

Effect of feeding frequency on the reproductive efficiency of two species of *Triatoma* with different epidemiological importance

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ABSTRACT

Introduction: In Triatominae, reproductive efficiency is an important factor influencing population dynamics, and a useful parameter in measuring a species' epidemiological significance as a vector of *Trypanosoma cruzi* (Chagas, 1909). The reproductive efficiency of triatomines is affected by food availability; hence, we measured and compared the effects of feeding frequency on the reproductive parameters of *Triatoma patagonica* (Del Ponte, 1929) and *Triatoma infestans* (Klug, 1934), and the effects of starvation on *T. patagonica*. **Methods:** Couples from both species were fed weekly, or every 3 weeks; in addition, females in couples of *T. patagonica* were not fed. Each couple was observed weekly and reproductive efficiency was assessed on the following parameters: fecundity (eggs/female), fertility (eggs hatched/eggs laid), initiation and end of oviposition, initiation of mating, number of matings/week, and number of reproductive weeks. Relative meal size index (RMS), blood consumption index (CI), and E values (eggs/mg blood) were also calculated. **Results:** Changes in feeding frequency affected the reproductive parameters of *T. patagonica* only, with a decrease in fecundity and number of reproductive weeks for those fed every 3 weeks, or not fed. The reproductive period, RMS index, and CI were lower for *T. patagonica* than *T. infestans*. However, despite the lower fecundity of *T. patagonica*, this species required less blood to produce eggs, with an E values of 2 compared to 2.94 for *T. infestans*. **Conclusions:** Our results suggest that the differences in fecundity observed between species reflect the availability of food in their natural ecotopes.

Keywords: Blood-sucking insect. Chagas disease. Fecundity. Fertility. Triatominae.

INTRODUCTION

In Latin America, triatomines (Hemiptera: Reduviidae) are recognized vectors of *Trypanosoma cruzi*, the etiological agent of Chagas disease. Although these hematophagous insects are of wild origin, several species show varying levels of ecological adaptation to human habitats^{1,2}, and this trait is relevant in characterizing the epidemiological importance of these species¹.

Of the 140 species in this subfamily³, 18 occupy wild habitats in Argentina, in addition to intradomicile and peridomicile environments⁴. *Triatoma infestans* is one species that has successfully adapted to human habitats. This primary vector has a wide distribution in southern South America, and is the most epidemiologically important species in Argentina, colonizing

intradomicile and peridomicile environments, where it is associated with birds, and occasionally mammals⁴. In addition, *Triatoma infestans* has been shown to have a significant level of natural infection with *T. cruzi*^{1,5,6}.

Triatoma patagonica occupies wild and peridomestic habitats, and has only been reported in Argentina to date, with its southernmost distribution limited to the Chubut province of Patagonia⁷. This secondary vector⁸ has been shown to establish significant colonies in peridomestic ecotopes⁹ where it feeds on both birds and mammals⁷, and a few instances of intradomicile colonization have been recorded^{10,11}. *Triatoma infestans* and *T. patagonica* can colonize different peridomestic structures, feeding on both birds and mammals; in rural areas of Argentina, chicken coops are the most common of such structures^{12,13}, and thus, in these habitats *T. infestans* feeds predominantly on chickens, as opposed to dogs or goats^{12,14}.

The reproductive efficiency of a species is strongly associated with its potential to colonize or recolonize a habitat; thus, information on its effects on population dynamics may help to determine the epidemiological significance of different triatomine species^{15,16}. Reproductive efficiency, as determined by parameters related to fecundity and fertility^{15,17}, may vary between species of triatomines; however, within species,

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this variation is significantly affected by factors such as environment (temperature), physiology (insect age, and gonadotrophic cycle status) and food (volume, quality, and availability)¹⁸. Food availability in the wild varies and insects may feed daily or undergo prolonged fasting, with each species having a critical feeding frequency at which reproductive parameters begin to be affected¹⁹.

In adult female triatomines, blood meals are essential for egg production, as they stimulate endocrine regulation of ovarian development²⁰. However, females that have high nutritional reserves from the fifth-instar nymph stage can undergo the first cycle of egg production without feeding²⁰. This phenomenon, known as autogeny, has been described for several triatomine species²¹⁻²³, including *T. infestans*²³ and *T. patagonica*²⁴. However, reproductive parameters under fasting conditions for the latter have yet to be fully described.

