



Feeding rates, nutritional status and flight dispersal potential of peridomestic populations of *Triatoma infestans* in rural northwestern Argentina

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Abstract

Triatoma infestans, the main vector of Chagas disease in Southern Cone countries, frequently infests peridomestic structures housing domestic animals. A total of 814 *T. infestans* collected from 35 different peridomestic sites in rural northwestern Argentina over 1–4 consecutive seasons was examined for recent blood meals and nutritional status. Bugs from goat or pig corrals had lower qualitative nutritional status and mean weight to length ratios (W/L) than those captured in chicken coops. Males systematically had lower qualitative nutritional status and W/L than females. Using logistic multiple regression, the daily feeding rates of *T. infestans* were significantly associated with season and stage but not ecotope, whereas the proportion of well-fed bugs varied significantly with all three factors. The seasonal trends in feeding rates and nutritional status were consistent with the local availability and breeding timing of domestic animals. The observed data fed into an empirical model predicted that the probability of flight initiation would peak in summer from pig or goat corrals, not chicken coops, and be insignificant in all ecotopes in spring and fall. Male *T. infestans* outnumbered females as potential fliers. This is the first study conducted in well-defined habitat units that shows significant heterogeneities in the feeding rates and nutritional status of triatomine populations linked to host demographics and management, and how these affect flight dispersal potential over seasons. Peridomestic bug populations are of great relevance as a source of domestic reinfestation and for the elimination of *T. infestans*.

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1. Introduction

The nutritional status of insect populations affects their vital parameters and flight dispersal. In Triatominae (Heteroptera, Reduviidae), the regulation of population size is mediated by density-dependent

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host irritation due to triatomine bites (Rodríguez and Rabinovich, 1980; Schofield, 1980a). These determine the interruption of blood-feeding and a reduced blood intake which translates into lower vital rates, and possibly, an increased probability of dispersal. The probability of flight initiation of *Triatoma infestans* Klug, the main vector of Chagas disease in Southern Cone countries, was found to be significantly associated with low nutritional status (measured by the weight to length ratio, *W/L*) and high temperatures (Schofield et al., 1992; Lehane et al., 1992). The physical features of domestic or peridomestic structures modified microsite temperatures (Vazquez-Prokopec et al., 2002b) and the population growth rate of *T. infestans* in experimental huts (Cecere et al., 2003). The joint effects of triatomine density per host, type of habitat, and host species (Guarneri et al., 2000) determine the population size of *T. infestans* and therefore affect our ability to control infestations.

Triatoma infestans is highly adapted to human-made or modified domestic or peridomestic ecotopes. In semiarid rural Argentina, goat or sheep corrals and other structures housing chickens sustain abundant populations of *T. infestans* and other triatomines both before and after the residual application of pyrethroid insecticides (Canale et al., 2000; Gürtler et al., 2004). Peridomestic sites are of great relevance to the elimination of *T. infestans* because they are the first to be recolonized after insecticide spraying, sustain more abundant populations of *T. infestans* than domestic sites, and increase the risk of domiciliary reinfestation (Cecere et al., 2002, 2004). Surprisingly, our understanding of the temporal and spatial dynamics of peridomestic populations of *T. infestans* is very limited. *T. infestans* from chicken coops had high feeding rates and nutritional status during spring-summer, and were predicted to have a low potential for flight dispersal (López et al., 1999), but this study neither included other ecotopes or seasons nor examined variations among sites. As part of a wider study on the spatial and temporal patterns of reinfestation by *T. infestans* in northwestern Argentina, we sought to determine the joint effects of ecotope-host, season and bug stage on the feeding rates and nutritional status of peridomestic bug populations using each peridomestic site as the unit of analysis. We fitted the observed *W/L* ratios and field temperatures into the empirical model by Lehane et al. (1992) to predict the probability of

flight initiation of bugs from different ecotopes over seasons. These results are relevant to understanding and modeling (Cohen and Gürtler, 2001) the dispersal and recolonization dynamics of a major vector species.

2. Materials and methods

2.1. Study area

Field studies were carried out in the rural villages of Amamá, Trinidad and Mercedes (27°12'33"S, 63°02'10"W), Santiago del Estero, Argentina. The villages, which are situated within 9 km of each other in semiarid hardwood, thorny forest habitat (Gürtler et al., 1999), had 114 houses with some 500 inhabitants in May 2000. Most houses had adobe walls and thatched roofs, and the peridomestic area consisted of a patio and 3–8 peridomestic structures separated from human habitations (Canale et al., 2000). Goat or sheep corrals (mean size, 35 m²; range 6–79 m²) usually had a fence made with piled thorny shrubs and vertical posts, and a small thatched enclosure. Pig corrals (mean size, 7 m²; range, 2–23 m²) usually had solid walls and roofs made of wooden planks, sometimes thatched roofs, and were more closed than goat corrals. In the peridomicile, chickens mainly nested in storerooms with mud-brick or mud-stick unplastered walls and thick thatched roofs, and more rarely in kitchens (of similar structure) or under mud ovens; all of these structures hereafter will be referred to as chicken coops. After a community-wide spraying with pyrethroids in 1992, villagers conducted selective insecticide sprays since 1996 (Cecere et al., 2002) but the study sites herein reported were not sprayed with insecticides or space sprayers neither by vector control staff nor by villagers during the current study.

