

Vital Statistics of Triatominae (Hemiptera: Reduviidae) Under Laboratory Conditions: IV. *Panstrongylus geniculatus*

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ABSTRACT A cohort of 100 eggs of *Panstrongylus geniculatus* (Latreille) was reared in the laboratory under constant conditions (temperature $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH), with mortality and fecundity data recorded weekly. We calculated stage-specific development times, age-specific mortality and fecundity (18.4 eggs/♀/wk), and stage-specific and total preadult mortality (31.6%), and the weekly intrinsic rate of natural increase ($r_0 = 0.096$), the finite population growth rate ($\lambda = 1.109$), the net reproductive rate ($R_0 = 60.45$), and the generation time ($T = 46.34$ wk). Elasticity analysis showed that the dominant life-history trait determining λ was survival (particularly the adult female's survival). Adult females dominated the stage-specific reproductive value, and the egg stage dominated the stable stage distribution (SSD). The damping ratio ($\rho = 1.096$) suggests a relatively rapid period of recovery to a disturbed SSD. Results were compared with one previous study and conform relatively well, considering that environmental conditions were not the same. We estimated the colonizing ability of *P. geniculatus*, using as a criterion the *ro/b* index, and obtained the value of 0.74, an indicator of a good colonizer, and similar to well-known invasive species such as *Rhodnius prolixus* and *Triatoma infestans*. The life history traits and demographic parameters here presented for *P. geniculatus* are discussed in terms of their usefulness for evolutionary studies and vector control activities.

RESUMEN Una cohorte de 100 huevos de *Panstrongylus geniculatus* (Latreille) fueron seguidos de manera simultánea en el laboratorio bajo las condiciones constantes (temperatura $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ HR), registrándose semanalmente la mortalidad y la fecundidad. Estimamos los tiempos de desarrollo por estadios (tiempo total = 39,4 semanas), estadísticas vitales (mortalidad y fecundidad específica por edades, y por estadios), y parámetros de crecimiento poblacional: la tasa intrínseca de crecimiento natural ($r_0 = 0,096$), la tasa finita de crecimiento poblacional ($\lambda = 1,109$), la tasa de neta de reproducción ($R_0 = 60,45$), y el tiempo generacional ($T = 46,34$ semanas). El análisis de elasticidad indica que la supervivencia, especialmente la de la hembra adulta, domina la determinación de λ , y además tienen el mayor valor reproductor por estadios, aunque la fase del huevo dominó la distribución estable de estadios (DEE). La tasa de amortiguación ($\rho = 1,096$) sugiere un período relativamente rápido de recuperación a una DEE si la misma fuera perturbada. Los resultados se compararon con un estudio previo y se encontró una concordancia satisfactoria, considerando que las condiciones ambientales no eran idénticas. Estimamos la capacidad colonizadora de *P. geniculatus*, en base al índice *ro/b*, obteniendo 0.74, indicando que se trata de una buena colonizadora, muy similar a dos especies muy conocidas por su alta capacidad de colonización: *Rhodnius prolixus* and *Triatoma infestans*. Se discuten los rasgos de historias de vida y los parámetros demográficos de *P. geniculatus* en cuanto a su utilidad en estudios evolutivos y actividades de control vectorial.

KEY WORDS Chagas, triatomines, population parameter, colonization, life-history trait

With this paper, we continue a series of publications with the life history features (life cycle, reproduction, and mortality) and population parameters (population

growth rates, age-specific reproductive values, stable stage distribution) of triatomine species (Heteroptera, Reduviidae). The previous three articles covered the species *Triatoma infestans* (Rabinovich 1972), *Triatoma maculata* (Felicciangeli and Rabinovich 1985), and *Rhodnius neglectus* (Rabinovich and Nieves 2011). Here we analyze a *Panstrongylus geniculatus* (Latreille 1811) cohort, and provide results similar to the ones presented for *R. neglectus*, providing statistical information about the demography of another triatomine species under controlled laboratory conditions, and using the most recent analytical methodologies developed in

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animal and plant demography. Absolute and relative variation of demographic parameters are particularly important in the analysis of the competition outcome among different triatomine species, thus contributing to explain triatomine species coexistence and diversity in a given habitat; they are also important for applications in the laboratory (e.g., to optimize the design of colony rearing of triatomines) and in the field (e.g., to design an optimal vector control strategy). The quantitative analysis of life-history traits, and particularly the population growth parameters, is also related to the geographic dispersal of triatomines, so it will find application in the epidemiology of Chagas disease; additionally, those parameters are also related to their potential geographic ranges in the face of global climatic changes.

