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The biting rate of *Triatoma infestans* in Argentina

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Abstract. 1. The daily proportion of fed individuals in a population of the reduviid bug *Triatoma infestans* (Klug), maintained under natural climatic conditions in experimental chicken houses in central Argentina, was estimated from the proportion of bugs retaining colourless urine in the rectum.

2. From the estimates of feeding frequency throughout a 1 year period, it was shown that temperature has a dominant effect on biting rate, but density-dependent effects became apparent during the warmest months.

3. These and other data on the determinants of blood consumption by *T.infestans*, were incorporated into a detailed hypothesis of density regulation in this species.

Key words. *Triatoma infestans*, Chagas disease, population dynamics, feeding strategy, density-dependence, temperature-dependence, Argentina.

Introduction

Triatoma infestans (Klug) (Hemiptera: Reduviidae) is an important vector of *Trypanosoma cruzi* Chagas, causative agent of Chagas disease in Latin America. Transmission of this parasite depends crucially on the population dynamics of the vectors and, in particular, on the rate of contact between vector and host. All five nymphal stages of the vector, and both sexes of adults, are obligate blood-suckers, and must take at least one bloodmeal during each developmental stage. Thus all stages can become infected with *T.cruzi*, and can then pass on the infection in their faeces when taking subsequent bloodmeals. Since the development of individual bugs – and hence development of the bug population – is critically dependent on the quantity of blood ingested, the biting rate is a key determinant of vector population dynamics.

Feeding frequency of triatomine bugs can be measured directly in the laboratory by periodically weighing individual bugs maintained with continuous access to a host (Schofield, 1982). However, estimation of feeding frequency in the field can only be carried out using indirect methods. Rabinovich *et al.* (1979) estimated the feeding frequency of *Rhodnius prolixus* Stål in Venezuelan houses, based on the argument that the distribution of bloodmeal weights in a large sample of a bug population would represent the distribution of times since last feeding. They derived the relationship between bug weight and time since feeding from laboratory observations. This method, also used by Schofield (1981) for *T.infestans* in Brazilian houses, gives useful estimates of biting frequency from which estimates of daily host blood loss can be derived. However, this method relies on several assumptions, including a stable age-distribution for the

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bug population, which is seldom the case – at least not for *T.infestans* in chicken houses in Argentina (Gorla & Schofield, 1989). Also, the method assumes a constant profile of bug weight loss since feeding, and requires complex statistical manipulation to allow for multiple small feeds, and for the typical bimodal distribution of nymphal weights representing fed and newly-emerged unfed nymphs. An objective of the present work, therefore, was to develop a method to estimate the biting rate of *T.infestans* that did not rely on the distribution of bug weights. The new method, based on evaluation of urine content in the bugs, was then used to estimate the relationship between feeding frequency, climate and bug population density.

Materials and Methods

Colourless urine retention as an indicator of recent feeding

This study used the presence of colourless urine in the bug rectum as an indicator of recent feeding. In triatomine bugs, rapid diuresis follows a bloodmeal (Maddrell, 1964), resulting in the elimination of most of the aqueous part of the ingested blood within a few hours after feeding (Wigglesworth, 1931). This colourless urine is then followed by white or yellowish fluid containing a suspension of uric acid, urates and carbonates. Subsequently, the excreted material contains a higher proportion of dark material representing undigested haem and haematin. The faeces of triatomine bugs thus show a very typical pattern of white and black streaks, for example on the walls of infested houses, which can be used as indicators for the presence of bugs (Garcia-Zapata *et al.*, 1985; Schofield *et al.*, 1986).

Production of colourless urine by triatomine bugs occurs only during the first few hours after a bloodmeal, and so the presence of such material in the rectum of a bug is a good indicator of a recent meal – irrespective of the total quantity of blood ingested at that time. Examination of the bug's rectum can be carried out either in the field or laboratory, but does not require instruments such as a precision balance (which is required to measure the bug's weight). As the rate of excretion of colourless urine depends on temperature, the model to predict the proportion of bugs in a population that have fed during the last 24 h requires modification as follows.

