

Active Dispersal of Natural Populations of *Triatoma infestans* (Hemiptera: Reduviidae) in Rural Northwestern Argentina

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ABSTRACT An empirical model of flight initiation coupled with data from a longitudinal study predicted that the flight dispersal of *Triatoma infestans* from peridomestic sites was more likely to occur in late summer. To partially test this prediction, we operated 11–12 black light traps from 1945 to 2200 hours in March 2003 in two villages in northern Argentina. All peridomestic sites around the light traps were later inspected to assess the relative abundance and nutritional status of *T. infestans* at each site. Traps were located 19–94 m from the nearest infested site. A total of 2 female, 10 male, and 3 fifth-instar nymphs of *T. infestans*; 4 adult *Triatoma garciabesi*; and 1 *Triatoma guasayana* fifth-instar nymph were collected in 64 trap nights. Nearly two-thirds of the bugs arrived to the traps during the first hour after sunset, when ambient temperatures were 22–28°C; 80% of adults were unfed. The number of *T. infestans* that flew to the traps was significantly and negatively associated with wind speed, and the number of males positively associated with the abundance of adult *T. infestans* in peridomestic sites within 200 m around each light trap. This is the first successful application of light traps for collecting dispersing nymphal and adult *T. infestans* on a village-wide scale. We attribute this success to the placement of traps with consideration to spatial infestation patterns and seasonal variation in nutritional status of peridomestic triatomine populations.

KEY WORDS flight, light trap, vector ecology, Triatominae, Chagas' disease

Triatoma infestans (Klug), the main vector of Chagas' disease, infests almost exclusively domestic and peridomestic habitats (Zeledón and Rabinovich 1981, Noireau et al. 2000). Transmission of *Trypanosoma cruzi* (Kinetoplastida: Trypanosomatidae) mostly occurs in human habitations (Cohen and Gürtler 2001), but in the Gran Chaco region peridomestic foci of *T. infestans* are very frequent and persist after insecticide spraying (Cecere et al. 2002, Gürtler et al. 2004). Flight dispersal of *T. infestans* from infested residual foci is considered one of the mechanisms determining domestic reinfestation after control interventions (Carcavallo 1985, Schofield 1985).

Flight initiation by triatomine bugs was associated with low nutritional status (measured by the weight/length ratio, W/L) and high temperatures (Ekkens 1981, Lehane and Schofield 1982, Lehane et al. 1992). The probability of flight initiation of *T. infestans* in the laboratory was closely associated with their W/L and maximum temperature (Lehane et al. 1992), and so was the likelihood of flight initiation of laboratory-reared *T. infestans* bugs under natural climatic condi-

tions (Lehane et al. 1992, Schofield et al. 1992). Flight dispersal of *T. infestans* was recorded at 1.5–2.0 km from their putative sources (Schweigmann et al. 1988). However, in a mark-release trial conducted in goat corrals, the high recapture rate of adult *T. infestans* suggested a very low dispersal rate during the following 1–4 mo (Ronderos et al. 1980). The lack of an effective and simple method for sampling flight-dispersing *T. infestans* accounts for the near absence of field reports, and hindered investigations on the determinants of house invasion by triatomines.

Poor nutritional status of bug populations can lead to more dispersive flights, and thus regulate triatomine population density (Schofield 1985). Higher bug densities per host would reduce the population nutritional state and increase the likelihood of flight initiation. In northwestern Argentina, the nutritional status and daily feeding rates of *T. infestans* varied among seasons in chicken coops (Lopez et al. 1999) and other peridomestic ecotopes (unpublished data). Fitting the observed W/L ratios and field maximum temperatures into the model by Lehane et al. (1992), the probability of flight initiation was predicted to peak in summer, when adult triatomines also peaked in abundance and reached the lowest W/L ratio (unpublished data). As a part of a wider study on the spatial and temporal

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patterns of reinfestation by *T. infestans* in northwestern Argentina, we conducted simultaneous light trap collections in two neighboring rural villages during the most likely flight dispersal period, and related the flight activity of *T. infestans* to weather and demographic variables.

