

# Preliminary Studies on Temperature Selection and Activity Cycles of *Triatoma infestans* and *T. spinolai* (Heteroptera: Reduviidae), Chilean Vectors of Chagas' Disease

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J. Med. Entomol. 34(1): 11-17 (1997)

**ABSTRACT** Preferred temperature and activity patterns of *Triatoma infestans* Klug and *Triatoma spinolai* Porter were studied, both are vectors of Chagas' disease in Chile. In the laboratory, 24 *T. spinolai* and 18 *T. infestans* were exposed to a temperature gradient between 50 and 15°C and a photoperiod of 14:10 (L:D) h. Temperature and hourly position of bugs in an experimental chamber were recorded for 24 h. Both species showed a cycle of preferred temperature, and both selected higher temperatures beginning at 1600 hours, although *T. infestans* maintains this preference over a longer period. For both species, activity patterns were synchronized with the light-dark cycle, although these activity rhythms were significantly different. *T. spinolai* had higher activity during the photophase, and *T. infestans* showed a lower activity in the photophase and a higher one during the scotophase. The similar pattern of preferred temperatures may facilitate the selection of similar environments in the event of colonization of houses by *T. spinolai*. Diurnal activity of this species might be a disadvantage (in terms of more exposure to defensive responses of the vertebrate hosts) but may allow *T. spinolai* to share the same habitat with *T. infestans* without competitive interference.

**KEY WORDS** *Triatoma infestans*, *Triatoma spinolai*, preferred temperature, light-dark activity, Chagas' disease, Chile

MUCH ATTENTION is currently given to the relative importance of sylvatic vectors in the transmission of South American trypanosomiasis and to their capacity to colonize human dwellings in suburban areas (Schofield and Patterson 1977, Apt and Reyes 1990, Salvatella et al. 1991). However, investigation of the biology of domestic vectors continues because several aspects remain unknown. To understand the capacity for spatial and temporal dispersion within the domiciliary habitat, it is necessary to understand feeding behavior, home range, density, spatial distribution, and preferred temperatures, among other variables (Schofield 1979; Lazzari 1991a, b). Di Luciano (1983) showed that *Triatoma infestans* Klug prefers temperatures between 26 and 27°C, and Lazzari (1991a, 1992) found a circadian cycle of *T. infestans* related to preferred temperature.

Only 2 triatomine vectors of Chagas' disease are known in Chile, the domiciliary species *T. infestans* (the most important South American vector) and the sylvatic *T. spinolai* Porter (Schenone and Rojas 1989, Apt and Reyes 1990). The latter is thought to be responsible for ≈5% of the occurrence of Chagas' disease in Chile (Canals et al. 1993). However, *T. spinolai* is found in houses either alone or

in conjunction with *T. infestans* (Donckaster et al. 1962, Lent and Jurberg 1967). Human blood is also part of the diet of *T. spinolai* (Schenone et al. 1985, Apt and Reyes 1986), and ≈7-11% of *T. spinolai* are infected with *Trypanosoma cruzi* (Schenone et al. 1980; Apt and Reyes 1986, 1990). Moreover, *T. infestans* and *T. spinolai* are sympatric throughout their distribution in Chile.

The objectives of this research were to detect in these 2 sympatric species, their differences in preferred temperatures, and daily activity cycles, and to determine why *T. spinolai* is not an active colonizer of houses.

## Materials and Methods

Preferred temperatures and activity patterns of *T. spinolai* and *T. infestans* were studied in an experimental temperature gradient from 15 to 50°C. Twenty-four *T. spinolai* adults captured in the wild (1 mo before the beginning of the experiments) and 12 adults and 6 nymphs (5th instar) of *T. infestans* from a long established laboratory colony were used. The specimens were maintained in the laboratory at 28°C, 70% RH, and a photophase of 14:10 (L:D) h (in local time, photophase was from

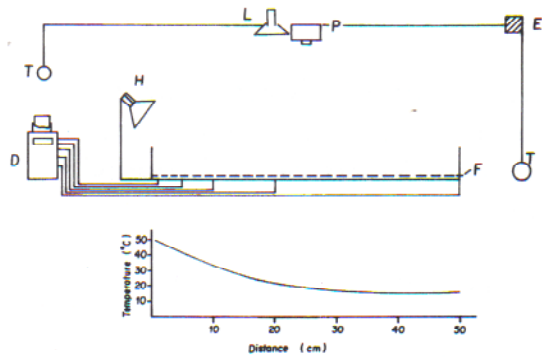


Fig. 1. Schematic view of experimental temperature gradient system. D, data logger; T, timer; H, heater; L, light; F, filter; P, camera; E, device for automatic flash exposure.