3. Study design

All 74 (65%) houses that had peridomestic sites positive for *T. infestans* in 1999 or March 2000 or both were visited in October 2000, and all its peridomestic sites were searched for triatomines by two skilled bug collectors using 0.2% tetramethrin dislodgeant (Icona, Buenos

Aires, Argentina) (Gürtler et al., 1999). Searches were conducted for 30 min per peridomestic compound (1 person-hour) usually between 8:00 and 14:00 h on non-rainy days, but sometimes searches had to start later because householders were not available. Follow-up surveys restricted to peridomestic sites positive for *T. infestans* in October 2000 were conducted in February, May and August 2001 by the same bug collectors. To increase bug sample size, two peridomestic sampling boxes were installed at each study site in October 2000 and inspected for the presence of triatomine bugs in each survey as described by Vazquez-Prokopec et al. (2002a).

In each survey householders were asked about the numbers of fowls and corral animals (goats, sheep, cows, horses and mules) they owned; the breeding season of these animals and when they were enclosed; recent construction changes in peridomestic structures; the use of insecticides, and the place where chickens usually nested. Here we report domestic animal census data from 29 (25%) households that had complete data for all surveys and include all of the study sites. Temperature and relative humidity were recorded in a pig corral, a goat corral, a chicken coop, and a store-room located in Amamá using data loggers (HOBO® H08, Onset Computer Corporation, Bourne, MA) for 4–7 consecutive days in each survey, and the results have been reported elsewhere (Vazquez-Prokopec et al., 2002b). Mean ambient temperatures during the surveys were 21.7 °C in October, 28.5 °C in February, 20 °C in May and 23 °C in August; microsite temperatures in goat corrals were the most variable.

All the triatomine bugs collected were kept in a cooler at 10–12 °C to depress their metabolism during the observation period, and identified to species and counted by stage at the field laboratory (Canale et al., 2000). Each bug was individually examined for the presence of colorless urine, and the local proportion of *T. infestans* that fed during the preceding night was estimated as the number of bugs with colorless urine relative to the number of triatomines examined, as described by Catalá (1991). The observed proportion of fourth and fifth instar nymphs with colorless urine was multiplied by a correction factor c ($c = 0.0533t - 0.585$) to give an adjusted proportion of colorless urine (Catalá, 1991), where temperatures (t) were calculated from the mean recorded in each type of ecotope from 20:30 h of the day preceding capture to

the catch time, instead of using ambient temperatures as in the original calibration.

The qualitative nutritional status of adult *T. infestans* 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 as described by Montenegro (1983). A similar classification of fourth and fifth instar nymphs into four categories of nutritional status was based on a cross-sectional view of the abdomen and the degree of cuticle distension following Rossell Reyes (1984), modified by pooling the original categories 4 and 5. This rather subjective categorization into a scale of appearances proved consistent among several observers (Rossell Reyes, 1984). All triatomines were weighed individually in an electronic balance (precision, 0.1 mg, OHAUS, Pine Brooks, NJ) and measured from clypeus to abdominal tip with a hand-held vernier caliper accurate to 0.02 mm within 8 days of capture. The fresh weight of all eggs laid by each individual female during this period was added to the females' weight. Adult W/L and the maximum temperature (T) between 20:00 and 6:00 h of the night preceding capture were used to estimate an individual (unadjusted) probability of flight initiation of peridomestic bugs from a given site (P_b) (Lehane et al., 1992):

$$\text{Logit}(P_b) = -A + B \left(\frac{W}{L} \right) - C \left(\frac{W}{L} \right)^2 + D(T),$$

where $\text{Logit}(P_b) = x$; $P_b = e^x / (1 + e^x)$; $A = 18.37$; $B = 1.97$; $C = 0.18$; $D = 0.43$. Adult *T. infestans* with a probability of flight initiation greater than 0.05 were taken as fliers.

4. Data analysis

Sites were classified into three types of ecotope (goat corral, pig corral, and chicken coop) according to the main local host, although in rare cases a chicken was nesting in a corral. All sites were assumed independent. As bugs collected by timed collections and sampling boxes did not display significant differences in feeding frequency and nutritional status, they were pooled to increase sample size. The relationship between daily feeding rates or qualitative nutritional status (well-fed bugs, after pooling bugs with large

blood content and good reserves for creating a binomial variable) and potential predictors was studied by maximum likelihood logistic multiple regression analysis. Because triatomine bugs were clustered at each individual peridomestic site, the data might violate the standard regression assumption of independent response probabilities across observations and underestimate standard errors. To avoid this, we used the logistic-binomial random effects model from EGRET software (Egret, 1993), which includes a random effects parameter that measures a residual site effect on the response probability. The explanatory variables were type of ecotope (goat corral, pig corral, chicken coop), season (spring, summer, fall and winter), and stage (fourth and fifth instars, males, females); goat corrals, spring and fourth instars were taken as reference levels for each variable, respectively. Interaction terms were added to this model and tested for significance at the 5% nominal level. The *W/L* ratios of *T. infestans* males and females were normally distributed and were tested separately by two-way ANOVA for ecotope and season; a posteriori comparisons for samples with unequal size were made using the Tukey–Kramer test (Zar, 1996). As fourth and fifth instar nymphs showed a bimodal distribution of *W/L* within each season and ecotope, data for each instar are shown separately for unfed and fed groups following Rabinovich et al. (1979) and Schofield (1980b). Ecotope and season effects on *W/L* were examined using Kruskal–Wallis test and a posteriori comparisons using Dunn's test (Zar, 1996).

5. Results

5.1. Population abundance and structure

Of 939 *T. infestans* (all stages) collected from 35 different sites between spring (October) and winter (August), 60% were from goat corrals and 34% from pig corrals (Fig. 1). Total catches increased from spring (195) to fall (315) and fell in late winter (222). Males outnumbered female *T. infestans* (2:1) over most seasons in corrals, but less so in chicken coops (1.7:1). The percentage of males significantly differed between goat corrals (range 61–67%) and pig corrals (54–77%) when stratified by season (Mantel–Haenszel test, $\chi^2 = 5.0$; d.f. = 1; $P = 0.03$).

