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Seasonal variations in active dispersal of natural populations of *Triatoma infestans* in rural north-western Argentina

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Abstract. The flight dispersal of *Triatoma infestans* Klug (Hemiptera: Reduviidae) is one of the main mechanisms determining community re-infestation after control interventions. An empirical model of flight initiation coupled with data from a longitudinal study predicted that the flight dispersal of *T. infestans* would peak in summer. To test this prediction, longitudinal light trap collections were conducted during 3–8 nights in March (late summer), July (winter) and November (spring) 2003, and in March 2004 in a rural community in north-west Argentina. Following each light-trapping collection date, all peridomestic sites around light traps were inspected to assess the relative abundance and nutritional status of *T. infestans* at each site. A total of 21 adult and five nymph *T. infestans*, six *Triatoma guasayana* Wygodzinsky & Abalos, and nine *Triatoma garciabesi* Carcavallo *et al.* were collected in 96 light-trapping nights, whereas 696 *T. infestans* were collected from the peridomestic sites that surrounded the light traps. The arrival of *T. infestans* in the light traps occurred in 64% of catch stations and peaked in the summer surveys (10–14 bugs) compared with spring and winter surveys. When winds were < 5 km/h, the arrival of adult *T. infestans* at the light traps was significantly associated with maximum temperature and relative humidity. This is the first field report of seasonal variations in the flight dispersal activity of *T. infestans*.

Key words. Triatominae, Chagas' disease, light trap, seasonal flight, vector ecology.

Introduction

The control of Chagas' disease vectors is based on the application of pyrethroid insecticides and entomological surveillance (World Health Organization, 2002). In the Gran Chaco region of South America, the elimination of the main vector, *Triatoma infestans* Klug, proved to be much harder in the peridomestic environment (Cecere *et al.*, 1997; Gürtler *et al.*, 2004). Peridomestic sites are the first to be recolonized by *T. infestans* after control interventions, sustain more abundant populations than domestic sites, and are considered one of the main sources of community re-infestation during the early surveillance phase (Cecere *et al.*, 2004).

The passive transport of bugs from infested neighbouring communities and flight dispersal from infested peridomestic residual foci are considered the two main mechanisms determining the re-infestation of rural communities (Carcavallo 1985; Schofield & Mathews, 1985; Schofield, 1985; Cecere *et al.*, 2004). An empirical model predicted that flight initiation of laboratory-reared *T. infestans* was associated with a low nutritional status (measured by the weight : length ratio, w : l) and high temperatures (Lehane *et al.*, 1992). When data on the w : l

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ratios of peridomestic bugs and field temperatures were fitted into the Lehane *et al.* (1992) model, the flight initiation activity of *T. infestans* was predicted to peak in summer, when adults also peak in abundance and reached the lowest w : l ratio (Ceballos *et al.*, 2005). None of the previous field studies of flight dispersal of *T. infestans* explored seasonal variations (Lehane & Schofield, 1981; Schweigmann *et al.*, 1988; Schofield *et al.*, 1992; Vazquez-Prokopec *et al.*, 2004). Building on these results, and as a part of a wider study on the spatial and temporal patterns of community re-infestation by *T. infestans* in northwest Argentina, we conducted longitudinal light trap collections during 3–8 nights in March (late summer), July (winter) and November (spring) 2003, and in March 2004 in a rural community to determine whether there is a seasonal variation in the flight dispersal activity of natural populations of *T. infestans*.

Materials and methods

Study area

The study was carried out in the rural community of Amamá (27°12′33″ S, 63°02′10″ W) in the province of Santiago del Estero, Argentina (Fig. 1). The landscape and climatic characteristics of this area have been described previously (Vazquez-Prokopec *et al.*, 2004). Most houses have adobe walls and thatched roofs. Domestic animals are raised by residents for subsistence in the compound that surround human habitations. This peridomestic environment includes mostly storerooms, chicken coops and corrals (Canale *et al.*, 2000). Houses are commonly illuminated by one to three kerosene lamps for a few hours after sunset, with the exception of two households (in which we did not operate light traps), which have had electricity since November 2003. Amamá and neighbouring communities have been under communitywide domestic triatomine surveillance since 1992 (Cecere *et al.*, 2004).