Abalos²⁵ has questioned whether *T. patagonica* could replace *T. infestans* as a permanent host of *T. cruzi* in intradomiciliary environments in southern Argentina. Considering that these species, which have a different epidemiological importance, coexist in peridomiciliary habitats, the objective of this work was to compare the effects of different food supply frequencies and starvation conditions on their reproductive parameters.

METHODS

Triatoma patagonica and *Triatoma infestans* were supplied by the Coordinación Nacional de Control de Vectores (Córdoba province, Argentina). These insects were originally obtained from chicken coops in the San Luis and La Rioja provinces (Argentina). First-generation insects were reared from eggs in our laboratory and maintained under controlled temperature ($26 \pm 1^\circ\text{C}$) and relative humidity ($60 \pm 10\%$), and a photoperiod of 12:12h (light: dark). Groups of 15 insects were kept in cylindrical (500cm^3) glass bottles covered with nylon mesh and containing vertically folded paper to allow insects' access to food and to avoid excess humidity. Triatomines were allowed to feed for 30 min on an immobilized pigeon (*Columba livia* Gamelin) placed on a plastic box. First-instar nymphs of each species were divided into 2 groups and fed either weekly, or every 3 weeks, from the nymphal to the adult stage.

Once triatomines had reached the adult stage (between August and September), couples from each group, for both species, were placed in separate glass bottles until both insects died. The 4 groups were defined as follows: G1: 13 couples of *T. patagonica* fed once a week; G2: 13 couples of *T. patagonica* fed every 3 weeks; G3: 10 couples of *T. infestans* fed once a week; and G4: 13 couples of *T. infestans* fed every 3 weeks.

In addition, an *autogenic group* comprised 13 couples of *T. patagonica*, which were fed every 2 weeks throughout the nymphal stage, and then females were not fed, and males were fed once a week, for the adult stage.

Reproductive parameters

Couples were observed weekly until females died, and the following data were recorded: initiation and end of

oviposition; initiation of mating; matings per week (determined by observation of spermatophores); reproductive weeks, fecundity (number of eggs laid/female); age-specific fecundity (m_x = mean eggs/female/week); and fertility (number of eggs hatched/number of eggs laid), calculated as: (number of eggs hatched/total eggs) \times 100. The length of the adult stage (days) for females was also recorded. Eggs were stored in Eppendorf tubes until nymphs hatched.

Relationships between feeding frequency and reproductive parameters

Females were weighed on the day of imaginal molt, and before and after each feeding event, to calculate the amount of blood consumed. The relative meal size index (RMS = meal size/insect weight before feeding) was calculated to allow comparison between species²⁶.

The blood consumption index (CI) was calculated for each group as per Catalá et al.²⁷ using the following formula: $CI = [(Bi + F) - Be]/T$, where Bi is blood in the stomach at moulting; F is the weight of ingested food (sum of intakes); Be is blood in the stomach after the last feeding event; and T is the duration of the adult stage (days). Blood contained in the stomach (BCS) was calculated using the following equations: $BCS = -69.76 + 0.54x$ and $BCS = -14.07 + 0.32x$, as described by Catalá de Montenegro²⁸ for *T. infestans* and Nattero et al.²⁹ for *T. patagonica*, respectively. E values were calculated as follows: $[\text{total number of eggs}/(\text{initial female weight} \times \text{amount of blood ingested})] \times 1,000$ ³⁰.

All weight measurements were performed using a Mettler Toledo precision balance (PG203-S) to a level of 0.001g.

Data analysis

Means and standard deviations were calculated for each variable. If data for variables did not show normal distribution or homogeneity of variance, as analyzed by the Kolmogorov-Smirnov and Levene's tests respectively, groups were compared using a non-parametric Mann-Whitney test (statistical index U) or Kruskal-Wallis one-way analysis of variance (statistical index U). Spearman's correlation coefficient (r_s) was used to evaluate correlations between reproductive parameters and feeding behavior for each species. Percentages were compared using Fisher's test. A p-value < 0.05 was considered statistically significant.

RESULTS

Only couples in which females laid eggs were considered in the analysis of reproductive efficiency and feeding behavior. All *T. infestans* females ($n = 23/23$, groups G3 and G4) and 65.38% ($n = 17/26$, groups G1 and G2) of *T. patagonica* females laid eggs at least once, and data from these groups was further examined (**Table 1**).