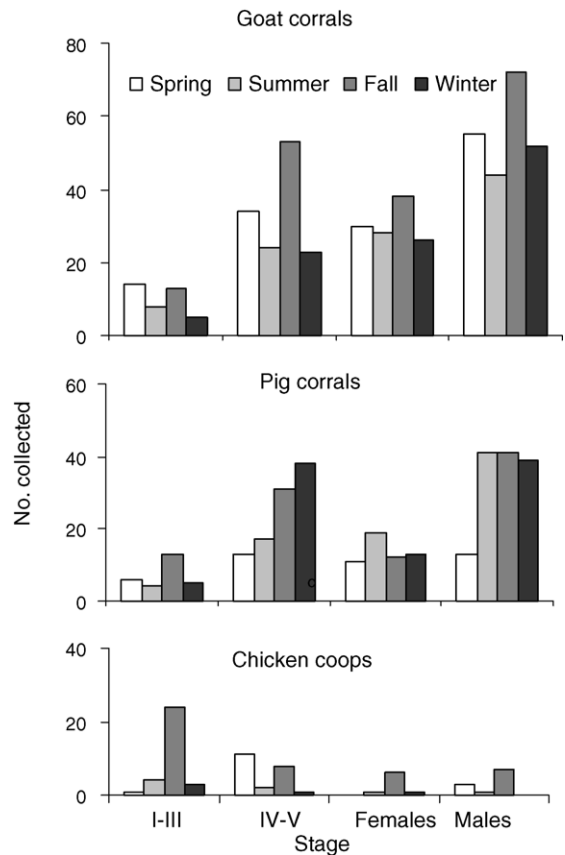


Fig. 1. Stage structure of *T. infestans* populations according to type of ecotope and season. Amamá, Trinidad and Mercedes, October 2000 (spring), February (summer), May (fall) and August (winter) 2001.

5.2. Feeding rates and nutritional status

A total of 814 fourth or fifth instars and adult *T. infestans* was examined for recent blood meals and nutritional status (Table 1). Mean daily feeding rates decreased significantly from 34% in spring to 23% in summer to 14% and 18% in fall and winter, respectively; mean feeding intervals were 2.9, 4.3, 7.0 and 5.6 days, respectively. Overall feeding rates were much less variable in goat corrals (range 18–28%) than in pig corrals (8–41%) or chicken coops (0–53%), and decreased markedly from spring to fall-winter in pig corrals. Adult *T. infestans* tended to have larger feeding rates than fourth or fifth instar nymphs, and females significantly larger rates than males in practically all surveys and ecotopes. Using logistic multiple regres-

Table 1
Stage-specific daily feeding rate of *T. infestans* according to type of ecotope and season

Ecotope	Season	Number of sites	Percentage of daily feeding rate (N)			
			IV–V	Males	Females	Total
Goat corrals	Spring	9	17 (32)	35 (52)	25 (25)	28 (109)
	Summer	9	26 (30)	19 (43)	32 (28)	25 (101)
	Fall	12	11 (58)	17 (75)	28 (43)	18 (176)
	Winter	10	14 (30)	18 (56)	30 (30)	20 (116)
Pig corrals	Spring	5	4 (11)	45 (11)	73 (11)	41 (33)
	Summer	7	39 (16)	25 (36)	10 (21)	24 (73)
	Fall	2	6 (31)	10 (41)	77 (13)	8 (85)
	Winter	3	12 (37)	11 (38)	36 (11)	14 (86)
Chicken coops ^a	Spring	4	40 (11)	100 (3)	–(0)	53 (14)
	Summer	4	0 (3)	0 (2)	0 (1)	0 (6)
	Fall	3	10 (5)	0 (4)	0 (4)	4 (13)
	Winter	2	0 (1)	–(0)	100 (1)	50 (2)
Total	Spring	18	23 (54)	39 (66)	42 (36)	34 (156)
	Summer	20	28 (49)	21 (81)	22 (50)	23 (180)
	Fall	17	10 (94)	14 (120)	22 (60)	14 (274)
	Winter	15	13 (68)	16 (94)	31 (42)	18 (204)

Amamá, Trinidad and Mercedes; October 2000 (spring)–August 2001 (winter). N, number of bugs examined.

^a Mainly includes storerooms where chickens nested.

sion analysis, the daily feeding rates of *T. infestans* were significantly associated with season and stage, but not ecotope (Table 2). The random effects parameter was highly significant, whereas the interaction between season and stage was not significant ($P = 0.086$).

5.3. Nutritional status

The qualitative nutritional status (bars) of *T. infestans* according to ecotope, season and bug stage is shown in Fig. 2. Bugs captured in goat or pig corrals always had a significantly lower qualitative nutritional status than bugs associated with chickens at every bug stage. The overall percentage of well-fed bugs (not shown in Fig. 2) from goat corrals varied very little from spring to fall (24–27%), to increase slightly in winter (34%). In contrast, well-fed bugs decreased steadily in pig corrals from spring to winter (56–12%) and in chicken coops from spring to fall (79–43%). Male *T. infestans* nearly always displayed the lowest qualitative nutritional status across ecotopes and seasons. Using logistic multiple regression analysis, the proportion of well-fed *T. infestans* was significantly modified by season, ecotope, and stage (Table 2). The random effects parameter was highly significant, thereby suggesting a residual cluster effect specific to each

peridomestic site. The interaction between season and stage was highly significant ($P < 0.001$), with fourth instar nymphs showing a significantly better qualitative nutritional status than every other stage in the fall in corrals.

