

Vital Statistics of Triatominae (Hemiptera: Reduviidae) Under Laboratory Conditions: III. *Rhodnius neglectus*

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ABSTRACT Five cohorts of 100 eggs of *Rhodnius neglectus* Lent 1954 (Hemiptera: Reduviidae) were reared simultaneously in the laboratory under constant conditions ($26 \pm 1^\circ\text{C}$ and $60 \pm 10\%$ RH), with mortality and fecundity data recorded weekly. We calculated stage-specific developmental times, age-specific mortality and fecundity, stage-specific and total preadult mortality, and the intrinsic rate of natural increase ($r_0 = 0.21$), the finite population growth rate ($\lambda = 1.23$), the net reproductive rate ($R_0 = 314.24$), and the generation time ($T = 21.45$ wk). Elasticity analysis showed that the dominant life-history traits determining λ were the adult female survival, and the survival of instar V nymphs (molting into adult females). Adult females dominated the stage-specific reproductive value, and the egg stage dominated the stable stage distribution (SSD). The damping ratio ($\rho = 1.11$) suggests a relatively rapid period of recovery to a disturbed SSD. Results were compared with previous values from the literature and conform relatively well, considering that environmental conditions were not always the same. Compared with two other species of the same genus, *Rhodnius neivai* Lent 1953 and *Rhodnius prolixus* Stål 1859, *R. neglectus* ranked higher in fecundity (total eggs/♀/life) and in female longevity, intermediate in the intrinsic rate of natural increase (r_0), and lower in developmental time and mortality. By fitting a logistic model of population growth to the density field values of a spontaneous colonization of two field experimental chicken coops we estimated the intrinsic rate of natural increase and carrying capacity parameters, and compared the former with our laboratory results.

RESUMEN Cinco cohortes de 100 huevos de *Rhodnius neglectus* Lent 1954 (Hemiptera: Reduviidae) SE criaron de manera simultánea en el laboratorio bajo condiciones constantes ($26 \pm 1^\circ\text{C}$ and $60 \pm 10\%$ HR), registrándose semanalmente la mortalidad y la fecundidad. Calculamos los tiempos de desarrollo por estadios (tiempo de desarrollo total = 15 semanas), las estadísticas vitales (mortalidad y fecundidad específica por edades, mortalidad preadulta específica por estadios), y los parámetros de crecimiento poblacional (la tasa intrínseca de crecimiento natural ($r_0 = 0,21$), la tasa finita de crecimiento poblacional ($\lambda = 1,23$), la tasa de reproducción ($R_0 = 314,24$), y el tiempo generacional ($T = 21,45$ semanas)). El análisis de elasticidad indica que el rasgo dominante de la historia de vida que determina λ es la supervivencia de la hembra adulta, y el tiempo en que las ninfas V permanecen en ese estadio. Las hembras adultas dominaron el valor reproductor específico por estadios, y la fase del huevo dominó la distribución estable de estadios (SSD). La tasa de amortiguación ($\rho = 1,11$) sugiere un período relativamente rápido de recuperación a un SSD si la misma es perturbada. Se compararon las estadísticas vitales con valores de la bibliografía y SE encontró una concordancia relativamente satisfactoria, tomando en consideración que las condiciones ambientales no siempre eran las mismas. En una comparación con otras dos especies del mismo género, *Rhodnius neivai* Lent 1953 y *Rhodnius prolixus* Stål 1859, *R. neglectus* evidencia valores más altos en la fecundidad (huevos totales/♀/vida) y en la longevidad de la hembra, valores intermedios en la tasa intrínseca de crecimiento natural (r_0), y valores más bajos en el tiempo de desarrollo y en la mortalidad. Se realizó un ajuste de los valores de densidad de una colonización espontánea de dos gallineros experimentales en el campo a un modelo logístico de crecimiento poblacional y SE pudo estimar la tasa intrínseca de crecimiento natural (r_0) y la capacidad de carga, y comparar la r_0 con nuestros resultados de laboratorio.