0600 to 2000 hours and scotophase from 2000 to 0600 hours). Before the experiments began, bugs were fed weekly on adult hens between 0900 and 1800 hours to avoid the generation of any timing pattern.

**Gradients.** The bugs were placed in an experimental chamber made of glass plates sealed with silicon rubber adhesive. The chamber had 4 channels, each 50 cm long and 6 cm wide, the walls of which were made of painted glass to make the corridor invisible. A strip of filter paper graduated in centimeters was laid on the bottom of each channel each time an experiment was conducted. The temperature gradient was created by placing an overhead heater at one end of the chamber and a cold water bath at the opposite end. A temperature of 50°C was maintained at the hot end; at the cold end, the temperature did not exceed 16°C. The experimental gradient was tested for 2 wk before to the experiments; temperatures were recorded for each centimeter of the channels (Fig. 1).

**Control and Recording System.** Five thermocouples were attached to the chamber 1, 5, 10, 20, and 50 cm from the hot end and connected to a data logger. Temperatures were recorded hourly for 24 h in each experiment. To record the position of bugs, a camera was located 1 m above the experimental chamber to cover the total area of the apparatus (50 by 50 cm). The camera was connected to an electronic device programmed to flash and fire hourly to record the insects and data simultaneously. A photoperiod of 14:10 (L:D) h was provided by a 100-lux lamp activated by a timer.

In each experiment, 1 bug (starved for 5 or 8 d previously) was introduced into the middle of each of 3 channels, leaving the 4th corridor free for the location of thermocouples. Hourly synchronous registers of both temperature and location of bugs in the channels were computed to analyze the decay of temperature along the gradient and to translate the location data (in centimeters) in terms of the exact temperature at this position in the chan-

nel. When a bug was very close to a thermocouple (exactly or adjacent), the temperature of the bug ( $T_b$ ) was assumed to correspond exactly to the temperature of the thermocouple ( $T_c$ ). When the bug was between 2 thermocouples, then  $T_b$  was calculated by linear interpolation. Experiments were started between 0900 and 1500 hours (local time) during the photophase. Because of the variability in starting times, occasionally there was a difference of  $\leq 5$  h between the data from any 2 experiments. The former data of position and temperature were recorded between 24 and 60 min after manipulation. Experiments were conducted daily between September 16 and October 28 1994.

**Data Analysis.** Two analysis matrices were constructed with hourly data of bug positions and simultaneous temperatures. After elimination of incomplete records (loss of the specimen during the experiment, misidentification of a bug in the records), in total 874 hourly position records (549 of *T. spinolai* and 325 of *T. infestans*) and 906 hourly temperature records (571 of *T. spinolai* and 335 of *T. infestans*) were analyzed. For comparisons of these data, nonparametric statistics were used because neither the data nor their standard transformations fit the normal distribution (Siegel and Castellan 1988).

Two different aspects of the data were analyzed: preferred temperature and activity of bugs. To analyze preferred temperatures, the effect of local time (hour) and the effect of light was studied separately for each species. To avoid pseudoreplication, the effect of light against preferred temperature was analyzed with the median temperatures selected by each individual during both photophase and scotophase as the response variable. This effect was studied by the Kruskal-Wallis test with the following treatments: T1 = *T. infestans* light; T2 = *T. infestans* dark; T3 = *T. spinolai* light; T4 = *T. spinolai* dark. We analyzed differences between *T. infestans* nymphs, *T. infestans* adults, and *T. spinolai* adults against the median preferred temperature for each hour. To study the differences, we used a Friedman test with *T. infestans* nymphs, *T. infestans* adults, and *T. spinolai* adults as treatments and hours as blocks. Multiple comparison tests also were made (Hollander and Wolfe 1972).

