Host-Feeding Patterns of Domiciliary *Triatoma infestans* (Hemiptera: Reduviidae) in Northwest Argentina: Seasonal and Instar Variation

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ABSTRACT Blood meal sources of 1,964 *Triatoma infestans* Klug collected in bedrooms in 3 rural villages in northwest Argentina were identified by agar double-diffusion tests. Bugs were collected in September (1988, end of winter), October (1992), December (1988, spring), and March (1989, 1992, summer), and tested for human, dog, cat, chicken–duck, and goat–sheep serum antigens. From late winter to late summer, the percentage of domiciliary *T. infestans* that fed on humans decreased from 81 to 50–51%, whereas the percentage of bugs that fed on dogs rose from 39 to 45–57%, on chickens from 8 to 40–54%, and on cats from 7 to 12–23%. Bugs that fed on goat–sheep (2%) were collected mostly from 1 house. In winter, most bugs fed on humans only (48%), followed by dogs only (13%), cats only, or chickens only (≈1%). In spring–summer, the percentages of bugs that fed exclusively on humans (19%), dogs (16%), or chickens (17%) were similar. The seasonal shift was associated closely with changes in the sleeping places of people from indoors in winter to verandahs in summer, and with the presence of brooding hens or ducks in or close to bedrooms in spring–summer. In spring–summer, at each instar, bugs had more identified blood meals, switched hosts from earlier instars, fed on a larger number of different host types, and took mixed meals more frequently than in winter. Bugs collected from walls, roofs and household goods showed similar blood-feeding patterns, whereas bugs from beds showed the highest frequency of human meals. The increased anthropophagy of domiciliary *T. infestans* populations at the end of winter and during spring precedes or coincides with the spring peak incidence of acute cases of Chagas disease in the region. This is the 1st report documenting seasonal variation in host selection of any triatomine species.

KEY WORDS *Triatoma infestans*, Chagas disease, epidemiology, blood meal sources, Argentina

TRIATOMA INFESTANS KLUG is probably the most important and widespread domiciliary vector of *Trypanosoma cruzi*, the cause of Chagas' disease. Available data indicate that >95% of *T. infestans* collected in bedrooms blood fed on either humans, dogs, cats, poultry, or bovids (Table 1); blood meals from peridomestic or sylvatic mammals and reptiles were rare (Minter 1976, Wisnivesky-Colli 1987).

Triatoma infestans populations reared in experimental chicken houses under natural climatic conditions in central Argentina have ≈2 generations per year (Gorla and Schofield 1989); indirect estimates of feeding frequency increased with temperature and were highly variable (every 2–10 d) during the warm season (Catalá 1991). In the laboratory, a single full blood meal usually is sufficient for molting to the next instar (Perlowagora-Szumlewics 1976), but in the field, more meals per instar may be frequent. Host blood antigens may remain detectable in the bug stomach for up to 4 mo (several references in Minter 1976). The duration of antigen detection increases with nymphal instar and may depend on bloodmeal size (Zárate and Tempelis 1981).

In mathematical models of vector-borne diseases transmitted to humans, the degree of anthropophagy of the vector is related closely to the risk of parasite transmission (Anderson and May 1991). The percentage of domiciliary *T. infestans* that fed on humans in 3 rural villages in northwestern Argentina varied from 15 to 67% (Wisnivesky-Colli 1987), although the prevalence of *T. cruzi* in each of the human populations was ≈50%. Why the percentage of bugs that fed on humans tended to be lower and more variable than recorded elsewhere (Table 1) remains unexplained.

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Table 1. Comparison of published feeding patterns of *T. infestans* collected in human sleeping areas of different countries

Country	No. bugs reactive[a]	No. antisera used	% bugs fed on				% mixed meals[c]	Reference
			Humans	Dogs	Cats	Chickens[b]		
Argentina	438	4	79.5	23.7	15.1	26.7	36	Mayer and Alcaraz 1955
Argentina	175	11	15.4	63.4	2.3	45.1	27	Wisnivesky-Colli et al. 1982
Argentina	132	11	67.4	43.9	22.0	34.1	19	Wisnivesky-Colli et al. 1987
Argentina	418	11	40.9	63.2	14.8	17.7	31	Wisnivesky-Colli 1987
Brazil	226	6	44.1	NR	NR	NR	NR	Andrade et al. 1979
Brazil	489	2	67.3	NR	NR	52.1	NR	Corrêa and Aguiar 1952
Brazil	631	4	57.2	35.7	15.1	33.8	35	Corrêa and Aguiar 1952
Brazil	42	11	76.2	0	11.9	14.3	10	Freitas et al. 1960
Brazil	371[d]	12	35.6	21.8	11.3	27.0	7	Barretto 1968
Brazil	1,241	10?	70.3	1.9	0	24.2	1	Marsden et al. 1979
Brazil	432[e]	10?	63.0	0.7	0	24.8	NR	Schofield 1980
Brazil	60[d]	6	91.7	1.7	23.3	8.3	43	Forattini et al. 1981
Brazil	360[d]	6	70.8	4.2	5.1	34.4	40	Forattini et al. 1982
Chile	87	13	86.2	1.1	8.0	11.5	23	Knierim et al. 1976
Chile	376	19?	68.4	3.2	6.1	6.6	NR	Schenone et al. 1985

NR, not recorded or not reported.
[a] Giving at least 1 positive host identification.
[b] Several authors employ antisera produced against chicken serum but report their findings either as chicken, poultry, bird, or avian.
[c] Mixed meals are those with ≥2 different sources.
[d] Pools of bugs collected in domestic and peridomestic sites.
[e] Includes 2 inhabited dwellings, and excludes 1 uninhabited dwelling.

Most studies on the bloodmeal hosts of triatomines have pooled results across villages, months, instar, or collection sites within houses (see Forattini et al. 1982). As a consequence of such aggregated data, many relevant features of triatomine biology remain undocumented or unexplored. Preliminary results for *T. infestans* in northwestern Argentina showed that host-feeding patterns varied across seasons (Gürtler et al. 1983, Solarz et al. 1986) and among instars (Wisnivesky-Colli et al. 1982). To our knowledge, no study has described seasonal variation in the feeding pattern of triatomine bugs adequately or searched for differences among instars in different seasons.