The genus *Panstrongylus* is composed by 13 species, and it is the triatomine genus with the largest geographical distribution in the American continent; this is so in particular for the species *P. geniculatus*, which has been found in Argentina, Bolivia, Brazil, Colombia, British Guiana, Costa Rica, Dutch Guiana, Ecuador, French Guiana, Nicaragua, Panama, Paraguay, Peru, Surinam, Trinidad and Tobago, Uruguay, and Venezuela (Dujardin et al. 2000). Rocha Leite et al. (2007a) provide more recently confirmed records of this species in Brazil, and Patterson et al. (2009) present a comparative summary of the biology, ecology, and epidemiological significance for each species in the genus *Panstrongylus*. *P. geniculatus*, based on the map given in Carcavallo et al. (1999), ranges between 21.1° N, 30.3° S, 38.8° E, and 94.9° W, and covers an area estimated in over 12 million km², which is characterized by an extremely variable environment, showing the high plasticity of this species: it is found at altitudes from sea level to over 4,000 masl (in the Colombian and Venezuelan Andes range), in places with almost nil annual average precipitation to over 9,000 mm, and with mean minimum and maximum annual temperatures (averaged from its whole range) between -3.9 and 34.3°C, respectively. Rocha Leite et al. (2007b) established that the most important variables determining the occurrence of *P. geniculatus* were terrain slope variability, isothermality, and annual precipitation, while altitude, temperature seasonality, maximum temperature of warmest month, temperature annual range, annual precipitation seasonality, precipitation of wettest quarter and of driest quarter were not significant.

This wide geographical distribution and its concomitant exposure to a variety of environmental conditions is probably the cause of the high phenotypic variability expressed by *P. geniculatus* in different areas, as shown by principal components of 25 morphological characters of specimens from the states of Aragua and Trujillo (Venezuela; Torres et al. 1997). Despite this morphological plasticity the genus *Panstrongylus* is often defined by a relatively constant character: a short head with antennal insertions closer to the eyes than found in most other South American species and more similar to the North American species of the genus *Triatoma*; the various species of the genus *Panstrongylus* are also often seen to cluster genetically with the North

American *Triatoma* (Schofield and Galvao 2009); however, since all species of *Panstrongylus* occur in South America this has been assumed to reflect a lack of resolution in the phylogenetic analyses (Hypsa et al. 2002, Marcilla et al. 2002). The basal *Panstrongylus* species may have been represented by *P. rufotuberculatus* or *P. geniculatus*, both of which are widespread species reported from Central America and southern Mexico, and Schofield and Galvao (2009) have postulate that the ancestral meso-American forms of this genus may have spread southwards after the joining of the isthmus of Panama, reaching a geographical bifurcation due to the northern part of the Andean Cordillera.

P. geniculatus is a relatively common sylvatic triatomine species, found in a variety of vegetation types—closed and open broad-leaved evergreen trees, herbaceous and shrubs sparse vegetation, broad-leaved deciduous woodland, broad-leaved and needle-leaved evergreen closed to open thickets, needle-leaved and broad-leaved evergreen closed to open trees, following the vegetation classification of Eva et al. (2004); however, the dominant vegetation type where *P. geniculatus* is found is the broad-leaved evergreen closed to open forest (48.1%), followed by cultivated and managed areas with natural and seminatural vegetation (closed to open shrubland and herbaceous vegetation; 25.6%). As to the microhabitat proper, *P. geniculatus* is mainly associated with caving animals such as the armadillo (*Dasypus novemcinctus*), but also with porcupines, mice, rat, guinea pig, opossum, and bat species (Lent and Jurberg 1969). For these characteristics this species is considered one the main elements maintaining the sylvatic transmission cycle of *Trypanosoma cruzi* (Pifano 1986); e.g., Molinari et al. (2007) found *T. cruzi*-infected *P. geniculatus* in bat-inhabited caves in Cueva del Guano, in the Paraguaná Peninsula, Venezuela, confirming the known role of cave-dweller bats as reservoir hosts of *T. cruzi* and part of the sylvatic cycle of *T. cruzi* through *P. geniculatus*.