To study activity pattern, we considered the hourly displacement ( $D_i$ ), defined as the difference between the positions ( $P_i$ ) recorded in 2 successive hours where  $D_i = P_i - P_{(i-1)}$ , to obtain an activity matrix, which included all the observations. Using the signed ranks Wilcoxon test, we compared activity of the nymphs and adults of *T. infestans* against the hourly median displacement. For both species, comparisons between activity in the photophase and in the scotophase were made. We considered the following 2 aspects: (1) the mean displacement (MD) and (2) the proportion of time (hours) in which bugs were in movement (PT). We defined mean displacement, as total displacement

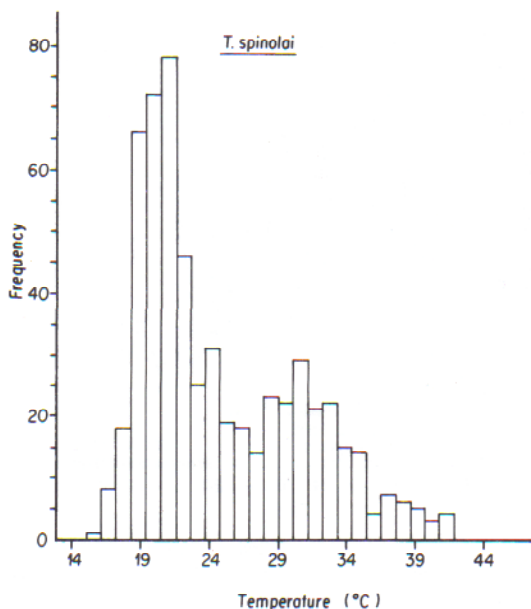


Fig. 2. Frequency distribution of temperature preferences of *T. spinolai*.

per hours. For each individual we obtained a mean displacement during photophase and another in the scotophase. Treatments T1–T4 were studied in the same way as temperature. Four orthogonal multiple comparisons were made as follows: light effects (1) *T. infestans*, T1 versus T2; (2) *T. spinolai*, T3 versus T4; and species effects (1) during

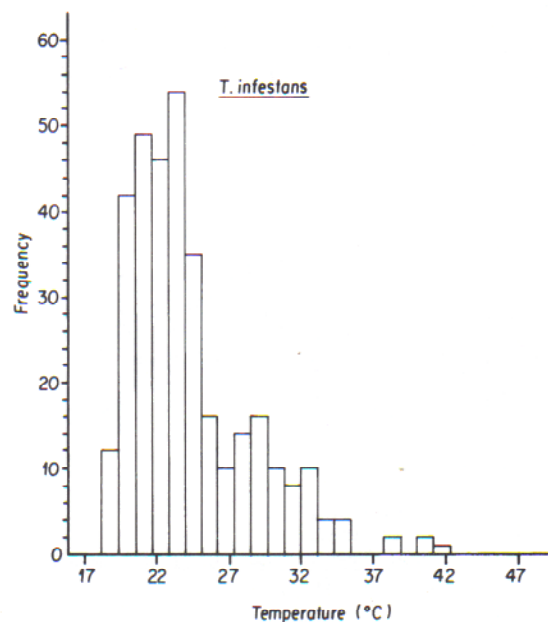


Fig. 3. Frequency distribution of temperature preferences for *T. infestans*.