Mixed blood meals may result from feeding on 2 different host species (patent) or on the same host species (cryptic) (Boreham and Garrett-Jones 1973). Patent mixed blood meals are common in *T. infestans* (Table 1) but not in other domestic triatomine species (Minter 1976). The proportion of mixed meals was first used as an index of feeding mobility by Barretto (1968). A low proportion of mixed meals could indicate that many bugs may have fed from the same host species (but not necessarily on the same individual) on consecutive occasions. Variation of mixed and unmixed blood meals by instar and season, not studied previously, may give clues to the degree of association of bugs with particular types of hosts during the year.

The current study describes seasonal and developmental changes in blood feeding by *T. infestans* collected from bedrooms because this is the place where transmission of *T. cruzi* to humans occurs. Our host-feeding data, spread over 4 yr, are compared with previous estimates made in the same area. This time series of host-feeding patterns constitutes the first for any triatomine bug.

Materials and Methods

Study Sites. Studies were carried out in 3 similar rural villages described by Gürtler et al. (1992): Trinidad, Mercedes, and Amamá, Province of Santiago del Estero, Argentina. The villages were situated within 9 km of each other in semiarid, hardwood thorny forest habitat at 27° 12′ S, 63° 02′ W. Trinidad and Mercedes were never sprayed with insecticides by official control services. Amamá was treated once with deltamethrin in 1985, but house reinfestation increased steadily after 1987 and returned to baseline levels by 1992 (Gürtler et al. 1994). In 1988, the population of Amamá consisted of 204 people, 121 dogs, and ≈25 cats in 41 houses; in Trinidad and Mercedes we censused 128 people, 86 dogs, and 31 cats in 31 houses. In Amamá, the prevalence of seroreactivity to *T. cruzi* in children <16 yr of age was 29.6% and in dogs was 39.8% (Gürtler et al. 1991). In Trinidad and Mercedes, 64.4% of dogs were seroreactive to *T. cruzi*, and 39.3% of cats had *T. cruzi* detected by xenodiagnosis (Gürtler et al. 1993a).

Houses typically had mud and brick or mud and stick walls, thatched roofs, floors of beaten earth, and an unfenced verandah at the front. Peridomestic structures included kitchens, storerooms, and goatpens and were separated 4–40 m from human sleeping quarters. Dogs, cats, and brooding hens (which had no special chicken coops and roosted on trees when not brooding) frequently rested inside or around bedroom areas. Ducks were less abundant than chickens, and turkeys or geese were rare. Goats, sheep, and pigs and fewer horses, mules, and cows wandered freely during the day but usually were housed at night in peridomestic corrals. Rats, mice, and cavies were seen or re-

ported rarely by housedwellers in domestic or peridomestic habitats.

Triatomine Collections. Collection procedures and results have been described previously (Gürtler et al. 1991, 1992, 1993b). Briefly, bug collections were made by a 2-person team by "flushing-out" or insecticidal knockdown or both in 19 houses in Trinidad (September 1988), in 12 houses in Mercedes and in 41 houses in Amamá (December 1988), in 40 houses in Amamá (March 1989), and in all 3 villages (47 houses in Amamá, 18 houses in Trinidad, and 5 houses in Mercedes) in March and October 1992. Mean monthly temperatures corresponding to the survey months were 18.3, 28.9, 24.1, 25.6, and 22.3 °C, respectively, at the closest meteorological station located at 27° 46′ S, 64° 18′ W. In most of the surveys and in May 1993, we recorded the nightly sleeping places of housedwellers and the type and number of their domestic animals.

In the flushing-out method, bug collectors first searched all bedroom areas for bugs, then sprayed walls and roofs repeatedly with a dislodging agent (0.2% tetramethrin) (Icona, Argentina) and captured triatomines as they emerged during 2 h (4 person-hour per house) in 1988, or 30 min (1 person-hour per house) in March 1992. In Trinidad in 1988, bedrooms were divided into quadrats and bugs were collected separately from each quadrat. In the 3 villages in 1992, bugs were collected separately from beds, household goods, walls, and roofs, and in Amamá from inside sensor boxes tacked to walls for vector surveillance. Sensor boxes were made of cardboard (41 cm wide, 22 cm high) with pleated pink paper inside and permanent entries for bugs at the bottom and both sides.

For knockdown collections, 1 γHCH (γBHC) fumigant tablet (Gammexane, Duperial, Argentina) per bedroom was used 3–5 d after flushing-out in 16 houses in Trinidad in September 1988 and in 3 houses in Mercedes in December 1988; both types of collection at each house were pooled to increase the sample size. Knockdown collections were made in 40 houses in Amamá in March 1989. To further reduce the densest bug infestations and help housedwellers in their control measures against bugs, insecticide fumigant canisters (Aguvac, Argentina) were used in 1988–1989 and 1992, but the bugs were not tested for blood meals. All domiciliary and peridomestic structures in the 3 villages were sprayed with deltamethrin (2.5% suspension concentrate at 25 mg [AI]/m^2 of sprayed surface) by staff of the National Chagas Control Service in October 1992. Collections of the knocked-down triatomines were made at each house ≈5–7 h after treatment.

Processing of Triatomines. Bugs were identified by instar, counted, and dissected or frozen within 10 d of capture. The thorax was cut at the level of the 3rd pair of legs, and the blood meal was expressed from the abdomen with the aid of tweezers into individual vials that contained 0.2 ml of buffered 0.85% saline (pH 7.2) with gentian violet added to a final concentration of 0.025%. For bugs with small blood meals, the promesenteron was transferred to the vial, even when possibly insufficient remnants of blood for host identification were observed. Each dissected bug was given a serial number to record its source house, place of capture, and instar. Bloodmeal vials were stored in a refrigerator in the field, and then frozen at −20°C until they were tested.

