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Comparison of Some Behavioral and Physiological Feeding Parameters of *Triatoma infestans* Klug, 1834 and *Mepraia spinolai* Porter, 1934, Vectors of Chagas Disease in Chile

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There are two vectors of Chagas disease in Chile: Triatoma infestans *and* Mepraia spinolai. *We studied the feeding behavior of these species, looking for differences which could possibly explain the low impact of the latter species on Chagas disease. Both species used thermal cues to locate their feeding source and consumed a similar volume of blood which was inversely related to the body weight before the meal and directly related to the time between meals. The average time between bites were 6.24 and 10.74 days. The average bite of* M. spinolai *lasted 9.68 min, significantly shorter than the 19.46 min for* T. infestans. *Furthermore, while* T. infestans *always defecated on the host, this behavior was observed in* M. spinolai *in only one case of 27 (3.7%). The delay between the bites and defecation was very long in* M. spinolai *and short in* T. infestans. *These differences may affect the reduced efficiency of transmission of Chagas infection by* M. spinolai.

Key words: *Mepraia spinolai* - *Triatoma infestans* - behavior - feeding - Chagas disease

There are two vectors of Chagas disease in Chile: *Triatoma infestans* Klug, 1834 and *Mepraia spinolai* Porter, 1934 (*sensu* Lent et al. 1994) (Schenone & Rojas 1989, Apt & Reyes 1990). Both species occur between latitudes 18° and 34° S in Chile (Schenone et al. 1980) and both can be naturally infected by *Trypanosoma cruzi*. Infected rates of 32.5% have been reported for *T. infestans* and 11.4 - 26 % for *M. spinolai* (Apt & Reyes 1990, Ordenes et al. 1996). *T. infestans* lives in domestic and peri-domestic habitats, while *M. spinolai* is generally silvatic, living among stones, holes, crevices and nests of birds and mammals (Apt & Reyes 1986), although it has also been found in human dwellings (Gajardo-Tobar 1960, Apt & Reyes 1986, Frías et al. 1995). *M. spinolai* is a diurnal insect, while *T. infestans* is nocturnal (Canals et al. 1997). Both species show similar preference for warm micro-environments (24°C) (Canals et al. 1997) and they are able to survive, mate and rear in human dwelling environments (Canals et al. 1994 a,b). Both species can feed on humans: 68% *T. infestans* (Schenone et al. 1985) and 7.4% *M. spinolai* (Canals et al. 1998).

In spite of these similarities, the epidemiological significance of these two species is very different. Epidemiological estimations suggest that *M. spinolai* is responsible for only 0.64 to 5.8% of all Chagas disease cases in endemic regions of Chile (Canals et al. 1993, 1998), and it is mainly infected with a silvatic strain of *T. cruzi* (Z1), rather than the strain normally found in humans (Z2) (Miles et al. 1987, Apt et al. 1987).

At the present time a new species of triatominae *Mepraia gajardoi* has been described by Frías et al. (1998). Possibly, the northern limit of *M. spinolai* was 26°S and all specimens between 18 to 26°S correspond to the new species.

The aim of this study is to compare the feeding behavior of *M. spinolai* and *T. infestans*, looking for differences that may help to explain the low impact of *M. spinolai* on Chagas disease transmission to humans. We compared the behavior of both species when exposed to a thermal stimulus, together with their bite frequency, the time between bite and defecation, and their subsequent weight loss after feeding.

MATERIALS AND METHODS

Behavior and thermal key - Individuals of *M. spinolai* were captured among rocks in Colina, a peri-urban zone, near Santiago, Chile. All individuals of *T. infestans* were obtained from the long established laboratory colony of the University of

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Chile. Both species were aclimatized during two weeks at constant temperature and humidity in climatic chambers (28°C and 70% RH) without feeding. Thirty fifth instar nymphs from each species were exposed to a thermal key at different distances (Fig. 1a).

The hot end was a glass chamber of 20x25x20 cm with water at a constant temperature of 37°C. The chamber was covered with insulating polystyrene except for a 4x5 cm window at one of its aspects. The chamber had a graduated glass channel of 4x30x5 cm next to the window. The entire system was maintained in a room at ambient temperature (20 ± 2°C) with artificial light. The experiments were conducted between 14 and 18 hr.