An analysis of the reproductive performance of *P. geniculatus* was made by Esteban and Angulo (2011a), and of the life cycle of this species by Galíndez Girón et al. (1997). However, only Cabello and Galíndez (1998) carried out a complete vital statistics analysis and estimation of demographic parameters of *P. geniculatus*; no other life table and population parameters' estimates have been made, except for the work of Rodríguez Morales (1978), a non-published Master's thesis. Here we present the results of a cohort study of *P. geniculatus* and our estimates of its life table and population parameters, with their variability and population growth rate sensitivity to life history traits.

Materials and Methods

Population Origin. The population of *P. geniculatus* used in this study was collected in Venezuela, although its precise geographical origin is unknown, and was reared in the laboratory for at least four generations, at the School of Health Sciences, University of Carabobo, Maracay, Venezuela.

Experimental Procedures. The experiment was carried out in Valencia, Venezuela, in a climatic room with constant temperature ($26 \pm 1^\circ\text{C}$) and humidity ($60 \pm 10\%$ RH) conditions. Photoperiod did not need to be controlled for at the latitude of Valencia its seasonal variation is very small (day length in December is 11:30h, and in June is 12:40h). The details of the experimental design and procedures can be found in Rabinovich and Nieves (2011). Hens were used for feeding with a weekly schedule, and the feeding time was 30 min. This feeding on restrained hens can be considered adequate (almost optimal) for *P. geniculatus* based on the well-known fasting capacity of most triatomine species, which is consistent with the fact that after 9 d of starvation insects of this species had stabilized their weights (Esteban and Angulo 2011b). All aspects of this research adhered to the protocols for animal care and use of laboratory animals given by CONICET (National Scientific and Technological Research Council of Argentina), and are consistent with the AVMA (American Veterinary Medical Association) Guidelines (<https://www.avma.org/KB/Policies/Documents/euthanasia.pdf>) (accessed 25 February 2015).

Statistical Analyses. A description of the methods of analysis can be found in Rabinovich and Nieves (2011), and particularly in their Appendix where definitions and formulae are given; the original equations and the conceptual basis of these methods are available in Birch (1948) and Fisher (1930). As in our experimental design (a group cohort) it was impossible to connect offspring with their parents (anonymous reproduction), so we used a simplified method to calculate the fecundity of an individual in the adult stage per unit of time: we divided total eggs produced in a given time period by all adult individuals alive in that same time period. The life table information (l_x and m_x) was also analyzed in the form of a Leslie matrix (Caswell 2001); see Rabinovich and Nieves (2011) as well as Ebert (1999) and Caswell (2001) for the methodology and the properties of population matrices. The elasticity analysis, and the damping ratio (ρ), as well as μ_1 were calculated from the Leslie matrix using PopTools, an Excel tool developed by Greg Hood (<http://www.cse.csiro.au/poptools/>). We also converted the age-structured matrix into stage-structured matrix, and were used to estimate the stage-specific reproductive values, the stable stage distribution, the damping ratio (ρ), as well as μ_1 ; however, they were not used to calculate population growth parameters, because of the bias that results from the information loss mainly in the grouping of all female adult ages into only one single stage.

Calculations were carried out with a special computer program (TV; Rabinovich and Nieves 2011) that uses bootstrap to estimate confidence intervals of some of the life history and demographic parameters. As the cohort was not followed individually but as a batch of individuals, it was not possible to resample directly for bootstrapping; so we developed a procedure that generated “virtual” individuals, following the FIFO rule (“First In, First Out”) method, as proposed by Fargo

(1986), which implies applying the arbitrary (and probably biologically questionable) rule that the first “virtual” individuals leaving a stage were also the first “virtual” individuals arriving to that stage (there is no way of verifying this assumption in a batch type cohort). The confidence limits obtained by this procedure mean that if we were to repeat this cohort study under the same experimental conditions and design (but always starting with one hundred eggs), we could expect that approximately in every 20 replications of the cohort experiments there would be one in which it would be outside the confidence limits of our original cohort. The TV program, although only with an interface in Spanish, is available under request from the first author.

Results

Vital Statistics. The survival and maternity curves of *P. geniculatus* are given in Figure 1. Table 1 provides a statistical summary of life-cycle statistics. Average time from oviposition to egg hatching was quite long for a triatomine: almost 4 wk; the development time of all instars oscillated between 4 and 8 wk, and was not extremely variable (coefficient of variation remained between 25 and 40%, except for instar 5 that was 50%). The sex-ratio ($\frac{\text{♀}}{\text{♂} + \text{♀}}$) when entering the adult stage favored females: however, the value was 0.476, not statistically different from 0.5 ($p = 0.1741$).