Preparation of Antisera. All antisera were prepared by injecting whole-serum antigens into New Zealand white rabbits according to standard procedures (Wisnivesky-Colli et al. 1982). Animals were treated according to standard practice (Anonymous 1980). Each antiserum was titrated against serial double dilutions of the homologous serum and each heterologous serum by agar double-diffusion tests. Antisera that cross-reacted with heterologous sera were adsorbed with undiluted sera (50:1) from the cross-reacting species with the highest titer, then retested to assure that cross-reactivity was eliminated. The cat antiserum, which still cross-reacted with dog serum diluted 1:4, was accepted as specific under our testing conditions (see below). The antigoat serum also detected sheep and cow serum antigens, so it was considered an antigoat–sheep. The antichicken serum was not adsorbed; it also detected serum antigens from columbiforms (pigeons and doves) and anseriforms (ducks and geese) and possibly served as a general anti-avian test. Blood meals that were positive against the antichicken serum were considered to be from chickens, although some of the bugs may have fed on ducks, the only other bird nesting indoors. Final homologous antisera titers ranged from 1:1,600 (chicken) to 1:4,000 (the other 4 antisera). In our test system, antisera titers in the range of 1:1,600 to 1:4,000 detected full blood meals taken as long as 3 mo previously in bugs stored at ≈20°C (Wisnivesky-Colli et al. 1980).

Testing of Blood Meals. Double-diffusion tests were carried out using 3.5 ml per slide of 1.3% purified agar (I. D. Oxoid Agar) in veronal–hydrochloric acid buffer (pH 8.6). The standard procedures of Wisnivesky-Colli et al. (1982) were modified for mass testing of samples and for verification of mixed feeds. Slides were composed of 5 linked sets of wells, each consisting of 1 central basin filled with ≈20 μl of an individual blood meal and 6 peripheral wells loaded with the 5 antisera (human, dog, cat, chicken, and goat–sheep) and normal rabbit serum. Cat and dog antisera were loaded in adjacent positions to check for partial and complete identity of precipitin bands through the presence of "spurs" (Ouchterlony and Nilsson 1986). Slides were kept for 48 h inside a humid chamber at room temperature. Readings were made at 24 and 48 h after loading the wells and after staining with 0.1% amido black. Dubious precipitin bands or unspecific arcs of unknown origin (both occurring in <5% of total blood meals)

Table 2. Temporal changes in host-selection patterns of domiciliary *T. infestans*

Survey date	No. (%) bugs		Blood source, no. (%)					All sources
	Tested	Reactive	Humans	Dogs	Chickens	Cats	Goat–sheep	
Winter								
September 1988	997	885 (89)	720 (81)	342 (39)	68 (8)	64 (7)	33 (4)	1,227
Spring								
October 1992	135	120 (89)	82 (68)	75 (63)	33 (28)	17 (14)	2 (2)	209
December 1988	170	147 (86)	93 (63)	75 (51)	82 (56)	23 (16)	0 (0)	273
Summer								
March 1989	179	155 (87)	79 (51)	89 (57)	84 (54)	36 (23)	1 (<1)	289
March 1992	705	657 (93)	326 (50)	295 (45)	265 (40)	79 (12)	4 (<1)	969
Overall	2,186	1,964 (90)	1,300 (66)	876 (45)	532 (27)	219 (11)	40 (2)	2,967

Comparisons among proportions of bugs that fed on different hosts among surveys (all df = 4): humans (χ^2 = 188.1, $P < 0.001$); dogs (χ^2 = 34.6, $P < 0.001$); chickens (χ^2 = 346.0, $P < 0.001$); cats (χ^2 = 40.8, $P < 0.001$).

were disregarded. Mixed blood meals (those in which ≥2 types of blood were identified) were repeated with the reacting antisera loaded in adjacent positions to check for specificity of reactions and to exclude potential cross-reactivity of the antisera with partially degraded proteins stored in the stomach (Perassi and Segura 1976). Unmixed blood meals are those in which only 1 type of blood is recognized, although the bug may have fed several times on the same type of host. For triatomine bugs, however, unmixed and mixed blood meals were termed single and multiple meals, respectively (Minter 1976, Wisnivesky-Colli 1987).

Data Analysis. To describe how bugs use the available hosts, we report the proportion of reactive bugs that contain each type of host blood. For example, the proportion of human-fed bugs is the number of bugs positive against human antiserum (whether or not the bugs were also positive against any other antiserum), divided by the number of reactive bugs (those positive against any antiserum). Because some bugs fed on as many as 4 types of host, the sum of the proportions of bugs that fed on each type of host category usually exceeded 1. The proportion of bugs that fed on each host can take values from 0 to 1 within the same survey because each bug may show several blood sources; thus these proportions are logically independent.

The relation between the percentages of bugs that fed on different host types among seasons or instars was analyzed by $R \times 2$ contingency tables using χ^2 tests; comparison of unmixed or mixed blood meals by instar between seasons was done by Mantel–Haenszel χ^2 (Fleiss 1981). For example, to analyze the percentage of bugs that fed on humans by season (rows), one column of the table represented the frequency of bugs fed on humans and the other the bugs that had not fed on humans. Another way of analyzing the data would treat each identified source of blood in each bug as a separate entity (Wisnivesky-Colli et al. 1982). This procedure assumes implicitly that bugs feed each time independently; in addition, it inflates the actual sample size of reactive bugs. For example, a bug positive against a human antiserum but not positive against any other antiserum would count as 1 human blood meal (although the bug may have fed on humans on several occasions), whereas a bug positive against a human antiserum and a dog antiserum would count as 1 human meal and 1 dog meal. Because many bugs had taken mixed blood meals, the proportion of human blood meals among all blood meals is necessarily lower than the proportion of human-fed bugs among all reactive bugs, and depends upon the number of blood meals detected on other hosts. The proportion of human-fed bugs among all reactive bugs may be interpreted as the proportion of bugs that fed at least once on humans, and possibly as an index of the probability of feeding on humans.

We attributed differences in samples from different months to seasonality on the assumption that the seasonal cycle was the same in different years. We tested this assumption by comparing samples taken in March 1989 and March 1992.