Materials and Methods

Study Area. The study was carried out in the rural villages of Amamá and Trinidad (27° 12' 33"S, 63° 02' 10"W), Province of Santiago del Estero, Argentina (Fig. 1). Both villages are situated within 9 km of each other in semiarid hardwood, thorny forest habitat. Amamá houses are relatively close together and surrounded largely by grasses, whereas Trinidad houses are widely dispersed and surrounded by high trees, abundant cactaceous plants, and little grass. The climatic characteristics of this area were described previously (Vazquez-Prokopec et al. 2002). The peridomestic environment includes mostly storerooms, chicken coops, and corrals (Canale et al. 2000). The houses were illuminated by one to three kerosene lamps for a few hours after sunset. The villages were under community-based domestic triatomine surveillance (Cecere et al. 2002).

Study Design. A pilot trial aimed at training local villagers in light trap collections was conducted in October 2002. A total of 9 light traps was operated in 9 Amamá houses for 4 nights. All 300 houses and peridomestic sites of Amamá and neighboring villages were searched for triatomines by timed manual collections with an irritant spray, and the bugs removed.

In March 2003, the light traps in Amamá and Trinidad were set up along two transects with five to six catch sites each (Fig. 1). The selected catch sites were close to peridomestic sites that had been infested by *T. infestans* in October 2002. Each light trap was set up in a way that enabled maximum visibility from all the surrounding structures. The mean distance from a light trap to the nearest peridomestic structure was 38 m (range 7–100 m) in Amamá and 52 m (range 17–102 m) in Trinidad. The light trap system consisted of a vertical white cloth (1.25 × 2 m) illuminated by a portable lantern (Energizer Multifunction Lantern Number 9450, Energizer, St. Louis, MO) with a 6 W black light tube (F6T5BLB; Satellite, Hong Kong, China).

After appropriate training, a householder, using disposable gloves and a flashlight, was left in charge of each light trap to collect the bugs in and around it; two to four family members usually accompanied him or her. All the insects collected during each 30-min interval were stored in separate plastic bags labeled with collection times. Light trapping was performed from 19:45 (15' before sunset) to 22:00 h because the flight activity of *T. infestans* is known to peak during the first hour after sunset (Lehane and Schofield 1982).

In each village, all catch stations along a given transect were operated simultaneously on alternate nights. This design was chosen to increase the chance of collecting bugs, to compare catches between vil-

lages, and to cover the whole community. Only nights with temperatures above 20°C and no rainfall were selected for light trapping because of the well-known temperature-dependent flight dispersal of *T. infestans* and the inhibitory effects of rainfall. Appropriate light-trapping nights occurred on 10, 11, 17, 18, and 19 March 2003, with a total trapping effort of 58 night traps, and a mean number of 5.8 traps per village night. In addition, six light-trapping nights were performed in Amamá near high-density peridomestic sites on 3, 8, and 12 March to increase the chances of bug collection.

A weather station (Weather Monitor II, Davis, Baltimore, MD) located in Amamá measured temperature, relative humidity, wind speed and direction, barometric pressure, and rainfall at 15-min intervals during the trapping period. Moon phase during each light-trapping night was measured as the percentage of the moon's surface that was lit. Each light trap and the surrounding domestic and peridomestic structures were located using a GPS (GeoExplorer II; Trimble, Sunnyvale, CA).

After the light-trapping period, two skilled bug collectors searched for triatomines in all peridomestic structures surrounding the light traps using 0.2% tetramethrin dislodgeant (Icona, Buenos Aires, Argentina) for 30 min per house (timed manual collections or flushing-out method) to assess the relative abundance and nutritional status of *T. infestans* at each site. A total of 51 peridomestic structures from 11 Amamá houses and 33 structures from 6 Trinidad houses was inspected for infestation.

