Shifting host choices of the vector of Chagas disease, *Triatoma infestans*, in relation to the availability of hosts in houses in north-west Argentina

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Summary

1. Data from a 4-year study on the blood meal sources of 1964 specimens of *Triatoma infestans* collected from human sleeping places in three rural villages of north-west Argentina were analysed using individual houses as the basic sampling unit. Logistic multiple regression analysis was used to test whether the proportion of domiciliary *T. infestans* that fed on humans, dogs, chickens or cats was related to the number of these hosts in the house and to vector density.

2. On average, dogs were 2·6 or 2·3 times more likely to be selected than humans, relative to availability, in summer 1992 (at 23 houses) or spring–summer 1988–89 (at 11 houses), respectively, but 0·8 less likely to be selected than humans, relative to their availability, in winter 1988 (at 12 houses). In the hot season, chickens were 4·8 times more likely to be selected than humans, relative to their assumed availability.

3. From data collected during the hot season, the proportion of bugs that fed on humans, among all bugs with any identified blood source (the human blood index, HBI), or on humans only (HBI ONLY), decreased significantly as both the number of dogs sharing human sleeping places (room-mate dogs) and the proportion of bugs that fed on chickens increased. The proportion of bugs that fed partly on dogs, or on dogs alone, increased significantly with increasing numbers of room-mate dogs and decreased significantly with an increasing proportion of bugs feeding on chickens.

4. From data collected during the winter, when fewer cases of feeding on chickens were detected and most people slept indoors, both HBI and HBI ONLY increased significantly with the number of humans and decreased with the number of room-mate dogs.

5. The effects of vector density on HBI or HBI ONLY were investigated by multiple logistic regression analysis. In summer 1992, after a backward elimination procedure, both HBI and HBI ONLY were significantly and negatively related to the density of domiciliary *T. infestans* per house, the number of room-mate dogs and the proportion of the bugs that fed on chickens. A marginally significant and negative relationship between HBI and the log-density of bugs was verified in two published datasets.

6. Analysis of 13 published host-feeding patterns of domiciliary *T. infestans*, and of another 27 datasets from 11 other triatomine species collected inside or around bedroom areas, showed that HBI was inversely and significantly related to the proportion of bugs that fed on chickens (in both groups of vector species) or on dogs (for *T. infestans*).

7. Our study is the first to show that: (i) the likelihood of feeding partly on humans, or on humans only, significantly decreased in the presence of dogs and chickens in bedroom areas; (ii) the HBI was also negatively related to the density of bugs per house after controlling for the effects of chickens and room-mate dogs; and (iii) the likelihood of feeding on dogs increased significantly with more room-mate dogs and decreased with an increasing proportion of bugs feeding on chickens. Some

epidemiological consequences of these relationships for transmission, control, zoo-
prophylaxis and modelling are discussed.

Key-words: feeding preferences, Triatominae, *Trypanosoma cruzi*, vector ecology,
zooprophylaxis.

Introduction

Host choice of haematophagous insects appears to be
dependent ultimately upon the local proportions of
available hosts (Lehane 1991). Hence, host abundance
and proximity are often considered the main deter-
minants of host choice. Other factors affecting host
choice are host defensive behaviour, the density of
blood-sucking insects, and the spatial and temporal
concurrence of hosts and insects. Examples of fixed
(intrinsic) host-feeding preferences are few, and con-
vincing evidence with both experimental and field sup-
port is scarce (Washino & Tempelis 1983; Lehane
1991).

Triatoma infestans (Klug) (Hemiptera: Reduviidae)
is the main vector of *Trypanosoma cruzi*, the agent of
Chagas disease (Schofield 1985). Like most species
of triatomine bugs, *T. infestans* shows eclectic host-
feeding patterns (Minter 1976a; Wisnivesky-Colli
1987). Hence, the proximity of particular types of
host has been considered more important than any
preference of the hungry bugs seeking to feed (Minter
1976a; Marsden *et al.* 1979). During simultaneous
exposure of different vertebrate hosts to three tri-
atomine species, the bugs showed no clear feeding
preferences among dogs, chickens and opossums, but
did not feed on toads (Jirón & Zeledón 1982); *T.
infestans*, however, showed some preference for dogs
in short day-time experiments and for chickens in all-
night trials.

In human habitations, *T. infestans* feeds pre-
dominantly on humans, dogs and chickens. However,
in north-west Argentina we recorded ample seasonal
variations in host-feeding patterns (Gürtler *et al.* 1996a)
and found that the density of *T. infestans* increased
with the number of humans and dogs sharing human
sleeping areas (Gürtler *et al.* 1992). Moreover, the
probability of a bug becoming infected with *T. cruzi*
when feeding on a dog was estimated to be 50 times
greater than if the bug fed upon humans (Gürtler *et
al.* 1996b). Throughout this paper, we shall refer to
bugs (both individuals and populations) actually
found in people's bedrooms as 'domiciliary' bugs.

Clearly, the host-feeding patterns of domiciliary tri-
atomine bugs are a key to understanding the epi-
demiology of Chagas disease. In this paper, we report
on the results from the first field study to test whether
host-feeding patterns of triatomine bugs are deter-
mined by host availability. Since domiciliary *T. infest-
ans* populations have a low rate of active dispersal

(Schofield 1985), we considered each house to be the
basic sampling unit. This approach has not been used
before to study the host-feeding preferences of tri-
atomine bugs.

Host availability will influence whether or not
domiciliary triatomines deviate from feeding on their
normal hosts. It therefore has serious implications for
assessing the risk of *T. cruzi* transmission to humans.
A detailed understanding of the relationships between
host availability and triatomine feeding behaviour is
necessary to help predict the effects of zooprophylaxis
(i.e. introducing animals, such as chickens, which are
bitten by the bugs but are not susceptible to infection
by *T. cruzi*) or removing reservoirs of infection (such
as domestic cats and dogs).

In this study, logistic multiple regression is used to
analyse how the proportion of domiciliary *T. infestans*
that fed on humans, dogs, cats or chickens was related
to the numbers of each host within the house. Host
blood antigens may remain detectable in the bug's
stomach for up to 3 or 4 months (Minter 1976a), and
the percentage of bugs that fed on a single class of
host can be taken as an index of repeated feedings on
this host class (Gürtler *et al.* 1996a). We also consider
the effects on host-feeding patterns of vector density,
which may possibly regulate the size of domiciliary
populations of triatomines through an effect on host
irritation and defensive grooming behaviour (Scho-
field 1985). Finally, we examine the published host-
feeding patterns of domiciliary *T. infestans* and other
triatomine species collected inside or around bedroom
areas to verify the generality of some of the relation-
ships observed in our study.

Materials and methods

FIELD SITE

Studies were carried out in three similar rural villages
in the Province of Santiago del Estero, Argentina:
Trinidad, Mercedes and Amamá with 19, 16 and 41
houses, respectively, in 1988. The villages were within
9 km of each other in a semi-arid area covered with
a thorn forest of hard-wood located about 27°12′S,
63°02′W. The mean annual temperature was about
22°C and annual precipitation averaged about 600
mm and was concentrated during the hot season
(October–March). Other characteristics of the study
area are described in Gürtler *et al.* (1992, 1996a).

Houses were typically made of mud-brick or mud-

stick walls, thatched roofs and floors of beaten earth; an unfenced veranda stood at the front of one or two bedrooms. Associated (peridomestic) structures included kitchens, store-rooms and goat-pens, and were 4–120 m from human sleeping quarters. Dogs, cats and fowls were not restricted in their movements at any times. Brooding hens (which in most cases had no special chicken coops and roosted on trees when not brooding) or ducks were frequently sighted or reported to nest inside or around bedrooms. Ducks were less abundant than chickens. Other livestock (goats, sheep, pigs, geese, horses, mules) were usually distant from bedrooms; peridomestic and commensal rodents were rarely seen in domiciliary and associated habitats or reported by house-dwellers.

STUDY DESIGN AND DATA COLLECTION

Study designs, vector collection methods and the distribution of bug infestations are described in detail elsewhere (Gürtler *et al.* 1992, 1993b, 1996a). Briefly, a two-person team searched for bugs in 19 houses in Trinidad (in September 1988), 12 houses in Mercedes and 41 houses in Amamá (in December 1988), 40 houses in Amamá (in March 1989) and a total of 70 houses from all three villages in March 1992.