KEY WORDS Chagas, Triatominae, population parameters, population growth, life-history traits

This article forms part of a series of studies about the demographic features and population parameters of Triatominae (Hemiptera: Reduviidae). The first two

articles dealt with *Triatoma infestans* Klug 1834 (Rabinovich 1972) and *Triatoma maculata* Erichson 1848 (Felicangeli and Rabinovich 1985), and here we provide results for *Rhodnius neglectus* Lent 1954, under controlled laboratory conditions. Parameters such as

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developmental time, population growth rates, and mortality are important in the analysis of the competition outcome between different triatomine species, and they contribute to explaining triatomine species coexistence and diversity in a given habitat. Such parameters also help to optimize the design of laboratory rearing of triatomine colonies. The quantitative analysis of life-history traits, and particularly the population growth parameters, also is related to the geographic dispersal of Triatominae, and so will find application in the epidemiology of Chagas disease because it is directly linked to their potential geographic ranges.

R. neglectus is part of the *prolixus* group (also called the *R. prolixus* complex) (Barrett 1988; Chavez et al. 1999), together with *Rhodnius prolixus*, *Rhodnius nasutus* Stål 1859, and *Rhodnius robustus* Larrousse 1927, which can be difficult to distinguish on morphological features, a fact that has frequently led to misidentification (Monteiro et al. 2000). In Brazil, *R. neglectus* ranges between the latitudes of ≈ 5 and 25°S and between 5 and 500 m above sea level, although occasionally it can be found above that altitude (Lent and Wygodzinsky 1979, Galíndez Girón et al. 1996, Carcavallo et al. 1999, Schofield and Dujardin 1999, Galvão et al. 2003, Silva de Paula et al. 2005, Abad-Franch et al. 2009). The region of its occurrence is characterized by mean annual temperatures ranging between 19 and 30°C (average 23.3°C), and a mean precipitation of 1,246 (SD = 429.4) mm/yr, representing Holdridge Dry Forest and Very Dry Forest or Savannah life zones (Curto de Casas et al. 1999)

R. neglectus has been found in hollow trees or in the crown of palm tree species of the genera *Orbignya*, *Acrocomia*, *Mauritia*, *Arecastrum*, *Syagrus*, and *Scheelea* (Diotaiuti and Días 1984, Rocha et al. 1999, Abad-Franch et al. 2005, Gurgel-Gonçalves and Cuba Cuba 2009), and it has occasionally been encountered in Furnariidae bird nests (Lent and Wygodzinsky 1979). It has also been found in peridomestic habitats such as chicken houses and pigeon coops (Carcavallo et al. 1998; Días 1968, Días-Lima et al. 2003). Lent and Wygodzinsky (1979) considered this species a recent colonizer on the way to becoming a domestic species, and this was confirmed by field investigations of Forattini et al. (1984) and Silveira and de Rezende (1994). *R. neglectus* has been found naturally infected by *Trypanosoma cruzi* Chagas 1909 (Barretto and Carvalheiro 1966, Forattini et al. 1977, Silveira and Vinhaes 1999, Teixeira et al. 2001), but due to its dominant sylvatic condition is not considered an important vector species of Chagas disease transmission.

The main feeding sources of sylvatic *R. neglectus* are marsupials, rodents, birds, and bats (Barretto 1967a,b, 1968, 1971; Pedreira de Freitas et al. 1960; Barretto and Carvalheiro 1966; Barretto et al. 1966, 1969; Abad-Franch et al. 2009); occasionally they have been found to feed on amphibians and reptiles such as snakes (Diotaiuti and Días 1984) but Minter (1975) reports that birds invariably supply most feeds (46–80%). In peridomestic habitats, the main hosts of *R. neglectus* are bovines, goats, cats and dogs, as well as humans

(Forattini et al. 1971). However, in a study where *R. neglectus* were collected in a mixture of sylvatic, domestic, and peridomestic habitats, rodents in the diet were dominant, followed by birds, canids, and humans (Lorosa et al. 1999), although the number of insects analyzed was small ($N = 34$).

