Life History Traits and Demographic Parameters of *Triatoma infestans* (Hemiptera: Reduviidae) Fed on Human Blood

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ABSTRACT *Triatoma infestans* (Klug, 1834) (Hemiptera: Reduviidae), the main vector of Chagas disease in South America, feeds primarily on humans, but ethical reasons preclude carrying out demographical studies using people. Thus, most laboratory studies of *T. infestans* are conducted using bird or mammal live hosts that may result in different demographic parameters from those obtained on human blood. Therefore, it is of interest to determine whether the use of an artificial feeder with human blood would be operational to rear triatomines and estimate population growth rates. We estimated life history traits and demographic parameters using an artificial feeder with human blood and compared them with those obtained on live hens. Both groups of *T. infestans* were kept under constant conditions [28 ± 1°C, 40 ± 5% relative humidity, a photoperiod of 12:12 (L:D) h] and fed weekly. On the basis of age-specific survival and age-specific fecundity, we calculated the intrinsic rate of natural increase (r), the finite rate of population growth (λ), the net reproductive rate (R_o), and the mean generation time (T_g). Our results show differences in life history traits between blood sources, resulting in smaller population growth rates on human blood than on live hens. Although demographic growth rate was smaller on human blood than on hens, it still remains positive, so the benefit/cost ratio of this feeding method seems relatively attractive. We discuss possibility of using the artificial feeder with human blood for both ecological and behavioral studies.

KEY WORDS life table, vital statistics, blood meal source, Chagas disease, kissing-bugs

Chagas disease, caused by the protozoan *Trypanosoma cruzi*, affects about 8 million people from southern South America to Mexico (World Health Organization 2013). The main route of transmission of *Try. cruzi* to humans is mediated by kissing-bugs (Hemiptera, Reduviidae, Triatominae). *Triatoma infestans* (Klug, 1834) is the most important vector of Chagas disease in South America due to its wide geographic distribution and its capacity to attain high domiciliary densities (Zeledón and Rabinovich 1981). The most frequently infested ecotopes by *T. infestans* are domiciles and storerooms and, to a smaller extent, chicken coops and corrals of animals such as goats, pigs, and cows (Gurevitz et al. 2011), although there are also some records of sylvatic populations (Cortez et al. 2007, Gurevitz et al. 2011, Buitrago et al. 2013). Like many other species of triatomines, *T. infestans* shows an eclectic food habit with a wide range of hosts both wild (e.g., birds, rodents, and possums) and domestic (e.g., dogs, cats, and humans) (Rabinovich et al. 2011). Domestic animals such as dogs and cats act as reservoirs of *Try. cruzi*, whereas hens only contribute to bug population growth since they are not susceptible to infection (Cohen and Gürtler 2001, Gürtler et al. 2007).

It is well known that the food source depends on the ecotope, host availability, among other factors. A food niche breadth analysis for 30 triatomine species showed that human blood ranked among the five top species of feeding source (Rabinovich et al. 2011). These authors showed that *T. infestans* feeds primarily on humans (38.1%) and to a lesser extent on hens (23.3%), based on 13 cases of food preferences of four combinations of habitats from three countries. Buitrago et al. (2013) found that in Bolivia, feeding of *T. infestans* on human blood is relatively frequent (28%) even under sylvatic conditions. More recently, Gürtler et al. (2014) found that *T. infestans* inhabiting domiciles feed primarily on human blood (68.2%), which shows the importance of human blood as food source in domestic populations on this triatomine species. Nevertheless, most laboratory studies on triatomines, in general, and *T. infestans*, in particular, are conducted using live hosts as hens, pigeons, and mice for rearing (Marti et al. 2013). This procedure is operationally complicated and difficult to standardize, and may result in an estimation of demographic parameters quite different from those obtained when fed on human blood. Since life history traits

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affect population growth rates and population bug density (Schofield 1980), the estimation of triatomine life history traits under different specific sources of blood is relevant.