Mortality per instar follows the usual pattern in triatomines of a high mortality in the younger stages; in *P. geniculatus* stages I, II and III account for approximately 60% of the total mortality from egg to adult. However, instar II shows the highest mortality rate (23.3%). About 42% of all initial eggs of the cohort arrived to the adult stage. In general the l_x curve shows a relatively steep slope up to the instar I, a quite gentle decrease during the instars II, III and IV, and another abrupt drop during instar V (Fig. 1); survival remained stable for several weeks after becoming imagoes, as if

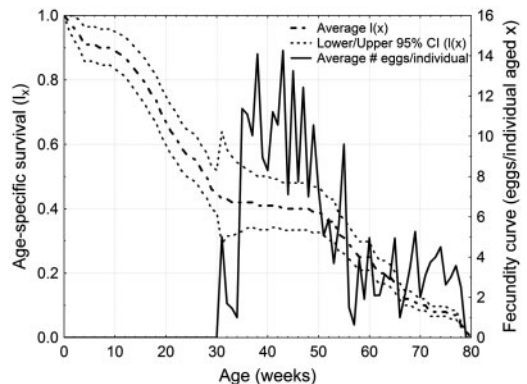


Fig. 1. Weekly age-specific survival (proportion surviving from the beginning of the egg stage to age x) and age-specific maternity curve (average eggs laid/individual/wk) of *P. geniculatus*. The dashed curves are the 95% confidence intervals of the survival curve from a bootstrap resampling with $N = 1000$.

Table 1. Average development time, mortality by stage, reproductive features, and sex-ratio of *P. geniculatus*

Development time (wk)					Mortality (%) ^a		
Stage	N	Avg.	Lower 95% CI	Upper 95% CI	Avg.	Lower 95% CI	Upper 95% CI
Egg	91	3.87	3.8	3.94	7.8	6.99	8.61
Instar I	86	6.58	6.21	6.95	9.24	8.31	10.17
Instar II	66	8.32	7.75	8.89	7.98	7.14	8.82
Instar III	54	8.39	7.5	9.27	2.08	1.54	2.62
Instar IV	48	4.08	3.68	4.49	1.52	1.02	2.02
Instar V	42	8.14	6.94	9.35	7.88	5.20	10.56
Egg to adult	42	39.38	38.61	44.72	31.6	28.88	34.32
♂ longevity	22	25.59	24.31	26.87			
♀ longevity	20	16.45	14.66	18.24			

Reproduction							
Reproductive statistics	N	Avg.	Lower 95% CI	Upper 95% CI	Reproductive performance		
Reproductive weeks/♀	20	16.25	14.3	18.2	Reproductive weeks by cohort	47	
Eggs/indiv./wk	48	5.7	4.6	6.8	Total eggs laid by cohort	6045	
Eggs/♀/life	20	302.25	240.84	363.66	1st reproductive week of the most precocious ♀	31	
Eggs/♀/wk	318	18.37	18.05	18.70	Last reproductive week of the most long-lived ♀	78	
♀ eggs/♀/wk	318	9.19	9.02	9.35	Cohort's reproductive period (wk)	47	
Week of first reproduction by cohort	20	43.45	38.58	48.32	Sex ratio	0.48	

^a Relative mortality within each stage i (N_i / N_{i-1}), where N is the number of individuals entering each stage. Sex-ratio [$\frac{\text{♀}}{\text{♂} + \text{♀}}$] was determined at time of adult emergence; reproductive features were based on a number of observations given by the number of reproductive weeks or the number of weeks-individuals.

with the last molt a severe mortality risk had been overcome; after those few weeks adult females showed a fairly linear age-specific schedule of survival. The average female's adult longevity was 16.5 wk while the adult males attained 25.6 wk of life. The probability of remaining alive in the same stage and of molting alive to the next stage as estimated from the stage-specific matrix (see below under the "Population growth parameters" subsection heading): 0.734 and 0.242 for the egg, 0.850 and 0.142 for instar I, 0.880 and 0.092 for instar II, 0.874 and 0.103 for instar III, 0.753 and 0.219 for instar IV, and 0.869 and 0.114 for instar V, respectively. The adult had an average weekly probability of survival of 0.953.

Figure 1 also shows the age-specific schedule of oviposition expressed as number of eggs/individual/wk. The general pattern can be considered as unimodal, even if very irregular; and the bell-shape is relatively similar to the one of other triatomine species, peaking shortly after entering the adult stage, at about an age of 40 wk from the egg stage in the case of the *P. geniculatus* cohort.