The insects were randomly placed in the channel at 5, 15 and 30 cm from the hot end (distance factor). Each individual was placed at each of the three distances in the lapse of two weeks. Before starting the experiments, the insects were placed in black cylinders during 2 min. Thereafter, the cylinder was picked up and the insect's behavior was filmed until it came in contact with the hot end. The films were examined at low speed in order to measure the number of antennae movements, the distance from the hot end, and the time that the insects took to reach the hot end.

The statistical treatment was made using a two way-ANOVA with repeated measurements, considering the species and the distances as the variation sources, the average frequency of antennal movements, and the average speed of approach (distance/time) as the response variables. A posteriori multiple comparisons were made with the Tukey test. The assumptions of normality and homocedasticity were tested by Kolmogorov-Smirnov and Bartlett tests respectively.

Frequency of bites - Fifty eight individuals of fourth and fifth instars of *M. spinolai* and 22 nymphs of *T. infestans* were studied with white rats as hosts (*Rattus rattus*, Sprage-Dowley). The rats were in an upper chamber of 20x25x20 cm, separated by a bronze grille to a lower chamber of 20x25x5 cm, which held the insects (Fig. 1b). Ten sackcloth ribbons stuck to the grille allowed the insects to climb and feed through the grille. The individuals of *M. spinolai* were observed for 27 days and the individuals of *T. infestans* for 22 days. Dead individuals were not replaced, but the date of death was registered. For the calculation of frequencies we considered only those days on which they were alive. The rats were changed daily.

The insects were weighed daily, to determine the occurrence of a bite, as indicated by changes in body weight. To estimate the frequency of bites and the period between bites we used two methods. First we considered an overall punctual estimator of the frequency f = total number of bites/ no. bugs/no. of days and the period between bites p = 1/f. Next, we determined the frequency of bites and the period between bites for each bug considering only those which bit more than once, obtaining an average frequency of bites and period between bites, their standard deviation and 95%- confidence intervals (x ± 1.96 E.S).

Correlation and exponential regression analyses between the weight before the meal and the change in weight (end weight/initial weight) were performed. We also made regression analyses of the periods between bites and the ingested volumes.

Defecation time - Eight adults of *T. infestans* and 27 adults of *M. spinolai* were placed on the surface of an immobilized mouse (*Mus musculus*). The mouse had only a 4.9 cm² circular zone of the skin exposed to the bites of the bugs (Fig. 1c). The time insects spent on feeding (Tp) was measured. They were also observed, looking for the occurrence of defecation. If this happened, the time between the beginning of the bite and the defecation was measured. The insects that did not defecate on the host were observed every 15 min for 1 hr, and the day after.

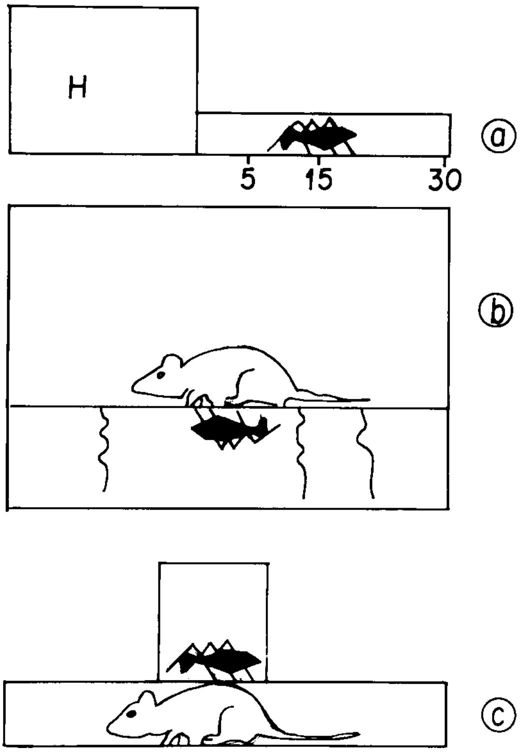

Fig. 1: experimental designs - a: exposure of the bugs to the thermal stimuli (H); b: exposure of rats to the bugs' bites, to estimate the bite frequency; c: exposure of a mouse to the bite of the bugs for defecation studies (see text).

