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Influence of the quality and quantity of blood ingested on reproductive parameters and life-span in *Triatoma infestans* (Klug)

Julieta Nattero*, Gustavo Leonhard, Claudia S. Rodríguez, Liliana Crocco

Cátedra de Introducción a la Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Avda. Vélez Sarsfield 299, piso 5. X5000JJC, Córdoba, Argentina

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ABSTRACT

In Triatominae, female fecundity and fertility may be affected by age, adult nutritional status (i.e., blood meal source and amount of blood ingested) and number of matings. *Triatoma infestans* (Klug) is the main vector of Chagas disease in southern South America and considering that reproductive success is intimately associated with the potential for colonizing or re-colonizing new ecotopes in endemic areas, we studied whether the blood meal source and the amount of blood ingested have influence on reproductive parameters.

We constitute two groups: couples feeding regularly on guinea pigs and couples feeding regularly on pigeons. We registered quantity of blood ingested, fecundity, fertility, number of matings, days between the first feeding and mating, copula initiation, oviposition initiation and adult life-span. Results showed that females that fed on guinea pigs exhibited high fecundity and fertility, higher number of matings and they needed a lower amount of blood to form an egg. The number of matings and fecundity increased linearly and significantly with the quantity of blood ingested for both meal sources. Results from lineal regression between life-span and fecundity showed a positive and significant relation for both meal sources. The number of matings showed a positive relation with fecundity for both meal sources but significant only for guinea pigs. In *T. infestans*, the quantity of blood ingested could be a determinant of their reproductive efficiency. This species is mainly adapted to human dwelling and peridomestic structures where there is low host diversity. Considering that this species is in contact with mammals over other food sources, a greater reproductive success may result from an adaptation to this environment.

1. Introduction

The bloodsucking bug *Triatoma infestans* (Klug) is the main vector of *Trypanosoma cruzi*, the causative agent of Chagas disease in southern South America (Lent and Wigodzinsky, 1979; Zeledón, 1983). It almost exclusively occurs in domestic or peridomestic habitats, with very rare records of selvatic populations (Ceballos, 2010; Dujardin et al., 1987; Noireau et al., 2002, 2005).

In Triatominae, reproductive parameters like fecundity, oviposition period and egg fertility may be affected by factors such as, age, adult nutritional status (i.e., blood meal source and amount of blood ingested) and number of matings (e.g., Costa et al., 1987; Daflon-Teixeira et al., 2009; Guarneri et al., 2000; Pires et al., 2004; Rabinovich, 1985). Adult age may affect fecundity. For example, in *Rhodnius prolixus* it has been observed that there is a decrease in the rate of age-related oviposition (e.g., Sulbaran and Chaves, 2006). In Triatominae, blood meal source has been considered an important factor affecting fertility and the conversion blood ingested/number of deposited eggs, depending, among other factors, on the natural history of each species (because each species may be adapted to different host feeding depending on the environment where they live) (Cabello et al., 1987; Guarneri et al., 2000). The amount of blood ingested is directly related to fecundity. Since, for a female to oviposite continuously they should not have prolonged fasting periods (Davey, 1967; Stoka et al., 1987). Besides blood meal ingestion, mating is a stimulus that appears to enhance egg production. The number of matings promotes more numerous ovipositions and increases fertility (Asin and Crocco de Ayerbe, 1992; Daflon-Teixeira et al., 2009; Mundal, 1978; Stoka et al., 1987).

According to Reznick (1985), reproduction is costly and there is a trade-off between reproduction and longevity. The relationship between fecundity (egg production) and longevity predicts that the first is costly and reduces longevity. It has been shown that in other Triatominae bug, life expectancy in adults is negatively correlated with fecundity, indicating the existence of a cost of reproduction (Sulbaran and Chaves, 2006).

In Triatominae reproductive success is intimately associated with the potential for colonizing or re-colonizing endemic areas.

* Corresponding author. Tel.: +54 351 4332100x248; fax: +54 351 4332100.
E-mail address: jnattero@efn.uncor.edu (J. Nattero).