Table 1 also provides a statistical summary of the reproductive characteristics of the females of *P. geniculatus*. The age of first reproduction of the cohort (which represents the most precocious individual) is a very important parameter in population dynamics, and resulted in 31 wk from the egg stage. On average a female laid eggs at a rate of 9.19 (CI: 9.02–9.35) ♀ eggs/wk/♀, and the reproductive period of an average female was 16.25 (CI: 14.3–18.2) wk after the start of reproduction.

Population Growth Parameters. The main population growth parameters and stage-specific demographic features of *P. geniculatus* are given in Table 2.

The net reproductive rate (R_0) indicates that, on average, 60.45 (CI: 44.12–77.70) eggs will replace each egg in the population in the course of one generation, being the generation time $T = 46.34$ wk (CI: 45.48–47.25 wk).

We show below the stage-specific projection matrix. The diagonal represents the stage-specific probability of survival per week, and the subdiagonal represents the probability of surviving and molting to the following stage, also per week; if both probabilities do not add to one, the difference (not shown) represents the per week probability of dying within a given stage. The right-most cell of the first row of the projection matrix represents the fecundity (in number of eggs laid per individual per wk).

Egg	N1	N2	N3	N4	N5	Adult
0.734	0	0	0	0	0	5.78
0.242	0.850	0	0	0	0	0
0	0.142	0.880	0	0	0	0
0	0	0.092	0.874	0	0	0
0	0	0	0.103	0.753	0	0
0	0	0	0	0.219	0.869	0
0	0	0	0	0	0.114	0.953

Figures 2 and 3 show the stable stage distribution (SSD) and the stage-specific reproductive values of *P. geniculatus*, calculated from the stage-structured matrix created from the l_x and m_x curves. The SSD is

Table 2. Demographic and population growth parameters of *P. geniculatus*

Population growth parameter	Avg.	Lower 95% CI	Upper 95% CI
Finite rate of population increase (λ)	1.109	1.090	1.111
Intrinsic rate of natural increase (r_0)	0.096	0.086	0.105
Net reproductive rate (R_0)	60.45	44.12	77.70
Generation time (T)	46.34	45.48	47.25
Instantaneous birth rate (b)	0.130	0.127	0.165
Instantaneous mortality rate (d)	0.035	0.034	0.044

All parameters were calculated from the age-structured life table and based upon a 1-wk time unit. Confidence intervals (CI) were estimated from a 1,000 resampling bootstrap.

Table 3. Results of the elasticity analysis of the life history cycle components of *P. geniculatus* and their effect on its finite rate of population growth (λ) based upon the Leslie matrix, and expressed as stages by accumulating the elasticity values over each stage using the average development time of each instar, in weekly time units

Matrix element description	Matrix element value	Matrix element elasticity
Adult female longevity (wk)	45.16	0.344
Proportion of eggs hatched	0.922	0.104
Proportion molting alive from instar I to II	0.908	0.090
Proportion molting alive from instar II to III	0.920	0.113
Proportion molting alive from instar III to IV	0.979	0.102
Proportion molting alive from instar IV to V	0.985	0.117
Proportion molting alive from instar V to ♀	0.921	0.174
Fecundity (average ♀ eggs/♀/wk)	7.224	0.047

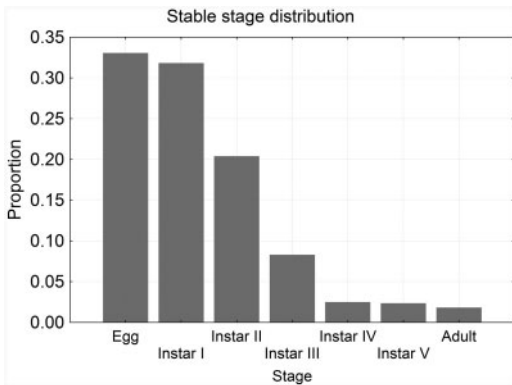


Fig. 2. Stable stage distribution of a *P. geniculatus* based on the l_x and m_x , and calculated by considering the average development time of each stage.

dominated by eggs, followed by the other stages in the form of a classical age pyramid. The adults are the ones with the highest reproductive value, followed by instar V. The estimation of μ_1 was 59.6 wk (CI: 57.0–62.3), very close to the value estimated for R_0 (60.45), as theoretically expected. The average damping ratio (ρ) was 1.096, indicating that, if perturbed from the SSD, it would return to it rather rapidly.