Materials and Methods

Population Origin. The population of *R. neglectus* used in this study was made available by Dr. Rodolfo Carcavallo and came from the insectaria of the Instituto Oswaldo Cruz (Rio de Janeiro, Brazil), although its exact geographical origin and the number of generations in the laboratory are not known. Taxonomic identification was provided by Dr. Carcavallo.

Experimental Procedures

The experiment was carried out in Caracas, Venezuela, in a climatic room with constant conditions of temperature ($26 \pm 1^\circ\text{C}$) and humidity ($60 \pm 10\% \text{RH}$). Photoperiod did not need to be controlled, for at the latitude of Caracas its seasonal variation is very small (daylength in December is 1129 hours and in June is 1242 hours). The experimental design involved the follow-up of five independent cohorts initiated simultaneously. Each cohort was started with 100 recently laid (0–48 h-old) eggs, kept in 150-cc glass containers until all viable eggs hatched. The first instar nymphs were transferred to 3.8-liter jars, covered with nylon mesh, and with vertically placed strips of paper inside that served both as resting places and for climbing to the top at feeding time. The experimental work was carried out while J.E.R. was a researcher at the Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.

Each cohort was fed weekly using hens placed on a wooden box with holes at the bottom, through which the tops of the cohort jars could be tightly inserted. The insects climbed to the top and fed through the nylon mesh. Food was offered for 1 h, and during the following hour the jars were horizontally exposed to a fan, to avoid the accumulation of excessive moisture in the glass containers, which is common after the insects become engorged. The hens were sedated using an intramuscular dose of midazolam (0.25 mg/kg). We allowed the hens to rest for 5–10 min after the sedative application and then carefully plucked them on one side on a surface not larger than a diameter of 7 cm (the mouth size of the jars). A towel was used to restrain the hens to minimize stress from being restrained. This procedure was carried out by two people who would gently wrap the towel around the hen, letting the head and legs stick out for better freedom of movement. This procedure was approved by the Animal Use Institutional Review Board of Venezuelan Institute for Scientific Research and is in conformity with Venezuelan law.

After being exposed to the fan, each jar was opened weekly to check the number of dead individuals (identified by instar), and number of eggs laid; identifica-

tion by sex was made only as adults. In a few instances the strict weekly feeding and counting schedule could not be maintained (although they were never out of phase for >3 d), and as the biodemographic methods require a constant time unit for analysis, the recorded information was subjected to linear interpolation to keep 1 wk as the time unit for the calculation of population statistics.

Statistical Analyses. The weekly death schedule of the cohort follow-up provided the necessary information to construct a life table (Deevey 1947). Calculations followed the method of Dublin et al. (1949); definitions of the components of a life table, with the formulae used, are given in the Appendix. As members of the cohorts were not followed individually, a frequency table of time in each instar was used to provide an estimate of the average and standard deviation of the developmental time of each instar. The frequency tables were based on time and number of individuals 1) entering a particular instar, 2) dying in that instar, and 3) molting to the following instar; from 1, 2, and 3, a table with the number of weeks (X) lived by groups of individuals (N) could be calculated, and the average and SD of this table produces results in an estimation of female adult longevity. The result is the same as calculating the expectation of life (or average future lifetime, e_x), where x represents the first age of a female emerging from an instar V nymph, but easier to carry out in a spreadsheet.

The weekly mortality data were used to calculate survival as a function of age (l_x) which, coupled with the weekly female age-specific fecundity [$m(x)$, also called the maternity curve], allowed the calculation of such statistics as the intrinsic rate of natural increase r_0 (using the Euler equation), the net reproductive rate R_0 , the instantaneous birth and death rate b and d (Birch 1948), the generation time T , the age-specific reproductive value V_x (Fisher 1930), and the stable age distribution (SAD). Calculation of total nymph mortality was carried out by converting age-specific mortality to age-specific survival and then multiplying those survival values and reconvert to its complement (mortality). All definitions and formulae are also given in the Appendix. Age-specific mortality was not included for it was already analyzed by Rabinovich et al. (2010). Parameters were calculated based exclusively upon the female population, so we converted all eggs/♀/wk values to ♀ eggs/♀/wk values multiplying by 0.5 [a sex ratio expressed as ♀/(♂ + ♀)]; as no specific studies have been carried out on the sex ratio of the eggs laid by *R. neglectus* females, we selected the 0.5 sex ratio value because unbiased sex ratios have been found in other triatomine species (Ronderos 1972, Paz Rodríguez 1996).