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Information of the relation between the nutritional status (both in quality and in quantity of blood ingested) with reproductive parameters and life-span will help to understand better reproductive biology, life history and the vectorial capacity of these species. Studies that address the effects of quality and quantity of blood ingested and reproductive parameters in Triatominae are still few (e.g., Gomes et al., 1990; Marassá et al., 1998; Guarneri et al., 2000; Aldana et al., 2001) and little is known about how these variables affected life-span and the number of copulas. In *T. infestans*, studies related to reproduction have been considered elsewhere (e.g., Asin and Crocco de Ayerbe, 1989, 1992; Catalá de Montenegro, 1989; Catalá et al., 1992; Giojalas and Catalá, 1993) but to our knowledge there is only one work where the quality and quantity of blood meal was related to reproductive parameters by comparing this species with other ones (Guarneri et al., 2000). Such data are important not only to better understand aspects related with the reproductive biology and vectorial capacity of this species but also to allow comparison with other peridomestic species that may eventually invade dwellings in endemic areas of southern South America (e.g., Lent and Wigodzinsky, 1979; Canale et al., 2000; Wisnivesly-Colli et al., 2003).

Specifically, the aims of this study are (1) to examine whether the blood meal source and the amount of blood ingested influenced different reproductive parameters and the life span of the female in *T. infestans*, (2) to look for the existence of a relation between female age with fecundity in *T. infestans*, (3) to examine the existence of a relation between the number of matings and the life-span with fecundity in *T. infestans*.

2. Materials and methods

2.1. Insects

T. infestans bugs were collected as fifth instar nymphs from two peridomestic structures of the Capital department of San Luis province, Argentina in April 2010. Peridomestic environment usually includes a wide array of structures, such as goat and pig corrals; chicken coops and storerooms. In northern Argentina, these ecotopes are very frequently infested mostly by *T. infestans* and other Triatominae species (Canale et al., 2000; Cecere et al., 1997, 2002).

Nymphs were taken to the laboratory, maintained at a temperature of $26 \pm 1\,^{\circ}C$, $60 \pm 10\%$ relative humidity and a photoperiod of 12:12 h (light:dark). Bugs fed regularly (15 days) on pigeon *Columba livia* until molt. Once molted to adult stage they were weighed, separated by sex and left without feeding until blood meals were completely digested. To determine this, we followed the methodology of the "shape of the stomach" proposed by Catalá de Montenegro (1983). Once, previous meals were completely digested we offered the first feeding and immediately we constituted the couples.

Both females and males were assigned haphazardly to one of the following two groups. Group 1: couples of adults regularly fed once every 15 days on guinea pig *Cavia porcellus*. Group 2: couples of adults regularly fed once every 15 days on pigeon *Columba livia*. Nineteen couples for group 1 and twenty for group 2 were followed until death. Couples were held in cylindrical glass vials. The females were weighed on the day of imaginal molt and before and after feeding to know the quantity of blood ingested in adult stage.

Twice a week we registered, on all the 41 couples, the following variables: number of eggs laid (fecundity), number of eggs hatched (fertility) and the number of spermatophores (number of matings). Moreover, we registered the days between the first feeding and the initiation of mating and oviposition. The number of reproductive weeks and life-span in adult stage for each female was also registered. These variables allowed us to calculate: the conversion of blood to eggs (mg blood/egg).

2.2. Data analysis

We tested the assumptions of normality for all traits included in analysis using the Shapiro–Wilks test. We performed one-way ANOVA to determine whether reproductive parameters and life-span vary between blood meal sources (guinea pig and pigeon). Lineal regressions were used to analyze the relationship between the quantity of blood ingested with the number of matings and fecundity for the two blood meal sources. To test whether reproduction is costly for females, lineal regression analysis was also performed between life-span and fecundity. We also used lineal regression to test the relation between the number of matings and fecundity.

3. Results

Independently of the blood meal source, female initial weight was 264.03 ± 57.65 mg and fed on average 1106.69 ± 438.66 mg of blood. The number of matings, fecundity, fertility and the conversion of blood to eggs showed significant differences between bugs fed on guinea pigs than those fed on pigeons (Table 1). All these parameters has highest values for those bugs that fed on guinea pigs except for the blood to egg conversion that exhibit a smallest value, i.e., need a lower amount of blood to form an egg (Table 1). On the other hand, the initiation of copula and oviposition did not show significant differences between feeding sources (Table 1). It is interesting to note that bugs that fed on guinea pigs present a lower life-span than those that fed on pigeons, although this difference was only marginally significant (Table 1).

The number of matings and fecundity increased linearly and significantly with the quantity of blood ingested for both the females fed on guinea pigs and those fed on pigeons (Fig. 1).