At time t, the total number of bugs in a population that have colourless urine in their rectum (N_T) will represent the sum of bugs that fed at different intervals previously $\Sigma(N_{t-i})$, each modified by the proportion of such bugs that would still retain colourless urine (PRI_{t-i}):

$$\mathrm{NT} = \sum_{i=1}^{i=n} (N_{t-i} \times \mathrm{PRI}_{t-i}). \qquad (1)$$

This sum is dominated by the number of bugs that have fed during the previous 24 h (N_{t-1}), which is the quantity we wish to estimate. Hence, by assuming that over the few previous days a similar proportion of bugs feed during each night (i.e. $N_t - 1 = N_{t-i}$), equation (1) can be modified to:

$$N_t - 1 = \mathrm{NT} \times C$$

where $C = 1/\sum_{i=1}^{i=n} (\mathrm{PRI}_{t-i})$

To estimate C implies knowing the proportion of bugs that maintain some colourless urine in their rectum for different times at different temperatures. Estimates of C were obtained separately for nymphs and adults. Groups of nymphs representing all stages were fed in the laboratory on pigeons and then maintained at 18, 25 and 28°C in controlled temperature rooms. Groups of adults were treated similarly, but maintained at either 15 or 26°C. Bugs in each group were checked at intervals of 2–12 h for the proportion with colourless urine in the rectum. By regression analysis, this allowed prediction of the proportion of bugs at each temperature that retained colourless urine in the rectum after 1, 2, 3 or 4 days (Fig. 1).

From these results, again by regression, a simple linear relationship was derived between C and mean temperature: $C = 0.0533(\mathrm{temp}) - 0.585$ ($r = 0.98$; $n = 3$; $P < 0.02$). This relationship was used to describe the profile of colourless urine loss for all nymphal stages for temperatures between 18 and 28°C (Table 1). For adults, however, it was found that colourless urine was not retained for longer than 30 h at either 15 or 26°C, so that for the field studies, C could be taken as unity for adult stages.

Feeding rates under natural climatic conditions

Field studies were carried out on three populations of *T.infestans* maintained in artificial

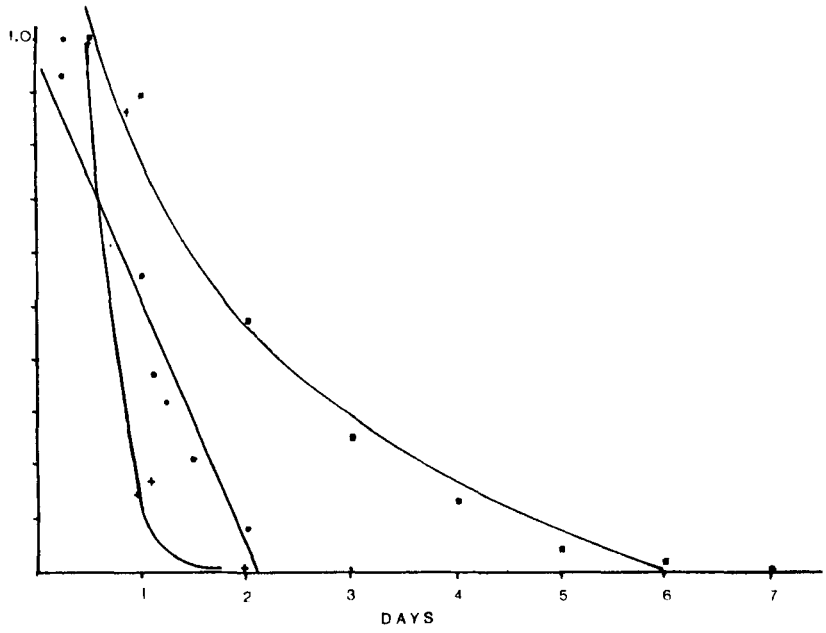

Fig. 1. Proportion of *Triatoma infestans* with colourless urine in the rectum, during the post-feeding period, at temperatures of 18°C (■), 25°C (•) and 28°C (+).

Table 1. Site temperature (°C) and temperature correction factors for rate of urine retention by *Triatoma infestans* nymphs.

Month	External temperature	Predicted internal temperature*	Correction factor
May	14.33	18.74	0.414
June	11.87	16.98	0.320
July	9.62	15.38	0.230
August	22.62	24.64	0.728
September	22.62	24.64	0.728
October	14.17	18.62	0.407
November	(no data)		
December	25.70	26.83	0.845
January	(no data)		
February	29.96	29.87	1.010
March	22.54	24.58	0.725
April	12.42	17.37	0.341

* Internal temperatures were predicted from the regression model proposed by Gorla (1985): Internal temperature = 8.52 + 0.71(external temperature).

chicken houses in a field site in an endemic area of the Argentine chaco. These were three of the chicken houses (those designated SAD4, each with four chickens as hosts) use by Gorla & Schofield (1985, 1989). They are constructed of locally made adobe blocks in such a way that

they can be dismantled and rebuilt at intervals, allowing a complete census of all bugs in each population.