The life table (l_x) and fecundity (m_x) information also was analyzed in the form of a Leslie matrix and the population parameters λ_1 (the largest positive real eigenvalue), r_0 [as $\ln(\lambda_1)$], R_0 , and T , were calculated (Caswell 1989). The subdominant (second-largest) eigenvalue (λ_2) produces oscillations which usually decrease over time as the population approaches the stable age distribution (Mollet and Cailliet 2002). The

rate of convergence to the stable stage distribution is governed by the other eigenvalues: the larger the value of λ_1 relative to λ_2 the faster the recovery to the stable stage distribution, which leads to the definition of the damping ratio $\rho = \lambda_1 / \lambda_2$ (Mollet and Cailliet 2002).

Calculations were carried out using a computer program for PC developed by the authors for this purpose in Delphi 2007 language (the program is available upon request to the first author). The Leslie matrix, the sensitivity and elasticity analyses as well as the damping ratio calculation were carried out with PopTools, an Excel tool developed by Greg Hood (<http://www.cse.csiro.au/poptools/>). Although methods to convert age-structured matrices into stage-structured matrices (called Lefkovitch matrices, Lefkovitch 1965) exist, they were not used here to calculate population growth parameters, due to the bias that can result in the estimate of some population parameters as a result of information loss, mainly in the grouping of all female adult ages into only one single stage (Mollet and Cailliet 2002). However, we used the "popbio" package developed by Stubben and Milligan (2007) for language R (R Development Core Team 2007) to calculate the Lefkovitch matrix to estimate the probability of molting or remaining in each stage, and the stable stage distribution. Differences in mortality values between the five cohorts were tested with a Friedman analysis of variance (ANOVA) and a Kendall coefficient of concordance test (StatSoft, Inc. 2009). The confidence intervals of p (the probability that the observed sex-ratio at emergence of the adults was different from 0.5), was calculated using the built-in binomial proportions test "prop.test" of language R (R Development Core Team 2007).

Results

Vital Statistics. Although each cohort was analyzed independently, we also present results by pooling them because there was no significant difference between the mortality rates among cohorts (ANOVA: $\chi^2 = 5.902$, $P = 0.21$; coefficient of concordance = 0.0168, average rank $r = 0.00547$). The survival and maternity curves of *R. neglectus* for the average of the five cohorts, in terms of female individuals, is given in Fig. 1.

Table 1 provides a statistical summary of life-cycle statistics. Average time from oviposition to egg hatching was just >2 wk. Developmental times of all instars were very similar, except for instar V, which took almost as twice as long as the other instars to complete development. However, instars I and IV show the most variable developmental times. The average developmental time from egg to adult was 15 wk (SD 1.5); the average minimum and maximum developmental times from instar I to the adult stage were 8.4 wk (SD 0.55) and 23.8 wk (SD 8.5), respectively. The sex ratio [$(\text{♀}/(\text{♂} + \text{♀}))$] when entering the adult stage favored males, but the average among cohorts (0.421) was not statistically different from a 0.5 sex ratio ($N = 342$, $P = 0.0461$, 95% CI of p [0.0016–0.1563]).

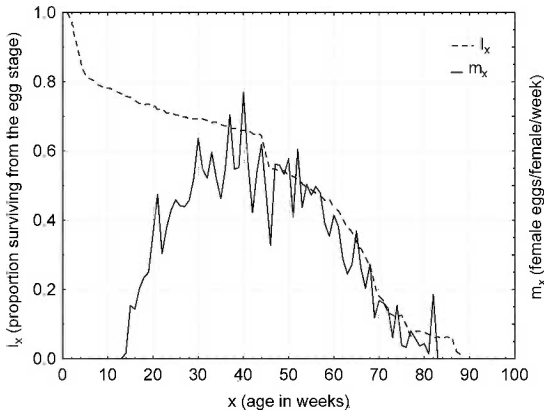


Fig. 1. Weekly age-specific survival (proportion surviving from the beginning of the egg stage to age x) and age-specific maternity curve (average ♀ eggs/♀/wk) of *R. neglectus* from the average among five cohorts.