Both females that feed on guinea pigs and those that feed on pigeons started oviposition during the fifth week in adult stage and after the first feeding (Fig. 2). Oviposition along adult stage showed a relatively regular pattern for females fed on both meal sources (Fig. 2). It is interesting to notice that a few weeks before they died, and for both meal sources, there was a peak in the number of eggs laid that then declines sharply. The maximum reproductive effort was observed in weeks 23 and 24 for guinea pigs and week 30 for pigeons (Fig. 2). During these weeks a female laid on average 23 ± 4.3 eggs and 23.67 ± 8.17 for guinea pigs and pigeons respectively (Fig. 2). These weeks, of maximum reproductive effort, did not show significant differences in the number of eggs laid between blood meal sources ($F_{(1,23)} = 0.032$; $p = 0.95$). The number of reproductive weeks matches with the life-span, since females laid eggs until death. Feeding showed an irregular pattern along adult life for both meal sources (Fig. 2) and this could be due to the fact that in many cases although we offered meal sources, they did not feed.

Results from lineal regression between life-span and fecundity showed a positive and significant relation for both meal sources (Fig. 3). Moreover, when the number of matings was regressed with the fecundity, there was a positive relation for both meal sources but was significant only for guinea pig ($y = 4.18 + 0.04x$, $p = 0.0018$; $y = 6.07 + 0.02x$, $p = 0.212$ for guinea pig and pigeon respectively).

4. Discussion

It is known that in Triatominae blood meal is essential for eggs formation. This has been reported not only for *T. infestans* but for other Triatominae species (e.g., Friend et al., 1965; Schofield, 1982; Wigglesworth, 1936). When *T. infestans* fed on pigeons, it was seen