Bug collections were made by 'flushing-out' and/or insecticidal 'knock-down'. In the flushing-out method, bug collectors first searched all bedroom areas, beds and household goods for bugs, and then sprayed walls and roof with a dislodging agent (0·2% tetramethrin); triatomines were collected as they emerged and put in labelled plastic bags. Flushing-out searches were carried out for 2 h (4 person-hours per house) in 1988, or 30 min (1 person-hour per house) in March 1992. For knock-down collections, one γ-HCH ($= \gamma$-BHC) fumigant tablet (Gammexane®, Duperial, Argentina) per bedroom was used 3–5 days after flushing-out collections in 16 houses in Trinidad in September 1988, and in three houses in Mercedes in December 1988. All knocked-down bugs were collected 2–4 h after treatment. Flushing-out and knock-down collections with γ-BHC tablets gave comparable estimates of relative bug density and host-feeding patterns at each house (Gürtler *et al.* 1993b, unpublished); bugs collected from each house were pooled to increase the sample size. In this study, density of bugs means the number of bugs per house.

In each survey we identified the resident people, dogs and cats by their house number and name, and asked where each slept at night. Dogs or cats reported by their owners to rest close to their beds during the night are hereafter referred to as room-mate dogs or room-mate cats to indicate their close proximity to humans and bedroom areas. The classification of room-mate dogs or cats in 1992 was principally based on the habits reported by owners in previous years. Nesting hens or ducks (or the location of their clutch of eggs) were recorded on a sketch map whenever they

were spotted. Complete censuses of poultry and other livestock were made in September 1988 and in March 1992. In May 1993 house-dwellers were asked whether fowl were allowed to nest indoors in previous years.

The methods used in the processing of triatomines, preparation of antisera and identification of blood meals are given in Gürtler *et al.* (1996a). In summary, the individual blood meal sources were identified by agar double-diffusion tests using five antisera representing the most common domiciliary hosts (humans, dogs, cats, chickens/ducks and goat/sheep). Blood meals that reacted against the chicken/duck antiserum are reported as chicken feedings because of the numerical predominance of chickens over ducks in bedroom areas. Mixed blood meals (i.e. those in which at least two types of hosts can be recognized) were reanalysed with the reacting antisera loaded in adjacent positions in order to check for the specificity of reactions. Unmixed blood meals are regarded as those in which only one host type is recognized, although the bug may have fed many times on the same type of host. A reactive bug is one that shows a positive result to at least one of the antisera employed. The proportion of all reactive bugs that had fed on humans will be called the human blood index (HBI); by extension, the proportion of reactive bugs that fed on humans only will be called the human blood index only (HBI ONLY). Similar terms are used for feedings on dogs (DOGBI and DOGBI ONLY), chickens (CKBI and CKBI ONLY) and cats (CATBI). The HBI may be interpreted as the probability of having fed on humans, regardless of whether the bugs have fed on another host; the HBI ONLY may be taken as an index of repeated feedings on humans, to the exclusion of other potential hosts.

DATA ANALYSIS

The primary database included the blood meal sources of 1964 specimens of domiciliary *T. infestans* collected from bedrooms during 1988–92 (Gürtler *et al.* 1996a). Because host-feeding patterns differed substantively among seasons, all analyses performed were stratified by season to reduce variability. From the database, we selected those houses with at least 10 reactive bugs in any one survey to calculate the house-specific feeding index (FI) and the proportion of bugs that fed on each class of host. The Appendix contains the complete data for each selected study house. FI was calculated as the ratio of the number of bugs that fed on host X to the number that fed on host Y (whether or not the bugs that fed on X also fed on any other host, and whether or not the bugs that fed on Y also fed on any other host), divided by the ratio of the number of hosts of type X to the number of hosts of type Y present in the house (Kay, Boreham & Edman 1979). An FI higher than one indicates an excess of feeding on host X relative to host Y. The FI for dogs over humans was taken as infinity in houses that had no

dogs at the time of the survey but where blood meals on these hosts were detected; this did not affect the calculation of median feeding indices. A similar procedure was followed for households where we did not spot, or dwellers did not report having, fowl nesting indoors but where blood meals on chickens were detected.

The presence of fowl nesting indoors was recorded when we observed them there. However, we had no precise data on their presence inside bedrooms during the previous 3–4 months (the period in which blood serum antigens might remain detectable). Observations from 1988 to 1992 indicated that usually not more than one hen or duck nested inside bedrooms at the same time (M. C. Cecere *et al.*, unpublished). For the analyses, we therefore assumed that there had been one hen in each of the houses where we spotted them inside or around bedrooms or where residents reported allowing hens or ducks to nest indoors.

The total host count per house included humans, dogs, cats, plus one hen or duck for households with fowl nesting indoors. Other fowl (turkey and geese), which nested far from bedrooms, and livestock (goats, sheep, horses, pigs, etc.), which usually do not appear as a blood meal source of domiciliary *T. infestans* (Wisnivesky-Colli 1987), were excluded from the total host count. Over 90% of cats were reported as room-mate cats; hence, we considered all cats to be in this category.

Multiple logistic regression analysis (Statistics for Windows: Release 4.3) was used to describe the effects of the numbers of available hosts on each host's blood index. Before analysis began, the numbers of hosts by house (g) were transformed to $(g+0.5)^{1/2}$ to stabilize variances and normalize the distribution of variables; we denoted the transformed number of humans as h, of room-mate dogs as d, and of cats as c. The number of triatomine bugs collected per man-hour (x) in each house was transformed to $\log_{10} x$ and denoted as t.

The general regression model was fitted to the data by maximum likelihood; it differed according to hosts' blood indices, and between summer or spring–summer and winter datasets because of substantive differences in the host-feeding patterns of the bugs. The dependent variable in each model was one host blood index: HBI, HBI ONLY, DOGBI, etc.; the independent variables were h, d and CKBI. The chicken blood index was used as direct evidence of the continuing presence of chickens in bedroom areas; it was considered a more objective measure than the house-dweller's reports or our visual assessment during time-limited field surveys. To explain variations in human and dog blood indices in spring–summer and summer collections (when humans, dogs and chickens were important host blood sources), the logistic regression model in its linearized form was:

$$\text{logit } i = b_0 + b_1 * h + b_2 * d + b_3 * \text{CKBI} \qquad \text{eqn 1}$$

where i is the host blood index, the logit of i is $\log_e [i/(1-i)]$ and b_0–b_3 are regression coefficients. We

ignored the potential effect of cats because the frequency of feedings on cats was small overall, and correlation analyses showed that all hosts' blood indices were unrelated to the number or proportion of cats in the three surveys. When the dependent variable was the chicken blood index, the abundance of chickens was described by a dummy variable (HENS) based on dwellers' reports and visual inspections; this variable took values of 0 when fowl did not nest indoors, and 1 when they did. To describe variations in the CATBI, the transformed number of cats was included as an independent variable in eqn 1. In the smaller winter dataset, chickens were a marginal host blood source; to simplify the fitting of the model given the small sample size, the regression models of hosts' blood indices included h and d as independent variables. Residuals were inspected visually for consistent deviations from normality and the presence of outliers. In the final stage of analysis, backward stepwise removal of non-significant variables was used to find the best set of predictor variables. The likelihood for the null model, where all slope parameters are zero, was compared with the likelihood of the fitted model and a χ^2 test was computed. All statistical tests were judged at the nominal level of significance ($P = 0.05$).

We analysed the published data on the host-feeding patterns of domiciliary *T. infestans* summarized in Gürtler *et al.* (1996a), and of other triatomine species collected inside or around bedrooms. Most of these data were primarily compiled by Minter (1976a) and Wisnivesky-Colli (1987); references appearing in these sources are not repeated here. The data were checked against the original sources and re-expressed as host blood indices. Information available up to the end of 1995 was used; results appearing in scientific meetings were included insofar as the data in them included all the information needed for analysis. We excluded from the analyses two studies that did not report data for both chickens and dogs, studies where bugs were collected mostly or only from associated sites, and data collected from uninhabited houses. Whenever possible, only data for domiciliary bug collections were considered, but in several cases the original sources pooled data from bedrooms with other associated sites. Blood meals reported as originating from 'primates and avian' were considered as human or chicken, whereas a few feedings reported as originating from carnivores were divided proportionally between dog and cat blood meals. Blood meals reported as from 'birds or chickens' (and very few from pigeons, parrots or other birds) were assigned collectively to chicken blood meals. Blood meals that were not identified to family were excluded and not computed as reactive bugs. The proportion of bugs that fed on each host can take values from zero to one within the same survey because each bug may show more than one blood source; thus these proportions are logically independent.