All triatomines collected were identified to species and counted by stage, as described by Canale et al. (2000). Each adult and fifth-instar nymph were weighed individually in an electronic balance (precision, 0.1 mg; OHAUS, Pine Brook, NJ), measured from clypeus to abdominal tip with a hand-held vernier caliper accurate to 0.02 mm, and microscopically examined for *T. cruzi* infection at ×400. Females collected by light trapping were also dissected to determine whether they were inseminated or not, and to count the number of eggs in the ovaries. Because of the high number of females collected by timed collections, their reproductive state was determined indirectly by the number of eggs laid by each individual female after a 10-d period. The wings, legs, and head of all triatomines were stored in ethanol for other studies. The qualitative nutritional status of adult bugs 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 (Montenegro 1983).

Statistical Analysis. W/L ratios and the mean maxima (26.2°C) or the absolute maxima (29.4°C) between 20 and 22 h during the light-trapping period (T) were used to estimate the probability of flight initiation of peridomestic bugs collected by timed catches (P_b) (Lehane et al. 1992): $\text{Logit}(P_b) = -A + B(W/L) - C(W/L)^2 + D(T)$, where $\text{Logit}(P_b) = x$; $P_b = e^x / (1 + e^x)$; $A = 18.37$; $B = 1.97$; $C = 0.18$; $D = 0.43$.

(A) Amamá

Legend

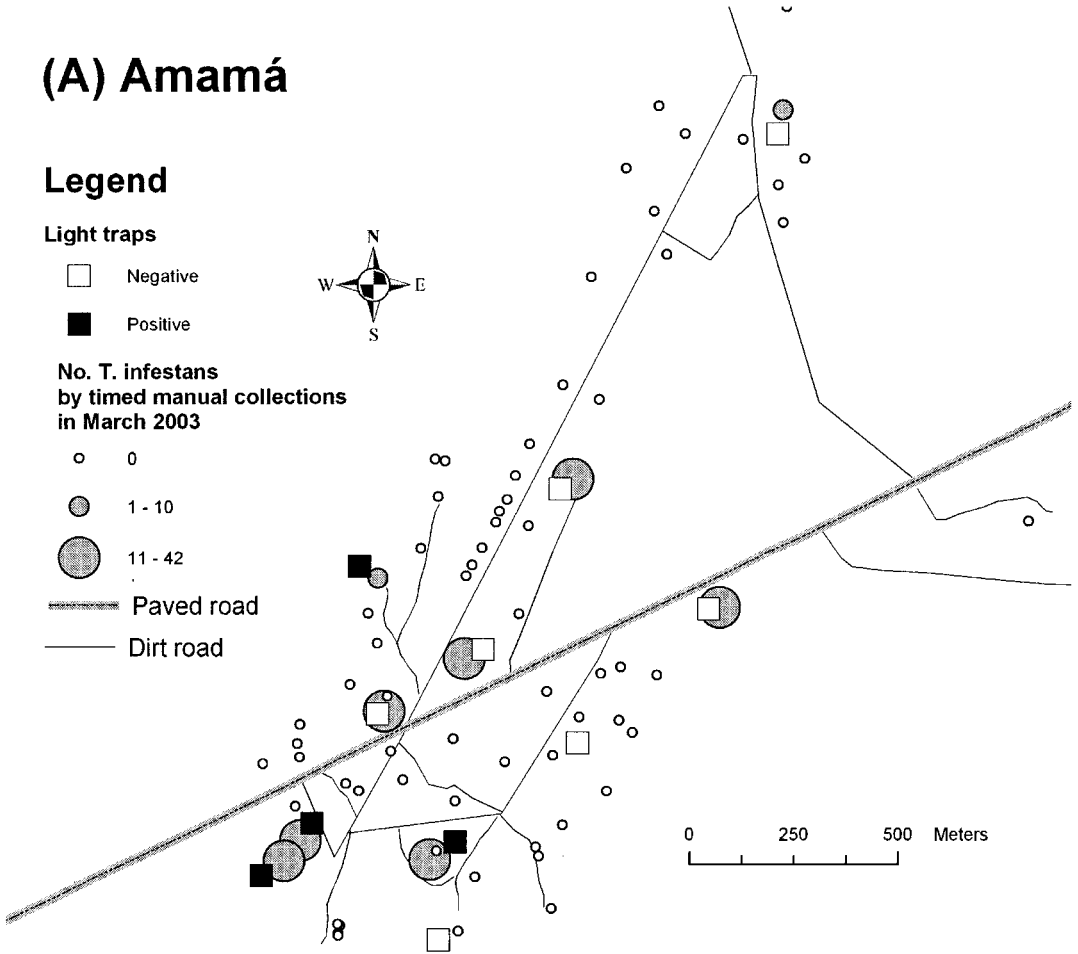
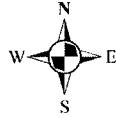
Light traps