During each monthly census of the chicken houses, at least seventy bugs from each (ten of each nymphal stage plus ten male and ten female adults) were examined for the presence of colourless urine in the rectum. Examinations were made by squeezing out the abdominal contents, and were completed during the early hours of the morning. Temperature and humidity records are routinely collected at this site using a SIAP thermohygrograph, and the records of external temperature can be adjusted to give estimates of the internal temperatures of the chicken houses using the equation derived by Gorla (1983) as follows: Internal temperature (for the range 10–30°C) = 8.52 + 0.71(external temperature). Results obtained in this way allowed estimation of the following parameters:

(1) Proportion of bugs of all stages that fed during the preceding 24 h (PFV), estimated as the number of bugs with colourless urine/number of bugs examined, multiplied by C (the temperature correction factor, which takes the monthly values cited in Table 1 for nymphs, and is unity for adults).

(2) Feeding frequency (average interval in days between feeds for each bug) (FP), estimated as 1/PFV.

(3) Number of bites per day per host (BR), estimated as [(PFVnymphs × total nymphs) + (PFVadults × total adults)]/number of hosts.

(4) Average amount of blood taken by each bug population, and average daily blood loss per chicken. Theses were estimated by summing the number of fed bugs of each stage weighted by the blood intake of each stage as measured in laboratory studies by Szumlewicz (1976), to give the average daily blood intake of each bug population during each month. Since there were four chickens in each chicken house, this estimate was then divided by 4 to give an estimate of the average daily blood loss per chicken.

Results

Proportion of bugs feeding

The daily proportion of bugs feeding showed a similar seasonal pattern for each stage, and can be illustrated by the monthly variation in PFV (Fig. 2). Accordingly, the average feeding frequency (FF) followed a similar seasonal pattern, reaching a predicted maximum of 71

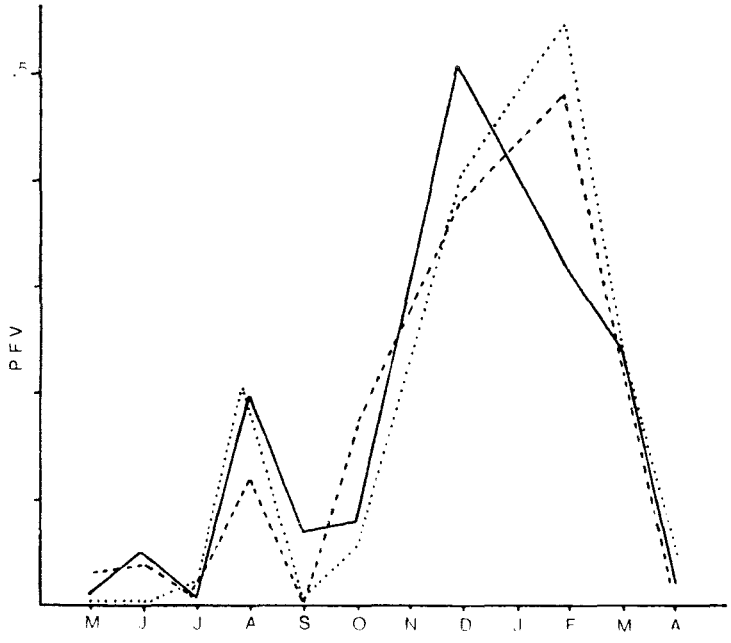

Fig. 2. Estimated proportion of fed *Triatoma infestans* (PFV) in three experimental chicken houses throughout the year.

days in the winter compared to a minimum of 2 days between feeds during the summer months (Fig. 3). By ANOVA, PFV shows significant variation between months ($P<0.01$), peaking during the warmest months from the end of spring through summer to the beginning of autumn (November–March). In August, nymphs showed a small PFV rise (Fig. 4b) which did not occur with adults (Fig. 4a), while during the summer, adults showed a substantially higher PFV than nymphs.