We sought to verify the relationship between HBI and bug density by surveying the published literature. Rabinovich *et al.* (1990) published data on the HBI, the number of resident people and the density of domiciliary *T. infestans* assessed by flushing-out (4 person-hours per house) in 12 infested houses of Amamá surveyed both in 1982 and 1984, before the first indoor-spraying with residual insecticides was ever conducted in the area. The published results were stratified by place of capture (walls versus beds); because most bugs were collected from the walls, only these were included in the analyses. The number of people and the density of bugs were transformed as before. In the absence of the raw data, the proportion of bugs that had fed on humans that were collected from walls was transformed to logits. To calculate the logit-human blood index when 100% of bugs had fed on humans, we assigned the human blood index a symbolic value of 0·99. The data were fitted by ordinary least squares to the model:

$$\text{logit HBI} = b_0 + b_1 * h + b_2 * t \qquad \text{eqn 2}$$

Results

FEEDING INDICES

We calculated the dog/human feeding indices (FI) for specimens of *T. infestans* collected in summer 1992, spring–summer 1988–89 and winter 1988 (Table 1). The FI clearly favoured dogs over humans both in summer (median = 2·3) and spring–summer collections (median = 2·6). In winter collections, the median dog/human FI favoured humans (median = 0·8), although it favoured dogs when only room-mate dogs, instead of any dogs, were considered (median = 2·0). FI estimates varied widely between houses within each season; hence, differences between seasons were not statistically significant (Kruskal-Wallis test, $H = 2·16$, $P > 0·3$). The mean FI calculated community-wide (i.e. for total numbers of

bugs that fed on dogs to bugs that fed on humans, divided by total numbers of dogs to humans) favoured dogs in all seasons (summer, mean = 2·4; spring–summer, mean = 2·2; winter, mean = 1·1).

The presence of nesting fowl inside or around bedrooms was measured less precisely than that of dogs, as explained above; therefore, estimates of FI for humans or dogs over chickens are to be taken as gross approximations. We pooled data for spring–summer 1988–89 and summer 1992, and included houses where we spotted one or more hens sitting in bedrooms or whose dwellers reported allowing fowl to nest indoors ($n = 28$ houses); we estimated that chickens were selected 4·8 times as often as humans relative to their assumed availability during the hot season (first quartile Q_1, 1·6; third quartile Q_3, 17·0). In the same period, the FI for dogs over chickens was 0·4 (Q_1, 0·1; Q_3, 1·6; $n = 28$ houses).

HOST BLOOD INDICES AND HOST AVAILABILITY

The multiple regression analyses for HBI, DOGBI and other indices in the larger sample taken from 23 houses in summer 1992 are summarized in Table 2. All regression models were statistically significant. For a more immediate interpretation of the main trends, some of the significant relationships obtained in the multiple regressions are shown as univariate scatterplots using untransformed variables (Figs 1–3). To summarize, the likelihood of feeding on humans or on humans only decreased significantly with the presence of dogs and chickens in bedroom areas; the likelihood of feeding on dogs increased with the number of room-mate dogs and decreased with an increasing proportion of bugs feeding on chickens; and the likelihood of feeding on cats increased with the number of cats and decreased as the number of dogs in bedroom areas increased.

The HBI decreased significantly with the CKBI and

Table 1. Distribution of dog/human feeding indices for individual houses according to season: winter (September 1988), spring–summer (December 1988–March 1989) and summer (March 1992)

Dog/human feeding index range*	Number (%) of houses in		
	Summer 1992	Spring–summer 1988–89	Winter 1988
0–0·6	4 (17)	1 (9)	6 (50)
0·61–1	1 (4)	2 (18)	0
1·01–2	5 (22)	3 (27)	2 (17)
>2	13 (57)	5 (45)	4 (33)
Total	23	11	12
Median feeding index	2·3	2·6	0·8

* Dog/human feeding index is calculated as the ratio of the number of bugs that fed on dogs to the number of bugs that fed on humans, divided by the ratio of the number of dogs to the number of humans present in the house.

Table 2. Logistic multiple regression analysis and backward elimination of non-significant variables for the model that fitted the host blood index (dependent variable) on the transformed number of humans (h), the transformed number of room-mate dogs (d) and the chicken blood index CKBI (the independent variables). Data taken at Amamá in March 1992 (see Appendix). Number of houses $n = 23$

Dependent variable	Independent variables	Coef.*	SE†	P‡
Logit HBI	Intercept	0·94	0·48	0·06
	Number of humans	0·23	0·16	0·16
	Number of room-mate dogs	−0·71	0·20	<0·001
	Chicken blood index	−2·76	0·50	<0·001
	$\chi^2 = 78\cdot8$ with 3 d.f., $P < 0\cdot001$			
Backward model	logit HBI $= 1\cdot52 - 0\cdot58*d - 1\cdot94*$CKBI			
	$\chi^2 = 76\cdot9$ with 2 d.f., $P < 0\cdot001$			
Logit HBI ONLY	Intercept	0·70	0·60	0·25
	Number of humans	0·07	0·19	0·70
	Number of room-mate dogs	−1·18	0·30	<0·001
	Chicken blood index	−2·47	0·51	<0·001
	$\chi^2 = 85\cdot6$ with 3 d.f., $P < 0\cdot001$			
Backward model	logit HBI ONLY $= 0\cdot89 - 1\cdot18*d - 2\cdot50*$CKBI			
	$\chi^2 = 85\cdot4$ with 2 d.f., $P < 0\cdot001$			
Logit DOGBI	Intercept	−0·42	0·49	0·40
	Number of humans	−0·28	0·16	0·08
	Number of room-mate dogs	1·35	0·22	<0·001
	Chicken blood index	−2·36	0·39	<0·001
	$\chi^2 = 59\cdot1$ with 3 d.f., $P < 0\cdot0001$			
Backward model	logit DOGBI $= -1\cdot17 + 1\cdot41*d - 2\cdot37*$CKBI			
	$\chi^2 = 55\cdot9$ with 2 d.f., $P < 0\cdot001$			
Logit DOGBI ONLY	Intercept	−1·10	0·66	0·10
	Number of humans	−0·33	0·21	0·13
	Number of room-mate dogs	0·99	0·30	0·002
	Chicken blood index	−2·96	0·55	<0·001
	$\chi^2 = 36\cdot0$ with 3 d.f., $P < 0\cdot001$			
Backward model	logit DOGBI ONLY $= -1\cdot98 + 1\cdot06*d - 2\cdot90*$CKBI			
	$\chi^2 = 33\cdot6$ with 2 d.f., $P < 0\cdot001$			
Logit CKBI	Intercept	−2·41	0·52	<0·001
	Number of humans	−0·24	0·18	0·19
	Number of room-mate dogs	1·31	0·19	<0·001
	Hens	1·11	0·27	<0·001
	$\chi^2 = 83\cdot2$ with 3 d.f., $P < 0\cdot001$			
Backward model	logit CKBI $= -2\cdot95 + 1\cdot36*d + 0\cdot96*$HENS			
	$\chi^2 = 81\cdot5$ with 2 d.f., $P < 0\cdot001$			
Logit CATBI	Intercept	−2·02	0·78	0·01
	Number of humans	−0·07	0·25	0·79
	Number of room-mate dogs	−0·96	0·32	0·005
	Number of cats	1·49	0·59	0·02
	CKBI	−0·25	0·47	0·60
	$\chi^2 = 25\cdot2$ with 4 d.f., $P < 0\cdot001$			
Backward model	logit CATBI $= -2\cdot13 - 1\cdot02*d + 1\cdot43*c$			
	$\chi^2 = 24\cdot9$ with 2 d.f., $P < 0\cdot001$			

* y-intercept and regression coefficients.
† Standard error of coefficients.
‡ t-values were computed as the coefficient estimate divided by its standard error.

the number of room-mate dogs (Fig. 1a, b), as did the HBI ONLY. The number of humans had no effect at all on HBI or all other hosts' blood indices. HBI ONLY was also negatively related to DOGBI ($r = -0\cdot50$, $P < 0\cdot01$; not shown). In this model and others that follow in this section, all the initially significant variables remained significant in the final model obtained by eliminating non-significant vari-

ables. In addition, when we used CKBI ONLY instead of CKBI, this change did not, in general, affect the selection of significant variables.