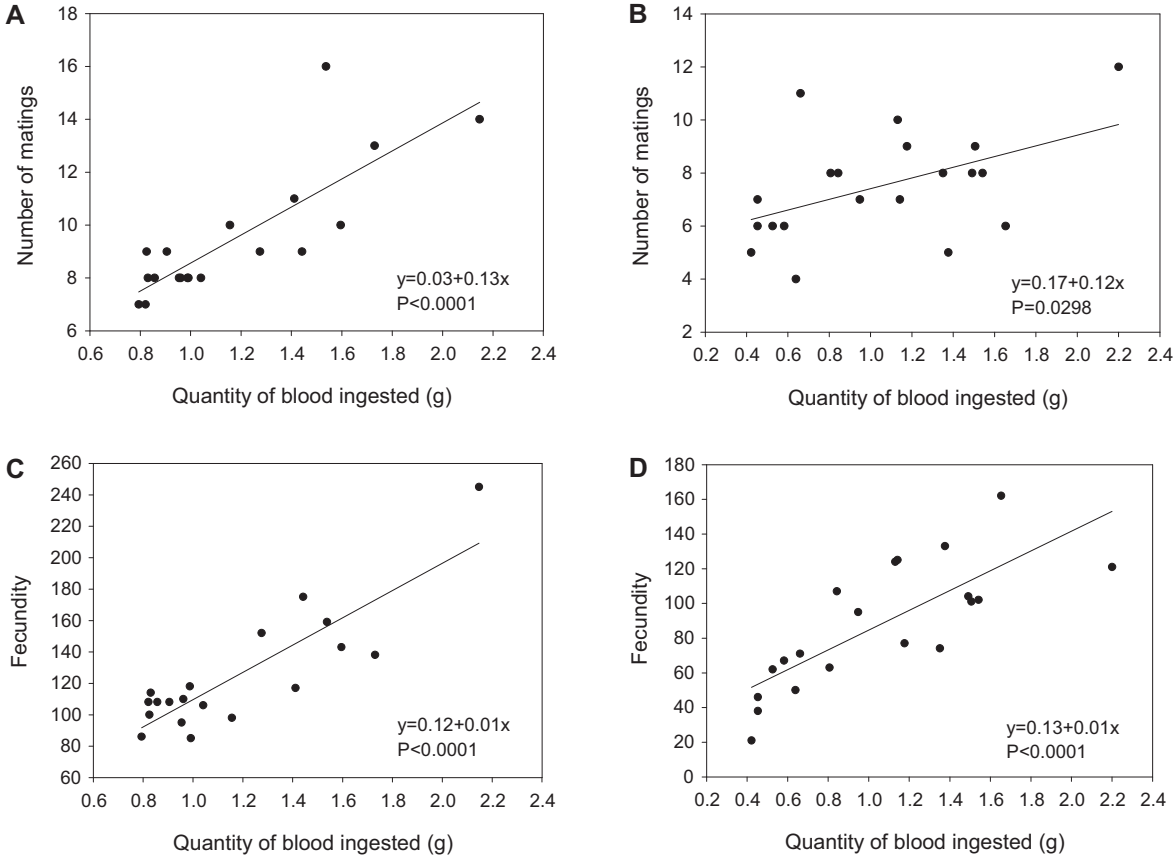

Fig. 1. Relationship between the quantity of blood ingested with the number of matings and fecundity for *Triatoma infestans* fed from two different sources. **A** and **C**: Guinea pig. **B** and **D**: pigeon.

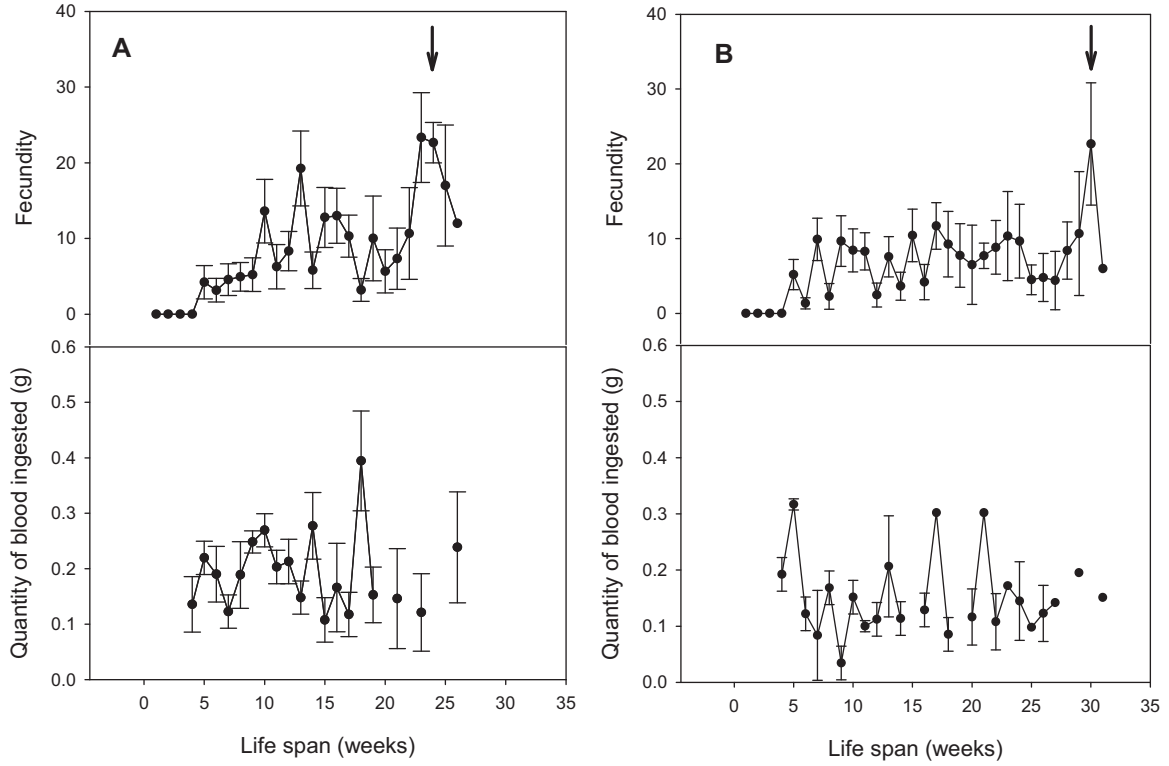

Fig. 2. Oviposition rhythm and quantity of blood ingested across life in adult stage for females of *Triatoma infestans* fed from two different sources. **A**: guinea pig. **B**: pigeon. Arrows indicate the maximum reproductive effort for each blood meal source.

Table 1
Reproductive parameters and life-span for couples of *Triatoma infestans* fed from two different sources. ANOVA test was conducted to compare, for the different variables, the two meal sources. The days before the initiation of copula and oviposition were calculated from the first feeding in the adult stage.