Female longevity was similar within each species for both feeding regimens. However, *T. patagonica* females had a significantly shorter lifespan than *T. infestans* females with a mean age of 77.92 ± 64.81 days compared to 316.60 ± 95.58 days ($H = 33.91$, $p < 0.001$).

TABLE 1 - Reproductive parameters for *Triatoma patagonica* and *Triatoma infestans* females with different feeding regimens (G1 and G3: fed weekly; G2 and G4: fed every 3 weeks).

	<i>Triatoma patagonica</i>			<i>Triatoma infestans</i>		
	G1 $\bar{x} \pm SD$ n = 9	G2 $\bar{x} \pm SD$ n = 8	Mann-Whitney test U (p-value)	G3 $\bar{x} \pm SD$ n = 11	G4 $\bar{x} \pm SD$ n = 12	Mann-Whitney test U (p-value)
Initiation of oviposition (days)	31.33 \pm 17.65	23.25 \pm 6.75	33.5 (0.06)	6.22 \pm 7.08	4.80 \pm 10.04	26.5 (0.36)
Fecundity (eggs/female)	72.11 \pm 66.0	20.50 \pm 14.48	15.0 (0.04)	183.3 \pm 118.33	132.61 \pm 113.21	41.1 (0.14)
Reproductive weeks	10.0 \pm 7.14	4.12 \pm 2.85	13.5 (0.06)	26.24 \pm 9.22	33.61 \pm 18.24	49.5 (0.33)
Initiation of mating (days)	31.33 \pm 17.65	23.25 \pm 6.75	43.0 (0.87)	6.22 \pm 7.08	4.80 \pm 10.04	32.0 (0.10)
Number of matings	10.0 \pm 7.14	4.12 \pm 2.85	24.5 (0.26)	33.61 \pm 18.24	26.4 \pm 9.22	56.0 (0.79)
Fertility (%)	72.1 \pm 66.0	20.5 \pm 14.5	18.0 (0.24)	56.3 \pm 22.3	66.7 \pm 34.9	44.5 (0.30)

$\bar{x} \pm SD$: mean \pm standard deviation; n: number of insects; U: statistical index of Mann-Whitney test.

Reproductive parameters

Fecundity was significantly higher in *T. patagonica* females fed once a week (G1) than those fed every 3 weeks (G2; $p < 0.05$; **Table 1**); however, there were no significant differences between feeding frequency for other reproductive parameters measured for this species (**Table 1**). For *T. infestans* there were no significant differences between groups for any of the reproductive parameters measured (**Table 1**).

Oviposition ($H = 16.62$, d.f. = 3, $p = 0.0008$) and mating ($H = 16.17$, d.f. = 3, $p = 0.01$) began earlier in *T. patagonica* than *T. infestans*; however, fecundity and reproductive weeks were higher for *T. infestans* ($H = 17.62$, d.f. = 3, $p = 0.005$ and $H = 25.58$, d.f. = 3, $p < 0.0001$ for fecundity and reproductive weeks respectively).

Of all couples observed, 88.2% ($n = 15/17$) of *T. patagonica* and 78.3% ($n = 18/23$) of *T. infestans* mated at least once, with no difference between species ($p = 0.209$, Fisher exact test). The mean mating number was significantly higher for *T. infestans* than *T. patagonica* ($H = 7.94$, d.f. = 3, $p = 0.04$), and the fertility rate was below 62.0%, with no differences between species ($U = 132.00$, $p = 0.307$; **Table 1**).

In *T. patagonica* reproductive activity began at week 2 and week 3 for G1 and G2 respectively, with the maximum reproductive effort (m_x) recorded at week 6 for G1 and week 4 for G2 (mean m_x 9.24 ± 6.18 and 5.90 ± 4.52 eggs/female/week for G1 and G2 respectively) with no significant difference between groups ($U = 24.00$, $p = 0.24$). From week 7 for G1 and week 13 for G2, m_x values began to decrease until females stopped laying eggs; however, there were a number of additional reproductive peaks for G2 (**Figure 1A**). In *T. infestans*, reproductive activity began at week 2 for both groups, and mean m_x values did not differ significantly between groups ($U = 36.00$, $p = 0.07$) (mean m_x 7.43 ± 4.51 and 4.56 ± 3.91 eggs/female/week for G3 and G4 respectively). The maximum reproductive effort for this species was recorded at the end of the reproductive period, at week 41 for G3 (26 eggs/female) and at week 65 for G4 (32 eggs/female; **Figure 1B**).