Results

Distribution of Blood Meals by Season. In total, 4,793 *T. infestans* were collected in bedrooms and dissected. Of these, 2,186 (46%) were judged to contain some blood, 90% of which gave at least 1 positive result.

The distribution of 1,964 domiciliary *T. infestans* by source of blood meals and date of survey are shown in Table 2. Overall, most bugs fed on humans (66%) and dogs (45%). Bugs fed less frequently on chickens (27%), cats (11%), and goat–

Table 3. Host availability in Amamá and Trinidad in 1988 and 1993

Village, yr	No. houses	Median density of hosts per house (interquartile range)				Proportion (%) of households with chickens–ducks brooding indoors
		Humans	Dogs	Cats	Chickens–ducks	
Trinidad, 1988	19	5 (3–7)	2 (1.5–3)	1 (0–1)	8 (4–20)	5/19 (26)[a]
Amamá, 1988	41	4 (3–7)	2 (2–3.5)	1 (1–1.5)	NR	9/27 (33)[a]
Trinidad, 1993	19	5 (4–6.5)	2 (1–3)	1 (0–1)	18.5 (10–50)	9/19 (47)[b]
Amamá, 1993	46	5 (3–6.7)	2 (1–3)	0 (0–1)	27 (13–43)	23/44 (52)[b]

NR, not recorded.
[a] Direct observations during vector collections.
[b] Reported by house-dwellers.

sheep (2%). This pattern, however, showed a marked seasonal progression from late winter to late summer. As the mean monthly temperature increased, the percentage of bugs that fed on humans showed a slightly decreasing trend from 81 to 50–51% ($r = -0.66$, $n = 6$, $P > 0.1$), whereas the percentage that fed on chickens increased from 8 to 40–54% ($r = 0.897$, $n = 6$, $P < 0.05$). Few bugs fed on goat–sheep; 2/3 of positives came from 1 house in Trinidad and included 4th and 5th instars. The mean number of identified blood meals per reactive bug increased from 1.39 in winter to 1.68 and 1.86 in spring and to 1.47 and 1.86 in summer. When each single host was compared with all remaining hosts, the percentages of bugs that fed on humans, dogs, chickens, and cats differed significantly among each and every survey, except for the percentage of bugs that fed on humans in March 1989 and in March 1992 (Table 2).

Results differed somewhat for the distribution of blood meals for all hosts jointly. Analyzing Table 2 as frequencies of blood meals, there were significant differences in the frequencies of blood meals on humans, dogs, chickens, and others combined among all surveys ($\chi^2 = 314.4$, df = 12, $P < 0.001$), or among October, December, and March ($\chi^2 = 22.5$, df = 9, $P = 0.007$). No statistically significant differences occurred between December and March ($\chi^2 = 8.9$, df = 6, $P = 0.179$) or March 1989 and March 1992 ($\chi^2 = 7.2$, df = 3, $P = 0.066$). This finding supported our assumption that feeding patterns were similar in the same season during different years.

Host Availability. Table 3 compares the frequency distribution of hosts per house in Amamá and Trinidad in September 1988 and May 1993. Both villages had similar host densities in both years, with slightly lower numbers of chickens and ducks in Trinidad in 1988. Nearly all households owned chickens (an important food resource) and dogs, and ≈50% owned a cat. The proportion of households that kept brooding hens indoors was similar in both villages and years. The median density per household was 5 people, ≈3 dogs, <1 cat, and 8–27 chickens and ducks.

Sources of Blood Meals by Instar. Because the stage composition of the bug population changed seasonally, it was necessary to examine whether the seasonal differences in host-feeding patterns could be the result of changes in the stage composition of the bug populations. In winter, the percentage of bugs that fed on humans ($\chi^2 = 4.7$, df = 5, $P > 0.4$) or dogs ($\chi^2 = 5.5$, df = 5, $P > 0.3$) did not differ significantly among instars or sex (Fig. 1). In spring–summer, the percentage of bugs that fed on chickens steadily increased from 22% in 1st and 2nd instars to 45–50% in adult bugs ($\chi^2 = 11.5$, df = 5, $P = 0.041$). Significant differences among instars and sex also were detected for proportions of bugs that fed on humans ($\chi^2 = 16.2$, df = 5, $P = 0.006$), or cats ($\chi^2 = 11.9$, df = 5, $P = 0.036$), but not on dogs ($\chi^2 = 7.3$, df = 5, $P > 0.2$). The sample sizes of reactive bugs for each instar and season are shown in Table 5.

A different way of analyzing these data statistically was as proportions of blood meals on each type of host among all the blood meals identified by instar within each season. No significant differences among instars were detected in winter (chicken, cat, and goat–sheep combined; $\chi^2 = 10.1$, df = 10, $P > 0.4$) or spring–summer collections (cat and goat–sheep combined; $\chi^2 = 20.1$, df = 15, $P = 0.167$).

Unmixed Blood Meals. Fig. 2 shows the distribution of domiciliary *T. infestans* with unmixed blood meals by instar in winter versus spring–summer. In winter collections, more bugs fed on humans only (48%) than on dogs only (13%) or on each of the other sources only (≈1%). In contrast, in spring–summer collections, the percentage of bugs that fed exclusively on humans (19%), dogs (16%), and chickens (17%) was similar and higher than on cats only (1%). The percentage of domiciliary *T. infestans* that fed on humans only stratified by instar was significantly higher in winter (48%) than in spring–summer (19%; Mantel–Haenszel $\chi^2 = 173.5$, df = 1, $P < 0.001$), and the reverse occurred with bugs that fed on chickens only (1% versus 17%; Mantel-Haenszel $\chi^2 = 128.3$, df = 1, $P < 0.001$). The percentage of bugs that fed on dogs only did not differ significantly between seasons (Mantel–Haenszel $\chi^2 = 0.5$, df = 1, $P > 0.5$).