The quantitative nutritional status of *T. infestans* indexed by W/L (lines) is also shown in Fig. 2 for comparative purposes. Female W/L ratios differed significantly among seasons ($F = 10.0$; d.f. = 3; $P < 0.0001$) depending on the type of ecotope ($P = 0.001$); in goat corrals female W/L ratios were significantly lower in spring, summer or fall than in winter, but in pig corrals they were significantly higher in spring or winter than summer or fall ($P < 0.05$). Male bugs had significantly larger W/L in fall or winter than in spring or summer both in goat and pig corrals ($P < 0.05$). The W/L ratios of fifth instars only differed significantly among ecotopes in spring ($H = 6.4$; d.f. = 2; $P = 0.042$), when bugs from pig corrals and chicken coops had a better nutritional status. The W/L ratios of fourth instars differed significantly between seasons both in goat ($H = 15.4$; d.f. = 3; $P = 0.001$) and pig corrals ($H = 7.8$; d.f. = 3; $P = 0.050$). Within each season and pooling over ecotopes and stages, both nutritional indices and the feeding rate of *T. infestans* were significantly associated by χ^2 -tests (not shown in tables).

Table 2

Logistic multiple regression analysis of the daily feeding rate and proportion of well-fed *T. infestans* (response variables) on season (summer, fall and winter in reference to spring); type of ecotope (pig corrals and chicken coops in reference to goat corrals); stage (fifth instar nymph, female and male in reference to fourth instars) (explanatory variables), and the random effects parameter

Response variable	Terms in model	Deviance	d.f.	LRS	<i>P</i>	Adjusted odds ratio (95% CI)
Daily feeding rate	Constant	274.30	0			
	+Random effects	264.17	1	10.13	<0.001	
	+Ecotope	262.62	2	1.55	0.462	
	Pig corrals					1.17 (0.57–2.38)
	Chicken coops					1.52 (0.58–4.01)
	+Season	240.94	3	21.68	<0.001	
	Summer					0.55 (0.32–0.92)
	Fall					0.29 (0.17–0.49)
	Winter					0.40 (0.23–0.69)
	+Stage	232.30	3	8.65	0.034	
	V					1.05 (0.50–2.18)
Female					2.16 (1.06–4.39)	
Male					1.63 (0.83–3.20)	
Well-fed bugs	Constant	378.75	0			
	+Random effects	343.97	1	34.78	<0.001	
	+Ecotope	336.14	2	7.83	0.02	
	Pig corrals					1.30 (0.79–2.13)
	Chicken coops					3.69 (1.28–10.62)
	+Season	317.67	3	18.47	<0.001	
	Summer					0.91 (0.53–1.56)
	Fall					0.51 (0.30–0.85)
	Winter					0.42 (0.24–0.74)
	+Stage	262.44	3	55.23	<0.001	
	V					1.15 (0.65–2.04)
Female					0.83 (0.46–1.48)	
Male					0.25 (0.14–0.44)	

d.f.: degrees of freedom; LRS: likelihood ratio statistic; CI: 95% confidence interval; Spring, goat corrals and fourth instars were taken as reference levels for each variable, respectively. Amamá, Trinidad and Mercedes, October 2000 (spring)–August 2001 (winter).

5.4. Host abundance

Host abundance per house differed by species across seasons (Fig. 3). The median number of goats per house increased steadily from 15 in spring to 27 in winter, whereas pigs decreased from 2.5 in spring to 1 per house in summer, to increase thereafter. Chickens averaged 15 per house throughout the year, and all households had chickens. Although goats delivered all year-round, peaks were reported in May (fall) and December (summer). Kids were always kept in small, thatched enclosures (very frequently found infested) up to 2–3 months old. Pigs were seen or reported to be enclosed at night only exceptionally. Chickens were allowed to roam freely, nesting either inside houses, storerooms or in shrubbery at various distances from

human habitations. Nesting peaked in spring (in 83% of houses) and was minimal in the fall (38%).

5.5. Flight initiation probabilities

The unadjusted probability of flight initiation, according to the model of Lehane et al. (1992), peaked in summer both in goat and pig corrals, tended to zero in all ecotopes in spring and fall, and showed a moderate increase in late winter (Fig. 4). None of the few adult bugs from chicken coops were predicted to fly. Male *T. infestans* outnumbered females as potential fliers from goat or pig corrals across seasons.

Because of the time period elapsed from field collection to *W/L* measurements, the actual fresh weight of *T. infestans* was almost certainly underestimated,