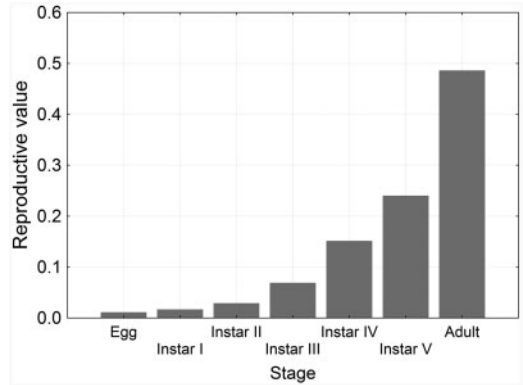


Fig. 3. Stage-specific reproductive value of *P. geniculatus*, based on the l_x and m_x , and calculated by considering the average development time of each stage.

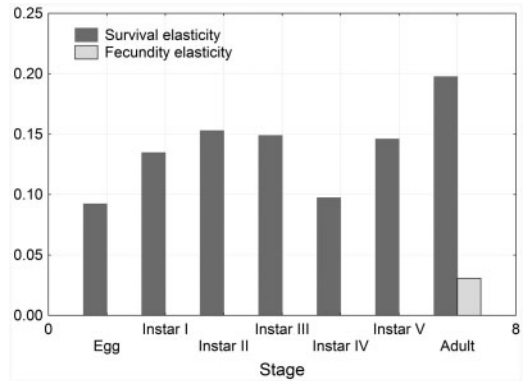


Fig. 4. Elasticity of finite rate of population growth (λ) of *P. geniculatus* to stage-specific fecundity and survival.

Elasticity Analysis. Figure 4 shows the elasticity of the finite rate of population growth (λ) to stage-specific fecundity and survival. Elasticity shows a clear dominance of the influence of survival on λ , particularly during the adult stage (the reproductive period) as compared with the elasticity of the fecundity (Table 3).

Discussion

Most of our results can only be compared with those published by Cabello and Galíndez (1998), keeping in mind the caveats stated in Rabinovich and Nieves (2011) when comparing life table results from different laboratories. In this particular case the environmental conditions are quite similar (except for the feeding time), making the results relatively comparable.

Esteban and Angulo (2011a) found that fecundity of a Colombian *P. geniculatus* laboratory-reared population was twice as large than a first generation sylvatic (forest) population (both fed on hens): 2.2 eggs/♀/day for the laboratory-reared population and 1.1 eggs/♀/day for the field population. Our results of 4.7 eggs/♀/day double the laboratory-reared values of Esteban and

Angulo (2011a), and as a possible explanation is based on the number of generations under laboratory rearing or (most plausible) to the different origin of the *P. geniculatus* population (Colombia and Venezuela).

Galíndez Girón et al. (1997) carried out a study on the life cycle of *P. geniculatus* in Venezuela, and their results show little similarity with our own. The development time was shorter than ours in the egg and the first two stages (3.6, 5.3, and 4.4 wk, respectively), while longer in the last three stages (10.3, 5.6, and 10.2 wk) and the adults (10 wk for both sexes). Differences range between -40 to 60%. We believe that the environmental conditions may explain these differences, for Galíndez Girón et al. (1997) had maintained the cohort under uncontrolled temperature (between 21 and 25°C), much higher relative humidity (90–100%), and most important of all, although they also fed the triatomines weekly on hens, the feeding time was “ad libitum,” while our cohort was fed weekly for only 30 min. Galíndez Girón et al. (1997) also estimated the mortality rate per stage during the development of *P. geniculatus*, and the discrepancy was even higher, for their cohort showed smaller mortality rates in all stages (except instar 3), with relative differences between -65 and 100%. We believe that the same reasons that may explain the differences in development time also may explain the differences in stage-specific mortality.