Host Fidelity. To represent host fidelity during the life cycle of the bug, from instar-specific data shown in Figs. 1 and 2, we calculated the per-

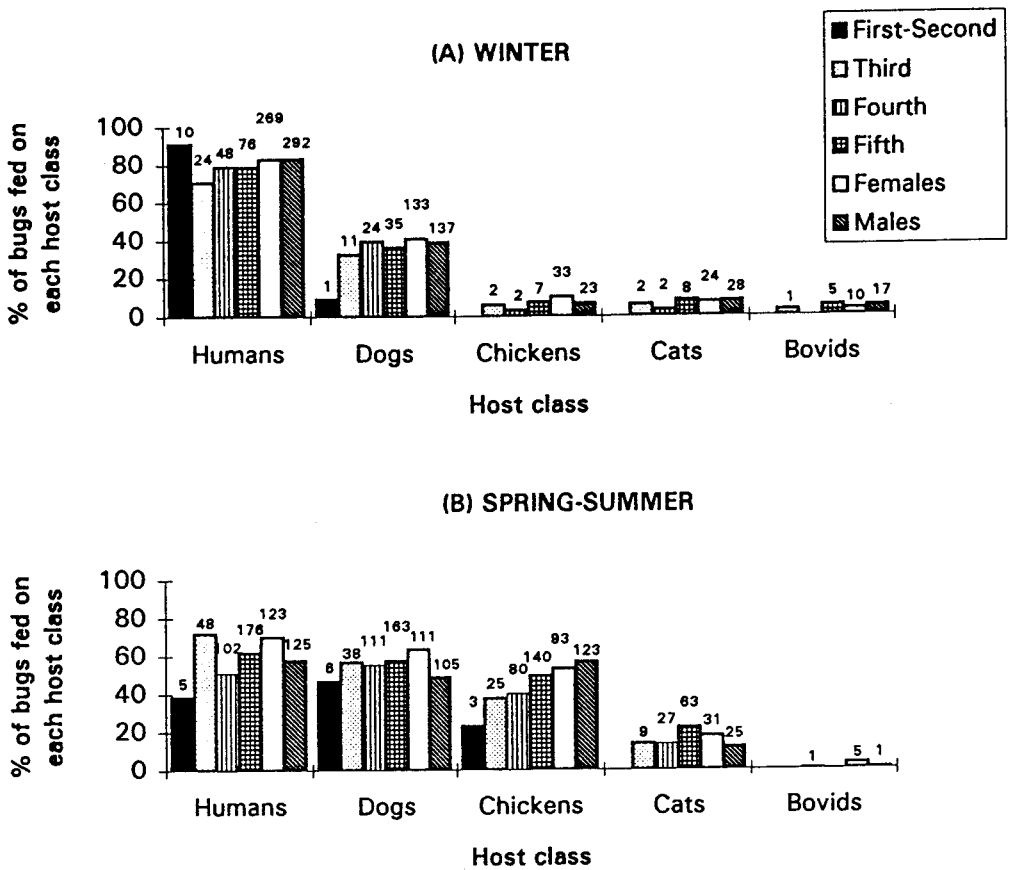

Fig. 1. Distribution by instar of the percentage of domiciliary *T. infestans* that fed on each host type. (A) Winter collections; Trinidad, September 1988. (B) Spring–summer collections; Amamá, Trinidad, and Mercedes, October–March 1988–1992. Numbers on top of each histogram bar represent the number of bugs with blood meals (mixed and unmixed) on each host type and instar.

centage of bugs that fed on each host type and had unmixed meals in winter versus spring–summer. For example, from a total of 10 human-fed 1st–2nd instars in winter (Fig. 1A, 1st bar), 10 had fed on humans only (Fig. 2A, first bar); thus the percentage of human-fed bugs with unmixed meals on humans for 1st and 2nd instars in winter was 100%. For large samples, this percentage represents the conditional probability of having fed on humans only among bugs that had fed on humans (the host fidelity index for humans).

In winter (Table 4), the fidelity index for humans was highest (59%), followed by dogs (35%), chickens (15%), and cats (13%). In spring–summer, fidelity indices for humans (35%), dogs (33%), and chickens (39%) were similar. For humans and dogs, the decreasing trend with instar started earlier and was sharper in spring–summer than in winter. The percentage of human-fed bugs that had unmixed human meals was significantly higher in winter (59%) than during spring–summer (35%; $\chi^2 = 73.2$, df = 1, $P < 0.001$), but those on dogs did not differ between seasons ($\chi^2 = 0.3$, df = 1, $P > 0.5$).

Mixed Blood Meals. Significantly more domiciliary *T. infestans* had patent mixed blood meals in spring–summer (46%) than in winter (35%) (Table 5). In winter, the percentage of bugs with mixed meals increased significantly from 0% in 1st–2nd instars to 37–40% among adult bugs. In spring–summer, the frequency of bugs with mixed meals also differed significantly among instars, but the pattern was less distinct than in winter.

Most bugs with mixed blood meals had fed on 2 and a few on 3 host species in winter, but 3 and 4 hosts were common in spring–summer (Table 5). More double and triple feeds appeared in earlier instars in spring–summer than in winter. Feeds on 4 hosts were detected only in spring–summer.

Site-Specific Feeding Patterns. The host-feeding patterns of domiciliary *T. infestans* were stratified according to site of capture (Table 6). Among bugs caught by flushing-out, the percentages that fed on humans in beds, household goods (includ-