Weight decrease after a blood meal - The daily variation of the body weight after one bite on *M. musculus* was studied in five adults of *T. infestans* and seven adults of *M. spinolai*, during 25 days. A linear regression analysis of the curve of the weight decrease was performed. The initial value was the weight reached immediately post-feeding (Po). Regression analyses were performed separately for each individual, studying the homogeneity of the response by means of analysis of the covariance (ANCOVA). A single regression for each species was performed. The weight values were expressed in percent of Po. To estimate a theoretical period between bites (Td), which was necessary to avoid a negative weight outcome, we determined the time in which the weight was P_{50} = 50% of Po, from the regressions: Td = (50-c)/m, where c and m are the intercept and the slope respectively. The value P_{50} was chosen, considering that a bug at least doubles its weight during a bite.

RESULTS

Behavior and thermal key - *T. infestans* and *M. spinolai* showed a different speed of approaching the thermal stimuli (F = 13.91, $p < 0.01$), but the differences in antennae movements between the species did not reach a significant level (F = 3.57, p = 0.07). There was an effect of the distance to the hot end on the frequency of antennae movements and on the speed of approach (F= 4.08, $p < 0.05$ for the frequency and F = 7.54, $p < 0.01$ for the speed). Furthermore, we found an effect of the interaction between species and distance on the speed (F = 6.67, $p < 0.01$), but not on the frequency of antennal movements (F = 2.59, p = 0.09). Analyzing both species, we found that each one responded in a different way (multiple comparisons, Table I). *T. infestans* showed differences in both parameters at different distances. For example, both the frequency of antennae movements and the speed of approach were higher at the distance of 30 cm. In contrast, *M. spinolai* did not change these parameters at different distances.

Frequency of bites - Both species showed comparable characteristics in their bite parameters (Table II). The frequency of bites was similar. Both methods of estimation of the frequency of bites and of the period between bites yield similar results. We include only the results of the second method in the Table. The 95%- confidence interval for the period between bites was [5.71-6.77] days for *M. spinolai* and [4.60 -16.88] days for *T. infestans*.

TABLE I

Frequency of antennal movements (am) and displacement speed of *Triatoma infestans* and *Mepraia spinolai* at different distances from a thermal key

	Distance (cm)	Frequency (am/s)	T	Speed (cm/s)	T
Triatoma infestans	5	0.70	a	0.21	a
	15	0.61	ab	0.37	ab
n = 30	30	1.21	b	0.95	bc
Mepraia spinolai	5	0.87	a	0.31	a
	15	0.61	a	0.34	a
n = 30	30	0.65	a	0.46	a

T represents the results of a Tukey's test; similar letters indicate homogeneous group.

TABLE II

Parameters of the bite of *Triatoma infestans* and *Mepraia spinolai*. The values, if necessary, are presented with ± 1 standard deviation

	M. spinolai (n = 58)	*T. infestans* (n = 22)
No. of bugs which bit	51 (87.9%)	19 (86.4%)
No. of bugs which bit more than once	33 (56.9%)	4 (18.2%)
Total bites	125	24
Frequency of bites (bites/insect·day)	0.1527 ± 0.066	0.1407 ± 0.083
Period between bites (days)	6.24 ± 1.54	10.74 ± 6.27
Blood ingested (mg)	90.5±77.6	27.11±32.04
Increase of weight in one bite (%)	129.4 ± 62.0	199.6 ± 109.5
Maximal increase of weight (%)	660.0	618.2
Maximal ingest (mg)	321.4	122.4
Blood ingested in the first bite (mg)	163.7 ± 81.5	39.3 ± 33.0
Weight increase after the first bite (%)	303.3 ± 58.19	285.3 ± 109.5

The latter species showed a broad interval because only four individuals bite more than once. Both species increased significantly their weight during feeding. In some cases it increased around six folds.

The change in weight when *M. spinolai* bites (pf/pi) was inversely correlated with the weight before the bite (pi) ($r = -0.795$, $R^2 = 63.29\%$, $p < 0.01$). *T. infestans* showed the same tendency, but the correlation did not reach statistical significance ($r = -0.176$, $R^2 = 3.1\%$, $p > 0.05$) (Fig. 2). Also, the volume of blood ingested by *M. spinolai* was positively correlated with the period between bites ($r = 0.3$, $R^2 = 9.02\%$, $p < 0.05$). In *T. infestans* it was not possible to perform this analysis because only four individuals bit twice or more times.

Defecation time - Several differences between *T. infestans* and *M. spinolai* were found (Table III). *T. infestans* took more time in its bite and showed a shorter defecation time than those of *M. spinolai*. The first species always defecated during the bite, whilst *M. spinolai* defecated over the host on only one occasion of 27 observations.