- Negative
- Positive

No. *T. infestans* by timed manual collections in March 2003

- 0
- 1 - 10
- 11 - 42

- Paved road
- Dirt road



(B) Trinidad

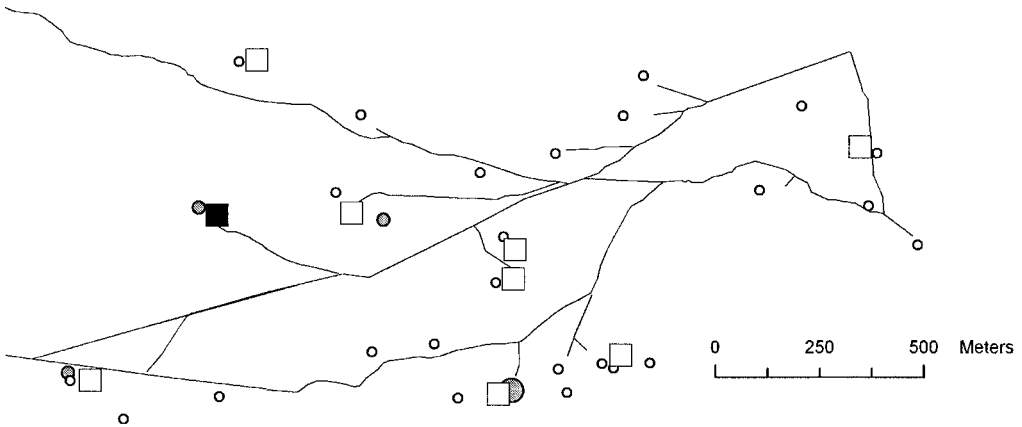


Fig. 1. Map of Amamá (A) and Trinidad (B) indicating the location of light traps, whether they collected *T. infestans* or not, and the number of *T. infestans* collected by timed catches in March 2003.

Table 1. Collections of *T. infestans* by timed manual catches and light traps in Amamá and Trinidad, March 2003

Collection method	Variable	Village	
		Amamá	Trinidad
Timed manual catches	% Sites infested (no. examined)	22 (51)	6 (33) ^a
	No. collected		
	Males	61	6
	Females	33	2
	Nymphs	81	18
	Mean bug abundance per infested site	14.6	6.5
Light trap catches ^b	No. traps positive/ No. trap nights	4/35	1/29
	No. collected		
	Males	10	0
	Females	2	0
	Nymphs ^c	2	1
	No. bugs per trapping night	0.40	0.03

^a Excludes one house infested by *T. infestans* as notified by householders.

^b Excludes 4 *T. garciabesi* (3 males, 1 female) and 1 fifth instar nymph *T. guasayana*.

^c Fifth instar nymphs.

As the exact source of the bugs that flew to each light trap was unknown, we pooled the abundance of *T. infestans* in all infested sites within a 200 m radius around each trap to assess the relationship between flight dispersal and bug abundance. This analysis was only performed for males because of the very low number of females collected by light trapping.

Results

In the pilot trial, 8 *Triatoma guasayana*, 1 *Triatoma garciabesi* and no *T. infestans* adults were collected by light trapping in October 2002. A total of 86 *T. infestans* (including 23 adult bugs) was collected by timed catches from 8 (21%) peridomestic sites around the light traps.