Cabello and Galíndez (1998) analyzed a cohort (initiated with 63 aged 0–48-h-old eggs) that was kept in a climatic chamber at $26 \pm 3^\circ\text{C}$ and $90 \pm 10\%$ RH, and fed on hens every 15 d, during 30 min. These eggs were obtained from a colony founded by a single female collected in a human dwelling in the area of San Jacinto, located in the city of Trujillo, Trujillo State, Venezuela. The results of these authors show some differences with our own, with lower development times, except for instar 3, but that compensate among them in such a way that they result having a similar total preadult development time; total mortality from the egg to the adult (23.8%) is significantly smaller than our results, but also the reproductive effort is lower (9 eggs/♀/wk for Cabello and Galíndez (1998) than our results (31.6% and 18.37 eggs/♀/wk, respectively). However, interestingly indeed, the estimation of the demographic parameters of Cabello and Galíndez (1998) showed small differences (with rather slightly higher values) as compared to our results (e.g., a higher finite rate of population increase (λ) of 1.13 vs ours of 1.109, and a net reproductive rate (R_0) of 89.4 vs ours of 60.45, but a lower generation time (T) of 36.1 wk vs ours of 46.34 wk, respectively); these differences and life history trait compensations are supported by the relative differences in the instantaneous birth and mortality rates (b and d) that were 20 and 10% higher for the former and the latter, respectively, when comparing Cabello and Galíndez (1998) and our own results. We believe that these differences are the result that the cohort of Cabello and Galíndez (1998) had been fed every 15 d, as compared to our weekly feeding regime (all other environmental factors being almost identical).

Cabello and Galíndez (1998) consider that *P. geniculatus* has a low population natural increase as well as a

low net reproductive rates, a long generation time, and a small general reproductive output, and conclude that this species is a K strategists, and so less likely than other species to become a significant household Chagas disease vector. We do not agree with this conclusion for, if we use the index ro/b as a colonizing species criterion (Rabinovich 1974), the larger the ro/b ratio, the larger the mean survival time of the population, which indicates a better colonizing species; the ro/b ratio of our results and those of Cabello and Galíndez (1998) are 0.74 and 0.77, respectively, while the well-known invasive species *R. prolixus* and *T. infestans* have a quite similar ro/b ratio of 0.74 and 0.65, respectively.

Elasticity analysis provides information about the relative sensitive of the finite population growth rate (λ) to changes in the age-specific elements of a Leslie transition matrix (or the elements in a stage-specific matrix). It is particularly useful in providing insight into which life history components should be under the most intense evolutionary selective pressure or, from a disease insect vector management point of view, which life history traits should be the main targets for population control (Ebert 1999). While the use of R_0 as a measure of fitness gives erroneous results, the population growth rate (λ) is an accepted measurement of fitness (Caswell 2009); how λ changes with changes in a trait a_i , that is, $\delta\lambda/\delta a_i$, has been called the “selective pressure” on that trait (Rabinovich and Nieves 2011) and, being a partial derivative, it is also called the sensitivity of λ to changes in a_i . As the elements a_i of a projection matrix usually have different units, the different contributions of the traits a_i to λ are better measured by their elasticity, which is a sort of proportional sensitivity, and defined as $e_i = (a_i/\lambda)(\delta\lambda/\delta a_i)$ (Caswell 2001). The elasticity of the life-history traits of *P. geniculatus*, as given in Figure 4, show a clear dominant contribution to λ by the survival components as compared to the fecundity component. The implications of these results for chemical pest control are important; e.g., Reyes et al. (2011) showed that fifth instars of *P. geniculatus* have a nine-fold higher resistance to deltamethrin than first instars (the lethal dose for 50 ng/insect was 9.9 (95% CI 8.4–11.4) for the former and 0.11 (95% CI 0.08–0.14) for the latter); our reproductive value results (see Fig. 3) and the elasticity analysis (see Fig. 4) indicate that the fifth instar is the stage that has the highest stage-specific reproductive value and the one with the highest elasticity, so deltamethrin effects seem inefficient for it is most effective with the least important stages from a population growth point of view. Thus our results may be used as guide in the search of triatomine pesticides that are more effective with the stages with the highest reproductive value and elasticity.

The damping ratio (ρ) is related to the period of recovery to a stable age distribution (SAD) or to a stable stage distribution (SSD) if a new population is being established or if a populations' age or stage distribution has been disturbed. To convert that ratio into a calendar value we have to specify the time required (t_x) for the contribution of the second root (λ_2) of a Leslie matrix to a reduction of a certain multiple (x) of the dominant root (λ_1). A decline of, say, 5% of that of the dominant

root implies calculating t_{20} ($x = 1/0.05 = 20$). Caswell (2001) shows that t_x can be estimated by $t_x = \ln(x)/\ln(\rho)$. As the value of the damping ratio for *P. geniculatus* was $\rho = 1.1$ (a value almost identical to the one calculated for *R. neglectus*, see Rabinovich and Nieves 2011), t_{20} becomes 24.5 wk (about 172 d). This is a relatively fast recovery period of a SAD/SSD, although it depends on the doubtful assumption that the vital rates remain constant during that recovery period.