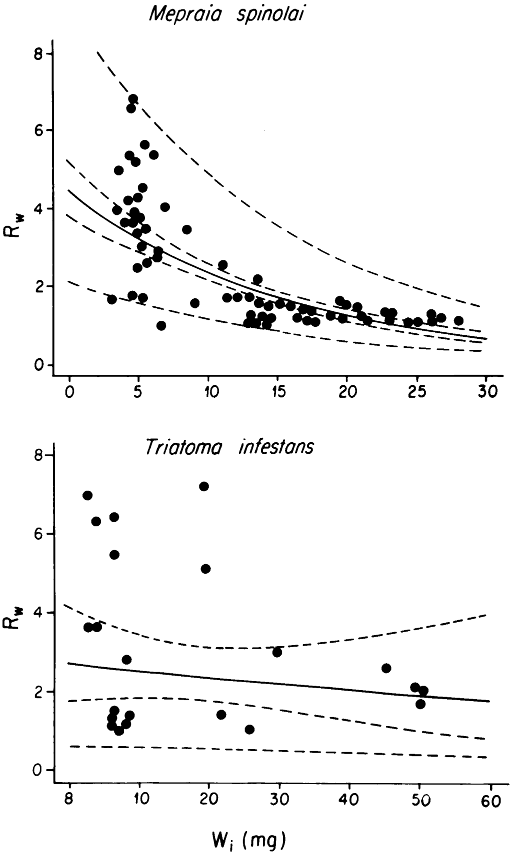

Fig. 2: exponential regressions between the increase in weight of *Mepraia spinolai* and *Triatoma infestans* during one bite (R_w = post ingest weight/ pre ingest weight) and the pre ingest weight (W_i).

TABLE III

Time that adult bugs *Triatoma infestans* and *Mepraia spinolai* took to perform one bite (Tp) and time of defecation (Tl)

	M. spinolai (n = 27)	*T. infestans* (n = 8)
Tp (min)	9.68 ± 5.5	19.46 ± 6.75
Tl (min)	24.4±16.6	3.62±2.84
Defecation during the bite (no. individuals)	1	8
1 to 15 min	2	0
15 to 30 min	2	0
30 to 60 min	5	0
1 to 24 hr	16	0
Total	27	8

Weight decrease after a blood meal - The weight decreased slowly in both species. There were individual differences in the weight decrease (ANCOVA: *M. spinolai* $F = 317.4$, *T. infestans* $F = 138.1$, $p < 0.001$). The common regression for *M. spinolai* was: $P = 93.51 - 1.65 \cdot t$, where P is the weight in percent of Po and t the time in days ($F = 65.1$, $R^2 = 40.41$, $p < 0.05$); for *T. infestans* the regression was: $P = 100.57 - 1.37 \cdot t$ ($F = 59.11$, $R^2 = 36.24$, $p < 0.05$). The estimated length of time to avoid a negative change in body weight were Td = 36 days and Td = 26 days for *T. infestans* and *M. spinolai* respectively.

DISCUSSION

Although both species showed all three characteristic components of the orientation to a thermal key: antennae movements, locomotive activity and extension of the proboscis (Wigglesworth & Gillet 1934), the specific responses were different. *T. infestans* showed fast displacements and antennae movements at 30 cm from the thermal key. However at 15 and 5 cm movements became slow, until contact or near touching the key. At that moment *T. infestans* extended its proboscis. In contrast, *M. spinolai* did not change the frequency of its antennae movements, and it showed a quite fast displacement at 30 cm, without statistical significance.

Despite the fact that *M. spinolai* is a diurnal species and can be found on stones exposed to the sun, it also used the thermal key for feeding (Schenone et al. 1980, Canals et al. 1997). In contrast to *T. infestans*, it did not change its behavior at the different distances tested. This could be an indication of a longer critical distance of heat perception. On the other hand, when it was exposed to the thermal key its general behavior could be interpreted as an expression of an apetitive display, with the exception of the extension of the proboscis. The latter was triggered by contact or by the close proximity of the thermal key. However this interpretation may be unlikely because *M. spinolai* always showed antennae movements of low frequency like those of *T. infestans* at short distances. *M. spinolai* is able to detect and to run toward an endothermic vertebrate at distances of several meters (Lent & Jurberg 1967).