In March 2003, *T. infestans* bugs were collected by timed manual catches from 22% of Amamá peridomestic sites (totaling 175 bugs) and 6% of Trinidad peridomestic sites (26 bugs) (Table 1). A total of 15 *T. infestans*, 4 adult *T. garciabesi*, and 1 fifth-instar *T. guasayana* were collected during the 5 light-trapping nights (Table 1). None of the triatomines was infected by *T. cruzi*. The catch rate of *T. infestans* per light trap night in Amamá (0.40) was 13 times greater than that in Trinidad (0.03). All *T. infestans* except 1 fifth-instar nymph were collected in Amamá. Both the light trap and timed collections of *T. infestans* were significantly biased toward males ($\chi^2 = 5.3$, $df = 1$, $P < 0.02$; $\chi^2 = 10.0$, $df = 1$, $P = 0.002$, respectively). Seven (62.5%) of the *T. infestans* fliers and 2 of the 3 nymphs that walked to the traps did so within the first hour after sunset.

The mean distance from each light trap to the nearest *T. infestans*-infested site was 39 m (range 19–82 m) in Amamá and 58 m (range 30–94 m) in Trinidad, whereas the mean distance from a *T. infestans* positive light trap to the nearest infested site was 50 m (range 30–82 m) and 42 m, respectively. The mean distance between *T. infestans*-positive light traps was 344 m (range 72–653 m) in Amamá. The three *T. infestans* fifth instars were collected in two light traps at 30 and 42 m from the nearest infested site.

Overall, 80% of male and 50% of female *T. infestans* that flew to the light traps were starved, whereas the remainder had scarce blood contents (Fig. 2). The time-collected bugs had a significantly better qualitative nutritional status than the light trap-collected bugs (Fisher test, $P = 0.002$), with only 31% of males and 23% of females unfed. Female and male *T. infestans* collected manually from peridomestic sites had a similar nutritional status ($\chi^2 = 2.41$, $df = 1$, $P = 0.12$). The three *T. infestans* fifth-instar nymphs that walked to the traps had scarce (one bug) or good blood contents (two bugs).

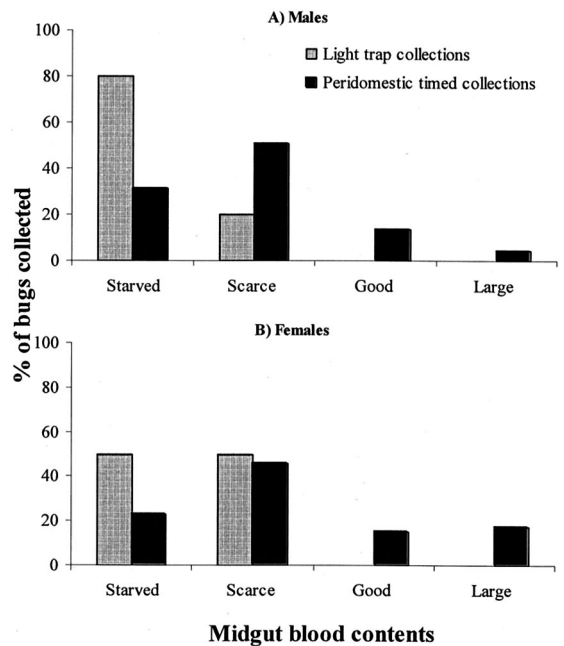


Fig. 2. Qualitative nutritional status of light trap and time-collected male (A) and female (B) *T. infestans* determined by transparency of the anterior midgut. Amamá and Trinidad, March 2003.