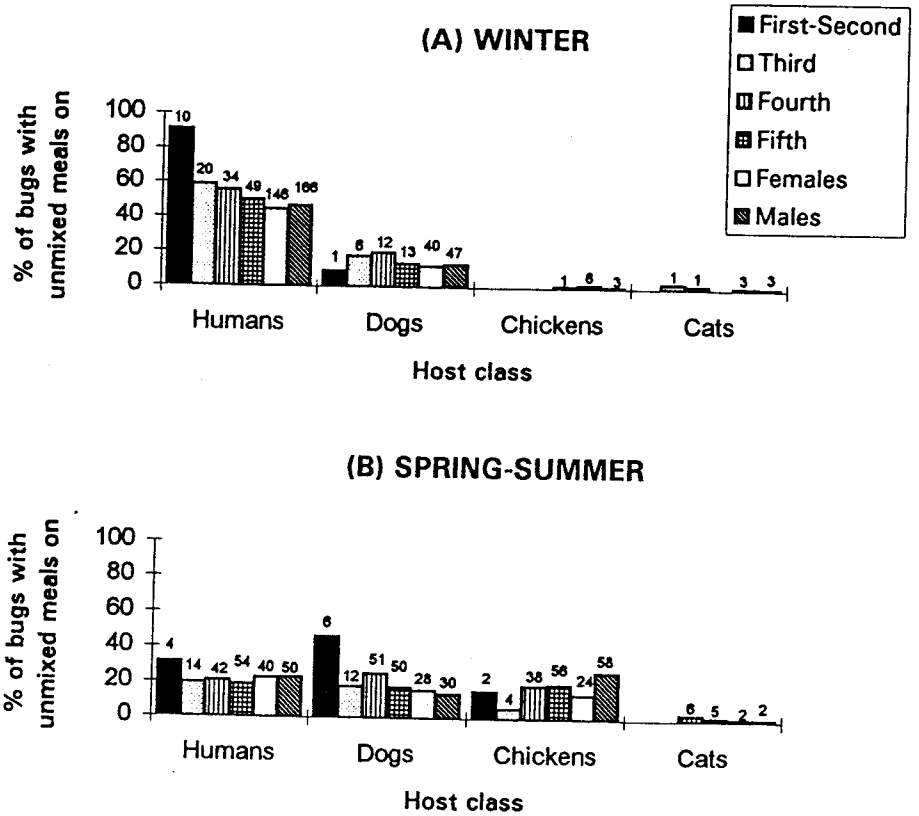

Fig. 2. Distribution by instar of the percentage of domiciliary *T. infestans* that fed only on humans, dogs, chickens, or cats (unmixed blood meals). (A) Winter collections; Trinidad, September 1988. (B) Spring–summer collections; Amamá, Trinidad, and Mercedes, October–March 1988–1992. Numbers on top of each histogram bar represent the number of bugs with unmixed blood meals on each host type and instar.

ing other furniture or clothes), walls, and roofs were not homogeneous (Table 6). Bugs collected from beds showed the highest percentage (90%) of human meals. The percentage of bugs that fed on humans did not differ significantly among walls, roofs, and household goods ($\chi^2 = 1.5$, df = 2, $P > 0.4$), and the same occurred with the bugs that fed on other hosts. Sensor boxes showed the highest frequency of bugs that fed on cats (37%), but most of these bugs came from 1 house.

In a house in Trinidad in September 1988, we obtained 254 reactive bugs captured from 10 different sites within bedrooms. We found no significant differences among sites in the proportion of bugs that fed on humans (mean, 82%; range, 68–91%) or dogs (mean, 28%; range, 10–48%) (not shown). Similar results were obtained in 4 other houses with >70 reactive bugs each.

Discussion

Study Design. Because our observations were spread over 4 yr and mainly 2 villages, potential confounding between time (months, years) and place (villages) would limit the interpretation of results in terms of seasonal variations if, for example, Trinidad differed in some essential respect from Amamá (for instance, no chickens in the former), or March 1989 differed from March 1992 (annual trends). However, the 3 villages were comparable with respect to patterns of house construction and cultural practices, host density, and the habit of keeping brooding hens or ducks indoors (M.C.C., unpublished data). Although the numbers of chickens or ducks showed some variation among and within villages from year to year, the habits of breeding poultry were consistent over years as reported by housedwellers or observed by us during collections. In addition, the host-feeding patterns observed in March 1989 and March 1992 in Amamá were similar, indicating homogeneity over time.

Seasonal Variation. The shift in host-feeding patterns from a predominance of human blood sources and almost no chickens in winter to a more balanced feeding on chickens, dogs, and humans

Table 4. Percentage of domiciliary *T. infestans* that fed on each host and had unmixed blood meals (host fidelity index)

Season	Host fidelity index[a] (range)[b]			
	Humans	Dogs	Chickens	Cats
Winter[c]	59 (100–56)	35 (100–32)	15 (0–16)	13 (50–12)
Spring–summer[d]	35 (80–36)	35 (100–27)	39 (67–38)	10 (0–7)

[a] Percentage of bugs that fed on each host that had unmixed blood meals.
[b] Range of host fidelity index from 1st–2nd instars to adult bugs.
[c] Trinidad, September 1988.
[d] Amamá, Trinidad, and Mercedes, October–March 1988–1992.

in spring–summer was associated closely with (1) changes in nightly sleeping places of most people (indoors during cold weather from April–May to September–October, outdoors in the verandah during the rest of the year), and (2) the presence of brooding hens (or ducks) in or close to bedroom areas (to protect eggs and chicks from predators). During cold weather, people sleeping indoors very probably had an increased risk and frequency of triatomine bites, whereas probably dogs and cats more often were restricted to outdoor sites (according to family customs) and hens were not allowed to brood indoors. In contrast, during the hot season, people moved beds to sleep in the open verandas, with dogs lying beside or below them at night, and 1 or 2 hens (sometimes a duck) entered or were placed inside empty bedrooms to sit on eggs. Our data confirm preliminary evidence of seasonal variation in the feeding patterns of domiciliary *T. infestans* either at the house (Gürtler et al. 1983) or at the community level (Solarz et al. 1986).

Because of the 3-mo period of serum antigen detection, blood meals from mid-September may correspond to the winter period (June to September), whereas those in December may represent spring and those in March, summer feeds. The rate of digestion of blood meals increases with temperature, therefore it is likely that more old feeds would be detected during or after the cool season than during the warm season. The 10% of bugs not reacting with any antisera in our study is among the lowest reported for *T. infestans* tested with as many as 13 antisera (Table 1) and may be attributed to the testing of bugs with almost empty stomachs rather than to an important blood source being missed by the antisera used.

It is noteworthy that one of the highest proportions of domiciliary *T. infestans* that fed on humans in northwestern Argentina (67%) corresponds to bug collections made in September, whereas the lowest (15%) corresponds to December (Table 1). No date was given for collections corresponding to the highest figure (79%) for Argentina (Mayer and Alcaraz 1955). Therefore, seasonal variation in the host-feeding patterns of *T. infestans* may, in part, explain the wide variability in the degree of anthropophagy observed in this area. Data showing that the availability of animal hosts explains the variation in host-feeding patterns among houses within each survey will be reported separately.

