weather station (Weather Monitor II, Davis Instruments) was installed in Patquia Viejo and Salinas de Busto during the three trapping days per month in each period to record temperature, relative humidity, and wind speed and direction at 30-min intervals from 19:00 to 22:30, known to be the main period of dispersion activity (Lehane and Schofield 1982).

Statistical analysis

Weather variables, W/L, and TR of adult dispersers of *T. infestans* were compared among dispersion periods using the non-parametric Kruskal-Wallis test. The physiological characteristics of dispersers of *T. infestans* captured in the two periods post-spraying were analyzed together by sex due to the low number of individuals.

The total number of dispersers was compared before and after spraying by Chi-square test. The number of *T. infestans* and *T. guasayana* captured by LT and DB before and after spraying were compared using Chi-square test. Infostat (Di Rienzo et al. 2011) was used for non-parametric analysis and the R software was used for GLM (R Development Core Team 2013).

RESULTS

Weather variables

Temperature and relative humidity were similar during all dispersion studied periods. Median temperature values varied between 25.9 and 28.3° C (H=2.89, df=2, p=0.24, Kruskal Wallis test). Relative humidity fluctuated between 40.3 and 46.2% (H=1.53, df=2, p=0.47). Wind speed was lower in 11-15 months post-spraying than in previous periods (H=7.22, df=2, p<0.03), although median wind speed values were always below 5 km/h. Table 1 shows the descriptive statistics of the climatic variables recorded during the studied period.

Active dispersal of *T. infestans* after spraying

Four flying *T. infestans* were captured by LT during the 270 trap-nights, two to six months post-spraying, representing 50% (4/8) of fliers captured pre-spraying. Only one *T. infestans* female in 234 trap-nights was captured 11-15 months post-spraying. Other triatomine species were also captured in each period. The number of individuals by species, sex, and date is detailed in Table 2.

One *T. infestans* 5th instar nymph was collected two to six months post-spraying in goat corrals DB. Other triatomines were also captured. One *T. eratyrusiformis* female and three *T. guasayana* females in goat corrals DB, and a male and one female of *T. guasayana* were captured in chicken coop DB at two to six months post-spraying.

Total dispersers of *T. infestans* and other triatomine species

The comparison between the total number of *T. infestans* dispersers pre-spraying (data from Abrahan et al. 2011) and two to six months post-spraying showed that there was a very significant decrease in total post-spraying (χ^2=12.45, df=1, p=0.0004). In contrast, the number of dispersers of sylvatic triatomine species did not differ from pre-spraying and two to six months post-spraying (χ^2=3.04, df=1, p=0.081).

Total number of *T. infestans* and sylvatic species did not show significant differences pre-spraying (χ^2=3.57, df=1, p=0.059),

Table 1. Climatic conditions of the Independencia department (La Rioja, Argentina) during the studied period of disperser collection. Median values of temperature, relative humidity, and wind speed (first and third quartiles, Q1 and Q3, respectively), recorded between 19:00 and 22:30.

Period	Temperature (°C)	Relative Humidity (%)	Wind speed (Km/h)
	Median (Q1-Q3) NS	Median (Q1-Q3) NS	Median (Q1-Q3)S
Pre-spraying	26.6 (24.9-28.9)	40.8 (34.1-50.9)	4.2 (2.2-7)
2-6 months post-spraying	28.3 (25.8-29.9)	46.2 (35.4-54.8)	4.9 (3.7-5.1)
11-15 months post-spraying	25.9 (21.3-28.0)	40.3 (23.0-53.5)	2.7 (2.2-3.5)

NS: No significant difference (p > 0.05); S: Significant difference (p < 0.05). Kruskal-Wallis test.

Table 2. Number of *T. infestans* and other species of triatomines collected by LT (flying insects) in six DUs of the Independencia department (La Rioja, Argentina) pre- and post-spraying. F: Females, M: Males.

Period	*T. infestans*		*T. guasayana*		*T. eratyrusiformis*		*T. platensis*		*T. garciabesi*	
	F	M	F	M	F	M	F	M	F	M
Pre spraying [a]	3	5	13	8	2	6	2	0	0	0
2-6 months post spraying [b]	1	3	8	3	13	9	0	1	3	3
11-15 months post spraying [c]	1	0	7	1	1	2	1	0	3	2

[a]Data from Abrahan et al. (2011). The capture effort was 270 trap-nights.
[b]Capture effort was 270 trap-nights.
[c]Capture effort was 234 trap-nights.

although sylvatic triatomine showed higher number of dispersers than *T. infestans* post-spraying (χ^2= 42.64, df=1, p<0.0001). Figure 3 shows the comparison between the total number of *T. infestans* dispersers and other triatomines.