Both DOGBI and DOGBI ONLY increased significantly with the number of room-mate dogs and decreased significantly with the CKBI (Table 2). Variations in the CKBI were significantly and positively related to the number of room-mate dogs and the
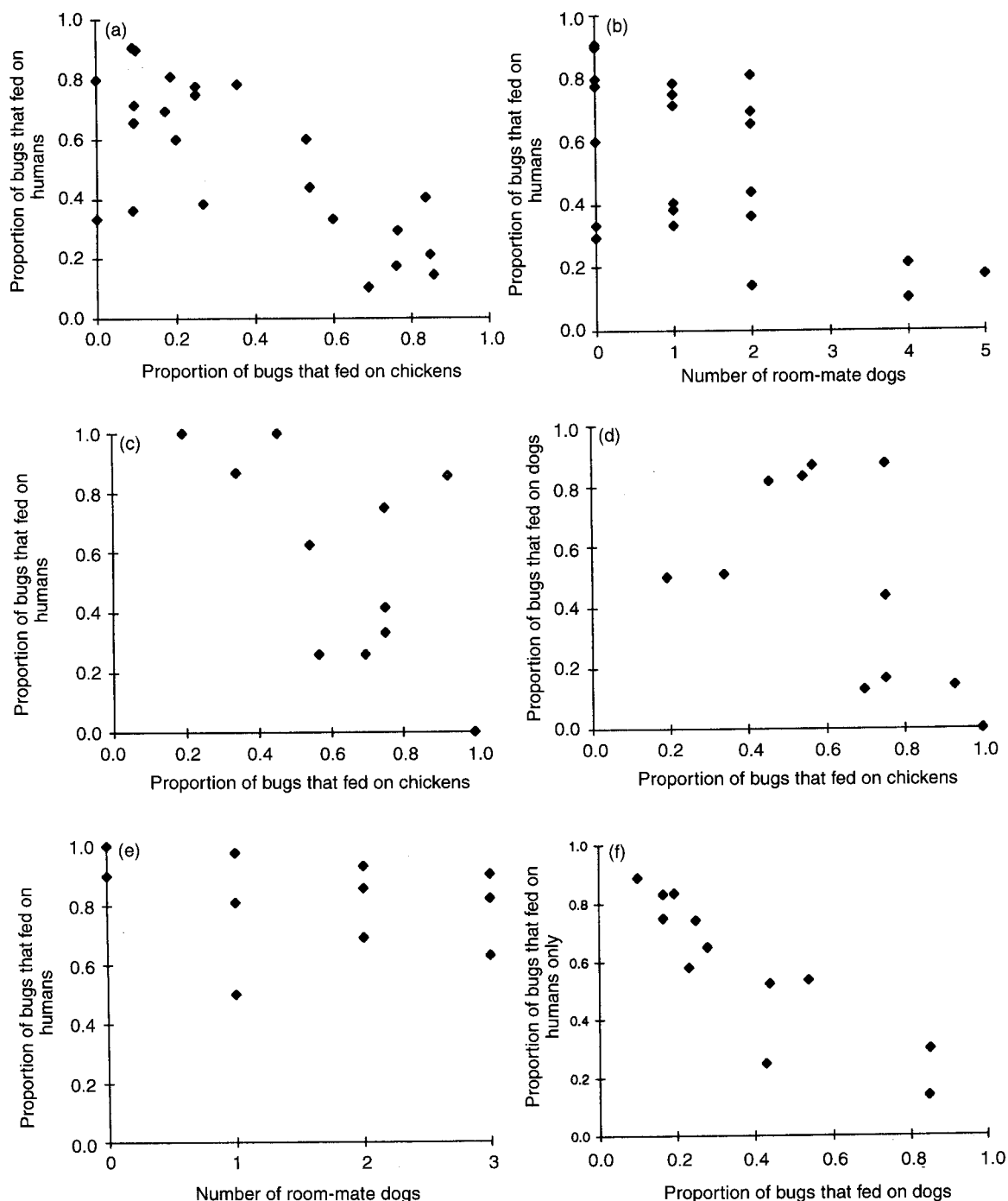
Fig. 1. Proportion of domiciliary *Triatoma infestans* that fed on humans, humans only or dogs in relation to the proportion of bugs that fed on chickens, or the proportion of bugs that fed on dogs, or the number of room-mate dogs. (a, b) Amamá, March 1992; (c, d) Mercedes and Amamá, December 1988–March 1989; (e, f) Trinidad, September 1988.

presence of brooding fowl; the CKBI ONLY showed similar relationships (not shown). The CATBI decreased significantly with the number of room-mate dogs and increased with the number of cats.

In similar backward step-wise regression analyses of the spring–summer data on 11 houses, variations in the HBI were also negatively and significantly related to the CKBI ($P < 0.001$) (Fig. 1c) and the number of room-mate dogs ($P = 0.006$) (not shown in tables). The model was: logit HBI-

$= 6.06 - 5.60 * CKBI - 1.47 * d$, $\chi^2 = 61.5$ with 2 d.f., $P < 0.001$). The HBI ONLY was significantly and negatively related to the CKBI (logit HBI ONLY $= -0.06 - 3.56 * CKBI$, $\chi^2 = 16.5$ with 1 d.f., $P < 0.001$). The DOGBI also decreased significantly with the CKBI (Fig. 1d) (logit DOG-BI $= 1.13 - 1.86 * CKBI$, $\chi^2 = 10.9$ with 1 d.f., $P < 0.001$). The CATBI was significantly and negatively related to the number of room-mate dogs ($P = 0.01$), and positively related to the numbers of

cats ($P = 0.005$), humans ($P = 0.001$) and the CKBI
($P = 0.03$)   (logit   CATBI $= -6.20 + 1.60 * h$
$+ 1.37 * c + 2.52 * \text{CKBI} - 1.90 * d$, $\chi^2 = 38.7$ with 4
d.f., $P < 0.001$).

In the winter data obtained from 12 houses, the
regression model included numbers of humans and
room-mate dogs as independent variables (not shown
in tables). HBI increased significantly with the number
of humans ($P = 0.008$) and decreased significantly
with the number of room-mate dogs ($P = 0.02$) (Fig.
1e) (logit HBI $= 1.07 + 0.62 * h - 0.70 * d$, $\chi^2 = 14.8$
with 2 d.f., $P < 0.001$), and so did HBI ONLY. Both
HBI ($r = -0.82$, $P < 0.001$) and HBI ONLY
($r = -0.93$, $P < 0.001$; Fig. 1f) were significantly and
negatively related to DOGBI (or DOGBI ONLY),
but not to other hosts' blood indices. The DOGBI
(or DOGBI ONLY) was significantly and negatively
related to the numbers of humans ($P < 0.01$) and mar-
ginally positively related to the number of room-mate
dogs ($P = 0.07$) (logit DBI $= 0.05 - 0.45 * h + 0.39 * d$,
$\chi^2 = 11.2$ with 2 d.f., $P = 0.004$). Variations in the
CATBI were not significantly predicted by any vari-
able.

VECTOR DENSITY AND HOST BLOOD INDICES

The effects of vector density on HBI or DOGBI and
related indices were also studied by multiple logistic
regression analysis of the models used in the preceding
section. In the summer collection, after backward
elimination of independent variables, HBI was sig-
nificantly and negatively related to the CKBI
($P < 0.001$), the number of room-mate dogs
($P = 0.02$) and the log-density of bugs ($P = 0.02$)
(Fig. 2a) (logit HBI $= 3.04 - 1.46 * \text{CKBI} - 0.50$
$* d - 1.07 * t$; $\chi^2 = 82.8$ with 3 d.f., $P < 0.001$). The
contribution of the CKBI and bug density, as mea-
sured by the standardized regression coefficients,
clearly surpassed that of the number of room-mate
dogs. Similar results were obtained with HBI ONLY
as the dependent variable, and with CKBI ONLY
instead of CKBI as an independent variable. Figure
2b shows that the proportion of bugs that fed on
chickens increased significantly as the density of bugs
increased. The DOGBI (or DOGBI ONLY) was sig-
nificantly and positively related to the number of
room-mate dogs ($P < 0.001$) and log-bug density
($P = 0.01$), and negatively related to the CKBI
($P = 0.01$)   (logit   DOGBI $= -2.97 + 1.35$
$* d + 1.24 * t - 2.98 * \text{CKBI}$; $\chi^2 = 63.3$ with 3 d.f.,
$P < 0.001$).

A similar analysis was made for the spring–summer
data including log-bug density as an independent vari-
able (not shown); after step-wise elimination, HBI was
significantly and negatively related to the CKBI and
the number of room-mate dogs but not to log-bug
density. The DOGBI was significantly and negatively
related to the CKBI ($P = 0.004$), and positively
related to log-bug density ($P = 0.03$) but not to the

number of room-mate dogs (logit DOGBI
$= -0.75 + 1.35 * d + 1.12 * t - 1.93 * \text{CKBI}$; $\chi^2 = 17.0$
with 2 d.f., $P < 0.001$). For the winter dataset, no
significant effect of log-bug density on HBI was found.