Most of the variation in PFV is explained by mean temperature, showing good linear correlation with the mean monthly temperature at the site (Table 3). In contrast, PFV showed no correlation with total bug density, nor with the densities of adults or nymphs considered separately. The variance of PFV also showed no trend associated with either temperature or with bug population density. The regression of PFV on mean monthly temperature (Table 3) predicts that at site temperatures below 11.3°C (equivalent to 16.5°C inside the chicken houses) no recently fed bugs would be found. This accords with the most recent estimates of the theoretical

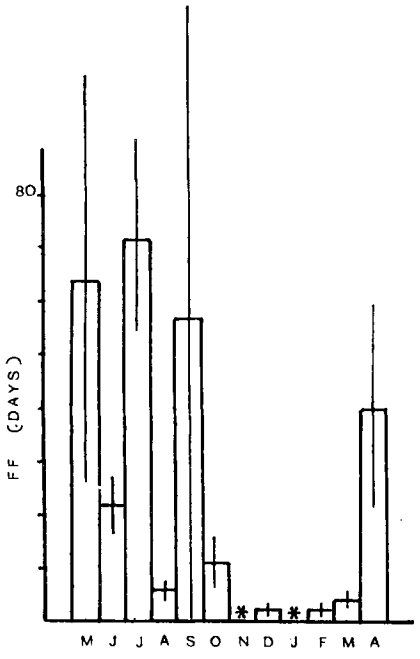

Fig. 3. Seasonal changes in the estimated feeding frequency of *Triatoma infestans* (FF) in three experimental chicken houses. Vertical bars show 95% limits of confidence. *no data.

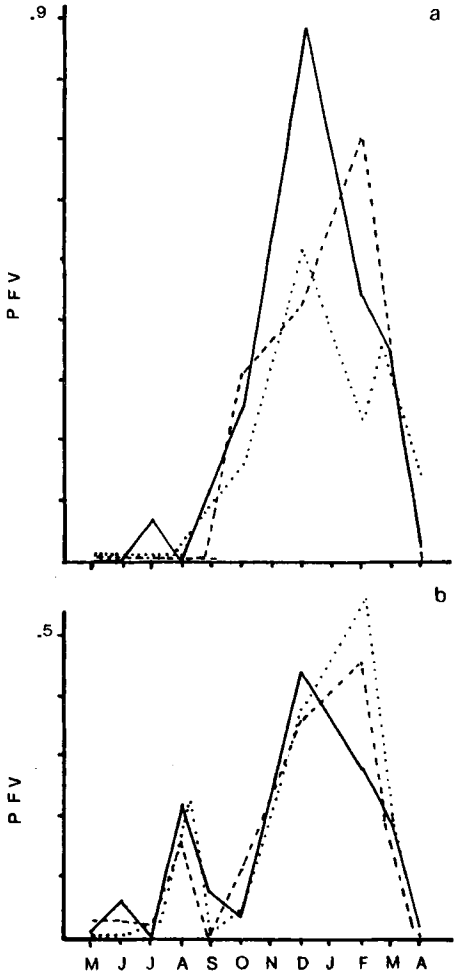

Fig. 4. Proportion of fed *Triatoma infestans* (PFV) in three experimental chicken houses throughout the year: (a) adults; (b) nymphs.

developmental zero temperature for *T.infestans* derived from laboratory cohort studies, which indicate an overall developmental zero of 15.8°C (range 13.9–17.7°C) (Stemp, 1988).

Biting rate and blood loss

As the number of hosts (four) in each chicken house was constant throughout this study, the daily biting rate per host (BR) followed a similar seasonal pattern to the overall daily proportion of bugs feeding (PFV) modified by effects of

bug density. Similarly, the estimates of daily blood loss per chicken also followed the seasonal pattern of PFV, modified by effects of bug density, bug population age-structure, and stage-specific blood intake. Each chicken house showed different bug densities and population age-structures during each month, but with no consistent trend in density or age-structure related to temperature.

Estimates of both the biting rate (average daily number of bites per chicken) and blood loss (average daily blood loss per chicken), showed a similar seasonal pattern, rising sharply in the summer months (Table 2). The estimates indicated that each chicken suffered around two to four bites per day during the winter months, losing around 0.25 g of blood per day as a result. However, the peak biting rate of over thirty bites per day during December translated to an average daily blood loss of over 3.25 g (Table 2).

Regression analysis again showed that temperature was the dominant factor influencing changes in biting rate and average daily blood loss (Table 3). However, unlike changes in PFV, both these regressions were improved by a multiple regression involving bug density, although the improvement was significant only for changes in biting rate. The regression of average daily blood loss on temperature was improved by considering adult density (rather than total bug density), which reflects the greater blood intake of adult stages (Table 3).