Several studies have analyzed the effects of the blood meal source and the feeding process on mortality and fecundity (de Souza Garcia et al. 1975, Lima Gomes et al. 1990, Braga et al. 1998, Guarneri et al. 2000, Nattero et al. 2012), as well as on mean development time (Cabello et al. 1987, Martínez-Ibarra et al. 2003) of various triatomine species, and particularly for *T. infestans*, those effects were analyzed by Guarneri et al. (2000) and Nattero et al. (2011). Since mammal blood has a lower DNA content than bird blood, we would expect a decreasing metabolic cost and an increasing energetic efficiency in triatomines when fed on the former than on the latter (Lehane 2005). We would also expect that triatomines fed on human blood show differences in development time, stage-specific mortality, and female fecundity when compared with those fed on bird blood, and in consequence, we expect to find differences between population growth rates. To our knowledge, there is only one study on Rhodnius neivai (Lent, 1953) that compared life history traits and demographic parameters of a triatomine species feeding on mammal and bird blood (i.e., rabbits and hens) (Cabello et al. 1988). Nevertheless, no studies have addressed the relationship between blood meal sources and population demographic parameters for *T. infestans*.

Currently, the most common feeding practice in triatomine insectaries is based on live hens and on pigeon or mice (Marti et al. 2013). Triatomines can feed on live hosts under fairly normal conditions with the host supplying all of the necessary signals such as heat gradients, CO_2, and various volatile signals, to elicit feeding, and the insects also receive unadulterated sterile blood in its freshest form. However, the major disadvantages of using live hosts are that they must be maintained, which is expensive in money, time, and space; restraining the hosts and applying feeding cages is time consuming and consequently hard to do on a large scale; the diet cannot easily be altered by the addition or subtraction of substances; and some of the hosts can develop resistance to feeding as was reported on rabbits (Hill et al. 1976).

Additionally, as mentioned earlier, feeding triatomines on live hosts make control and standardization of breeding conditions difficult when compared with the use of artificial feeders (Nuñez et al. 1996). The use of artificial feeders offers several advantages over the use of live hosts, since it is cheaper and it avoids host maintenance circumventing ethical concerns related to the well-being of live hosts when exposed to the triatomines and the need to house the live hosts in a government-approved animal care facility (Huebner et al. 1994, Issmer et al. 1994). Additionally, artificial feeders facilitate the control of diet composition to identify the function of chemicals on development performance (Friend and Smith 1977, Lima Gomes et al. 1990). Therefore, the use of an artificial feeder with human blood may be an alternative method for demographic studies and laboratory rearing of *T. infestans*.

For these reasons, the main goal of this work is to investigate whether the use of an artificial feeder to feed *T. infestans* on human blood may be adequate in terms of population growth rates, for both rearing and research. To address this goal, we compared life history traits and associated population growth rates of *T. infestans* under two feeding conditions: an artificial feeder with human blood and the classical procedure of feeding on live hens. We discuss our results in the light life history traits and demographic parameters of triatomines.

Materials and Methods

Origin of the Population. A second laboratory generation of a *T. infestans* population was used; the parental insects were collected from a chicken coop from the locality of Pinedo, Chaco Province, Argentina (−27° 07′42″ −61° 30′45″).

Experimental Procedures. Ninety 0–48-h-old first-instar nymphs (nymphs I) were the base of a cohort study; they were divided into two groups (cohorts) of 45 nymphs each which were kept in 0.5-liter jars covered with a nylon mesh and provided with vertically placed strips of paper as resting places. Both cohorts were followed-up collectively and simultaneously and maintained under constant conditions [28 ± 1°C, 40 ± 5% relative humidity, a photoperiod of 12:12 (L:D) h]. The feeding was offered weekly for 40 min.

One cohort (called group HuB) was fed using an artificial feeder (Marti et al. 2015) with human blood, free of infection (*Try. cruzi*, human immunodeficiency virus, HTLV, brucellosis, hepatitis, and syphilis) and containing Adenine–Dextrose–Phosphate–Citrate as anticoagulant. The blood was provided by the *Instituto de Hemoterapia* of the city of La Plata (Argentina) from stocks discarded for human transfusions because of the volume of each unit was exceeded, which affects the optimal concentration of anticoagulants required for human safety. The human blood discarded from blood center was maintained at a temperature of 4°C and was replaced weekly.

The other group (called group HeB) was fed on live hens, immobilized in a wooden box, following the ethics guidelines for biomedical research from our institution, based on resolution No. 1047 (2005) of the National Scientific and Technical Argentinean Research Council. In both groups, and immediately after each feeding occasion, the number of individuals with different degree of abdominal stretching was recorded; this was done qualitatively using only two categories: individuals that fed to repletion (i.e., fully engorged, showing a convex abdomen) and unfed individuals (i.e., a flat or concave abdomen). Individuals that showed an incompletely filled abdomen were considered as unfed individuals.