Table 1. Temperatures preferred by *T. spinolai* and *T. infestans*

| Hour | Phase <sup>d</sup> | <i>T. spinolai</i> adults <sup>a</sup> |        | <i>T. infestans</i> |        |                     |        |
|------|--------------------|----------------------------------------|--------|---------------------|--------|---------------------|--------|
|      |                    |                                        |        | Nymphs <sup>b</sup> |        | Adults <sup>c</sup> |        |
|      |                    | Mean                                   | Median | Mean                | Median | Mean                | Median |
| 0600 | P                  | 23.5                                   | 22.1   | 22.8                | 20.5   | 22.1                | 20.9   |
| 0700 | P                  | 24.2                                   | 22.3   | 23.4                | 20.3   | 21.8                | 20.6   |
| 0800 | P                  | 23.9                                   | 23.4   | 24.4                | 21.7   | 21.2                | 20.4   |
| 0900 | P                  | 23.0                                   | 20.6   | 21.5                | 21.5   | 22.6                | 21.3   |
| 1000 | P                  | 23.2                                   | 20.6   | 22.0                | 21.3   | 22.9                | 21.4   |
| 1100 | P                  | 23.5                                   | 20.2   | 21.9                | 21.5   | 24.1                | 22.4   |
| 1200 | P                  | 25.8                                   | 21.3   | 21.4                | 20.6   | 22.4                | 21.5   |
| 1300 | P                  | 24.5                                   | 20.8   | 20.9                | 20.9   | 23.1                | 22.5   |
| 1400 | P                  | 25.3                                   | 20.7   | 22.9                | 22.3   | 24.7                | 23.7   |
| 1500 | P                  | 26.7                                   | 25.3   | 24.6                | 22.2   | 26.9                | 23.9   |
| 1600 | P                  | 27.2                                   | 27.3   | 23.6                | 21.9   | 26.8                | 24.7   |
| 1700 | P                  | 25.3                                   | 22.4   | 23.1                | 20.8   | 26.3                | 24.9   |
| 1800 | P                  | 27.4                                   | 27.4   | 23.8                | 22.7   | 26.0                | 24.3   |
| 1900 | P                  | 27.1                                   | 28.7   | 23.9                | 23.1   | 25.6                | 24.3   |
| 2000 | S                  | 27.1                                   | 26.2   | 23.2                | 21.8   | 25.4                | 24.9   |
| 2100 | S                  | 26.3                                   | 24.3   | 26.2                | 26.3   | 24.8                | 24.3   |
| 2200 | S                  | 25.0                                   | 21.9   | 23.2                | 24.7   | 24.7                | 24.3   |
| 2300 | S                  | 24.7                                   | 21.8   | 28.3                | 27.0   | 25.5                | 24.1   |
| 0000 | S                  | 24.9                                   | 23.0   | 24.0                | 22.1   | 25.9                | 24.6   |
| 0100 | S                  | 23.4                                   | 21.5   | 23.6                | 21.0   | 27.1                | 24.0   |
| 0200 | S                  | 23.4                                   | 22.1   | 23.7                | 21.5   | 25.6                | 22.9   |
| 0300 | S                  | 23.1                                   | 22.2   | 25.2                | 24.4   | 23.0                | 22.9   |
| 0400 | S                  | 23.4                                   | 22.8   | 24.4                | 23.0   | 25.7                | 23.4   |
| 0500 | S                  | 22.6                                   | 21.2   | 23.1                | 19.8   | 22.9                | 22.6   |

<sup>a</sup>  $n = 24$ .

<sup>b</sup>  $n = 6$ .

<sup>c</sup>  $n = 18$ .

<sup>d</sup> P, photophase; S, scotophase.

photophase, T1 versus T3; (2) during scotophase, T2 versus T4.

The same analysis was performed to study the variable proportion of time of movement, which was defined as  $100(\text{number of hours where DI} > 0/\text{total hours})$ .

## Results

**Preferred Temperature.** *T. spinolai* was active between 15 and 42°C. The frequency distribution of the temperatures for *T. spinolai* (Fig. 2) show a bimodal pattern with peaks at 21 and 31°C. The mean preferred temperature was  $24.8 \pm 5.8^\circ\text{C}$ . (mean  $\pm$  SD); median and mode were 22.4 and 20.3°C, respectively. *T. infestans* was active between 18 and 42°C with an average of  $24.2 \pm 4.3^\circ\text{C}$ , a median of 23.1 and a mode of 24.3 1C (Fig. 3). Comparing preferred temperatures of nymphs of *T. infestans* and adults of both species, a significant difference was detected (Friedman test,  $= 8.08$ ,  $P < 0.05$ ) supported by the differences detected among the nymphs of *T. infestans* and the adults of the 2 species (*T. infestans* nymphs versus *T. infestans* adults,  $P < 0.05$ ; *T. infestans* nymphs versus *T. spinolai* adults,  $P < 0.05$ ; *T. infestans* adults versus *T. spinolai* adults,  $P > 0.05$ ). The mean difference in preferred temperatures of nymphs and adults of *T. infestans* was 0.9°C (Table 1). Considering the hourly distribution of pre-