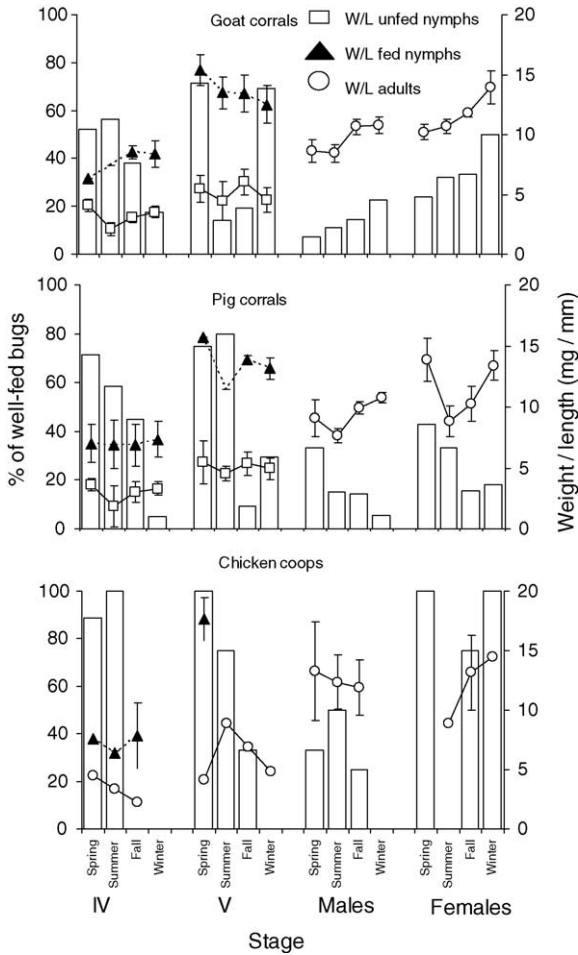


Fig. 2. Qualitative (histogram bars) and quantitative (lines, showing 95% confidence interval of the mean of weight to length) nutritional status of *T. infestans* fourth or fifth instar nymphs and adults according to type of ecotope and season. Amamá, Trinidad and Mercedes, October 2000 (spring), February (summer), May (fall) and August (winter) 2001.

and this would affect the estimated probabilities of flight initiation. In support of the above, the mean fresh weights of male and female *T. infestans* collected in February 2001 (mean \pm S.D., 200.8 ± 45.5 mg, $n=90$; 255.3 ± 84.3 mg, $n=50$, respectively) were significantly lower (*t*-test, $P < 0.001$) than those determined on the same day of capture at the same village in March 2003 (259.6 ± 41.0 mg, $n=67$; 320.6 ± 88.4 mg, $n=35$, respectively) (Vazquez-Prokopec et al., 2004). In contrast, the mean length of male and female *T. infestans* in February 2001

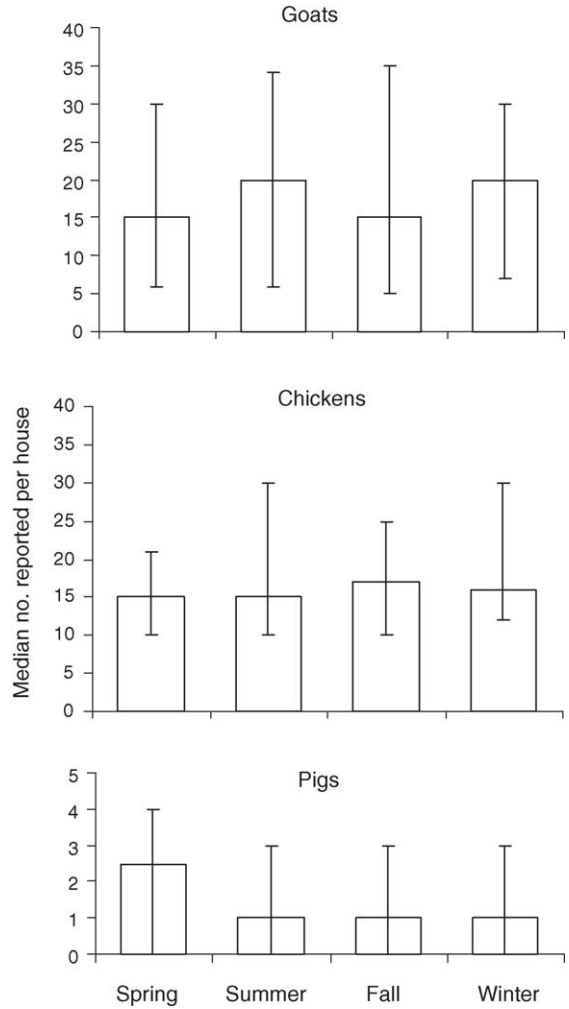


Fig. 3. Reported numbers of goats, chickens and pigs per house (bars, median; lines, first and third quartiles). Amamá, Trinidad and Mercedes, October 2000 (spring), February (summer), May (fall) and August (winter) 2001.

(24.6 ± 1.9 mm, $n=90$; 26.2 ± 1.6 mm, $n=50$, respectively) did not differ significantly from measurements in March 2003 (24.6 ± 0.7 mm, $n=67$; 26.1 ± 0.6 mm, $n=35$, respectively). On the assumption of similar distributions of weight by sex over different years in Amamá, the mean weight ratios between 2003 and 2001 (1.293 and 1.256 for males and females, respectively) were used to adjust individual W/L ratios in February 2001 and to calculate an adjusted probability of flight initiation. Relative to the unadjusted summer estimates in Fig. 4, the adjusted proportion of fliers