Figure 2c shows the marginally significant negative
relationship between HBI and log–density of domi-
ciliary *T. infestans* collected from walls in 1982 in the
dataset published by Rabinovich *et al.* (1990). After
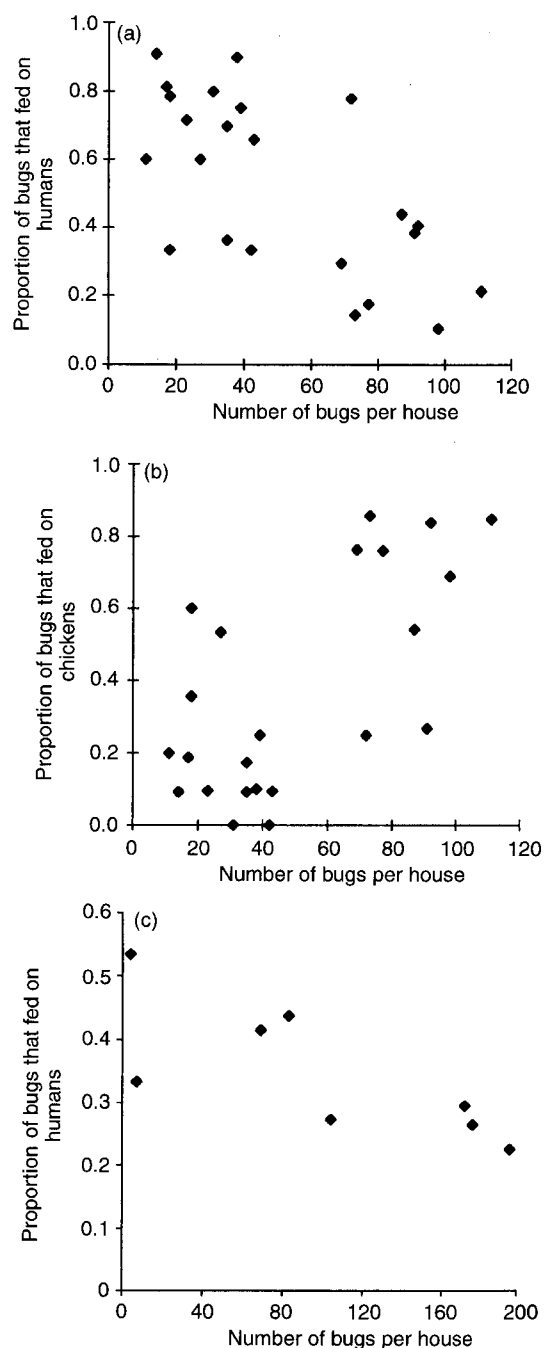backward elimination, the fitted equation was: logit

Fig. 2. Proportion of domiciliary *Triatoma infestans* that fed
on humans or the proportion of bugs that fed on chickens in
relation to the density of triatomine bugs in bedroom areas
(number of bugs collected per person-hour). (a, b) Amamá,
March 1992; (c) data taken from Rabinovich *et al.* (1990)
collected in Amamá, November 1982.

HBI $= 0.19 - 0.48 * t$; $r^2 = 0.47$, $F = 5.31$, 1 d.f., $P = 0.06$, $n = 8$. A similarly negative trend was obtained for data collected in 1984, but only one extreme point turned the correlation into marginally significant (logit HBI $= 4.97 - 3.08 * t$; $r^2 = 0.41$, $F = 4.78$, 1 d.f., $P = 0.06$, $n = 9$). In both datasets, the number of resident people was not a significant predictor and was eliminated from the model.

ANALYSIS OF DATA FROM LITERATURE

Figure 3a, b shows the host-feeding patterns of domiciliary *T. infestans* from 13 published studies. HBI was significantly and negatively correlated with the proportion of bugs that fed on dogs, or on chickens, reported within the same surveys. This negative trend was also verified when the data from either Argentina, or Chile, or both were excluded.

Figure 3c, d shows a similar analysis for 11 other triatomine species collected inside or around bedrooms, within several countries (data shown in Table 3). HBI was negatively correlated with the proportion of bugs that fed on chickens, but not on dogs. Considering only those datasets where bugs were col-

lected from bedrooms yielded a similar negative relationship between HBI and CKBI ($r = -0.83$; $n = 15$, $P < 0.01$) and lack of relationship between HBI and DOGBI ($r = -0.29$; $n = 11$, $P > 0.3$). In these analyses, we used an entire study as the unit of analysis, rather than individual houses within each study. Hence, the results are not directly comparable with our analysis based on individual houses. Nevertheless, the results are consistent overall.

Discussion

MAIN FINDINGS

Our study is the first to show for domiciliary triatomine populations that: (i) the likelihood of feeding on humans, or on humans only, decreased significantly with the presence of dogs and chickens in bedroom areas; (ii) the likelihood of feeding on humans was related negatively to the density of bugs per house, after controlling for the effects of chickens and room-mate dogs; and (iii) the likelihood of feeding on dogs increased with more dogs in bedrooms and decreased when the bugs fed upon chickens.
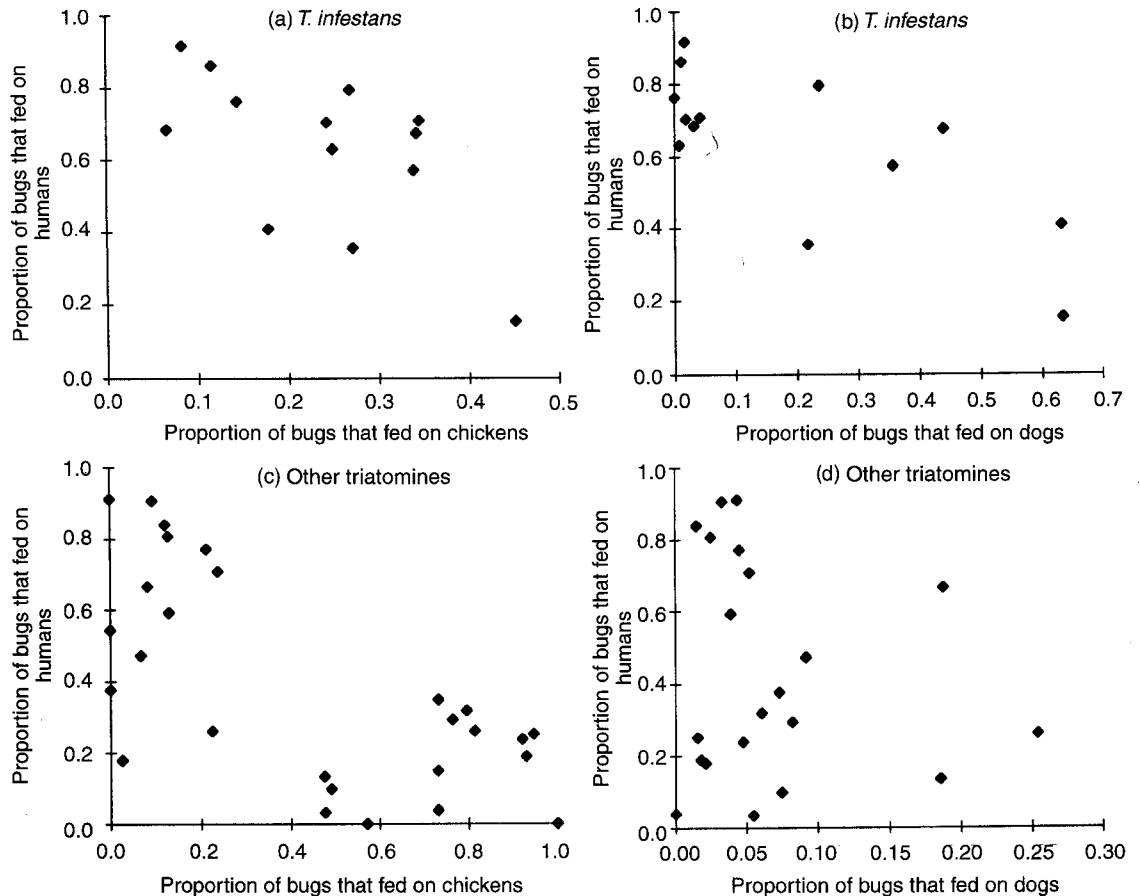
Fig. 3. Proportion of triatomines collected from or close to bedroom areas that fed on humans in relation to the proportion of bugs that fed on dogs or chickens in published datasets. (a) and (b) for domiciliary *Triatoma infestans* in 13 datasets taken from Gürtler *et al.* (1996a); (c) and (d) for 11 other triatomine species collected inside or around bedroom areas in 27 datasets shown in Table 3. (a) $r = -0.60$, $0.01 < P < 0.02$, $n = 13$; (b) $r = -0.74$, $0.001 < P < 0.01$, $n = 13$; (c) $r = -0.67$, $P < 0.001$, $n = 27$; (d) $r = -0.08$, $P > 0.1$, $n = 22$.