Variables	Blood meal source		ANOVA between blood meal sources
	Guinea pig $x \pm SD$	Pigeon $x \pm SD$	
Initiation of copula (days)	12.74 ± 7.94	12.60 ± 8.79	$F_{1,38} = 0.00$; $p = 0.957$
Number of copulas	9.47 ± 2.44	7.50 ± 2.04	$F_{1,38} = 7.56$; $p = 0.009$
Initiation of oviposition (days)	24.37 ± 16.55	25.05 ± 13.53	$F_{1,38} = 0.02$; $p = 0.889$
Fecundity	124.47 ± 38.25	87.15 ± 36.14	$F_{1,38} = 9.82$; $p = 0.003$
Fertility	0.89 ± 0.06	0.77 ± 0.09	$F_{1,38} = 25.90$; $p = 0.000$
Female initial weight (mg)	278.95 ± 48.83	249.85 ± 62.89	$F_{1,38} = 2.59$; $p = 0.116$
Total blood ingested (mg)	1171.53 ± 377.51	1045.10 ± 491.57	$F_{1,38} = 0.81$; $p = 0.375$
Conversion of blood to eggs (mg blood/egg)	9.47 ± 1.63	12.33 ± 3.66	$F_{1,38} = 9.77$; $p = 0.003$
Life-span (days)	115.32 ± 15.57	137.65 ± 55.06	$F_{1,38} = 2.90$; $p = 0.097$

that an increment in fecundity was related with the quantity of blood ingested (Catalá de Montenegro, 1989). Our results support those found by Catalá de Montenegro (1989) not only when females fed on pigeons, but also, for those that fed on guinea pigs. This means that, in *T. infestans*, independently of the food source offered in adult stage, a greater blood meal results in a higher fecundity.

In *T. infestans*, the food reserve brought from the last nymph state is determinant of the first oviposition (Asin and Crocco de Ayerbe, 1989). Moreover, when adult molt occurs with a deficient nutritional status, females should have a blood ingestion to achieve a basic weight so that the ovary begins to produce eggs (Asin and Crocco de Ayerbe, 1989). In this study, when bugs molt to adult state, we left without feeding until blood meals were completely digested. This methodology was applied because we want to know the influence of the nutritional status (both in quality and in quantity) on different reproductive parameters and not the influence of the reserves brought from fifth instar. In this sense, the data obtained in this research on the reproductive parameters of *T. infestans* are difficult to compare due to the differences in methodologies used in this and other studies. Results found in this study showed that fecundity, fertility and the conversion of blood to eggs were influenced by the blood meal source. For this species, Guarneri et al. (2000) did not find differences in these parameters but, they did not wait until blood meals, brought from fifth instar, were completely digested. This would imply that, when considering only the nutritional status in adult stage, the blood meal source will influence differently some reproductive parameters.