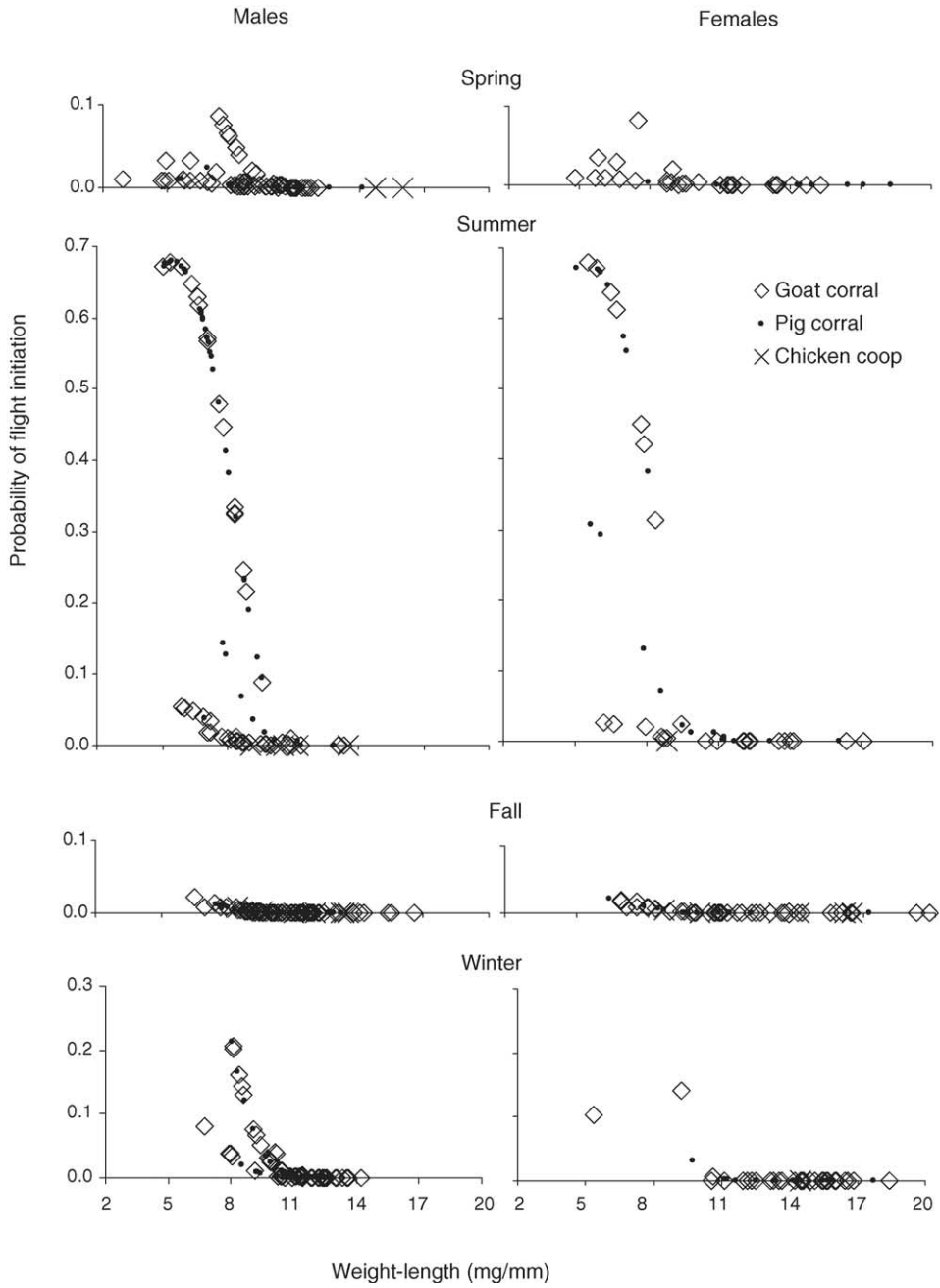


Fig. 4. Unadjusted probability of flight initiation of *T. infestans* per site according to type of ecotope, season and sex. Amamá, Trinidad and Mercedes, October 2000 (spring), February (summer), May (fall) and August (winter) 2001.

was reduced by 24% among males but only by 8% among females. In summer, the adjusted proportion of male fliers from pig corrals (55%, 22 of 40) was 2.75 times larger than from goat corrals (20%, 9 of 45); female fliers would originate from pig corrals (43%, 9 of 21) twice as likely as from goat corrals (21%, 6 of 28).

6. Discussion

Our longitudinal study shows for the first time significant heterogeneities in the feeding rates and nutritional status of peridomestic *T. infestans* populations linked to host demographics and management, and how these heterogeneities translate into variable flight dispersal probabilities from different source sites over seasons. Our data fed into the model by Lehane et al. (1992) predict that fliers were more likely to be males and originate from pig or goat corrals in summer. Subsequent light-trap surveys validated these predictions to a large extent (Vazquez-Prokopec et al., 2004; unpublished data).

Goat corrals provided most of the peridomestic *T. infestans* collected and maintained abundant populations of bugs and hosts year-round, whereas pig corrals had similar bug abundance per site although less persistent populations with more variable nutritional status. These variations may balance the relative contribution of each ecotope to the pool of potential fliers. Peridomestic *T. infestans* from goat or pig corrals had lower feeding rates and nutritional status as well as smaller wing size (Schachter-Broide et al., 2004) than bugs associated with chickens in spring-summer in our study area and elsewhere (López et al., 1999). However, in our study area permanent chicken coops were rare, nesting sites were relatively unstable, and nesting activity varied seasonally. These factors determined small peridomestic bug populations associated with chickens that did not persist year-round. As chickens left its transient nesting sites after a few months, in the absence of hosts the starved bugs presumably dispersed elsewhere.

Host species and age affect bug feeding success through host defensive behavior (Lehane, 1991). Our study also shows that the feeding rate and nutritional status of *T. infestans* is also modified by management practices of domestic animals and the timing of breeding seasons, which affect host availability locally. For example, in goat corrals the feeding rates and nutri-

tional status of adult *T. infestans* were the least variable and peaked by late winter, coinciding with the increasing abundance and availability of goats (especially kids) from spring to late winter. In winter, all goats usually were enclosed at night for protection against cold weather and kids were kept enclosed permanently, whereas in summer goats were allowed to roam freely and forage the scarce grass available. The abundance of pigs decreased sharply by mid-summer because of increased sales prior to end-of-year feasts, and this reflected in a sharp decrease in bug feeding rates and *W/L*. In consequence, most female fliers were predicted to originate from pig corrals than from other ecotopes in summer. This result is consistent with pig corrals being the ecotope most frequently found infested and the most productive of *T. infestans* in Amamá during 1993–1997, with one particular large pig corral being the recurrent source that propagated most infestations after insecticide spraying (Cecere et al., 2004). Chicken numbers were high and stable year-round, but they usually nested in human habitations in spring and early summer (Cecere et al., 1997) when they were bitten preferentially by domestic *T. infestans* (Gürtler et al., 1997). When not nesting, most chickens roosted in uninfested peridomestic trees and thus were less available for *T. infestans*. We conclude that domestic animal availability in the peridomestic environment varies seasonally and asynchronously depending on host species and local management practices. These heterogeneities are a major driver of triatomine population dynamics and reinfestation patterns.