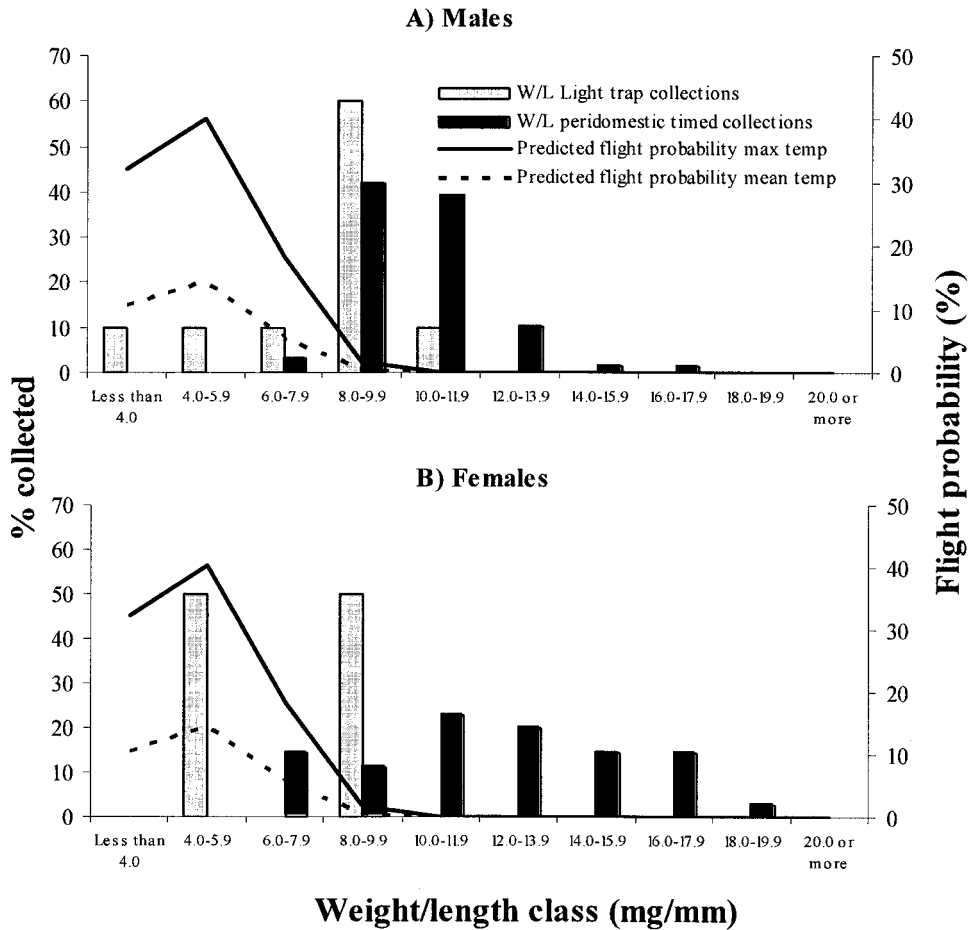


Fig. 3. Percentage of male (A) and female (B) *T. infestans* collected by light trapping or in peridomestic sites according to their nutritional status measured by the W/L ratio (bars). The figure also shows the percentage of bugs predicted to fly according to the model by Lehane et al. (1992) using W/L ratios and the period mean maxima (26.2°C, - - -) or absolute maxima (29.4°C, —) during light trap collections. Amamá and Trinidad, March 2003.

The mean weight of the *T. infestans* male fliers was significantly lower than the time-collected males (t test, $t = 3.92$, $df = 69$, $P = 0.0002$). The two light trap-collected females (150.9 and 222.2 mg) were also lighter than the time-collected females (mean \pm SD, 320.6 ± 88.4 mg). The length of light trap- and time-collected males did not differ significantly ($t = 1.45$, $df = 69$, $P = 0.15$). Only one of the light trap-collected females was inseminated and had six eggs (two vitellogenic and four chorionated), whereas 60% of time-collected females laid eggs (mean \pm SD, 16.6 ± 8.7 eggs).

Male *T. infestans* fliers had a significantly lower mean W/L ratio than the time-collected males ($t = 3.75$, $df = 69$, $P = 0.0004$) (Fig. 3). The two females collected by light trapping had a lower W/L (5.9 and 8.2 mg/mm) than time-collected females (12.3 ± 3.3 mg/mm). The extreme W/L values for the light trap-collected *T. infestans* were 3.6–10.3 mg/mm (males) and 5.9–8.2 mg/mm (females), whereas for the time-collected bugs, the extreme W/L were 7.9–16.7 and

6.6–18.6 mg/mm, respectively. If the extreme W/L of each sex captured by light trapping is taken as the extreme value allowing flight, twice as many time-collected male (53.7%) as female *T. infestans* (25.7%) would be expected to fly.