Study design

In March (late summer), July (winter) and November 2003 (spring), and in March 2004, between eight and 11 light traps per survey were set up in houses along two perpendicular transects with 3–6 catch sites in each (Fig. 1). The selected catch sites were 40–60 m distant from peridomestic sites that had been infested by *T. infestans* in October 2002. In July 2003 and March 2004 light traps could not be set up at all catch stations due to the absence of some homeowners. In November 2003 and March 2004 two additional catch stations were placed 1–2 km from Amamá, with the aim of collecting sylvatic triatomines from the surrounding forest. In each survey, all catch stations along a given transect were operated simultaneously on alternate nights. Catch sites were located in a way that enabled maximum visibility from all the surrounding structures. In each survey, light traps were set up in the same household compound, with the same position and orientation. The mean distance from a light trap to the nearest peridomestic structure was 38 m (range 7–100 m).

The light trap system consisted of a vertical white cloth illuminated by a portable lantern with a black light tube (Vazquez-Prokopec *et al.*, 2004). On each survey night, light trapping started 15 min before sunset and continued for the following 2 h. A trained householder was left in charge of each light trap and collected the bugs in and around it every 30 min. In March 2003, only nights with temperatures over 20°C and no rainfall were selected for light trapping (Vazquez-Prokopec *et al.*, 2004). On the day after each light-trapping period, two skilled bug collectors searched for triatomines in all peridomestic structures of the house in which the light trap had been operated using 0.2% tetramethrin dislodgant (Icona, Buenos Aires, Argentina) for 30 min per compound (timed manual collection, TMC, or flushing-out method) to assess the relative abundance and nutritional status of *T. infestans* at each site. The study sites were not sprayed with insecticides during the study period. In April 2004, all domestic and peridomestic sites in Amamá and the nearby communities were inspected by TMC before communitywide insecticide spraying.

All triatomines collected by light trap or TMC were identified to species, counted by stage, weighed individually in an electronic balance (to a precision of 0.1 mg; OHAUS, Pine Brooks, NJ, U.S.A.), measured from clypeus to abdominal tip with a hand-held vernier calibre accurate to 0.02 mm, and microscopically examined for *T. cruzi* infection at 400× magnification. The qualitative nutritional status of adults was determined by direct observation of the volume and shape of the anterior midgut against a flashlight and classified as starved or with scarce, good or large blood contents (Ceballos *et al.*, 2005). The quantitative nutritional status of adults was determined by the w : l ratio (Schofield, 1980).

A weather station (Weather Monitor II; Davis Co., Baltimore, MD, U.S.A.) located in Amamá measured temperature, relative humidity, wind speed and direction, barometric pressure and rainfall at 15-min intervals during each light-trapping period. The moon phase on each light-trapping night was obtained from digital records and expressed as the percentage of the moon's surface that was lit. Each light trap and its surrounding domestic and peridomestic structures were located using a geopositioning system (GeoXM; Trimble, Sunnyvale, CA, U.S.A.) in March 2003.

Statistical analysis

Multiple linear regression (Zar, 1996) was used to identify the environmental variables associated with the arrival of bugs in the light traps. The rate of collection of *T. infestans* (number of *T. infestans* arriving in the traps/number of light traps) per night was square root-transformed to increase the model fit. Multicolinearity between independent variables was assessed, and only non-intercorrelated variables were included in the final model. The Kruskal–Wallis test (Zar, 1996) was used to determine the differences in the w : l ratio of peridomestic bugs collected by TMC. The association between the number of bugs collected in light traps and total bug abundance or total number of adults collected by TMC within 200 m of each light trap was assessed by simple linear regression.