Table 5. Distribution of mixed blood meals of domiciliary *T. infestans* according to instar; Trinidad, September (winter) 1988, and Mercedes-Amamá, October–March (spring–summer) 1988–1992

Instar	Season	No. bugs reactive	No. blood sources in mixed meals			Total	%
			Double	Triple	Quadruple		
First–second	Winter	11	0	0	0	0	0
	Spring–summer	13	1	0	0	1	8
Third	Winter	34	6	0	0	6	18
	Spring–summer	67	22	14	1	37	55
Fourth	Winter	61	13	1	0	14	23
	Spring–summer	214	51	19	6	76	36
Fifth	Winter	97	30	2	0	32	33
	Spring–summer	332	129	33	5	167	50
♀♀	Winter	327	118	12	0	130	40
	Spring–summer	208	77	28	7	112	54
♂♂	Winter	353	118	13	0	131	37
	Spring–summer	244	78	21	5	104	43
Total	Winter	883[a]	285	28	0	313	35
(%)		—	(32)	(3)	(0)	—	—
	Spring–summer	1,078[a]	358	115	24	497	46
		—	(33)	(11)	(2)	—	—

Differences between spring–summer and winter: Mantel–Haenszel $\chi^2 = 27.7$, df = 1, $P < 0.001$. Differences among instars: in winter, $\chi^2 = 17.1$, df = 4, $P < 0.002$); in spring–summer, $\chi^2 = 18.3$, df = 4, $P = 0.001$.
[a] Excluded 2 bugs in winter and 1 in spring–summer with instar not recorded.

Table 6. Host-feeding patterns of domiciliary *T. infestans* by site of capture in Amamá, Trinidad, and Mercedes during March (summer) 1992

Collection site	No. bugs		Blood source (% bugs fed on)[a]				
	Tested	Reactive	Human	Dog	Chicken	Cat	Goat/sheep
Beds	44	40	90.0	22.5	7.5	7.5	0.0
Goods	78	76	40.8	38.2	50.0	11.8	0.0
Walls	303	286	48.6	43.0	44.1	12.9	0.7
Roofs	172	156	47.4	49.4	48.7	7.1	1.3
Sensor boxes	33	27	55.6	40.7	33.3	37.0	0.0

[a] Categories are not mutually exclusive and sum to >100% because of mixed blood meals.
[b] Differences among beds, household goods, walls and roofs: $\chi^2 = 28.8$, df = 3, $P < 0.001$.

Feeds on dogs showed the least variation among seasons and villages, whereas the proportion of bugs that fed on cats was highly variable. Despite their low density and well-known nocturnal activity (which might decrease their exposure to triatomines), cats were fed upon frequently by *T. infestans* in this and other areas (Table 1).

The few goat–sheep meals came mostly from 1 house in Trinidad, with some of them occurring as nymphal instars (presumably less mobile than adults); the remainder came from individual adult bugs in several houses. Blood meals from goat–sheep in domiciliary triatomines usually are regarded as markers of dispersal from peridomestic corrals. However, we observed in 2 houses that people kept goat kids in or near their bedrooms for protection or to feed them. Thus, although a direct interpretation of goat–sheep feeds may not be assured, data from other houses indicated that some bugs moved from goat corrals into dwellings.

Comparative Time Series in Amamá. In Amamá and adjacent villages in December 1982, most domiciliary *T. infestans* had fed on dogs (63%), humans (41%), or chickens (18%) (Table 1). A strikingly similar host-feeding pattern again was found in this area in November 1984 (674 bugs tested) (Solarz et al. 1986). In contrast, our October and December data show that more bugs fed on humans (63–68%) or chickens (28–56%) and a similar proportion fed on dogs (51–63%) than in 1982–1984, despite comparable methods of bug collection and identification of blood meals.

The higher frequency of bugs that fed on humans and chickens in 1988–1992 than in 1982–1984 cannot be attributed to any effect of the 1985 deltamethrin spraying because (1) house reinfestation after spraying most likely originated from unsprayed peridomestic foci of *T. infestans* (Gürtler et al. 1994), (a local vector strain reinfested houses); (2) the host-feeding pattern in March 1989 (when house reinfestation was expanding rapidly) was very similar to that observed in March 1992 (when ≈90% of houses were infested); (3) there is no known mechanism by which the insecticide could affect selectively the host-selection behavior of the bugs after ≥3 yr (6 or more *T. infestans* generations). In addition, the size and resting habits of the human population appeared to be stable across years. We believe that the observed differences in host-feeding patterns across years in Amamá may reflect the flexible host selection behavior of *T. infestans*, a highly opportunistic species feeding readily on humans throughout its distribution range (see Table 1).

Instar and Site-Specific Feeding Patterns. Minter (1976) concluded that "there appeared to be no striking difference between the feeding pattern of adults and younger instars of triatomine bugs," whereas Wisnivesky-Colli (1987) identified 3 cases in which significant differences existed. In our study, although the host-feeding patterns of *T. infestans* showed statistically significant differences among instars in spring–summer (but not in winter), the differences were variable and likely of minor biological relevance. The percentage of bugs that fed on chickens in spring–summer was the only one that showed a clear (increasing) trend with instar, similar to that reported by Wisnivesky-Colli et al. (1982). Contrary to the latter survey, we did not detect a decreasing trend in the percentage of bugs that fed on dogs with instar.

The increasing frequency of bugs feeding on chickens among instars in spring–summer may be explained by the increased opportunities of older (larger) bugs to ever have fed on chickens (part of such meal remaining detectable), concurrently with more brooding hens and young chickens within bedrooms as the warm season progressed. Interestingly, higher frequencies of chicken blood meals in adults than in nymphs appeared in the 3 data sets identified by Wisnivesky-Colli (1987), who attributed this shift to differential location and mobility of nymphs and adult bugs. In addition, in our study ≈40% of 4th and older instars that fed on chickens had unmixed meals. This indicates repeated feedings and increasing reliance on the chicken blood source for those instars that have larger requirements of blood and higher reproductive value. This may have important consequences for the populations dynamics of *T. infestans*.