Both species ingested similar volumes of blood, but these were smaller than the maximal volumes reported for other triatomines: 433 mg for *Rhodnius prolixus*, 618 mg for *T. infestans*, 600 mg for *T. dimidiata* and 1,008 mg for *Panstrongylus megistus* (Miles et al. 1975, Zeledón & Rabinovich 1981, Zeledón 1983). Also, the average volume ingested was smaller than the 260 mg reported for *T. rubrovaria* (Garcia da Silva 1985). Our values are similar to the range of 30 to 90 mg found in *T. infestans* feeding on hamsters (*Cricetus auratus*) of diverse grade of irritability (Schofield 1985). In this study, Schofield found the ingested volume to be inversely related with the irritability of the host. Our bugs fed on *R. rattus* and they could only bite the host from below. Furthermore our experimental rats showed several movements to avoid the bites. This fact could explain the small volumes ingested by the bugs. In spite of these factors, both species were capable to increase nearly six fold their weight, ingesting maximal volumes of 321 and 122 mg. The volume ingested in the first bite was always larger than the following ones.

The volume ingested during the bite was inversely related to the pre-feeding weight and directly related to the period between bites. These findings are in agreement with Friend and Smith (1977) who found that the period between bites and the grade of abdominal distention determine the volume of feeding.

The bite frequencies of both species were lower than 15 days. The estimated frequencies would correspond to the optimal frequencies reported by Cabello et al. (1988). These figures are also comparable with those reported for *R. prolixus*: between 0.089 and 0.119 bites/insect/day [periods between bites from 8.4 to 11.2 days (Rabinovich et al. 1979)]. From the curves of the decrease in weight, times Td = 36 and Td = 26 days to a negative outcome of weight were estimated for *T. infestans* and *M. spinolai* respectively. These values suggest critical frequencies (*sensu* Cabello et al. 1988) of 0.028 and 0.038 bites/insect/day for these species. Below these values, vital parameters would be depressed. However, the decrease in weight showed individual variability. Most of the curves were in agreement with Td between 20 and 30 days [Td = (50-c)/m] but in some cases, Td of 8.5 and 129.6 days were estimated.

The main difference between *T. infestans* and *M. spinolai* was found in the free bite on *M. musculus*. *M. spinolai* showed an aggressive behavior, quickly initiating its feeding, but spending a very short time on its bite: 9.68 min in average. In contrast, *T. infestans* took 19.46 min. Long feeding times have been reported in other triatomines: 17, 21 and 30 min for *R. prolixus*, *T. infestans* and *T. dimidiata* (Zeledón & Rabinovich 1981). However, some individuals can take from 4 to 10 min to feed (Zeledón et al. 1977). It is relevant that *M. spinolai* defecated on the mouse in only one occasion of 27 (3.7%) whilst *T. infestans* always defecated on it. *M. spinolai* showed a fleeing behavior after a short time of feeding. Also, its defecation time was very long in comparison to that of *T. infestans* (Table III).

T. infestans and *R. prolixus* show short defecation delays, whilst *M. spinolai* fell in the range between 15 and 45 min likes other triatomines such as *T. dimidiata*, *T. protracta*, *T. recurva* and *Psammolestes hirsuta* (Wood 1951, Zeledón et al. 1977, Zeledón & Rabinovich 1981).

These differences suggest that *M. spinolai* would be less efficient in transmitting *T. cruzi*. For example, considering a probability of transmission of 0.01 as a reasonable estimate in bugs which usually defecates on the host (following Rabinovich & Rossel 1978 and Canals et al. 1998), in *M. spinolai* this value would decrease to $0.037 \cdot 0.01 = 0.00037$. Furthermore, considering that the proportion of infected bugs in Chile are: *T. infestans* 32.5% and *M. spinolai* 11.4% (Canals et al. 1993), the probabilities of transmission of the *T. cruzi* infection through one bite (Vectorial efficiencies (E_i), *sensu* Canals et al. 1993) would be $E_i = 0.01\text{x}\ 0.325 = 0.00325$ for *T. infestans* and $E_i = 0.00037\text{x}\ 0.114 = 0.0000421$ for *M. spinolai*. The latter value represents approximately 1% of the efficiency of *T. infestans*. This finding joined with the bad capacity to colonize human dwellings of *M. spinolai* may help to explain the low epidemiological impact of *M. spinolai* as well as the low prevalence of strain Z1 in patients with Chagas disease.

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