T. infestans vs *T. guasayana* dispersers

T. guasayana, the most active sylvatic species, showed greater number of dispersing females than *T. infestans* on pre-spraying, two to six months post-spraying and 11-15 months post-spraying (χ^2=6.25, df=1, p=0.012; χ^2=15.21, df=1, p=0.0001; χ^2=4.5, df=1, p=0.034, respectively) (Figure 4A). For males, *T. infestans* and *T. guasayana* did not differ in the number of flying dispersers pre-spraying (χ^2=0.69, df=1, p=0.4) or two to six months post-spraying. Only *T. guasayana* flying males were captured 11-15 months post-spraying.

There were fewer *T. guasayana* than *T. infestans* walking females on pre-spraying captures (χ^2=3.85, df=1, p=0.049) but was the only species observed post-spraying (Figure 4B). The number of walking males of both species did not differ significantly pre-spraying (χ^2=0.33, df=1, p=0.56) and only walking males of *T. guasayana* were captured post-spraying.

Physiological characteristics of *T. infestans* dispersers

Nutritional status: Median value of W/L in males was 7.8 mg/mm (7.1-11.1, first and third quartiles, respectively), whereas in females it was 10.1 mg/mm (9.2-10.9, first and third quartiles) in the post-spraying. No significant difference in W/L was found pre- and post-spraying (H=5, df=1, p=0.39; H=0.33, df=1, p=0.2, for males and females, respectively; KW test).

Thoracic muscle status: The minimum observed value of TR was 19.5%. Median value of TR in males was 26.7% (23.2-32.1, first and third quartiles, respectively), whereas in females it was 22.9% (9.2-10.9, first and third quartiles) in the post-spraying. No significant difference in TR was found pre- and post-spraying (H=0.2, df=1, p=0.57; H=0.33, df=1, p=0.8, for males and females, respectively; KW test).

Reproductive status: No significant difference was found in the number of chorionated eggs (H=0.0, df=1, p=0.6) in the female oviducts, pre- and post-spraying. The two flying females captured in the post-spraying period were fertilized with seven and eight chorionated eggs. Flying males had accessory glands filled with secretory fluid and seminal vesicles and efferent ducts with abundant sperm.

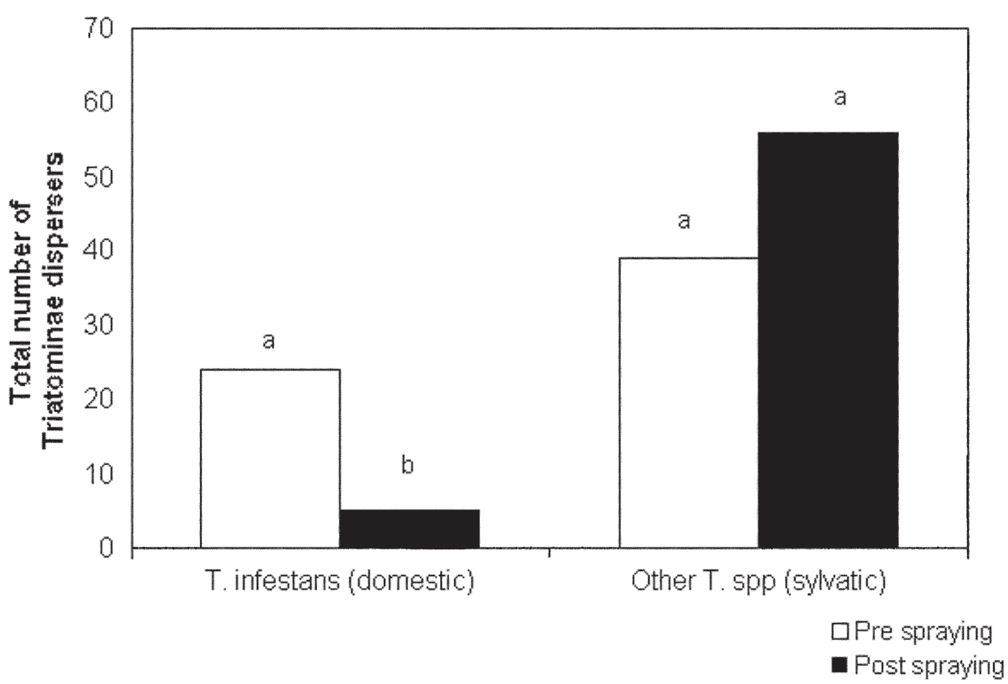

Figure 3. Total number (flying + walking) of sylvatic (4 spp) and domestic Triatominae (*T. infestans*) trapped pre-spraying and total two to six months post-spraying in Los Llanos (La Rioja, Argentina). Different letters indicate significant differences (p<0.0005).