For both species, the number of matings positively correlated with fecundity ($r_s = 0.64$, $p = 0.004$ and $r_s = 0.56$, $p = 0.006$, for *T. infestans* and *T. patagonica* respectively). For *T. infestans* females, there was also a correlation between initiation of oviposition and mating ($r_s = 0.53$, $p = 0.013$).

Initiation of oviposition (20.23 ± 8.2 days), first mating (14.33 ± 3.70 days), and fertility ($53.75 \pm 40.85\%$) for the autogenic group of *T. patagonica* (autogenic group) showed similar values to those for G1 and G2 ($H = 3.78$, $p = 0.15$; $H = 3.52$, $p = 0.17$ and $H = 5.90$, $p = 0.052$ respectively). However, the number of reproductive weeks (2.92 ± 1.75) of the autogenic group was lower than that for other groups ($H = 9.07$, $p = 0.01$), and fecundity (16.38 ± 7.81 eggs per female) was significantly lower than G1 and similar to G2 ($H = 9.57$, $p = 0.008$).

Relationships between feeding frequency and reproductive parameters

Only G1 and G2 groups were analyzed in terms of relationships between feeding frequency and reproductive parameters.

The weight at moulting of the *T. patagonica* G1 group was higher than that of G2; however, there were no significant differences between the G3 and G4 groups of *T. infestans*. For both species, the volume of blood ingested in the adult stage was similar for females fed weekly or every 3 weeks (**Table 2**). *T. infestans* females had a higher RMS index and blood CI than *T. patagonica*, when fed weekly ($U = 10.00$, $p = 0.007$ and $U = 5.00$, $p = 0.002$ for RMS and CI, respectively) and every 3 weeks ($U = 0.00$, $p = 0.006$ and $U = 11.00$, $p = 0.003$ for RMS and CI, respectively; **Table 2**).

For *T. patagonica*, oviposition began before the first feeding event for 33.3% and 62.5% of females for G1 and G2 respectively; however, for *T. infestans*, no females laid eggs without being fed at least once.

For *T. patagonica* females, there were no statistically significant differences for E values in relation to feeding frequency, and standard deviations were high. However, these