Both groups were checked weekly for mortality and ecdysis until the death of the last individual. Sex ratio and the total number of laid and hatched eggs were recorded after the cohorts produced the adult stage. As both groups were followed collectively (i.e., not

individually), we recorded the date and the total number of individuals that 1) entered a given stage, 2) died in that stage, and 3) molted to the next stage; these data were used as input for life table calculations (Deevey 1947). The proportion of hatched eggs produced by the females of the cohort was used to estimate mortality at the egg stage and to calculate the number of initial eggs of each group that was initiated with 45 nymphs I.

Statistical Analyses. Weekly mortality records were used to calculate survival from the first day at the nymph I stage as a function of age (l_x); the number of eggs laid weekly was used to calculate the age-specific fecundity (m_x), by dividing total number of eggs laid each week (x) by the number of individuals alive at the end of that week. The l_x and m_x schedules allowed the estimation of demographic parameters such as the intrinsic rate of natural increase (r), the finite rate of population growth (λ), the net reproductive rate (R_o), and the mean generation time (T_g); complete definitions of these parameters and the formulae used for their calculation are given in the Appendix of Rabinovich and Nieves (2011). For each demographic parameter, we also estimated the confidence interval at the 95% significance level based on 1,000 bootstrap samples by random resampling with replacement from the initial individuals of each group. The bootstrap method is appropriate to estimate demographic parameter uncertainties and particularly useful for small cohorts with high early mortality (Alvarez-Buylla and Slatkin 1991). These calculations were carried out using a computer program developed in our laboratory in Delphi Language, which was previously tested on a triatomine life table study (Medone et al. 2012). Statistical comparison of demographic parameters and fecundity was carried out with the t-student test, and power t-test analyses were performed with $\beta = 0.95$. We estimated the duration of the reproductive period as the difference between the average age at last reproduction (ω) and the average age at first (α) reproduction. For each group, we estimated the cumulative oviposition pattern (M_x) standardized as percentage, by calculating the proportion of eggs laid each week as $M_x = \frac{\sum_{x=\alpha'}^{\omega'} E_x}{M}$, where E_x is the total number of eggs laid by the cohort during week x, M is the total number of eggs laid during the lifetime of the cohort, and where α' and ω' are the first and last oviposition ages of the cohort, respectively. To facilitate the comparison between both groups, we expressed M_x in relation to a standardized reproductive period (i.e., we scaled each reproductive week with respect to the total amount of reproductive weeks from α' to ω' and expressed it as percentage). We estimated the weekly average female fecundity ($\overline{F_x}$) as the total number of eggs laid per week divided by the total number of females alive at the end of that same week; and we estimated the average number of eggs laid per female per lifespan ($\overline{F_T}$) as the total number of eggs laid by the cohort divided by the total number of females produced by each cohort.

Table 1. Proportion of fully engorged individuals of *T. infestans* fed on human blood (group HuB) and fed on hens (group HeB)

Stage	Group HuB		Group HeB		*P* chi-square
	N	Fully engorged (%)	*N*	Fully engorged (%)	
Nymph I	152	82.24	92	72.83	0.1145
Nymph II	180	90.56	57	92.98	0.7696
Nymph III	232	68.97	101	89.11	0.0002*
Nymph IV	284	84.86	102	93.14	0.0495*
Nymph V	404	82.18	285	84.91	0.3994
Male	147	64.63	280	72.86	0.0984
Female	169	56.21	214	68.22	0.0209*

N, accumulated number of individuals in a given stage that were offered a meal during the time they were found in that stage. Fully engorged (%): ratio between *N* and the accumulated number of individuals alive (i.e., fed and unfed) during the time they were found in that stage.

*Significant differences between the HuB and HeB groups (<0.05).