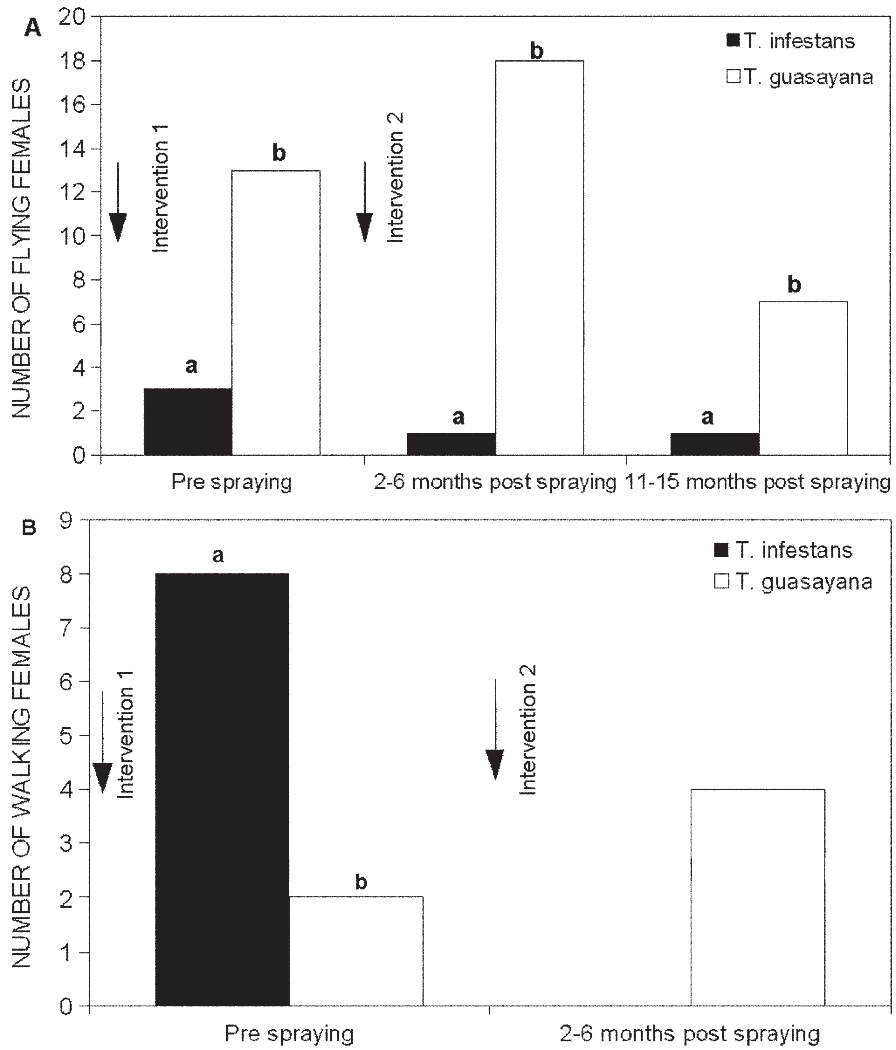

Figure 4. Number of female dispersers of *T. infestans* and *T. guasayana*. A. flying insects collected by light trap (LT). B. walking insects collected by dispersal barriers (DB). Different letters represent significant differences among species in each period ($p < 0.05$). Intervention 1: Indoor residual spraying and treatment of domestic animals with pour-on veterinary formulations. Intervention 2: insecticide spray in peridomestic and intradomestic structures.

Infestation index and nutritional status of T. infestans adults in peridomestic populations after 15 months post-spraying

In March, 2011, 15 months post-spraying (end of the study), six of the 11 peridomiciles (54.5%) and one of the six intradomiciles (16.67%) were positive for *T. infestans*. However, no eggs, feces, or exuviae were found in this intradomicile where one starved adult and a 5th instar nymph were captured.

In peridomestic sites, the median value of W/L in adults was 10.25 mg/mm (6.28-17.75, minimum and maximum respectively, n=80). The percentage of probable fliers (W/L< 8 mg/mm) was 10% (8/80).