The feeding rate and nutritional status of *T. infestans* peaked in spring and dropped to a minimum in the fall rather than in late winter because of the prevailing temperatures during the surveys and the relatively lower availability of pigs and goats. Local temperatures in fall and winter surpassed the threshold for *T. infestans* locomotory activity (18–20 °C) on 25% of the days (Vazquez-Prokopec et al., 2002b), and would allow the bugs to feed sporadically on such nights despite the fact that developmental and fecundity rates are largely reduced in fall-winter (Cecere et al., 2003). Sporadic blood meals and low metabolic rates explain the high *W/L* ratios in late winter. On average, peridomestic *T. infestans* fed very frequently; every 2.9 and 4.3 days in spring and summer, and every 7 and 5.6 days in fall and late winter, respectively. These feeding intervals should be taken as approximands to the actual values because

a fraction of actual adult blood meals is not detectable experimentally at summer temperatures within the recommended time window for bug examination (Marcet et al., unpublished results), and operational constraints sometimes determined delays in processing the bugs. The large feeding rates estimated suggest that bugs tend to feed small meals rather than at repletion.

The predicted probability of flight initiation from pig or goat corrals peaked in summer and was nil from chicken coops in spring-summer, in agreement with more extensive chicken coop data (López et al., 1999). These qualitative predictions are robust to small sample sizes in chicken coops and errors in *W/L* estimates. Had *W/L* ratios in spring, fall or winter been adjusted for weight loss, the very low flight probabilities during these seasons (Fig. 4) would become trivial. Conversely, because the model of Lehane et al. (1992) tended to underestimate the actual flight initiation probabilities of field populations of *T. infestans* during summer (Vazquez-Prokopec et al., 2004), the predicted flight chances most likely underestimate the actual values.

Most fliers were predicted to be males because of their lower *W/L* and because males outnumbered female *T. infestans* in corrals throughout the year. This unexpected pattern agrees fully with subsequent light-trap collections nearby infested peridomestic sites (Vazquez-Prokopec et al., 2004, unpublished data). Field surveys recorded skewed sex ratios toward male *T. infestans* whereas laboratory or experimental hut studies recorded the reverse (reviewed by Cecere et al., 2003). In principle, such skewed sex ratios may not be attributed to the dislodgment agent tetramethrin, which flushed out *T. infestans* females more easily than males and exerted no additional mortality in a laboratory setting (Wood et al., 1993). However, as peridomestic *T. infestans* females had a better nutritional status than males and most were full of developing eggs, their motivation status and reaction toward tetramethrin may differ from those displayed by laboratory-reared triatomines under a different, more homogeneous physiologic status. Asymmetries in flight dispersal patterns by sex may also contribute to skewed sex ratios in manual timed samples.

Peridomestic structures housing domestic animals compose a heterogeneous physical environment showing site-specific seasonal variations in host and bug abundance. Variable host management practices among

households jointly with variations in host density reflected in significant cluster effects of individual sites on bug feeding rates and nutritional status. Host and bug density-dependent effects on feeding rates and nutritional status will be reported separately. These heterogeneities make broad generalizations from chicken coops (López et al., 1999) to all peridomestic habitats, or from one ecologic region to another probably misleading. Store-rooms and other structures with chickens nesting for limited periods may also become relevant source sites for reinfestation. Goat and pig corrals made of wood or shrubs are key sites for *T. infestans* because they sustain persistent bug populations with a variable nutritional status that triggers bug dispersal under adequate conditions, and because residual insecticide spraying there is less effective than in domestic sites (Gürtler et al., 2004). This problem is further compounded by the insensitivity of timed manual collections with dislodgment sprays in peridomestic structures (Gürtler et al., 2001). Targeted surveillance of key peridomestic sites is needed for the elimination of *T. infestans* in the Gran Chaco.

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References

- Canale, D.M., Cecere, M.C., Chuit, R., Gürtler, R.E., 2000. Peridomestic distribution of *Triatoma garciabesi* and *Triatoma*