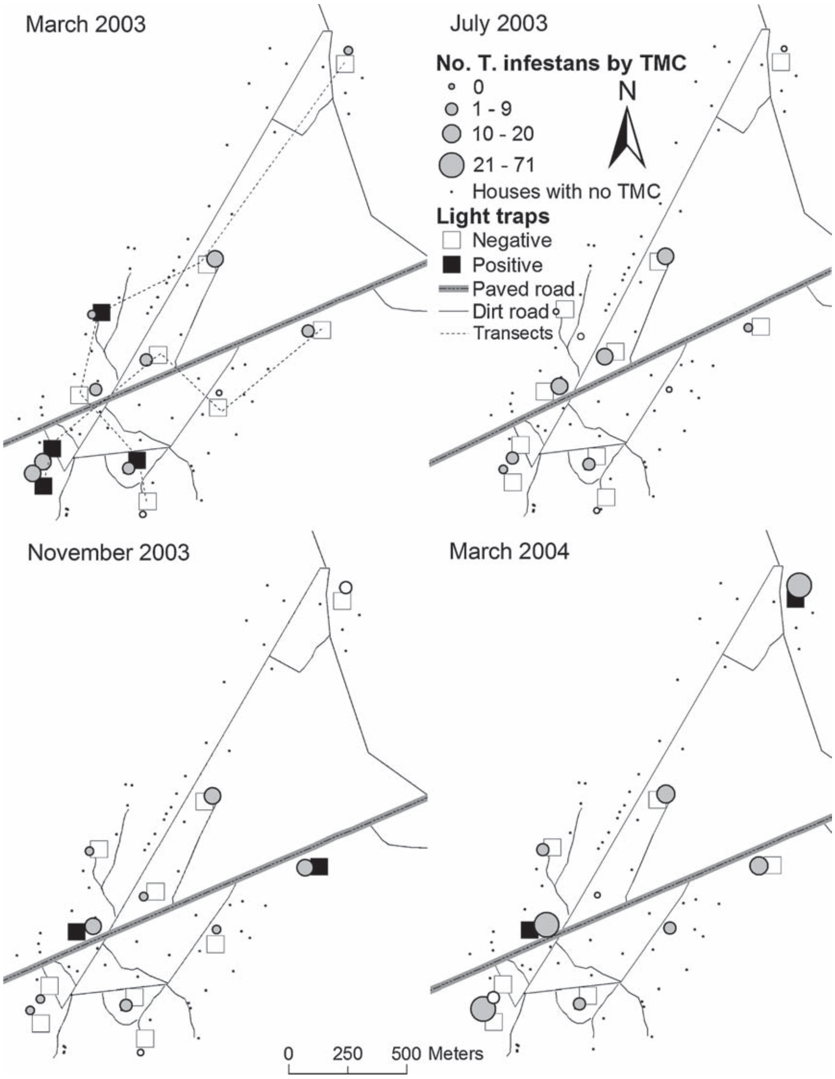

Fig. 1. Map of Amamá indicating the location of light traps, whether they collected *T. infestans* or not, and the number of *T. infestans* collected by timed collections in March, July and November 2003 and March 2004.

Results

A total of 26 *T. infestans* bugs (14 males, seven females, four V and one IV instar nymphs), six *T. guasayana* (five males and one V instar nymph), and nine *T. garciabesi* (five males and four females) were collected during 96 light-trapping nights between March 2003 and March 2004 (Table 1). In contrast, no *T. infestans*, six *T. guasayana* (four males and two females) and one female *T. garciabesi* were collected during 38 trapping nights in the forest around the community (data not shown). Overall, 64% of the 11 catch stations collected at least one *T. infestans* during the study period (Table 1). The percentage of positive light traps varied from 0% to 36%. Collection of *T. infestans* in light traps occurred mostly in March (10–14 bugs), compared with November (two bugs) and July (no bugs). The mean number of *T. infestans* per positive light trap was 3.3 (range 1–5) (Table 1). The male : female ratio of light trap collections ranged from 5 : 1 to 0.6 : 1.

A total of 696 *T. infestans*, one *T. guasayana* and 59 *T. garciabesi* was collected by TMC around the light traps. The percentage of peridomestic sites infested by *T. infestans* (15−23%) varied only slightly between surveys (Table 1). Adult *T. infestans* abundance peaked in March surveys (54–60% of total catch), whereas nymphs peaked in November (80% of total catch). The overall sex ratio was male biased (1.7 : 1) (Table 1). *T. cruzi* infection was detected only in March 2004 in 11 *T. infestans* (five adults collected in one light trap and six adults collected by TMC in a domicile 8 m distant from this light trap). In a subsequent survey of all Amamá compounds in April 2004, a total of 207 *T. infestans* were collected from 21 compounds (38%), none of which were infected by *T. cruzi*.