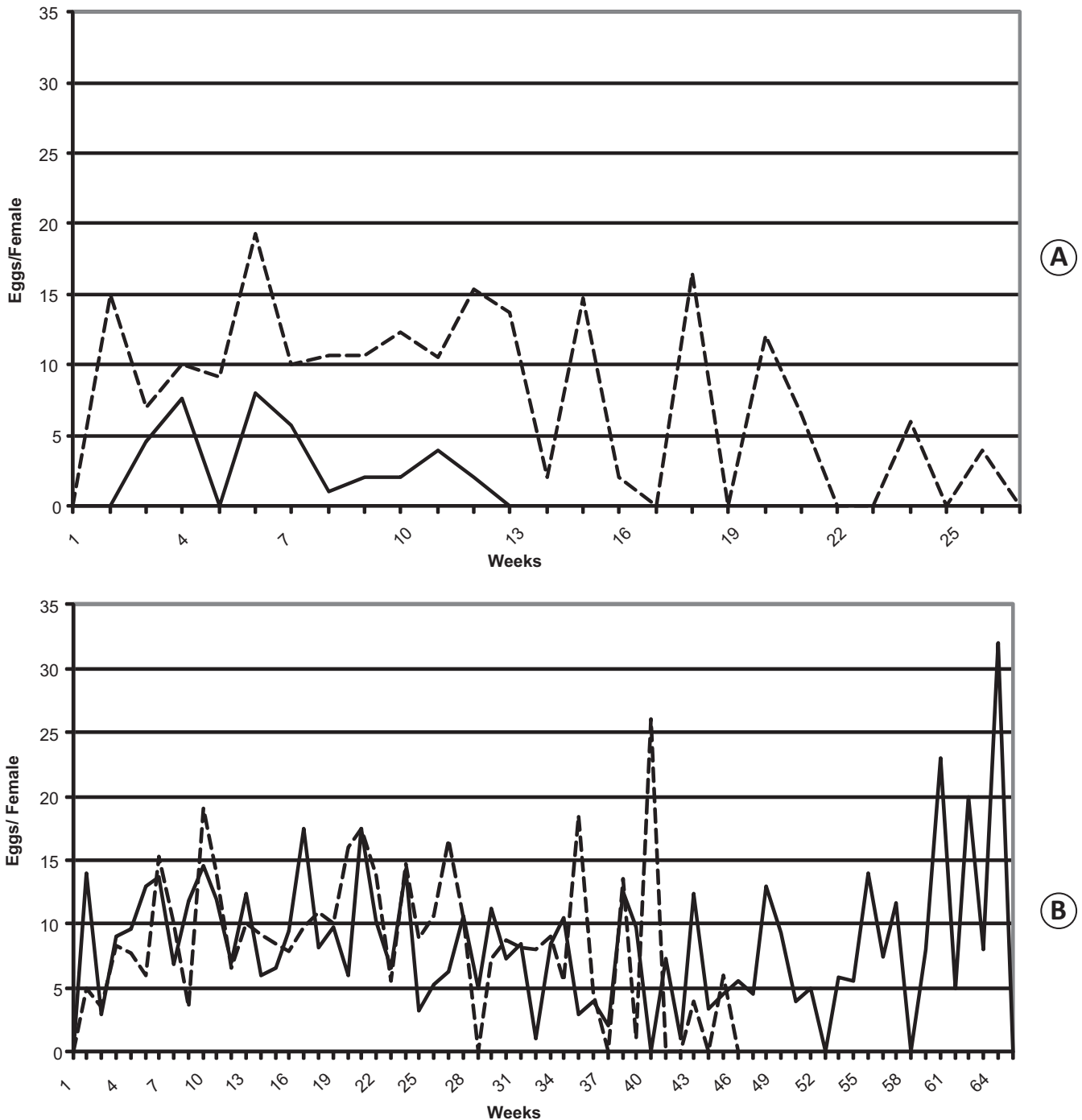


FIGURE 1 - Age-specific fecundity curves (m_x) for (A) *Triatoma patagonica* and (B) *Triatoma infestans* females with different feeding regimens. Dotted lines: groups fed weekly (G1 and G3); Continuous lines: groups fed every 3 weeks (G2 and G4).

E values were significantly higher than those recorded for both groups of *T. infestans* females ($H = 20.47$, d.f. = 3, $p = 0.0001$; **Table 2**).

For both species, the volume of blood ingested during the adult stage correlated positively with fertility ($r_s = 0.62$, $p = 0.030$ for *T. patagonica* and $r_s = 0.60$, $p = 0.05$ for *T. infestans*) and reproductive weeks ($r_s = 0.85$, $p = 0.0003$ for *T. patagonica* and $r_s = 0.54$, $p = 0.05$ for *T. infestans*).

DISCUSSION

Feeding has a direct effect on the reproductive efficiency of triatomines. Variations in reproductive parameters within species relate to food availability, quality, and nutritional status¹⁸, whereas differences between species may be due to the relationship between reproductive behavior and the insects'

TABLE 2 - Amount of blood ingested, relative meal size index, blood consumption index and E values for *Triatoma patagonica* and *Triatoma infestans* (G1 and G3: fed weekly; G2 and G4: fed every 3 weeks).

	<i>Triatoma patagonica</i>			<i>Triatoma infestans</i>		
	G1 $\bar{x} \pm SD$ n = 7	G2 $\bar{x} \pm SD$ n = 4	Mann-Whitney test U (p-value)	G3 $\bar{x} \pm SD$ n = 10	G4 $\bar{x} \pm SD$ n = 13	Mann-Whitney test U (p-value)
Weight at molting (mg)	186.1 ± 30.6	146.5 ± 45.2	33.5 (0.009)	247.5 ± 56.4	218.2 ± 60.2	45.0 (0.21)
Blood ingested (mg)	439.5 ± 350.5	116.0 ± 114.4	16.0 (0.09)	2071.7 ± 798.5	2192.6 ± 1221.0	64.0 (0.95)
RMS	3.95 ± 3.84	0.69 ± 0.71	8.0 (0.04)	10.76 ± 6.49	8.67 ± 4.42	51.0 (0.38)
CI (mg/day)	3.35 ± 1.47	2.37 ± 2.07	18.0 (0.14)	7.08 ± 2.14	6.13 ± 2.42	39.0 (0.19)
E value (eggs/mg blood)	1.58 ± 1.25	2.40 ± 4.49	9.0 (0.16)	0.50 ± 0.39	0.21 ± 0.09	24.0 (0.01)