To roughly determine whether any of the two methods was inadequate in the feeding process, we compared the proportion of fully engorged individuals in each nymphal stage between groups using a chi-square test for two independent samples. The proportion of fully engorged individuals was estimated for each stage based on individuals-observation units. That is, after each feeding, we recorded the total number of individuals alive at every stage and how many of them were fully engorged (convex abdomen). The individuals that not showed a convex abdomen were considered as unfed individuals. Then, we added the total amount of fully engorged individuals among observation units (i.e., for each stage, we added all fully engorged individuals among all feeding events), and then divided this quantity by the total amount of individuals-observation units (i.e., the total number of individuals alive offered a feeding during the whole duration of the cohort).

We also carried out an elasticity analysis of the finite rate of population increase (λ), for that purpose we converted the age-specific survival (l_x) and the fecundity (m_x) schedules into a Leslie matrix using the spreadsheet utility PopTools (http://www.poptools.org/, accessed 3 September 2015). The mean development time was tested for normality with the Shapiro test using the R software (R Core Team 2012): if normality was not rejected (i.e., P value Shapiro test > 0.05), we used the t-student test to compare groups, whereas if normality was rejected, we used the Mann–Whitney test. The significance of a departure from a 50% sex ratio and the stage-specific mortality among groups were tested using the chi-square test for two independent samples. These statistical analyses were performed using MedCalc, version 12.7.5 (MedCalc 2013).

Results

The proportion of fully engorged individuals was significantly different between groups only in the nymph III, nymph IV, and female adult stages (Table 1). The

Table 2. Stage-specific development time (DT) and mortality (*M*) of *T. infestans* fed on human blood (group HuB) and on hen blood (group HeB)

Stage	Group HuB				Group HeB			
	N	DT (weeks)	Lower–upper 95% CI	*M* (%)	*N*	DT (weeks)	Lower–upper 95% CI	*M* (%)
Egg	55	2.1*	1.5–2.7	18.2	57	2.3*	1.7–2.9	21.1
Nymph I	44	3.4*	3.2–3.6	2.2	45	2.7 *	2.5–2.9	0.0
Nymph II	43	4.3*	3.8–4.7	2.3	44	2.2 *	2.1–2.4	2.2
Nymph III	41	5.7*	5.3–6.0	4.6	43	2.6 *	2.3–2.8	2.3
Nymph IV	36	6.7*	4.9–8.4	12.2**	43	2.7 *	2.4–3.0	0.0**
Nymph V	22	9.6	7.6–11.6	38.9**	38	7.0	6.4–7.7	11.6**
Egg to NV	22	29.2*	25.7–32.7	60.0**	38	18.9*	17.9–20.0	33.3**
Males	11	16.3	13.5–19.1	—	24	15.1	10.8–19.4	—
Females	11	17.4	15.0–20.0	—	14	19.8	15.6–23.9	—

N, number of individuals that completed each stage. DT, average development time of immature stages and adult lifespan (wk). Lower–upper 95% CI: limits for a confidence level of 95%. *M*: stage-specific mortality (%). Note: the number of eggs for life table analyses was estimated (see Materials and Methods) as 55 and 57 for group HuB and group HeB, respectively.

*Significantly different between groups ($P < 0.05$, Mann–Whitney test).

**Significantly different between groups ($P < 0.05$, chi-square test).

Table 3. Reproductive traits of *T. infestans* fed on human blood (group HuB) and hen blood (group HeB)

Reproductive trait	*N*	Group HuB	CV%	*N*	Group HeB	CV%
Average eggs laid per female per reproductive week ($\overline{F_x}$)	31[a]	3.68	64.98	41[a]	3.79	77.8
Average number of eggs laid per female per lifespan ($\overline{F_T}$)	11[b]	63.45	40.32	14[b]	72.5	32.02
Average age at first reproduction (α, wk)	11[b]	31.73*	26.26	14[b]	20.7*	15.43
Average age at last reproduction (ω, wk)	11[b]	46.45*	14.45	14[b]	38.4*	28.66
Average reproductive period ($\omega - \alpha$, wk)	11[b]	15.73	37.19	14[b]	18.6	47.21

CV%, coefficient variation as percentage.

[a] Total number of reproductive weeks in each group (*N*).

[b] The total number of emerged females (*N*).

*Significantly different between the HuB and HeB groups ($P < 0.05$, *t*-student test).

greatest difference was observed for nymph III: the proportion of fully engorged individuals was 20% lower in group HuB (i.e., fed on human blood) than in group HeB (i.e., fed on hens). The proportion of fully engorged adult females was significantly lower in group HuB (56%) than in group HeB (68%). For both experimental groups, all nymphal stages show a proportion of fully engorged individuals above 68%, whereas adult stage shows values above 56%.