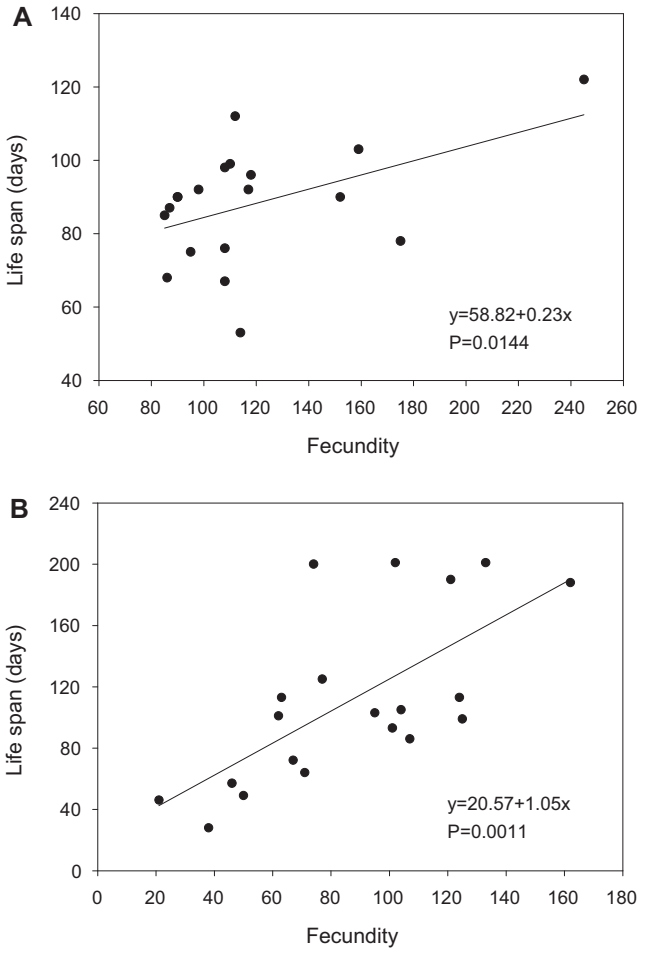

Fig. 3. Relationship between fecundity and the life-span in females of *Triatoma infestans* fed from two different sources. **A**: guinea pig. **B**: pigeon.

The fact that this species showed differences in the conversion of blood to eggs when the feeding sources were compared means that females feeding on pigeons need more blood to produce an egg. That may reflect a low efficiency of conversion of blood to egg for females feeding on pigeons. These results are consistent with those reported for Triatominae by Braga et al. (1999), Diotaiuti and Dias (1987), Gomes et al. (1990) and Guarneri et al. (2000) that suggest that mammal's blood has a higher nutritional quality. It has been described that bird blood contains a higher concentration of DNA than that of mammals, because of its nucleated blood cells. The catabolism of nucleic acid and the resulting excretion of uric acid probably require an increased energy consumption that may also influence reproductive parameters of bugs fed on pigeons (Lehane, 1991).

We found a positive relation between the quantity of blood ingested and the number of matings, independently of the meal source. This means that, as for the number of lay eggs, the amount of blood ingested also affects positively the number of matings. It is known that in Triatominae, nutritional status can affect mating occurrence by modulating the motivation of bugs to copulate (Lima et al., 1986; Malo et al., 1993; Manrique and Lazzari, 1994; Pires et al., 2004). For example, in other Triatominae like *Triatoma brasiliensis*, nutritional status affects the receptivity of females (Vitta and Lorenzo, 2009). On the other side, as was describe above, the quantity of blood ingested affected the number of matings positively, also, blood meal source affected the number of matings being higher when bugs fed on guinea pigs.

Results showed that a greater amount of blood ingested implies a higher number of matings and a high fecundity lay independently of the feeding sources. Moreover, the number of reproductive weeks is coincident with the life-span for much of the bugs included in this study. The result of a positive correlation between fecundity and adult life-span demonstrates that there is probably no cost of reproduction on life expectancy in *T. infestans*. However, as was proposed by Reznick (1985) the best way to assess the cost of reproduction in any species is to measure genetic correlations or correlated responses to selection in life history variables. For

Rhodnius prolixus, Sulbaran and Chaves (2006) found that life expectancy in adults is negatively correlated with gross fecundity, indicating a cost of reproduction.

In this study, we examined whether the quantity and the quality of the blood ingested influenced different reproductive parameters (fecundity, fertility and number of matings). Our data illustrate how, independently of blood meal source, the amount of blood ingested affected fecundity and the number of matings. While females feeding on guinea pig showed higher fecundity and fertility, and needed a lower amount of blood to form an egg, other parameters like initiation of copula, and initiation of oviposition did not show significant differences between blood meal sources. Furthermore, results from this study reveal that oviposition is regular all along female life and that the number of mating and life-span influence positively the fecundity in *T. infestans.*

Studies done on reproductive aspects of *T. infestans* were performed on bird blood meal (pigeon or chicken) rather than on mammal blood meal (e.g., Asin and Crocco de Ayerbe, 1989, 1992; Catalá de Montenegro, 1989; Catalá et al., 1992; Giojalas and Catalá, 1993) and most of them showed evidence of the high potential of this species as vector of Chagas disease. Results found on this research, showed an increase in the reproductive success when bugs fed on mammal blood, thus confirming the efficiency and vectorial capacity of this species. Under natural conditions it would be a selective advantage to this species to develop mechanisms which avoided a restriction on its reproductive success by careful choice of hosts (Lehane, 1991). Moreover, this study reinforces previous findings in other blood-sucking species that found that insects feeding on mammal blood showed an increase in their reproductive capacity (Hocking, 1971; Lehane, 1991). This species is mainly adapted to human dwelling and peridomestic structures where there is low host diversity. Considering that this species is in contact with mammals over other food sources, a greater reproductive success may result from an adaptation to this environment.

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