The locations of the *T. infestans*-positive light traps differed between dates except for a compound in the centre of the community, which was positive in both November 2003 and March 2004 (Fig. 1). The mean distance of a positive light trap to the nearest infested peridomestic site was 39 m (range 19–82 m) in March 2003, 30 m (range 23–38 m) in November 2003, and 16 m

Table 1. Collection of *T. infestans* by light traps and timed catches (TMC) during March, July and November 2003 and March 2004 in Amamá.

		Survey date				
Collection method	Variable	Mar 2003*	Jul 2003	Nov 2003	Mar 2004	Total
Light traps	No. of light-trapping nights	35	13	27	21	96
	% of *T. infestans* positive light traps	36	0	18	25	64
	No. of *T. infestans* collected					
	Males	10	0	1	3	14
	Females	2	0	0	5	7
	Nymphs	2	0	1	2	5
	Mean number of *T. infestans* per positive light trap (SD)	3.5 (2.7)	0	1.0 (0)	5.0 (4.2)	3.3 (2.8)
TMC	% sites infested (no. examined)	22 (51)	15 (52)	23 (57)	22 (46)	20 (206)
	No. of *T. infestans* collected					
	Males	61	15	22	58	156
	Females	33	8	23	30	94
	Nymphs	81	132	175	58	446
	Mean *T. infestans* mosquito abundance per infested site	14.6	15.5	16.9	12.3	14.8

*Vazquez-Prokopec *et al.* (2004).

(range 8–25 m) in March 2004. *T. infestans* nymphs walking to the light traps was observed in March and November 2003, and in March 2004 (Table 1). Dispersing nymphs were collected at a mean distance of 26 m (range 8–42 m) from the nearest infested site.

The number of *T. infestans* bugs caught per light-trapping night showed a seasonal pattern, peaking in March (late summer) surveys (Fig. 2). Low temperatures (mean $< 10°C$) probably explain the absence of bugs in July, whereas the fewer bugs collected in November with respect to March surveys could not be explained by period mean, minimum or maximum temperatures alone (Fig. 2). The number of *T. guasayana* collected in light traps was much higher in November (11 bugs) than in other surveys (one bug), whereas the arrival of *T. garciabesi* bugs at light traps did not show any temporal pattern (range 2–4 bugs) (data not shown). Most of the *T. infestans* bugs that arrived at the light traps (90%) were starved or had very low blood contents. The w : l ratio of peridomestic *T. infestans* bugs did not differ significantly between surveys for males (Kruskal–Wallis test; $H = 5.1$, d.f. $= 3$, $P = 0.17$) or females ($H = 4.03$, d.f. $= 3$, $P = 0.26$). Male *T. infestans* captured in goat or pig corrals had a significantly lower w : l ratio compared with males from ecotopes associated with chickens ($H = 5.4$, d.f. $= 1$; $P = 0.02$), whereas female w : l ratios did not differ significantly between ecotopes ($H = 1.47$, d.f. $= 1$, $P = 0.23$).

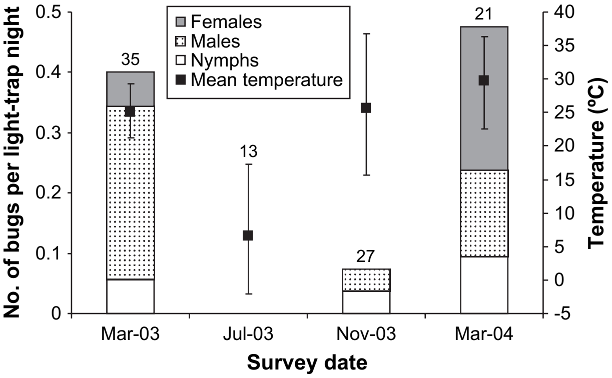

Fig. 2. Number of *T. infestans* males, females and nymphs per light-trapping night (bars), and mean, minimum and maximum temperature during light-trapping periods. Numbers on top of bars represent the total trapping effort. Amamá, March, July and November 2003 and March 2004.