Separate analysis of results from the hot season

Table 2. Population density of *Triatoma infestans*, proportion of fed bugs (PFV), daily biting rate per chicken (BR), and daily blood loss, grams per chicken (BLg) averaged for three experimental chicken houses in Argentina (SEM given in parentheses).

	Density			PFV				
Month	Nymph	Adult	Total	Nymph	Adult	Total	BR	BLg
May	634 (363.7)	58 (13.1)	692 (248.8)	0.022 (0.011)	0	0.020 (0.010)	4.23 (2.92)	0.138 (0.081)
June	364 (106.2)	51 (10.3)	415 (112.7)	0.031 (0.016)	0.032 (0.032)	0.036 (0.017)	4.09 (2.38)	0.286 (0.144)
July	303 (92.2)	43 (8.9)	346 (99.1)	0.014 (0.005)	0.021 (0.021)	0.014 (0.002)	1.14 (0.16)	0.206 (0.108)
August	218 (64.4)	35 (4.3)	253 (66.4)	0.178 (0.043)	0.012 (0.012)	0.155 (0.043)	11.02 (4.65)	0.697 (0.160)
September	171 (55.1)	24 (1.7)	195 (56.3)	0.029 (0.024)	0.032 (0.032)	0.030 (0.021)	1.95 (1.46)	0.175 (0.107)
October	147 (59.8)	28 (7.6)	175 (63.2)	0.062 (0.012)	0.248 (0.043)	0.103 (0.025)	4.07 (0.39)	0.783 (0.328)
November	No data							
December	196 (71.3)	42 (11.8)	238 (82.9)	0.442 (0.046)	0.610 (0.137)	0.470 (0.059)	30.34 (13.29)	3.270 (1.410)
January	No data							
February	149 (32.5)	28 (17.5)	177 (45.8)	0.416 (0.109)	0.436 (0.133)	0.432 (0.084)	17.96 (4.48)	2.110 (0.790)
March	145 (43.1)	42 (19.1)	187 (56.7)	0.191 (0.005)	0.346 (0.004)	0.224 (0.010)	10.72 (3.45)	1.580 (0.560)
April	90 (37.3)	30 (11.8)	120 (48.6)	0.018 (0.006)	0.060 (0.049)	0.031 (0.010)	0.98 (0.45)	0.200 (0.100)

Table 3. Regression analysis of the proportion of fed *Triatoma infestans* (PFV), daily biting rate per chicken (BR) and daily blood loss per chicken (BL), on temperature (T) and bug population density (D) (df=29).

$PFV=0.029T-0.473$ ($t=6.617$, $P<0.001$)
$BR=1.422T-22.304$ ($t=3.829$, $P<0.001$)
$BR=1.630T+0.155D-31.162$ ($t_1=4.417$, $P<0.001$) ($t_2=1.970$, $P<0.1$)
$BL=0.157T-2.470$ ($t=3.708$, $P<0.001$)
$BL=0.671T+0.003D-11.715$ ($t_1=3.778$, $P<0.001$) ($t_2=0.849$, ns)
$BL=0.730T+0.119D_{adult}-16.647$ ($t_1=4.958$, $P<0.001$) ($t_2=3.402$, $P<0.005$)

Table 4. Regression analysis of proportion of fed *Triatoma infestans* (PFV), daily biting rate per chicken (BR), and daily blood loss per chicken (BL), on temperature (T) and bug population density (D), for hot season months (August–March, inclusive) (df=17).

$PFV=0.034T-0.620$ ($t=3.470$, $P<0.005$)
$BR=1.736T-30.495$ ($t=2.032$, $P<0.1$)
$BR=1.610T+0.078D-43.327$ ($t_1=2.364$, $P<0.05$) ($t_2=3.202$, $P<0.01$)
$BR=1.616T+0.30D_{adult}-37.654$ ($t_1=2.103$, $P<0.1$) ($t_2=2.210$, $P<0.05$)
$BL=0.030D-0.466$ ($t=2.273$, $P<0.05$)
$BL=0.627T+0.029d-15.791$ ($t_1=1.789$, $P<0.1$) ($t_2=2.317$, $P<0.05$)
$BL=0.594T+0.203D_{adult}-15.760$ ($t_1=2.067$, $P<0.1$) ($t_2=3.916$, $P<0.005$)

(August–March) and the cold season (April–July) showed that the density-dependent effect on biting rate was confined to the hot season (Table 4) with no significant effect during the cold season. Moreover, multiple regression analysis revealed that during the hot season, bug density had a dominant effect over temperature both on the biting rate and on the average daily blood loss (Table 4).