Table 3. Selected host-feeding patterns of triatomine species collected from bedroom areas. Data taken from published studies

Species*	Country	Site†	Number of bugs reactive‡	Number of bugs that fed on				Authors§
				Humans	Dogs	Chickens	Cats	
R. prolixus	Venezuela	D,P	63	24	5	0	27	Torrealba 1970[W]
R. prolixus	Venezuela	D	122	102	2	15	3	Rossell 1976[W]
R. prolixus	Venezuela	D	90	82	4	0	NR	Pifano 1973[M]
R. prolixus	Honduras	D	53	48	2	5	4	Ponce et al. 1974[W]
R. pallescens	Panama	D	331	196	13	43	9	Christensen et al. 1981[W]
P. megistus	Brazil	D,P	804	26	44	384	9	Barretto 1968[M]
R. neglectus	Brazil	D	118	31	NR	96	NR	Rodriguez et al. 1992
P. megistus	Brazil	D	48	26	12	0	2	Steindel et al. 1994
P. megistus	Brazil	D	1172	175	NR	857	NR	Rodriguez et al. 1992
P. megistus	Brazil	D	244	64	62	55	NR	Rocha et al. 1975[W]
P. megistus	Brazil	D,P	1703	1314	77	366	432	Forattini et al. 1981
P. megistus	Brazil	D,P	329	105	20	262	23	Forattini et al. 1982[W]
P. megistus	Brazil	D	1378	1113	34	178	1	Minter 1976[M]
P. megistus	Brazil	D	421	298	22	101	10	Piesman et al. 1983
T. sordida	Brazil	D	54	0	NR	54	NR	Rodriguez et al. 1992
T. sordida	Brazil	D,P	884	87	66	434	32	Barretto 1968[M]
T. sordida	Brazil	D,P	232	81	NR	170	NR	Rocha et al. 1977[W]
T. sordida	Brazil	D,P	444	84	8	413	15	Forattini et al. 1982[W]
T. sordida	Brazil	D,P	882	211	42	812	11	Forattini et al. 1981
T. brasiliensis	Brazil	D,P	877	258	72	670	100	Forattini et al. 1981
T. pseudomaculata	Brazil	D,P	2852	719	44	2698	80	Forattini et al. 1981
T. arthurneivai	Brazil	D	63	0	NR	36	NR	Rodriguez et al. 1992
T. barberi	Mexico	D	250	118	23	17	36	Zárate et al. 1980[W]
T. dimidiata	Mexico	D,P	269	36	50	128	1	Quintal & Polanco 1977[W]
T. dimidiata	Costa Rica	D	522	347	98	43	40	Zeledón et al. 1973[M]
T. dimidiata	Ecuador	D,P	434	78	9	11	1	Arzube Rodriguez 1966[M]
T. maculata	Venezuela	D	52	2	0	38	3	Tonn et al. 1978[W]

* R., *Rhodnius*; P., *Panstrongylus*; T., *Triatoma*.

† Collection site: D, domiciliary; P, peridomestic.

‡ Reactive means giving a positive reaction against one of the antisera employed.

§ Original citations compiled by Minter (1976a) are followed by superscript M, and those by Wisnivesky-Colli (1987) by superscript W.

NR, not recorded.

HOST CHOICES

Our study shows that the host choice of domiciliary specimens of *T. infestans* was related to host proximity (represented by the classification of room-mate or nesting indoors), the number of dogs, and the presence of fowl in bedroom areas. There were no fixed host-preferences, as bugs preferred chickens and dogs rather than humans in the hot season but fed on humans more often in winter. Even more interesting is the fact that the frequency of feeding on humans or dogs was affected by the presence and species of other hosts.

Host-preference of triatomine bugs has usually been approached through the affinity index (i.e. the ratio of the number of bugs that fed on a given class of host to the absolute number of those hosts present in the village). This index has been criticized because it is based only on numbers of hosts and does not take into account host attractiveness and behaviour favourable or unfavourable to biting (Minter 1976a; Zárate *et al.* 1980; Wisnivesky-Colli 1987). More importantly, our results show that the proportions of

bugs feeding on humans or dogs were modified by the presence of chickens in bedroom areas. This makes affinity indices even more inappropriate to the consideration of host-preference. The FI addresses specifically the choice between two host species in terms of their relative abundance, and thus overcomes one of the limitations of affinity indices. However, FI estimates fail to take into account the effects of vector density or of a third host species with qualitative importance, such as chickens. In addition, in our study we calculated medians because of the overdispersed distribution of house-specific FI values, instead of relying on the community-wide average index based on total bugs that fed on a host type and total hosts. Using the data from winter collections, we showed that different conclusions may be suggested by house-based or community-wide estimates. Considering the relatively low rate of dispersal of domiciliary *T. infestans*, a meaningful analysis should be based on the household unit and should take into account variability among houses to avoid potentially misleading interpretations.

Median dog/human feeding indices indicated that

dogs were about 2·3–2·6 times more likely to be selected as humans during the hot season. In winter, however, humans were chosen more frequently relative to their availability, even though the exposed surface of humans during night-time was greatly reduced. Since about 60% of the dogs did not share humans' sleeping accommodations in winter (as reported by house-dwellers), it is likely that the median dog/human FI for all dogs (0·8) was the lower bound of the actual value, whereas the FI for room-mate dogs (2·0) was the upper bound.

Considering that there was usually one hen (or duck) nesting inside the house at a time during spring and summer, the proportion of bugs that fed on chickens tends to be disproportionately high relative to chicken numbers. The fowl nesting indoors most likely provided the chicken blood meal source for domiciliary *T. infestans*, as it is unlikely that nymphs or adult bugs would be able to feed on chickens roosting on trees 20–40 m away from human sleeping quarters or that they would repeat any such feeding trips to and from the bedrooms. However, migration of a few chicken-fed bugs from closely associated structures (such as kitchens and storerooms also used by brooding hens) might have occurred in some cases. All published studies in which affinity indices for chickens were calculated included all the chickens in the household, including those that did not rest in human sleeping quarters (e.g. Zárate *et al.* 1980). This practice is expected to underestimate strongly the real selectivity of triatomine bugs for chickens. As a gross estimate, we estimated that chickens were 4·8 times more likely to be selected than humans during the hot season, but as shown by the interquartile range (1·6–17), evidently this was highly variable. Most of this variability may be due to the seasonal effect on fowl breeding, which peaks in mid-spring and decreases during the hot summer months (M.C. Cecere *et al.*, unpublished). The host-preference for chickens and dogs relative to humans would increase even more if relative biomass or surface were considered instead of number of hosts.

Host exposure to triatomine bugs and host behaviour in reaction to bites probably explain most of the variation in host-feeding patterns between seasons and houses, although we cannot exclude possible differences in attractiveness between humans, dogs, chickens and cats. The shift in host-feeding patterns from a predominance of humans in winter to a more balanced feeding on humans, dogs and chickens during the hot season was associated closely with the change in sleeping places of people (indoors in winter, in the unfenced veranda during hot weather), and the presence of fowl sitting on eggs inside or around bedrooms in spring–summer (Gürtler *et al.* 1996a). During hot weather people moved beds to the unfenced veranda or under open sky, and dogs rested beside or below them at night; one brooding hen entered or was placed into or around bedrooms for protection. In addition, the fact that brooding hens

stayed in one place for an extended period probably attracted more bugs. The behaviour and attitudes of house-dwellers toward their domestic animals thus presented specific conditions of host exposure to each triatomine population. Variations in host availability and exposure probably explain most of the observed variability in the feeding patterns of domiciliary *T. infestans* between different regions (Fig. 3) and seasons.

The nocturnal habits of cats probably decrease their association with bedroom areas and hence exposure to domiciliary bugs; during kittenhood, however, the pattern is probably reversed. In the two datasets pertaining to the hot season, feedings on cats were positively related to their presence and inversely related to the presence of dogs in bedroom areas.

Defensive grooming behaviour by vertebrate hosts has been suggested as a general regulatory mechanism for populations of blood-sucking arthropods (Lehane 1991) and of domestic triatomine bugs (Weir-López 1982; Schofield 1985). More tolerant hosts would allow triatomines to take larger blood meals and thus increase the reproductive rate of bugs. In contrast to cats, both dogs and chickens appear to be tolerant hosts, as suggested by: (i) the high proportions of bugs that fed exclusively on them, and (ii) the high feeding success of *T. infestans* on unrestrained dogs and chickens held in cages during day-time and night-time experiments (Jirón & Zeledón 1982). When bugs take large blood meals, the probabilities of ingesting trypanosomes (Minter, Minter-Goedbloed & Ferro Vela 1977) and of emitting faeces (Trumper & Gorla 1991) also increase. It follows that tolerant and highly infectious hosts, such as dogs, would be expected to increase the probability of bug infection and transmission of *T. cruzi*.

HOST SHIFTS

Our results show for the first time that in the presence of chickens or dogs, domiciliary *T. infestans* fed less frequently on humans: (i) in different surveys conducted by house carried out either during the hot season or in winter; and (ii) in the published community-wide data on domiciliary *T. infestans* and other triatomine species collected inside or around bedroom areas. We conclude that this is a generalized, robust pattern and that the more the bugs feed on chickens or dogs, the less they feed on humans. Marsden *et al.* (1979) believed that 'If man puts chickens in the house the bugs will turn to chickens and maintain high populations'. Our data give strong support to that speculation.