The mean development time for all nymphal stages was significantly longer in group HuB than in group HeB ($P < 0.05$, Mann–Whitney test), except for nymphs V (Table 2). The average lifespan of males and females was not significantly different between groups ($P = 0.713$, Mann–Whitney test).

The stage-specific mortality of nymphs I, II, and III was not significantly different between groups ($P > 0.0574$,chi-square test); for nymphs IV and V, it was higher in group HuB than in group HeB ($P = 0.01$, chi-square test) (Table 2). Total accumulated mortality from egg to nymph V was significantly higher in group HuB (60.0%) than in group HeB (33.3%) ($P = 0.008$, chi-square test). Nevertheless, the egg-hatching rate was not significantly different between groups ($P = 0.885$, chi-square test) (Table 2).

The main reproductive features for both groups are summarized in Table 3. The two indicators used for fecundity ($\overline{F_x}$ and $\overline{F_T}$) were not significantly different between groups ($P = 0.865$, *t*-test). Nevertheless, there was a high coefficient variation and a low sample size, and the power *t*-test was low, indicating that for a power of $\beta = 0.95$, we could detect differences only greater than 40%. The total number of eggs laid by the group HuB was 698, whereas group HeB laid 1,015 eggs. Both groups showed a similar standardized cumulative oviposition pattern as a function of the standardized reproductive period (Fig. 1). The average age at first (α) and last reproduction (ω) were significantly larger for group HuB than for group HeB, with a statistical power (with $\beta = 0.95$) that permits to detect differences of at least of 20%. The average duration of the reproductive period was not significantly different between groups ($P = 0.355$, *t*-test). For both groups, the sex ratio (♀ : ♂) was not different from the expected 50% ($P > 0.05$, chi-square test). The difference of the sex ratio between groups was not statistically significant ($P = 0.467$) (Table 3). All demographic parameters (r, R_o, λ, and T_g) were significantly different between groups (Table 4), with population growth rates smaller and a mean generation time higher in the group HuB than in the group HeB.

For both groups, the survival elasticity was dominant during the prereproductive period, whereas the fecundity elasticity was dominant during the reproductive period. The survival elasticity shows a similar pattern between both groups (constant during the prereproductive period and decreasing during the reproductive period), with higher values in group HeB