Mortality per instar follows the usual pattern in Triatominae of a high mortality in the younger stages; in *R. neglectus* stages I and II account for ≈50% of the total mortality from egg to adult. Instars III and IV have a lower mortality rate, but that rate is extremely variable among cohorts. On average, ≈70% of all initial eggs of the cohorts arrive 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 a few weeks after becoming adults, as if 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 adult lon-

gevity was 45.16 wk, with a maximum of 65.8 wk. Calculations based upon the Lefkovitch matrix resulted in a probability of remaining alive in the same stage of 0.502, 0.547, 0.551, 0.551, and 0.817 and a probability of molting into the next stage of 0.347, 0.439, 0.449, 0.449, and 0.176, for instars I-V, respectively.

Figure 1 also shows the age-specific schedule of oviposition expressed as number of eggs/female/wk for the average among cohorts. The general pattern can be considered as unimodal, even if irregular, and the bell-shape is similar among cohorts (data not shown), peaking at about age 40 wk from the egg stage.

Table 1 also provides a statistical summary of the reproductive characteristics of female *R. neglectus*. The age of first reproduction of the cohort (representing the most precocious individual) is an important parameter in population dynamics, and resulted in 15.4 wk from the egg stage (SD 0.55 wk; coefficient of variation = 3.56%). On average a female laid eggs at a rate of 8.99 (SD 4.89) ♀ eggs/wk/♀, and the reproductive period of an average female was 45.37 (SD 4.34) wk after the start of reproduction.

It was of interest to determine if nymph mortality was related to developmental time, but linear regression analysis (data not shown) showed no significant relationship between total (all stages) nymph mortality and developmental time ($R^2 = 0.074$).

Population Growth Parameters. The main population growth parameters and stage-specific demographic features for each cohort of *R. neglectus* are given in Table 2. Population growth rates show very little difference between cohorts (coefficient of variation is between 2 and 15%, depending on the parameter). The net reproductive rate (R_0) indicates that,

Table 1. Average developmental time (weeks) and mortality by stages, reproductive features, and sex ratio (♀/(♂ + ♀)) of *R. neglectus*

Pop parameter	Cohort					Cohort statistics			
	1	2	3	4	5	Avg	SD	Coefficient of variation. (%)	
Developmental time									
Egg	2.4	1.9	2.3	2.3	2.3	2.2	0.2	9.1	
Instar I	2.1 (0.4:86)	1.4 (0.7:95)	1.9 (0.8:92)	2.7 (0.8:96)	1.5 (0.7:92)	1.9	0.5	25.8	
Instar II	2.3 (0.5:72)	2.5 (0.7:91)	2.3 (0.6:84)	2.4 (0.6:88)	2.5 (0.6:84)	2.4	0.1	5.1	
Instar III	2 (0.1:70)	2.1 (0.3:85)	2.2 (0.5:74)	2.5 (0.6:80)	2.1 (0.3:76)	2.2	0.2	8.7	
Instar IV	2 (0.2:70)	2.2 (0.5:85)	3.2 (1.2:72)	2.8 (1.4:77)	2.2 (0.5:73)	2.55	0.5	19.7	
Instar V	3.6 (0.8:70)	3.4 (0.6:83)	4.1 (0.8:72)	4.6 (1.4:74)	3.5 (0.8:72)	3.8	0.5	12.7	
Egg to adult	14.4	13.5	15.9	17.2	14.1	15.0	1.5	10.0	
Mortality (%)^a									
Egg	14.0	5.0	8.0	4.0	8.0	7.8	3.9	50.0	
Instar I	16.3	4.2	8.7	8.3	8.7	9.2	4.4	47.2	
Instar II	2.8	6.6	11.9	9.1	9.5	8.0	3.5	43.4	
Instar III	0	0	2.7	3.8	4.0	2.1	2.0	94.1	
Instar IV	0	2.4	0	3.9	1.4	1.5	1.7	108.7	
Instar V	2.9	2.4	9.7	21.6	2.8	7.9	8.3	105.0	
Instar I to adult	20.9	14.7	29.4	39.6	23.9	25.7	9.4	36.5	
Egg to adult	32	19	35	42	30	31.6	8.4	26.5	
Reproduction									
Age of first reproduction by cohort	16	15	16	15	15	15.4	0.6	3.6	
Reproductive weeks by cohort	60	64	68	63	67	64.4	3.2	5.0	
Total eggs laid by cohort	25,428	30,121	24,005	26,885	26,976	26,683	2,274.5	8.5	
Reproductive weeks/♀	38.6 (17.4)	46.4 (16.0)	44.7 (15.3)	50.5 (13.6)	46.7 (16.9)	45.4	4.3	9.6	
Eggs/♀/wk	20.8 (7.9)	18.3 (9.9)	17.0 (9.8)	19.2 (11.6)	15.0 (8.6)	18.1	2.2	12.2	
Sex ratio (at adult emergence)	0.44 (30.4)	0.40 (32.5)	0.45 (29.4)	0.38 (22.4)	0.44 (31.4)	0.42	0.03	7.45	
♀ adult mean longevity	39.5 (15.2:8-58)	42.8 (14.9:3-60)	46.2 (17.4:1-70)	47.1 (15.2:5-701)	50.2 (15.5:10-71)	45.2	4.1	9.1	