The range of w : l values for light trap-collected *T. infestans* was 3.6–10.3 mg/mm for males and 5.9–11.1 mg/mm for females. If the maximum w : l ratio of each sex captured by light trapping is taken as the upper extreme allowing flight, the predicted percentages of time-collected peridomestic males that would be able to fly were 54% in March 2003, 33% in July 2003, 41% in November 2003, and 43% in March 2004, whereas the predicted percentages for females were 46%, 13%, 35% and 33%, respectively. The percentage of all *T. infestans* adults able to fly that arrived at the traps (calculated as the number of light-trapped adults to the total number of TMC-collected adults with a w : l ratio less than the upper extreme compatible with flying) was 19% for males (range between dates 0–30%) and 21% for females (range 0–50%). Most of the *T. infestans* (57%) flew to the light traps when the wind speed was > 1 km/h and all flew when wind was < 5 km/h and when the temperature was $\geq 22°C$. The square root-transformed rate of collection of adult *T. infestans* bugs (number of bugs arriving at the traps/number of light traps) per night with winds < 5 km/h was significantly associated with maximum temperature (multiple linear regression coefficient, beta $= 0.58$, $P < 0.04$) and relative humidity (beta $= 0.66$; $P < 0.025$) during light trap collections (Fig. 3). No association with barometric pressure or phase of the moon was observed. The rate of collection of *T. infestans* nymphs was

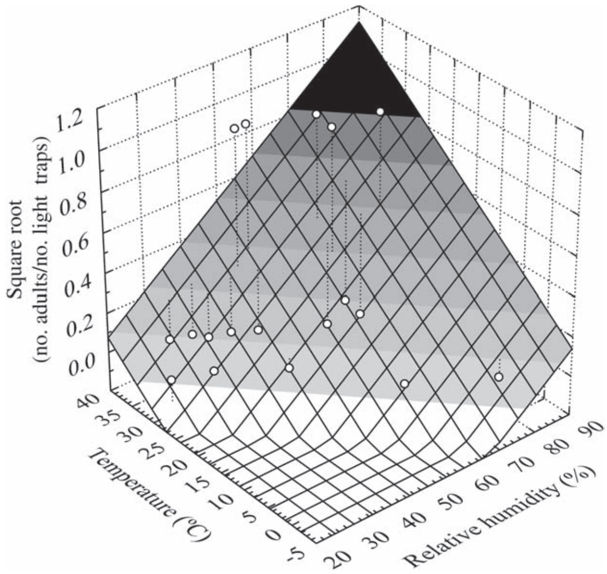

Fig. 3. Association between the square root-transformed rate of collection of adult *T. infestans* per light-trapping night, maximum temperature and relative humidity excluding those nights with winds speeds $>$ 5 km/h. Dots represent the total catch for each light-trapping night during March, July and November 2003 and March 2004 in Amamá.

not significantly associated with any climatic variable. The number of light-trapped adult *T. infestans* in the March surveys was positively and significantly ($P < 0.01$) associated with adult bugs abundance ($R^2 = 0.60$) and with total bug abundance ($R^2 = 0.57$) within 200 m of each light trap (data not shown).

Discussion

This is the first field demonstration of seasonal variations in flight dispersal activity of *T. infestans* in a well defined rural community. Active dispersal of *T. infestans* peaked in summer and males outnumbered females, validating the predictions of Ceballos *et al.* (2005). Moreover, the flight dispersal activity of *T. guasayana* appeared to peak in spring (November). The flight dispersal activity of *Triatoma protracta* Uhler and *Triatoma rubida* Neiva was found to peak in summer in the Arizona desert (Sjogren & Ryckman, 1966; Ekkens, 1981), whereas that of *Triatoma dimidiata* Latrielle, *Triatoma dispar* Lent, and *Panstrongylus geniculatus* Latreille peaked at the end of the dry season (spring) in the forests of Costa Rica (Zeledón *et al.*, 2001).

Several factors may contribute to the seasonal pattern of flight dispersal activity of *T. infestans*. In July (winter), the combination of low air temperatures and high w : l ratios inhibit the dispersal of bugs. In the context of adequate temperatures for flight dispersal ($>$ 22°C) in the November (spring) and March (late summer) surveys, a joint increase in adult bug abundance and decreased nutritional status (and w : l ratio) are the most likely explanations for the peak in dispersal in late summer. Adult bug abundance peaked in the March surveys, whereas w : l ratios did not differ significantly between seasons, probably because of the low number of bugs and peridomestic sites included in our current dataset. However, a larger prospective study based on 814 bugs from 70 peridomestic sites has shown that the w : l ratio of *T. infestans* was significantly lower in summer because domestic animals were less available and the metabolic rate of bugs was higher (Ceballos *et al.*, 2005). Because both summer light-trapping surveys were performed in March, the precise time window in which flight dispersal occurs and potential differences in dispersal timing between sexes (Ekkens, 1981) could not be assessed. These aspects may have important implications for designing optimal spraying regimes.