The predicted percentage of *T. infestans* that would fly, according to the model of Lehane et al. (1992), parameterized with the observed W/L ratios and mean or absolute maximum temperature during the light trap period, is also shown in Fig. 3. The model predicted that 60% of males and 50% of females that actually flew to the light traps would not be physiologically apt for flying, and that nearly all of the time-collected bugs with a W/L > 8.0 mg/mm would not be able to perform any dispersive flight at both temperatures. The observed number of *T. infestans* that flew to the traps was significantly higher than the expected number that would fly according to the model ($\chi^2 = 27839$, $df = 4$, $P < 0.001$).

Mean temperatures during the light-trapping nights were 22.3–27.8°C. The number of *T. infestans* that flew

T. infestans populations (Figs. 2B and 3B) probably explain why, in our study, females flew much less frequently than males. However, different flight activity patterns by sex (Ekkens 1981) or a higher attractiveness of male triatomines to black lights (Carcavallo 1985) cannot be excluded.

Winds of at least 6 km/h apparently inhibited *T. infestans*-dispersive flights, as incidentally observed by Schofield et al. (1992). Under laboratory conditions, the flight initiation of *T. infestans* was positively correlated with temperature, but no association was found with barometric pressure (Lehane et al. 1992). In our study, however, the lack of any relationship between flight dispersal and temperature or other weather conditions probably resulted from the exclusion of colder nights in which *T. infestans* flight activity was not expected to occur. The arrival of *T. infestans* bugs to the light traps was not associated with the phase of the moon, suggesting that this factor did not interfere with the orientation of bugs. The presence of a variable number of bug collectors among catch stations may have added an extra source of variation and differential attractiveness to the traps.

The model of Lehane et al. (1992) predicted the proportion of flight initiations from a given source population (although some of these flights were trivial), whereas the light trap collections are the effective number of bugs arriving from one or more infested sites. This difference should be taken into account when comparing the model with field data. According to the model (Lehane et al. 1992), 50–60% of the *T. infestans* bugs that effectively flew to the light traps would not have flown, and this difference would have been more marked had we considered the mean rather than the period maximum temperature. These discrepancies may originate from the use of *T. infestans* colonies kept under laboratory conditions for many years and the range of temperatures used for parameterizing the model. Compared with the *T. infestans* used by Lehane and Schofield (1982) (Table 2, p. 502), male and female bugs in our study were significantly longer (*t* tests, $P < 0.001$, and $P = 0.0003$, respectively), male fliers were significantly heavier ($P < 0.0001$), and W/L ratios would be strongly modified by disproportionate differences in weight. As laboratory-reared *T. infestans* colonies are shorter and lighter than natural populations, the exact quantitative predictions of the model with natural bug populations need to be adjusted.

T. infestans fifth-instar nymphs walked from 29 to 42 m to arrive at the light traps, assuming that they came from the nearest infested site. Schofield (1985) also mentioned these nymphs walking up to 60 m. The walking distances recorded in this study are consistent with the finding, in bedroom areas, of *T. infestans* nymphs that have fed on goats or bovids enclosed 50–80 m away (Gürtler et al. 1996). The active dispersal of large nymphs possibly plays an important role in the local propagation of *T. infestans* within and between neighboring households.

At a village level, the spatial patterns of reinfestation and gene flow are determined by flight dispersal and

may depend on distances between houses, the local abundance of bugs and hosts, and vegetation cover. Given a flight-dispersal capacity ranging from 200 to 2,000 m (Schweigmann et al. 1988, Schofield et al. 1992), *T. infestans* from a few peridomestic residual foci might reinfest the entire village. The spatial heterogeneity generated by the effects of landscape and vegetation cover may affect the spatial distribution of *T. infestans* infestations and the risk of house invasion if they act as a barrier for bug dispersal. In Amamá, the low vegetation cover allowed one trap to be seen 500–600 m away, whereas in Trinidad the visibility range of each trap was 100–200 m because of dense vegetation cover and higher trees. Thus, in addition to bug nutritional differences, differences in landscape and accessibility to the light traps may modify the numbers of *T. infestans* bugs that fly to the traps.

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