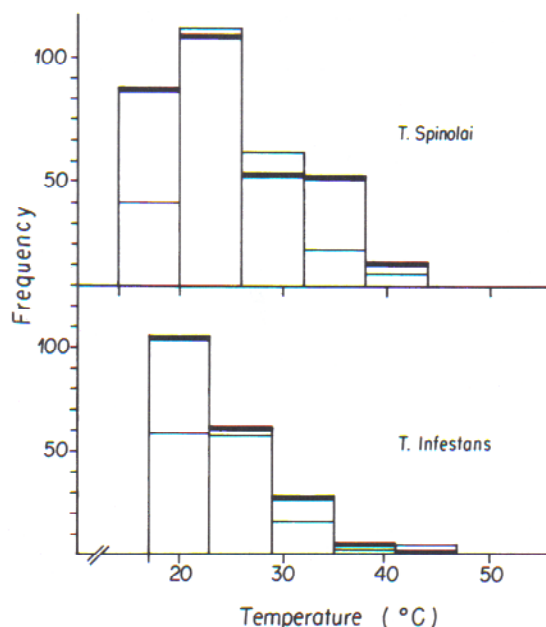


Fig. 4. Daily variation in temperature preferences.

ferred temperatures, it was noted that both species had cycles showing a preference for higher temperatures: between 1600 and 2000 hours for *T. spinolai* and between 1600 and 0400 hours for *T. infestans* (Fig. 4). Differences between preferred temperatures at different hours were significant for both species: Kruskal-Wallis test = 63.1,  $P < 0.001$  for *T. spinolai* and 49.4,  $P < 0.001$  for *T. infestans*. It was apparent that lack of light affected the selection of temperature when comparing those temperatures selected during the light period with those selected during the dark period for both species (Kruskal-Wallis test = 4.12,  $P > 0.05$ ) (Fig. 5).

**Activity.** *T. spinolai* showed a mean displacement of  $5.88 \pm 0.47$  cm between 2 successive hours and a proportion of time of movement of  $43.8 \pm 4.14\%$ . This was similar to the mean displacement of  $6.37 \pm 0.56$  cm and proportion of time of movement of  $56.7 \pm 4.99\%$  exhibited by *T. infestans*. However, activity was strongly related to light. *T. spinolai* showed the highest activity in the photophase (MD =  $7.97 \pm 0.72$  cm, PT =  $53.7 \pm 4.4\%$ ) and the lowest in the scotophase (MD =  $2.96 \pm 0.45$  cm, PT =  $33.9 \pm 6.4\%$ ). *T. infestans* showed a lower activity in the photophase (MD =  $4.73 \pm 0.62$  cm, PT =  $45 \pm 5.2\%$ ) and higher in the scotophase (MD =  $8.58 \pm 0.99$  cm, PT =  $69.3 \pm 7.4\%$ ). Notwithstanding the lower photophase activity of *T. infestans*, there was an activity zone between 0900 and 1500 hours, giving a bimodal pattern for the cycle of this species (Fig. 6).

Mean displacement and proportion of time of movement were affected by light (Kruskal-Wallis test: 21.25,  $P < 0.001$ ; 14.71,  $P < 0.01$ , respectively). Multiple comparisons showed differences in

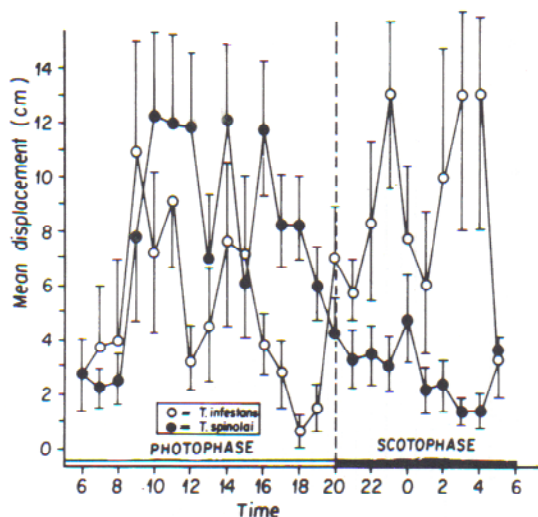


Fig. 5. Frequency distribution of preferred temperatures for both species. Thin line, limit of photophase; thick line, limit of scotophase.

activity patterns occurring between light and dark periods and in both species during the scotophase (Tables 2 and 3).