Pooling all dates of collection allowed us to cover a wide range of climatic conditions (24–91% RH, 1–36°C, wind speed 0–10 km/h) in order to determine the environmental factors that affect *T. infestans* dispersal. Bugs arrived at the light traps when temperatures were $>$ 22°C, which is very close to the 23°C threshold observed for the flight initiation of *T. infestans* in experimental huts under natural climatic conditions (Gurevitz *et al.*, 2006). The flight of *T. infestans* bugs to the traps occurred only when wind speed was $<$ 5 km/h; this is slightly lower than the 6 km/h reported previously (Vazquez-Prokopec *et al.*, 2004) because here we included a wider range of environmental conditions. Under these conditions, other environmental factors such as the maximum temperature during light trapping and the relative humidity were positively associated with the arrival of bugs in the light traps. The negative effect of wind on the flight dispersal of *T. infestans* has also been observed in many other bloodsucking insects (Lehane, 1991). When winds were $<$ 5 km/h and temperatures $>$ 22°C, only bugs with a w : l $<$ 10.3 mg/mm (males) or $<$ 11.1 mg/mm (females) arrived at the light traps. If these examples of extreme w : l ratios for each sex captured by light trapping are taken as representing the upper extreme values allowing flight, and assuming that the dispersers came from the infested peridomestic sites sampled by timed collections, some 50% of the latter bugs were in a condition compatible with initiating a dispersive flight. The occurrence of flights not directed towards the light traps and interindividual differences in flight dispersal capacity may in part explain the fewer than expected number of adults that arrived at the traps. More research on flight behaviour and the in-flight orientation of triatomine bugs is needed to understand the patterns observed.

All the light-trapped adult *T. infestans* were collected by the villagers directly from the traps, close to the light source. However, walking cannot be excluded as an additional mechanism of active dispersal of adult *T. infestans*. By searching for bugs around the light traps every 30 min, we detected five nymphs that had walked to the light traps but no adults. Thus, active flight appeared to be the most likely mechanism for the arrival of adults at the light traps.

The range, frequency and seasonality of triatomine flight are of particular importance to the epidemiology and control of Chagas' disease vectors because they affect the spatial patterns of re-infestation and parasite distribution in a rural community. The occurrence of *T. infestans*-positive catch stations (64%) was high, and although the total number of light-trapped bugs was low, the occurrence of flights was more frequent than previously supposed (Ronderos *et al.*, 1980). This is especially so because the local densities of *T. infestans* in the late summer surveys were very much lower than the typical densities found in the absence of control actions. This suggests that re-infestation of rural communities after insecticide spraying may be driven by flight dispersal from low-density residual foci. Moreover, the positive association observed between flight dispersal and the density of peridomestic bugs 200 m around the light traps suggests that a much higher number of flights can be expected to occur in heavily infested communities.

In the Gran Chaco region, goat and pig corrals are considered the likely sources of dispersers because they sustain dense *T. infestans* populations with a lower nutritional status (Ceballos *et al.*, 2005). In March 2004, dispersal from a domicile to the light traps was evidenced by both the finding of *T. cruzi*-infected adult bugs in one light trap and in a domicile 8 m away, and by the absence of infected bugs in other houses in Amamá. The w : l ratio of the bugs from that domicile was very low (< 9.8 mg/mm) because householders and dogs slept outdoors during the prevailing hot weather. Thus, under particular circumstances, domiciles can also be a source of dispersers. A clustered spatial pattern of bug infection within a rural community may follow the propagation of infected *T. infestans* from such domiciles.

Using spatial statistics and geographic information systems, Cecere *et al.* (2004) determined that to prevent the propagation of *T. infestans* from an epicentre of re-infestation, all houses and peridomestic sites 450 m around it should be sprayed with insecticides. Our data suggest that the spraying of epicentres should ideally be performed before the flight dispersal season in order to reduce the propagation of bug colonies around them. This may help vector control agencies to target control actions against *T. infestans* more effectively.

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