Discussion

The mean biting frequency of infective vectors is an important index of vector-borne disease transmission (OMS, 1972). Under field conditions, however, estimation of the biting rate of Chagas disease vectors is very difficult – as shown by the scarcity of published data on this subject. An indirect method, based on the relationship between bug weight and time since feeding, has been used for natural infestations of *R.prolixus* in Venezuelan houses (Rabinovich *et al.*, 1979) and of *T.infestans* in Brazilian houses (Schofield, 1981). However, as these authors acknowledge, the method is technically and statistically complex, of low accuracy, and requires several assumptions which are difficult to verify.

The method developed in the present work provides a simple estimation of feeding frequency without the use of accurate instruments. Colourless urine is produced by triatomine bugs for only a few hours after a bloodmeal (Maddrell, 1964; Wigglesworth, 1931) and is only retained for longer than 24 h by nymphs at low tempera-

tures (Fig. 1). Although estimates of the proportion of fed bugs required temperature correction during this work, mainly to allow for the cool temperatures prevailing during winter months, it is likely that this method could be used without temperature correction in warmer climates (such as Brazil). The method does assume that no bug will feed and excrete all resulting urine so quickly that it could then be recorded as unfed. Thus, at high temperatures, the proportion of bugs feeding may be underestimated if some bugs are taking very small meals and excreting the resulting urine very quickly. However, independent laboratory studies suggest that when bugs take very small meals their subsequent defaecation rates are slower (Trumper & Gorla, unpubl.; Kirk & Schofield, 1987), which could abnegate this possible source of underestimation.

The present work was carried out using artificial chicken houses which have been shown to provide excellent physical models of natural infestations of *T.infestans* (Gorla, 1983, 1988; Gorla & Schofield, 1985, 1989). The chicken houses are made of local materials and are subject to natural climatic conditions. Because they can be easily dismantled and rebuilt at intervals, this arrangement allows precise monitoring of all bugs in each population, so that variables such as the feeding frequency estimated here can be related to other factors such as bug population density and stage recruitment rate, as well as to climatic variables.

Monthly changes in the proportion of fed bugs during this study were clearly related to temperature changes. In this area, nymphal recruitment rate and female fecundity of *T.infestans* are greatly reduced during the cold winter months (Gorla & Schofield, 1985, 1989), primarily as a result of reduced metabolic rate at cooler temperatures (Catalá & Ayerbe, 1987; Catalá & Giojalas, 1986). This is in accordance with the present results, which imply that at cooler temperatures the feeding frequency of the bugs (and blood loss per host) will decline in association with the reduced metabolic rate of the bugs. Conversely, as temperatures increase, the metabolic rate of the bugs increases and so does their feeding rate.

Overall, the temperature effects on proportion of bugs feeding were much more important than any possible density-dependent effects. This could imply weak or absent density-dependence in feeding rates, or that under these conditions the experimental bug populations rarely reached critical densities. The latter possibility is supported by separate consideration of results for cool months (April–July) and hot months (August–March), which reveals a density-dependent effect during the hot months when bug populations were higher (Table 4), but not during the cool months. This idea is also supported by our observations on *T.infestans* populations in a similar experimental arrangement in Salta (a more northerly, and warmer, province of Argentina) using guinea-pigs as hosts: when bug population densities were high, the proportion of fed bugs declined markedly.

This interpretation builds from Schofield's (1980) working hypothesis of density-dependent regulation of triatomine bug populations operating within a framework of temperature constraints. We can now suggest more details for a system of density regulation mediated by the nutritional status of the bugs, which in turn modifies their developmental rates. Under this hypothesis, bug development rate depends on the rate of metabolism of ingested blood. At low temperatures, the metabolic rate becomes the limiting step (Catalá & Ayerbe, 1987; Catalá & Giojalas, 1986; Catalá & Pasina, 1984), while at higher temperatures the rate of blood ingestion becomes the limiting step, and both act in the same way on the rate of development (expressed, for example, as rate of recruitment from one stage to the next). The decline in metabolic rate associated with low temperatures implies a corresponding decline in feeding frequency, as shown by the present work (Fig. 3) whereas, as temperatures increase, the corresponding increase in metabolic rate leads to increased feeding frequency, increased rate of bug development and increased bug population density, until the density-dependent factors come into play (Schofield, 1985; Gorla & Schofield, 1989).

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