Our results impinge on a species that has shown increasing evidence of domiciliation. Although it has been recorded that *P. geniculatus* is attracted by lights and enters all kind of houses, there is an important debate about how this process takes place: if this species "invades the cities" or if suburban sprawl towards sylvatic areas that conserve mammal caves harboring *P. geniculatus* may best explain for the new contact between people and this typically sylvatic triatomine species. Our results on the demographic potential of *P. geniculatus* and our estimate of its invasive characteristic (as measured by the *ro/b* index, see above) justifies a deeper discussion of the domiciliation process in *P. geniculatus*. Pifano (1986) collected in Venezuela 349 specimens of *P. geniculatus* mostly captured in houses, and 135 (38.9%) were infected *T. cruzi*. Comparable evidence is available from Colombia: *P. geniculatus* was found infected with *T. cruzi* in human habitations in the municipality of Amalfi, Antioquia, Colombia (Wolff and Castillo 2002), who also found that the displacement of *P. geniculatus* toward the houses was not determined exclusively by electric light since 24% of the houses lacked electricity, and ecological changes and housing conditions probably favor the distribution of this species. There is also clear indication that *P. geniculatus* is not just a "visitor" but a colonizer of houses: Reyes-Lugo and Rodriguez-Acosta (2000) found 20 specimens *P. geniculatus* that were associated with the presence of *Rattus rattus*, which were living in a cavity inside one house in Hoyo de la Puerta, Miranda state, Venezuela; they captured adults and all nymphal stages as well as eggs, a clear indication of effective colonization. In a blood feeding sources study based on 88 *P. geniculatus* specimens captured in Metropolitan Caracas, Venezuela, and using seven host species antisera (including humans), Feliciangeli et al. (2004) and Carrasco et al. (2005) found that the human blood index (HBI) was 98.1%, and that 41% of those insects were positive for *T. cruzi*. These data show that feeding of *P. geniculatus* on humans does not seem to be accidental and that its rate of infection by *T. cruzi* is high in an area which is not regarded as endemic for Chagas disease by the National Control Program (despite in and around Caracas lives 20% of the whole population of Venezuela; Carrasco et al. 2005).

The invasive performance of *P. geniculatus* is not restricted to houses; Valente et al. (1998) found, in a scattered riverine community in the locality of Furo do Rio Pau Grande, on the island of Marajo, in the mouth of the Amazon River, Brazil, hundreds of *P. geniculatus* infesting 15 pigsties annexed to human dwellings, repeatedly attacking local inhabitants, and exposing

them to the risk of *T. cruzi* infection. Jaramillo et al. (2002) report that *P. geniculatus* nymphs were found inside a house in northeastern Antioquia, Colombia, as an indication of permanent colonization. Aldana et al. (2011) have postulated that the adaptation of *P. geniculatus* to an urban "artificial" environment is evidenced by the degree of sexual dimorphism (specially the wing dimorphism), considering it an evidence of its adaptation to domiciles. However, these results contrast with those of Jaramillo et al. (2002) that evaluated, using the techniques of geometric morphometry, the morphological differences between a wild population and its laboratory descendants over five generations as a proxy to house adaptation, in order to monitor the invasion processes. The results of Jaramillo et al. (2002) showed differences in size but not in shape, with a reduction in head size and wing size from sylvatic to laboratory populations; however, the decrease in head size occurred only up to the second generation while the decrease in wing size proceeded up to the fifth generation.

All these references, and more occasional ones (such as Añez et al. 2005, for the State of Mérida, Venezuela) are clear indications of an increasing process of domiciliation of *P. geniculatus*, which associated with medium to high positivity to *T. cruzi*, representing an additional domiciliary component to the existing vectorial transmission of the agent of Chagas disease. Under this perspective our contribution on the life history traits and demographic parameters of *P. geniculatus* should be useful for not only interpreting adequately the domiciliation process of this species, but also to design the optimal control strategies. Furthermore, in view of the global climatic change taking place, and its consequences in terms of new geographic ranges of triatomine species (Medone et al. 2015), this kind of studies gain more and more importance for the epidemiology of Chagas disease, and we encourage new studies to calculate these parameters for *P. geniculatus* under other environmental conditions.

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