Finally, concerning activity, no significant differences were detected between nymphs and adults of *T. infestans* ( $P > 0.05$ ).

## Discussion

The results show a daily cycle in the preference for high or low temperatures, with a similar average amplitude for both species ( $4.4^\circ\text{C}$  for *T. infestans* and  $4.6^\circ\text{C}$  for *T. spinolai*). *T. spinolai* selects the highest temperatures at the end of the photophase, whereas *T. infestans* does so over a longer

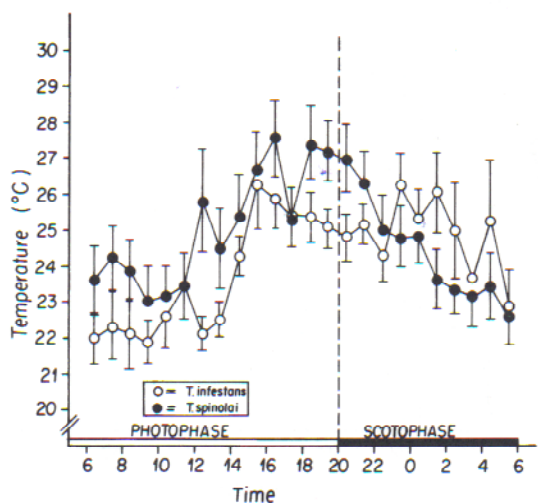


Fig. 6. Daily pattern of activity of *T. infestans* and *T. spinolai* measured as mean displacement.

**Table 2.** Multiple comparison (MC) for mean displacement

| Parameter                             | MC test | P      |
|---------------------------------------|---------|--------|
| Light effect                          |         |        |
| <i>T. infestans</i> ,<br>T1 versus T2 | 14.9    | >0.05  |
| <i>T. spinolai</i> ,<br>T3 versus T4  | 26.6    | <0.05  |
| Species effect                        |         |        |
| During photophase,<br>T1 versus T3    | 12.1    | >0.05  |
| During scotophase,<br>T2 versus T4    | 29.5    | <0.05  |
| Kruskal-Wallis test                   |         |        |
|                                       | 21.25   | <0.001 |

period of time, including parts of both photophase and scotophase. There are reports that indicate a preferred temperature between 26 and 27°C for *T. infestans* (Di Luciano 1983) and of incomplete development < 20°C (Jörg 1960). Moreover, Jörg (1989) pointed out that optimal fertility occurs near 27°C. Despite these reports, information on daily variation in temperature selection is scarce. Lazzari (1991a) described a daily rhythm, with a peak at the beginning of the scotophase and with preferred temperatures of 28 to 29°C immediately after feeding and 25 to 26°C 12 d after feeding. In the current study, with bugs fed 5–8 d previously, *T. infestans* showed a preference for a mean temperature of 24.2°C (mode, 24.3°C), somewhat lower than the figures of Lazzari (1991a). However, this does not explain the discrepancy in the data of Lazzari (1991a). The explanation for the differences may be that in the current work, all bugs were studied individually to avoid interference from endogenous rhythms of gregariousness triggered by the photoperiod (Lorenzo et al. 1991). The highest temperatures were selected between 1500 and 0300 hours. It seems that light does not play a role as a synchronizer of the preferred temperature cycle. There was no statistically significant difference between preferred temperatures from the light or dark periods. Although there were different activity patterns for each species, no significant differences were detected in the daily variation of preferred temperature (Fig. 4). Both adults and nymphs of *T. infestans* showed a similar pattern of preferred temperature but, in agreement with data of Di Luciano (1983) and Lazzari (1992), the selection made by 5th instar of *T. infestans* was 0.9°C (average) lower than adults (nymphs 23.5°C, adults 24.4°C).