$\bar{x} \pm SD$: mean ± standard deviation; **n**: number of insects; **U**: statistical index of Mann-Whitney test; **RMS**: relative meal size index; **CI**: consumption index.

natural habitat¹⁵. Consensus has not yet been reached in terms of the quality of ingested blood, with some species showing greater reproductive efficiency when fed on mammals or birds^{15,17,29}, but other species not¹⁵; variability has even been shown between different studies of the same species^{15,29}. For this reason, our results are discussed in the context of other studies using the same food source. The reproductive efficiency of *T. infestans* females does not appear to be affected by feeding frequency, as there were no differences between groups for any reproductive parameters. However, the reproductive efficiency of the secondary vector *T. patagonica* appears to be sensitive to feeding frequency, as fecundity, reproductive weeks, and blood consumption, were lower in females fed every 3 weeks than those that were fed weekly. Similarly, Zeledón et al.²¹ and Cabello et al.¹⁹ reported an increase in fecundity with increased feeding frequency for *Triatoma dimidiata* and *Rhodnius neivai*.

On the other hand, the fact that *T. patagonica* that were starved had similar fecundity and reproductive week values to those of females fed every 3 weeks suggests that this is close to the critical fasting limit for this species in terms of reproductive parameters.

Females of *T. patagonica* began to lay eggs earlier than *T. infestans*. This may be related to the stimulatory effects of mating on oviposition²⁰, as females of this peridomiciliary species copulated earlier than those of the domiciliary species. In *T. infestans*³¹ and other domiciliary triatomine species like *Panstrongylus megistus*³² and *Triatoma brasiliensis*¹³, virgin females were found to begin laying eggs later than those that had copulated. Accordingly, Carrizo²⁴ reported that virgin females of *T. patagonica* fed fortnightly began oviposition at 38.2 ± 14.4 days, later than that recorded here.

Fecundity and reproductive weeks were also different between species, with values for both higher in *T. infestans* than *T. patagonica*. However, the fecundity values under starvation for *T. patagonica* seen in this study were higher than those reported by Noriega²⁰ for *T. infestans* under similar conditions. This may be an advantageous characteristic in *T. patagonica*, allowing it to lay many eggs prior to first feeding

in a peridomicile habitat where food availability is variable. For both species, fertility rates were similar; however, they were lower than values previously recorded for these species^{7,26,33}, as well as other peridomiciliary and domiciliary species^{7,34,35} fed on birds blood. This decrease might be due to excessive insect manipulation during the performance of experiments, and is in agreement with results reported by Tolesano et al.³⁶ for *T. infestans*.

Reproductive efficiency in terms of fecundity was compared between species by calculating indices relating egg production to blood consumption. Although *T. patagonica* laid fewer eggs and had a lower RMS than *T. infestans*, they consumed a smaller volume of blood daily (CI) and were more efficient in converting blood into eggs (E values), producing approximately 2 eggs per mg blood ingested. To produce a similar number of eggs, *T. infestans* required approximately 4mg of blood when fed weekly. The E values obtained in this work are similar to those reported by Guarneri et al.¹⁵ for other domiciliary and peridomiciliary species. These authors indicated that differences in E values between species reflect the food availability of the insects' natural ecotopes.

In the natural environments of triatomine species, there are a number of interacting factors that cannot be reproduced in the laboratory, such as behavioral responses to the environment and to different food sources, and genetic variability of populations^{34,37}. Hence, although it is difficult to extrapolate the data presented here directly to populations developing in natural environments, our results do indicate trends in the behavior of these species relative to these environments.

Our comparison of the reproductive efficiency of these two species with different epidemiological importance indicates that, unlike domiciliary species, peridomiciliary species such as *T. patagonica* allocate a greater percentage of ingested blood to reproduction than maintenance. This characteristic may be related to the environmental conditions under which this species develops. Peridomiciliary species live in unstable ecotopes, and form small scattered colonies with infrequent access to food sources, whereas domiciliary species live in more stable ecotopes in high densities and with frequent food access.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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