DISCUSSION

The active dispersion of *Triatoma infestans* from residual foci of peridomiciles is considered one of the main mechanisms of intradomestic reinfestation after vector control interventions (Schofield 1994, Schofield and Matthews 1985). Here, for the first time, active dispersal of *T. infestans* (walking and flying) was studied in their natural domestic habitat before and after a traditional vector control intervention with pyrethroid insecticide in and around dwellings. Effectively, the total number of *T. infestans* dispersers moving among habitats diminished after total spraying in 2009. The six intradomestic habitats that received two insecticide applications were not recolonized throughout the study (PPCh, unpublished data). Fifteen months after the last spraying, only one 5th instar nymph and a male of *T. infestans* with very low nutritional status were found in the room of a house. As no signs of colonization (faeces, exuviae, eggs) were found in the house, we consider these insects as possible invaders.

Schofield (1985) and other authors (McEwen and Lehane 1993, Schofield et al. 1992) have suggested that a low nutritional status (< 8mg/mm) triggers the flight initiation in *T. infestans*. This study demonstrates that flying adults of *T. infestans* are always individuals with low nutritional status. Moreover, the nutritional status of 90% adults in the peridomestic populations at the end of the study showed median values above 10 mg/mm, indicating a low probability to disperse by flight. Some peridomestic adults (10%) presented nutritional values < 8mg/mm, compatible with flight initiation probability.

In other endemic areas, the connection between peridomestic and wild populations of *T. infestans* could influence peridomicile infestation prevalence. However, a simultaneous and intensive search of wild *T. infestans* in the study area was negative (G. Marti, unpublished data), indicating that the exchange of individuals occurred among peridomiciles but not between the wild and peridomestic habitats.

Low flight dispersal of *T. infestans* in peridomestic sites was reported by Vazquez-Prokopec et al. (2004, 2006), although during these studies no vector control interventions were performed. Our study demonstrates that the active dispersal of *T. infestans* decreases after the traditional spraying with pyrethroids. Fewer total dispersers after a traditional spraying (24 before vs five after) indicate that the vectorial control had an effect on the active dispersal of *T. infestans* in Los Llanos Riojanos.

Previous studies suggested that active dispersal in triatomines may be optimal between 26° and 29° C as it increases metabolism, frequency of feeding, and reproduction. One flight inhibition factor seems to be wind speed above 5 km/h (Curto de Casas and Carcavallo 1995, Schofield et al. 1992; Vazquez-Prokopec et al. 2006). Our study shows that climatic variables during the capture dates were within optimal values, with median temperature values of 25 and 29° C, less than 60% relative humidity, and low wind intensity (<5 km/h). The reduction of total *T. infestans* dispersers after spraying of intradomestic and peridomestic sites could not be attributed to weather variables, which remained favorable to dispersion activities during the study.

During the post-spraying period, sylvatic triatomine species showed higher invasion pressure than did *T. infestans*. *T. guasayana* had the highest potential for flight dispersion, as reported in other studies (Wisnivesky-Colli et al. 1993). No difference in the total number of sylvatic species was observed before or after total spraying. This was likely due to the sylvatic nature of their foci, unaffected by vector control activities. A relevant number of *T. eratyrusiformis,* a rupicolous species typical of northwest Argentina, was found as a second important sylvatic species, which has yet to demonstrate significant evidence of public health importance. According to Salvatella et al. (2014), because this and other secondary species invade but do not colonize the intradomicile, they should not be considered in the existing epidemiological surveillance routine. However, local people may confuse these species with *T. infestans* when they observe these insects arriving at the domestic area, creating a false alarm for people in charge of the control programs and/ to researchers working in the area (Abrahan and Cavallo unpublished data).

After 15 months of insecticide spraying, the six intradomiciles remained free of *T. infestans* colonies, supporting that traditional spraying with pyrethroids is effective in the human habitations (indoors) where the highest probability of *T. cruzi* vectorial transmission occurs. Although some peridomestic structures remained infested, a low probability of intradomestic recolonization by active dispersal from peridomiciles may be suggested. A similar situation was observed in the San Martín department near the Independencia department (Gorla et al. 2009). The present work as well as data provided by Abrahan et al. (2011) and Hernández et al. (2013) support the idea of a low exchange of individuals between intra- and peridomestic habitats in domiciliary units of the arid Chaco. We believe that assessing the effective number of dispersers in an area is a good predictor of house invasion risk and it is important in terms of vector transmission probability.

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