The host-feeding pattern of bugs collected from walls, roofs, and household goods were similar. The small nymphs collected from people's beds, however, showed an expected higher frequency of human meals than did other sites, as reported by Rabinovich et al. (1990). Bias in sampling some sites, in which easily catchable instars may be associated closely with 1 host (as in beds), may artificially pro-

duce a pattern of host preference for such instars. With this exception, and within the limitations of the sampling methods used, our data support the existence of homogeneous host-feeding patterns among collection sites and instars within the house.

Unmixed Blood Meals and Host Fidelity. Minter (1976) suggested that 1-host identifications may often represent several successive feedings from the same host type. Developing this idea, we propose that the percentage of bugs that fed on a single type of host among any bugs fed on that host (mixed or unmixed) can be used as an index of host fidelity or of repeated feedings on that host, measuring the strength of the feeding link. Another possible indicator of host fidelity, the percentage of all reactive bugs that fed on a given host only, is not as helpful as the host fidelity index because it is affected by other host choices of the bugs that are not relevant to the host at issue.

The high percentage of human-fed bugs with only human blood in September (59%) indicates that bugs fed only on people during the previous period (a strong host fidelity). Assuming that blood antigens remained detectable in the stomach of the bug for 3 mo and that domiciliary *T. infestans* fed about as frequently as *T. infestans* in experimental chicken houses from a similar rural area of Argentina (Catalá 1991), we estimated that bugs may have fed an average of 3 times during June–September and that most of these feedings were on humans. In addition, the host fidelity index for humans in winter implicitly indicates that 41% of bugs had fed on humans and another source, which in this case was dogs, the main reservoir of *T. cruzi*. Fidelity for humans or dogs declined with instar in both seasons, but in spring–summer, host switches from earlier instars were more frequent.

Mixed Blood Meals. Four or 5 different host sources were identified in the same domiciliary *T. infestans* (Corrêa and Aguiar 1952, Wisnivesky-Colli 1987) and up to 6 different host types in other domiciliary species (Zeledón et al. 1973, Zárate et al. 1980). The following 3 factors may explain this phenomenon: (1) large bloodmeal size in *T. infestans* (Perlowagora-Szumlewicz 1976); (2) repeated feedings during a prolonged life-span; and (3) extended detection of blood meals, even through 2 molting periods. Therefore, the older the bug, the greater the number of previous blood meals. However, among the few studies that reported separately the host-feeding patterns of nymphs and adults of any triatomine species (Corrêa and Aguiar 1952, Mayer and Alcaraz 1955, Zeledón et al. 1973, Zárate et al. 1980, Wisnivesky-Colli et al. 1982), none detected higher frequencies of mixed blood meals in adult bugs, possibly because of lumping of nymphal instars. We reanalyzed data from domestic *Triatoma dimidiata* Latreille (Zeledón et al. 1973) separating all instars and found that older instars had significantly more mixed meals than younger ones ($\chi^2 = 12.6$, df = 5, $P = 0.028$).

Our study showed a high percentage of mixed blood meals in domiciliary *T. infestans* (35–46%) that could not be attributed to nonspecific reactions; these percentages were within the range previously reported (Table 1). Considering that our blood meal identification tests could not determine successive blood meals taken from different individuals of the same host group, the actual degree of multiple feedings (or effective host change) would be higher than the 35–46% we estimated. *T. infestans* is a highly mobile species in both nymphal and adult stages when several alternative blood sources are available.

Mixed feeding habits of bugs in winter and spring–summer differed in 4 important respects. In spring–summer at each instar, bugs had more identified blood meals, fed on a larger number of different host types, took mixed meals more frequently, and switched hosts in earlier instars. These changes occurred in parallel with increasing temperature and bug population density, and possibly may have resulted from increased bug mobility during warmer periods and increased host availability. High feeding mobility from early instars onward also is indicated by 26% of *T. cruzi*-infected 4th instars fed only on chickens (which are refractory to *T. cruzi* infection) (unpublished data). This indicates that bugs had fed on some undetectable infective source at an earlier instar.

Feeding Patterns and Incidence of Chagas' Acute Cases. The frequency of symptomatic acute cases of Chagas' disease in northwestern Argentina increases steeply in September–October from a (non-0) minimum during June–August (Romaña 1963). In September–October in this region, however, the domiciliary density of *T. infestans*, the percentage infected with *T. cruzi*, and the density of infective trypomastigotes in the infected bugs were close to the minimum values recorded across seasons (Giojalas et al. 1990). In addition, the feeding frequency of *T. infestans* located in a similar area was well below its annual peak (Catalá 1991). The increased anthropophagy of domiciliary *T. infestans* populations during late winter and early spring would (1) likely compensate for marked reductions in parameters affecting the vectorial capacity of *T. infestans*, and (2) precede or coincide with the spring peak in incidence of acute cases of Chagas disease.

Consequences for Modeling and Control. Mathematical models of the domiciliary transmission of *T. cruzi* in northwestern Argentina (see Rabinovich et al. 1990) should allow for seasonal variation in contact among *T. infestans*, people, and domestic animals. The high degree of feeding mobility of domiciliary *T. infestans* from early instars onward has 2 consequences: (1) the host-feeding patterns are less likely to differ among instars or collection sites within the house; hence the bug population can be considered homogeneous in these respects, and (2) bugs have an increased probability of finding an infected host and then

transmitting the infection, thus increasing the chance of *T. cruzi* infection and superinfection of vectors and hosts. Bugs likely acquire the infection mainly from infected dogs (and secondarily from cats) all year round but more frequently during spring and summer, when both the feeding frequency of bugs and the percentage of bugs feeding from these animals are maximal. Bugs then have a higher probability of transmitting these infections to humans at the end of winter and during spring. Because of the timing of the events, we tentatively would recommend that vector control precede the expected spring and summer rise in bug density and the occurrence of acute cases of Chagas' disease.

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