Our field data are the first to show a significant negative relationship between HBI or HBI ONLY and the density of domiciliary triatomine bugs, while adjusting for the effects of chickens or dogs on the host-feeding patterns of the bugs at the end of summer. These effects were not detected in the winter

and spring–summer collections, which may be due to the much smaller sample sizes in these datasets or to a seasonal effect. More importantly, our analysis of the data published by Rabinovich *et al.* (1990) gives additional support for the significant and negative relationship between HBI and the density of domiciliary *T. infestans*.

The probability of feeding on humans was lower at higher bug densities and when there were chickens available. How could this pattern emerge? One possible argument is that bugs preferred chickens or dogs to humans; the bug population feeding on chickens or dogs would increase rapidly during the bug's reproductive season, while humans were less preferred hosts. Another possible explanation rests on human irritability and exposure to bugs; the increasing density of bugs and their increased biting rate during the hot season would increase the irritation of humans due to the bites (Schofield 1985). As a consequence, bugs would achieve a lower feeding success on humans and shift to the more accessible chickens or dogs. During our surveys, residents of houses which were densely infested complained frequently about bug bites and reported reacting defensively in several ways: moving away from bedrooms, applying smoke to repel bugs, sleeping with kerosene lamps on, lighting lamps to kill the emerging bugs, etc. While sleeping in beds away from bedrooms, human exposure to domiciliary triatomines may be greatly reduced, whereas chickens and dogs would rest closer to bugs' refuges. It is likely that the relative accessibility of chickens and dogs (or host-preference, if any) would combine with less exposure of humans due to temperature and the irritation produced by the bites to produce the pattern observed. Under either or both hypothetical mechanisms combined, the net effect is the same: bugs fed relatively less frequently on humans and relatively more frequently on chickens when more bugs were in the house. Interestingly, feeding on dogs was positively related to bug density in the two datasets pertaining to summer and spring–summer bug collections; this may possibly suggest that dogs were more tolerant to bites, in addition to being involved in the increase of the bug population. Examples of mosquitoes shifting from feeding on birds to mammals when vector density increased (i.e. the reverse of what we observed) have been reported by Reeves (1971) and Edman & Taylor (1968).

RESERVATIONS AND PROBLEMS

The issue our study deals with does not lend itself to planned experimental field studies for ethical reasons. Domiciliary triatomine populations reproduce within houses and are a threat to house-dwellers' health; there is no preventive treatment of acute Chagas disease without severe toxic side-effects. Therefore, it is not justifiable to leave people exposed to the bugs for the sake of measuring variations in vector host-feeding patterns or other variables related to transmission of *T. cruzi*. Ethical standards thus preclude planned vector samplings during successive seasons at well-defined houses, as well as interventions involving the addition or removal of chickens, dogs or bugs and the measurement of the effects on the hosts' blood indices. The data we present here were obtained in cross-sectional studies, following which control measures were applied to reduce or eliminate domiciliary populations of triatomines. This explains why our observations were spread over 4 years and mainly two villages, with very few repeated observations at the same houses. This may also explain why the present database has no published antecedent.

It could be argued that potential confounding between time (months, years) and place (villages) would limit the interpretation of FI results if, for example, Trinidad differed in some essential respect (such as abundance of chickens) from Amamá, or March 1989 differed from March 1992. However, the three villages were comparable with respect to cultural practices, host density, and the habit of allowing fowl to nest indoors over the years (Gürtler *et al.* 1996a). In addition, the host-feeding patterns observed in March 1989 and March 1992 in Amamá were very similar, indicating homogeneity over time. The focus of the present analyses is not on attempting to detect seasonal variations in host-feeding patterns (which are evident at the community-wide scale), but rather on testing the relationship between host-feeding patterns and host availability, while controlling for variability due to season.

Other problems also limit the interpretation of these results. First, an implicit assumption in our analyses is that host availability at each house was constant during the preceding 3-month period (the interval in which host serum antigens may remain detectable). The point census of dogs, cats and nesting fowl at each survey may not represent accurately their previous presence in the house, and there was obviously some mobility of animals among houses (e.g. shared ownership of dogs or cats between neighbouring households). This mobility may explain why a few blood meals on domestic animals were detected in some houses without dogs or cats, or where fowl were not considered to nest indoors. Another plausible explanation is that these bugs immigrated from associated structures or adjacent houses. In addition, the classification of animals as 'room-mate' or 'nesting indoors' based on the owners' report must be considered an approximation to their actual exposure to domiciliary bugs. In practice, animals reported as not related to bedroom areas may actually have a weaker or unstable relation with these areas rather than no relation at all (Gürtler *et al.* 1993a). Consideration of the resting habits of domiciliary animals during the previous period, and a more objective measure of exposure patterns, if possible, would probably reduce the observed variability around the regression lines.

Secondly, the relationship between the density of bugs per house and HBI was not analysed on the same scale of bug density in all surveys because of different sampling methods and efforts. However, sampling methods were consistent within each survey, and estimates of bug density by the flushing-out method correlated closely with successive estimates obtained by knock-down at each house. Estimates of bug density by the available sampling methods are inaccurate and at best provide an ordinal scale of measurements (Gürtler *et al.* 1993b). Therefore, the observed relationship between bug density and HBI should be interpreted qualitatively.

Thirdly, blood indices on different hosts were not mutually exclusive because the bugs had mixed blood meals, which may violate the assumption of statistical independence. However, as an individual bug may show 2–6 different host blood sources and the sum of the proportions of bugs feeding on each host need not equal 1, these proportions are logically independent. Hosts' blood indices only were mutually exclusive and therefore this statistical problem did not arise. Nearly all results obtained with hosts' blood indices were verified by the results using the hosts' blood indices only.

Fourthly, in some published studies on host-feeding patterns, the original authors pooled bug collections from domiciliary (bedrooms) and associated sites. Previous studies (Wisnivesky-Colli *et al.* 1982) and our data showed that peridomestic bugs fed predominantly on chickens and marginally on humans. Hence, the negative relation between HBI and the proportion of bugs that fed on chickens in peridomestic bug collections would be related to very different exposures of both hosts, and not due to a shift of bugs from humans to chickens. Such pooling would likely favour a 'false-negative' relationship between HBI and other hosts' blood indices. Nevertheless, an analysis restricted to bugs collected only from domiciliary sites yielded a stronger negative correlation between HBI and the chicken blood index.

CONSEQUENCES FOR CONTROL AND MODELLING

Our results have serious implications at three levels: (i) density of *T. infestans*; (ii) contacts between bugs and humans; and (iii) transmission of *T. cruzi*.

Domiciliary populations of *T. infestans* and other triatomines were reported to increase with the number of available blood sources in the house (Marsden *et al.* 1982; Gürtler *et al.* 1992), and the number of chickens in experimental chicken houses (Gorla & Schofield 1989). Several authors (Marsden *et al.* 1979; Minter 1976b; Schofield & White 1984) have suggested that the presence of chickens in the house might build up bug populations, but no data supporting that proposition were available. Our data show that the density of domiciliary *T. infestans* was correlated positively

with the percentage of bugs that fed on chickens, which in turn is direct evidence of previous availability of chickens in bedrooms. This relationship still holds after adjusting for the statistical effects of other determinants of bug density, such as the use of domiciliary insecticides and the surface structure of indoor walls (M.C. Cecere *et al.*, unpublished). Overall, our results suggest that, in the absence of compensatory effects due to feeding on humans, removal of chickens and dogs from bedroom areas would decrease the reproductive rate of domiciliary *T. infestans* populations.

Mathematical models of vector-borne diseases usually assume that the proportion of vectors that feed on humans does not vary with vector density or season (e.g. Anderson & May 1991). The same applies to some models of the transmission of Chagas disease (e.g. Rabinovich & Himschoot 1990). By not taking into account the inverse density-dependent relationship of feeding on humans, calculations of the probability of host infection with *T. cruzi* may overestimate the actual value during the hot season (when the density of bugs, their biting rate and the incidence of Chagas' acute cases all peak), and underestimate the value at the beginning of the bug's reproductive season in late winter and spring (when the HBI is highest). Similarly, calculations of the expected blood loss from people living in densely infested houses (Rabinovich, Leal & Piñero 1979; Schofield 1981) might be too high. Because the bugs prefer to feed on dogs and chickens during hot weather, they would feed on humans less frequently than predicted by a random (proportional) distribution of bites among all hosts.

The presence of dogs or chickens in bedrooms may reduce significantly the probability that one bug will contact a human. However, the number of bugs may increase and the total number of contacts between bugs and humans (which is the product of the number of bugs times the probability of human contact per bug) may increase or decrease. Using the data in Fig. 2a, c, we estimate the number of human–bug contacts as follows. Let p be the proportion of bugs that fed on humans (the vertical axis in Fig. 2a, c) and let T be the total number of bugs per house (the horizontal axis, per person-hour of searching effort in Fig. 2a, and per 4 person-hours of searching effort in Fig. 2c). Then the number N of human–bug contacts is the product $N = pT$. The observed relation between p and T may be approximated as a straight line with negative slope.