- guasayana* in north-west Argentina. Med. Vet. Entomol. 14, 383–390.
- Catalá, S., 1991. The biting rate of *Triatoma infestans* in Argentina. Med. Vet. Entomol. 5, 325–333.
- Cecere, M.C., Gürtler, R.E., Chuit, R., Cohen, J.E., 1997. Effects of chickens on the prevalence of infestation and population density of *Triatoma infestans* in rural houses of north-west Argentina. Med. Vet. Entomol. 11, 383–388.
- Cecere, M.C., Gürtler, R.E., Canale, D.M., Chuit, R., Cohen, J.E., 2002. Effects of partial housing improvement and insecticide spraying on the reinfestation dynamics of *Triatoma infestans* in rural northwestern Argentina. Acta Trop. 84, 101–116.
- Cecere, M.C., Canale, D.M., Gürtler, R.E., 2003. Effects of refuge availability on the population dynamics of *Triatoma infestans* in central Argentina. J. Appl. Ecol. 40, 742–756.
- Cecere, M.C., Vazquez-Prokopec, G.M., Gürtler, R.E., Kitron, U., 2004. Spatio-temporal analysis of reinfestation by *Triatoma infestans* (Hemiptera: Reduviidae) following insecticide spraying in a rural community in northwestern Argentina. Am. J. Trop. Med. Hyg. 71, 803–810.
- Cohen, J.E., Gürtler, R.E., 2001. Modeling household transmission of American Trypanosomiasis. Science 293, 694–698.
- Egret, 1993. Epidemiological Graphics, Estimation and Testing Package. Statistics and Epidemiology Research Corporation, Seattle, WA.
- Guarneri, A.A., Pereira, M.H., Diotaiuti, L., 2000. Influence of the blood meal source on the development of *Triatoma infestans*, *Triatoma brasiliensis*, *Triatoma sordida*, and *Triatoma pseudomaculata* (Heteroptera, Reduviidae). J. Med. Entomol. 37, 373–379.
- Gürtler, R.E., Cohen, J.E., Cecere, M.C., Chuit, R., 1997. Shifting host choices of the vector of Chagas disease *Triatoma infestans* in relation to the availability of hosts in houses in north-west Argentina. J. Appl. Ecol. 34, 699–715.
- Gürtler, R.E., Cecere, M.C., Canale, D., Castañera, M.B., Chuit, R., Cohen, J.E., 1999. Monitoring house reinfestation by vectors of Chagas disease: a comparative trial of detection methods during a four-year follow-up. Acta Trop. 72, 213–234.
- Gürtler, R.E., Vazquez-Prokopec, G.M., Ceballos, L.A., Lund Petersen, C., Salomón, O.D., 2001. Comparison between two artificial shelter units and timed manual collections for detecting peridomestic *Triatoma infestans* (Hemiptera: Reduviidae) in rural northwestern Argentina. J. Med. Entomol. 38, 429–436.
- Gürtler, R.E., Canale, D.M., Spillmann, C., Stariolo, R., Salomón, O.D., Blanco, S., Segura, E.L., 2004. Effectiveness of residual spraying with deltamethrin and permethrin on peridomestic populations of *Triatoma infestans* in rural western Argentina: a district-wide randomized trial. Bull. World Health Org. 82, 196–205.
- Lehane, M.J., 1991. Biology of Blood Sucking Insects. Harper Collins, London, 288 pp.
- Lehane, M.J., McEwen, P.K., Whitaker, C.J., Schofield, C.J., 1992. The role of temperature and nutritional status in flight initiation by *Triatoma infestans*. Acta Trop. 52, 27–38.
- López, A.C., Crocco, L., Morales, G., Catalá, S., 1999. Feeding frequency and nutritional status of peridomestic populations of *Triatoma infestans* from Argentina. Acta Trop. 73, 275–281.
- Montenegro, S., 1983. Determinación de las reservas alimenticias en *Triatoma infestans* Klug, 1834 (Hemiptera Reduviidae) en base a caracteres externos. I. Adultos. Physis (Buenos Aires) 41, 159–167.
- Rabinovich, J.E., Leal, J.A., Feliciangeli de Piñero, D., 1979. Domiciliary biting frequency and blood ingestion of the Chagas's disease vector *Rhodnius prolixus* Ståhl (Hemiptera: Reduviidae), in Venezuela. Trans. Roy. Soc. Trop. Med. Hyg. 73, 272–283.
- Rodríguez, D., Rabinovich, J.E., 1980. The effect of density on some population parameters of *Rhodnius prolixus* (Hemiptera: Reduviidae) under laboratory conditions. J. Med. Entomol. 17, 165–171.
- Rossell Reyes, O., 1984. A comparison of the feeding performance of *Rhodnius prolixus* Ståhl and *Rhodnius robustus* Larrousse (Hemiptera: Triatominae). A thesis submitted for the degree of Doctor. London University.
- Schachter-Broide, J., Dujardin, J.P., Kitron, U., Gürtler, R.E., 2004. Spatial structuring of *Triatoma infestans* (Hemiptera, Reduviidae) populations from northwestern Argentina using wing geometric morphometry. J. Med. Entomol. 41, 643–649.
- Schofield, C.J., 1980a. Density regulation of domestic populations of *Triatoma infestans* in Brazil. Trans. Roy. Soc. Trop. Med. Hyg. 74, 761–769.
- Schofield, C.J., 1980b. Nutritional status of domestic populations of *Triatoma infestans*. Trans. Roy. Soc. Trop. Med. Hyg. 74, 770–778.
- Schofield, C.J., Lehane, M.J., McEwen, P.K., Catalá, S., Gorla, D.E., 1992. Dispersive flight by *Triatoma infestans* under natural climatic conditions in Argentina. Med. Vet. Entomol. 6, 51–56.
- Vazquez-Prokopec, G.M., Ceballos, L.A., Salomón, O.D., Gürtler, R.E., 2002a. Field trials of an improved cost-effective device for detecting peridomestic populations of *Triatoma infestans* (Hemiptera: Reduviidae) in rural Argentina. Mem. Inst. Oswaldo Cruz 97, 971–977.
- Vazquez-Prokopec, G.M., Ceballos, L.A., Cecere, M.C., Gürtler, R.E., 2002b. Seasonal variations of microclimatic conditions in domestic and peridomestic habitats of *Triatoma infestans* (Hemiptera: Reduviidae) in rural northwest Argentina. Acta Trop. 84, 229–238.
- Vazquez-Prokopec, G.M., Ceballos, L.A., Kitron, U., Gürtler, R.E., 2004. Active dispersal of natural populations of *Triatoma infestans* (Hemiptera: Reduviidae) in rural northwestern Argentina. J. Med. Entomol. 41, 614–621.
- Wood, E., Licastro, S.A., Casabé, N., Sivori, J., Zerba, E., 1993. Evaluation of the flushing out activity of pyrethroids on *Triatoma infestans*. Insect. Sci. Appl. 14, 651–655.
- Zar, J.H., 1996. Biostatistical Analysis, 3rd ed. Prentice-Hall, Englewood Cliffs, NJ, 661 pp.