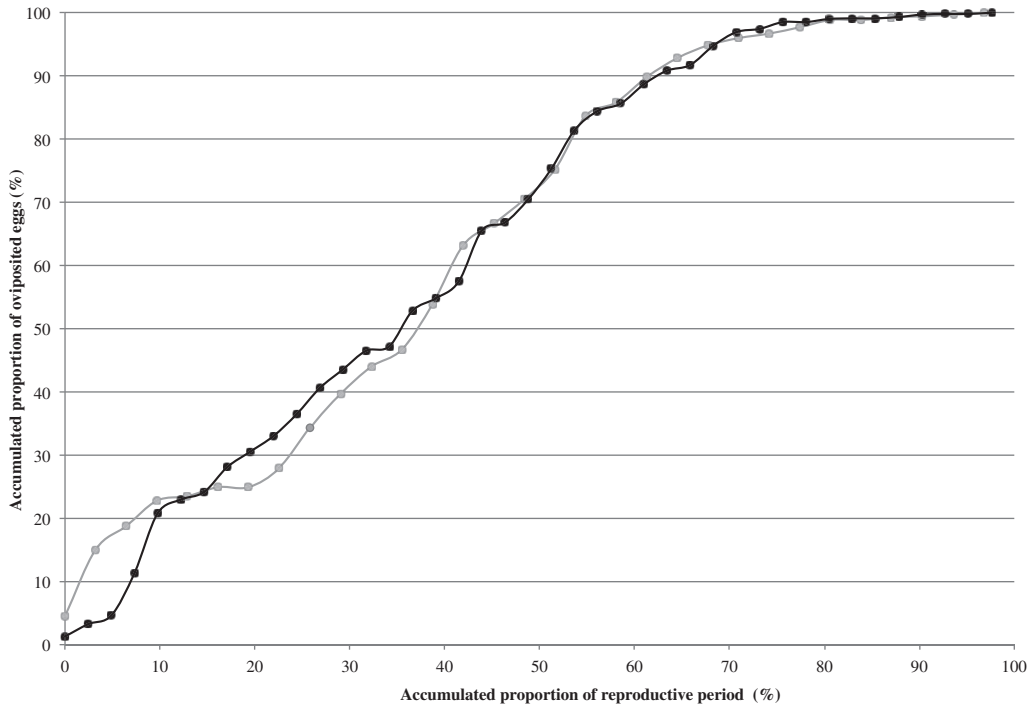

Fig. 1. Cumulative oviposition pattern (M_x) in percentage of *T. infestans* fed on human blood (black line) and hens (gray line).

Table 4. Demographic parameters of *T. infestans* fed on human blood (group HuB) and hen blood (group HeB)

Demographic parameter	Group HuB		Group HeB	
	Avg	Lower–upper 95% CI	Avg	Lower–upper 95% CI
Mean generation time (T_g)	36.97*	35.94–37.64	32.93*	32.87–32.93
Net reproductive rate (R_o)	12.71*	12.56–12.87	17.90*	17.74–18.07
Intrinsic rate of natural increase (r)	0.0611*	0.0606–0.0615	0.1058*	0.1055–0.1062
Finite rate of population increase (λ)	1.0630*	1.0625–1.0634	1.1117*	1.1112–1.1121

All time units in weeks. Lower–upper 95% CI: confidence interval limits at the 95% level.
*Statistically significant differences between the HuB and HeB groups ($P \leq 0.05$, chi-square test for two independent samples).

than in group HuB. The fecundity elasticity also shows a similar pattern between groups, with an almost equal maximum peak, though delayed with age in group HuB with respect to group HeB (Fig. 2).

Discussion

The artificial feeder using human blood offers several advantages over the use of live hosts (see the Introduction). However, no study has assessed whether an artificial feeder is efficient in terms of population growth rates for triatomine laboratory rearing. Our results show differences in life history traits between the two feeding methods resulting in smaller population growth rates feeding on the artificial feeder with human blood than feeding on live hens. However, despite being smaller, the growth rate still remains positive, so the use of the artificial feeder to analyze either the effect of chemical composition of the diet or the amount and quality of ingested blood on reproductive aspects seems relatively attractive. We discuss below in detail the life history traits with respect to the feeding methods.

Development Time. The life history trait of *T. infestans* most affected by the artificial feeder using human blood was the preadult development time (29.2 wk when compared with 19.0 wk when fed on live hens). Various studies have shown that there is a large variability in development times of triatomines depending on the blood meal source (Lima Gomes et al. 1990; Guarneri et al. 2000; Aldana et al. 2001, 2005; Nattero et al. 2013). The general pattern indicates that triatomine development time decreases on individuals fed on mammal blood (e.g., mice and guinea pigs) when compared with individuals fed on bird blood (e.g., hens and pigeons).

T. infestans developed faster when fed on mice than on pigeons (Guarneri et al. 2000); this might be explained due to a 30 times lower concentration of