For Fig. 2a, we estimate $p = 1 - T/120$ to ensure that $p = 1$ when $T = 0$ and $p = 0$ when $T = 120$. Hence, $N = pT = (1 - T/120)T = T - T^2/120$. Elementary calculus shows that N is maximal when $T = 60$. The number of human–bug contacts increases as the number of bugs per house (per person-hour of searching effort) increases up to 60 bugs per house and then decreases as the number of bugs per house increases beyond 60. There are $N = 0$ contacts in houses with 120 or more bugs because essentially

all bug meals are taken from nonhuman hosts. Similarly, for Fig. 2c, we estimate $p = 0.45 - T/1000$ to ensure that $p = 0.45$ when $T = 0$ and $p = 0.25$ when $T = 200$. In this case, the number of human–bug contacts increases as the number of bugs per house (per 4 person-hours of searching effort) increases up to a maximum of 225 bugs per house, i.e. over the entire observed range of 0 to 200 bugs per house.

As 4 person-hours of searching would be expected to yield several times more bugs, though perhaps not 4 times more bugs, than 1 person-hour of searching, the maximum number of human–bug contacts in Fig. 2c of 225 bugs per house is roughly consistent with the maximum number of human–bug contacts in Fig. 2a of 60 bugs per house, though the apparent consistency may be purely coincidental.

These calculations show that increasing numbers of bugs per house appear to be associated with increasing numbers of human–bug contacts, at least at the lower ranges of bug density. Caution is required in interpreting these calculations because the human-blood index does not distinguish a single human blood meal from repeated feedings on human hosts; it is possible that the number of repeated blood meals on human hosts per bug could vary at different levels of bug density.

Before it can be concluded that increasing numbers of human–bug contacts increase the risk of transmission of *T. cruzi*, it is necessary to investigate the prevalence of bug and host infection at different levels of bug density (Gürtler *et al.* 1996b). Hence, we refrain from drawing any conclusions here about the utility of chickens for zooprophylaxis, defined as 'the use of wild or domestic animals, which are not the reservoir hosts of a given disease, to divert the blood-seeking mosquito vectors from the human hosts of that disease' (Service 1991). While bugs are biting on chickens, the reproductive rate of *T. cruzi* in the bug population would in theory decrease in the short term (see Dye & Hasibeder 1986).

Our data suggest that the continuing presence of chickens in bedroom areas would reduce the fraction of bugs' blood meals taken from humans. In practice, however, during its long life cycle *T. infestans* shifted repeatedly from chickens to humans or dogs in the hot season, as shown by the increasing frequency of mixed blood meals with instar (Gürtler *et al.* 1996a). Bugs feeding on dogs were subjected to an increased risk of infection, hence resulting in an increase of the proportion of infected domiciliary *T. infestans* when more infected dogs were in the house (Gürtler *et al.* 1993a). In addition, because hens sit on eggs in bedroom areas during spring and summer and are mostly absent at other times, the increased bug population that fed on them would probably shift to humans or dogs when chickens were absent. Therefore, the exposure of chickens to bugs may increase the number of future contacts (per human) between bugs and humans. Because chickens are not susceptible to *T.*

cruzi and dogs are a highly infectious reservoir, the net effect of introducing sitting hens into a house on the transmission of *T. cruzi* remains to be evaluated.

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Appendix Host-feeding patterns of domiciliary *T. infestans* by house; Trinidad, Mercedes and Amamá, 1988–1992

No. of house	Bug density	Number of bugs reactive	Humans	Humans only	Dogs	Dogs only	Chickens	Chickens only	Cats	Bovids	People	Room-mate dogs	Dogs in total	Cats*	Brooding hens†
							Number of bugs fed on							Number of	
Winter															
T-01	50	78	54	29	42	19	5	0	5	1	3	2	4	2	0
T-02	215	254	209	136	71	28	12	3	27	22	6	3	5	1	1
T-03	20	20	10	3	17	9	0	0	1	0	2	1	1	1‡	0
T-04	45	44	43	32	11	1	0	0	1	1	6	1	3	0	0
T-08	87	92	58	8	78	31	3	1	3	3	5	3	3	1	0
T-09	79	82	74	43	19	2	17	3	7	1	5	3	3	1	1
T-13	10	12	12	10	2	0	0	0	0	0	3	0	1	1	0
T-14	36	24	24	18	4	0	2	0	1	0	3	0	1	1	1
T-15	66	148	120	63	65	20	18	1	14	3	9	1	1	0	1
T-16	73	72	67	56	14	4	3	0	1	0	10	2	2	1	1
T-17	5	14	12	3	6	1	3	1	3	0	7	2	2	0	1
T-18	23	20	18	16	2	1	1	0	1	0	2	0	0	1	1
Spring–summer															
A-02	56	14	12	1	2	0	13	2	2	0	2	0	0	0	1
A-05	19	24	8	0	21	5	18	1	8	0	5	2	3	4	1
A-15	208	23	6	0	20	6	13	1	5	0	10	2	2	0	1
A-17	38	23	6	6	3	1	16	5	11	0	8	2	2	2	1
A-19	30	14	0	0	0	0	14	14	0	0	2	4	4	0	1
A-23EX	151	16	12	1	7	0	12	2	6	0	16	3	3	1	1
A-27	23	26	26	6	13	1	5	0	4	0	7	2	2	1	1
A-31	29	12	5	0	2	0	9	0	7	1	8	0	4	1	1
A-35EX	54	11	11	1	9	0	5	0	0	0	4	1	5	1	1
A-40	65	24	15	1	20	4	13	2	3	0	7	2	2	0	1
M-06	51	53	46	17	27	6	18	0	1	0	9	3	3	1	1

Appendix (*Continued*)

No. of house	Bug density	Number of bugs reactive	Number of bugs fed on								People	Number of			
			Humans	Humans only	Dogs	Dogs only	Chickens	Chickens only	Cats	Bovids		Room-mate dogs	Dogs in total	Cats*	Brooding hens†
Summer															
A-05	73	28	4	2	2	1	24	19	4	0	6	2	2	1	1
A-06	72	36	28	19	7	2	9	4	5	0	5	0	0	0	1
A-10	17	16	13	6	6	2	3	1	3	0	5	2	2	1	0
A-11	87	50	22	3	26	7	27	17	2	0	8	2	2	1	1
A-12	43	32	21	7	22	10	3	0	6	0	5	2	2	1	0
A-13B	69	17	5	0	2	0	13	8	6	0	4	0	3	0	1
A-15	91	26	10	0	23	11	7	0	4	0	1	1	1	0	0
A-15B	111	33	7	1	18	4	28	12	1	0	6	4	4	0	1
A-18	35	23	16	7	11	5	4	2	1	0	3	2	2	0	1
A-19	92	37	15	2	6	0	31	18	6	0	10	1	1	1	1
A-21	27	15	9	5	1	0	8	6	1	0	2	0	2	1	1
A-23EX	39	32	24	7	18	2	8	1	12	0	6	0	4	1	1
A-24	11	10	6	4	4	1	2	1	2	0	4	0	2	1	1
A-27	42	36	12	6	28	19	0	0	6	0	8	0	2	1	1
A-29	23	21	15	8	9	4	2	2	5	0	12	0	3	0	1
A-30	14	11	10	10	0	0	1	1	0	0	12	0	1	0	1
A-31	18	15	5	1	11	5	9	2	0	0	2	0	4	0	0
A-32	98	29	3	0	13	7	20	15	0	0	3	4	1	0	1
A-39EX	18	14	11	4	4	1	5	2	4	0	4	1	5	0	0
A-41EX	77	46	8	1	29	7	35	15	0	0	3	5	1	0	1
M-04	38	10	9	8	0	0	1	1	1	0	2	0	1	0	0
M-06	35	11	4	2	7	5	1	1	0	1	6	2	2	2	1
T-14	31	10	8	5	4	1	0	0	2	0	4	0	1	1	1

T, Trinidad; A, Amamá; M, Mercedes. EX and B stand for new (non-numbered) houses built after the 1985 insecticide spraying.

Bug density: in winter 1988, number of bugs collected by flushing-out in 4 person-hours; in spring–summer, maximum density observed in December 1988 (by 4 person-hours) or March 1989 (by knock-down); in summer 1992, number of bugs collected by flushing-out in one person-hour. The last estimate of bug density omits bugs collected by knock-down.

Reactive bugs: giving a positive reaction against at least one of the antisera employed. This number may be larger than the bug density because bugs collected by knock-down were excluded from estimates of bug density.

Room-mate dogs: sleeping close to people in bedroom areas.

* Over 90% of cats were considered room-mate.

† Habit of keeping brooding fowls indoors or in veranda areas, as reported by house-dwellers and concurrent observations during vector surveys.

‡ Excludes three 10-day-old kittens.