The patterns of activity were different for each species. *T. spinolai* had its main activity in the photophase, and *T. infestans* was more active in the scotophase. It was clear that both species synchronized their activity rhythms to the light–dark cycle. This was recorded for several other triatomines (Wiesinger 1956, Nuñez 1982, Settembrini 1984, Lazzari 1992). Similar synchronous activity was

**Table 3.** Multiple comparisons for time proportion in movement (PT)

| Parameter                           | MC test | P     |
|-------------------------------------|---------|-------|
| Light effect                        |         |       |
| <i>T. infestans</i><br>T1 versus T2 | 19.5    | <0.05 |
| <i>T. spinolai</i><br>T3 versus T4  | 14.5    | <0.05 |
| Species effect                      |         |       |
| During photophase,<br>T1 versus T3  | 6.4     | >0.05 |
| During scotophase,<br>T2 versus T4  | 27.31   | <0.01 |
| Kruskal-Wallis test                 |         |       |
|                                     | 14.71   | <0.01 |

noted for triatomine circadian rhythms of oviposition (Ampleford and Davey 1989), moulting (Ampleford and Steel 1982, Ampleford 1985), hatching (Lazzari 1991b), attraction to  $\beta$  lights (Bertram 1971, Schofield 1979), and aggregation (Lorenzo et al. 1991). There were 2 activity periods during the cycle of *T. infestans*, the 1st between 0900 and 1500 hours and the 2nd during the dark phase, between 2000 and 0400 hours. This is similar to the results of Lazzari (1992) with a 12:12 (L:D) h cycle at a constant temperature. This bimodal pattern was noted also for several crepuscular species of Diptera (Brady 1972, 1981). It is remarkable that the activity pattern of nocturnal *T. infestans* does not differ from that of *T. spinolai* (Tables 2 and 3). The diurnal activity of *T. infestans* was not induced by manipulation, because the records were made 24–60 min after the insects were introduced into the experimental chamber.

It was clear that the activity pattern was synchronized by the light–dark cycle, whereas there were no significant differences in preferred temperature between light and dark periods. Moreover, we must point out that the adults of 2 congeneric species, one light-active and the other dark-active, did not exhibit significant differences in their preferred temperatures. This may mean that the endogenous cycle which regulates temperature preferences is not coupled with the activity rhythm cycle; moreover, this may be a common occurrence in triatomines. However, it will be necessary to make further experiments to expose and record the insects over several consecutive 24-h cycles to test such an hypothesis. The colony conditions before to the experiments were done might affect the results, but so far, there is no evidence of any entraining effect produced in this way.

Spatial distribution of *T. infestans* in a human dwelling is nonrandom. Critical aspects are the distance from blood meal sources (Schofield 1979, Zeledón and Rabinovich 1981), the physiological conditions of bugs and their aggregation pheromones (Schofield and Patterson 1977), and the microclimatic conditions of the cracks in the walls of houses (Canals et al. 1994). Microhabitat selection

hardly is affected by thigmotaxis and negative phototaxis (Schofield 1979). *T. infestans* shows preferences for mud, sand, and wood over paper, fur, and glass (Wiesinger 1956), and it prefers to rest on black paper rather than on white (Schofield and Matthews 1985). This species perceives radiant heat from a warm source and discriminates between different temperatures (Lazzari and Nuñez 1989).

The 2 Chilean vectors of Chagas' disease show a general similarity in their patterns for selection of temperature, suggesting preference for similar substrates. Wild habitats of *T. spinolai* are characterized by stones, cracks in rocks, the burrows of small animals, and bird droppings on rocky offshore islands (Schenone et al. 1980, Apt and Reyes 1990). In human dwellings, *T. spinolai* is found in bedrooms and other locations; it has a spatial distribution similar to that of *T. infestans* (Schenone et al. 1980). But the daily activity patterns of the 2 species are different. This fact is important in the transmission cycle of *Trypanosoma cruzi* (diurnal for *T. spinolai* and nocturnal for *T. infestans*). The diurnal activity of *T. spinolai* may be detrimental to the species in human environments because adults are easily visible. However, the younger developmental stages are small and cryptic, making sighting difficult. Differences in activity patterns are important in multispecies population dynamics because this allows the use of the same resources at different times.

### Acknowledgments

We thank the coeditor and 2 anonymous reviewers for several suggestions that improved the article. This research was supported by Grant No. 194-0373 from the Chilean Scientific and Technology National Fund.

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*Received for publication 21 April 1995; accepted 14 June 1996.*