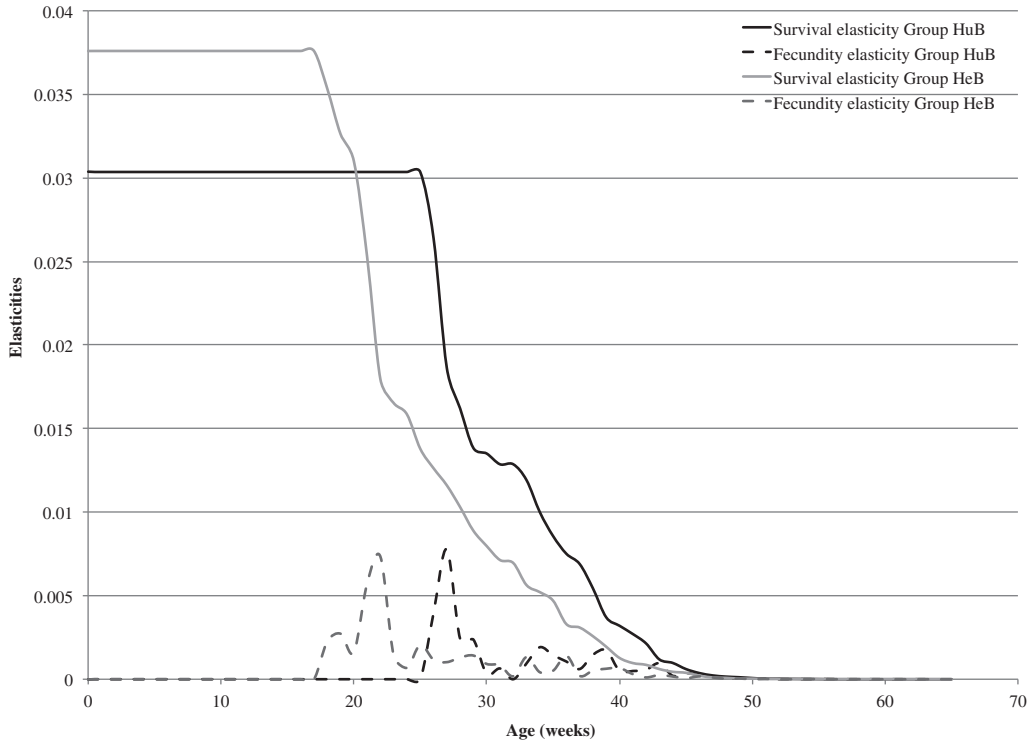

Fig. 2. Elasticity of the age-specific survival (full lines) and the age-specific fecundity (dotted lines) for *T. infestans* fed on human blood (black lines) and hens (gray lines).

DNA of mammal blood when compared with bird blood (0.136 and 4.216 g/100 ml, respectively), which in turn decreases the catabolic cost due to the lower amount of uric acid that must be excreted (Lehane 2005). Nevertheless, the results of our study show the opposite, so it seems that other factors (e.g., mechanical obstacles or inhibitions to feed adequately on the artificial feeder, and effectiveness of chemical clues) may be involved in the increase in the development time of *T. infestans* fed on human blood (see Influence of the Artificial Feeder). Since the Adenine–Dextrose–Phosphate–Citrate anticoagulant present in the human blood has never been used previously to feed triatomines, further analyses are required to study its possible effect on triatomine life history traits and demographic parameters.

Preadult Mortality, Adult Fecundity and Adult Lifespan. *T. infestans* fed on human blood showed a significant increase in the preadult mortality and decreasing but not significant female fecundity compared to live hens. These results (i.e., increasing pre adult mortality and decreasing fecundity) are in agreement with those reported for *Triatoma maculata* (Erichson, 1848) feeding on human blood when compared with live hens (Torres et al. 2010). Although these authors found significant differences between fecundity, we failed to find statistical differences possibly due to the low power of our test. However, no significant differences in female fecundity of *T. infestans* fed on different blood sources (i.e., mice and pigeons) were previously reported by Guarneri et al. (2000), which seems to be in agreement with our results.

Interestingly, in our study, the increased age at first reproduction in the group fed on human blood with the artificial feeder had no consequence on the duration of the reproductive period. That is, the increase in preadult development time represents only a shift in the starting and ending reproductive ages, which suggests no metabolic or somatic cost during the preadult stages. Nevertheless, the low statistical power of the comparison of reproductive parameters between cohorts does not allow to state strong conclusions about the effect of blood source on female fecundity. Therefore, further studies are required to determine the influence of human blood on the reproductive performance of *T. infestans*.

Our results showed no significant differences in adult lifespan between groups fed on artificial feeder with human blood and live hens. Female lifespan when fed on live hens (138.6 d) was similar and slightly larger than those reported in literature: 114.8 d (Rabinovich 1972) and 133 d (Nattero et al. 2011). Furthermore, female lifespan of *T. infestans* feeding on human blood (119 d) in our study was similar to that reported for *T. infestans* feeding on guinea pig (115 d) (Nattero et al. 2011).

Influence of the Artificial Feeder. Several studies have used artificial feeders to rear triatomines for scientific research (Harington 1960, Langley and Pimley 1978, Núñez and Lazzari 1990). It has been pointed

out that the lower population performance (e.g., longer development times, lower survival, and lower fecundity) of triatomines feeding on artificial feeders could be related to mechanical effects of the artificial feeders (Nuñez and Segura 1987). For example, Chiang and Chiang (2010) showed for *Rhodnius prolixus* (Ståhl, 1859) that feeding efficacy is reduced using an artificial membrane and demonstrated that the efficiency of turning the blood meal into eggs is also significantly reduced.

Our results seem to be in accordance with those previously reported by De Isola et al. (1980) for *T. infestans* feeding on an artificial feeder with hen blood. These authors showed that *T. infestans* had twice the preadult development time when fed on artificial feeder than when fed on a live hens, as well as a higher variability in the stage-specific development time. Additionally, these authors observed a decrease in female fecundity in individuals fed on the artificial feeder with respect to those fed on live hens. Based on the great similarity between our results and those obtained by De Isola et al. (1980), it seems likely that effects of the artificial feeder *per se* has increased the development time of *T. infestans*, as claimed by Schaub and Jensen (1990).

Demographic Parameters. The two feeding methods resulted in smaller population growth rates in the group fed with the artificial feeder using human blood when compared with the group fed on live hens. This result goes against the expectation based upon the lower DNA content in mammal blood than in bird blood (which for a blood feeder implies a decreasing metabolic cost and an increasing energetic efficiency; Lehane 2005). Aldana et al. (2001) showed that insects of the species *R. prolixus* fed only on human blood plasma did not complete their nymphal development, those fed only on human blood red cells reached the third nymphal instar, while individuals fed on whole blood completed successfully their life cycle. Hence, we put forward the hypothesis that the mechanical and other negative effects of the artificial feeder have counter balanced the positive effect of human blood with respect to live hens.

Previously, Cabello et al. (1988) found significant differences in the adult lifespan of *R. neivai*, the total number of laid eggs and population growth rates (r and R_o) between individuals fed on mammal and bird blood. Nevertheless, these authors showed no differences in the age at first reproduction (α) as well as the finite rate of population increase (λ) and the generation time (T_g) were observed between both blood sources. These heterogeneous effects of blood sources on life history traits and demographic parameters observed for *R. neivai* (Cabello et al. 1988) and for *T. infestans* in our work confirm the importance of the effects of the artificial feeder as a device affecting the performance of triatomines.

Nonetheless, the aforementioned effects are difficult to generalize for the response to the artificial feeder seems to be species specific in triatomines: Aldana et al. (2001) found that *Rhodnius pictipes* (Ståhl, 1872) never accepted feeding on an artificial feeder with human blood, but readily accepted to initiate feeding on the arm of the researchers, while this was not observed for other three species of *Rhodnius* under the same experimental conditions: *R. prolixus*, *R. neivai*, and *Rhodnius robustus* (Larousse, 1927). Our results could not separate the relative influence of the effects of the human blood from the effects of the artificial feeder on life history traits of *T. infestans*. Analyses of the relative effects of these two factors should be carried out using noninfected bugs and human volunteers such as has been previously done with disease vector mosquitoes (Epstein et al. 2007).

Despite population growth rates were smaller with the artificial feeder using human blood when compared with live hens, we did not observe any trade-off impinging on fitness among the life history traits here analyzed. This result is not surprising since even using the artificial feeder, the population growth rate stays positive, suggesting that the energetic conditions were not restrictive enough to produce detectable trade-offs. However, with the artificial feeder, we can investigate the possible trade-offs in comparing life history traits between a limiting and a nonlimiting energetic feeding resource, since in general, trade-offs are detected only under limiting conditions (Roff 1992, Stearns 1992). In consequence, we suggest that future research should investigate the relationship between traits under two feeding conditions: low quality and quantity versus high quality and quantity of the blood used.

To conclude, because of the lower demographic performance of *T. infestans* with the artificial feeder using human blood and the risk of getting infected from human blood manipulation (Schmuñis et al. 2000, Blejer et al. 2002, Flichman et al. 2014), we consider that our method is an appealing alternative only for specific purposes where the chemical composition of the diet needs to be controlled but not for mass rearing. Although the artificial feeder showed various advantages with respect to live hosts (e.g., the population growth rate remains positive, preserved human blood is cheap-even costless-, it avoids ethical concerns related to the use and maintenance of a live host, and it avoids the need to harbor live hosts in the laboratories and/or in a government-approved animal care facility), we discourage the routinely use of human blood to laboratory rearing of *T. infestans* due to the risk of getting infected from human blood manipulation (Zou et al. 2012, Medina 2014, Bruhn et al. 2015).

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