SDs and N are given in parentheses separated by a colon; numbers in parentheses separated by a dash represent the range.

^a Relative or stage-specific mortality ($q_i = 1 - (N_i/N_{i-1})$) for stage i , where N is the number of individuals entering each stage.

Table 2. Demographic and population growth parameters of *R. neglectus*

	Cohort					Cohort statistics		
	1	2	3	4	5	Avg	SD	Coefficient of variation (%)
Finite rate of pop increase (λ)	1.23	1.25	1.21	1.22	1.25	1.23	0.02	1.45
Intrinsic rate of natural increase (r_0)	0.20	0.22	0.19	0.20	0.22	0.21	0.01	6.99
Net reproductive rate (R_0)	281.82	372.19	264.51	351.75	300.91	314.24	46.01	14.64
Generation time (T)	21.17	20.39	23.61	22.82	19.25	21.45	1.77	8.27
Instantaneous birth rate (b)	-0.09	-0.07	-0.07	-0.07	-0.08	-0.08	0.01	-8.76
Instantaneous mortality rate (d)	0.29	0.29	0.26	0.27	0.30	0.29	0.02	5.75

All parameters were calculated from the age-structured life table and based upon a 1-wk time unit. See Appendix for the definitions and the formulae for the calculations of parameters.

on average, 314.2 (± 46.0 SD) females will replace each female in the population in the course of one generation, with generation time $T = 21.4 \pm 1.8$ wk.

Figure 2a and b shows the SSD and stage-specific reproductive values (V_x) of *R. neglectus*, calculated from the stage-structured matrix created from l_x and m_x curves as averages of the five cohorts (thus, not necessarily identical, although quite similar, to the values presented in Table 2). Female adults have highest reproductive value, followed by instar V; the SSD is dominated by eggs, followed by the other stages in

the form of a classical age pyramid. The average damping ratio (ρ) was 1.11, indicating that, if perturbed from the SSD, it would return to it rather rapidly.

Sensitivity and Elasticity Analysis. For the pool of the five cohorts, the sensitivities and elasticities of the finite rate of population growth (λ) are shown for age-specific (Fig. 3a) and stage-specific (Fig. 3b) fecundity and survival. During the period when the female is still not reproducing (prereproductive period), sensitivity and elasticity show a clear dominance of the survival of the instar V nymphs into females in its influence upon λ , whereas during the period when the female is already laying eggs (reproductive period) fecundity dominates the influence on λ .

Discussion

Vital Statistics. Few of our results can be compared with previously published information because most of the work with *R. neglectus* was limited to developmental times or mortality estimates. Furthermore, previous work with *R. neglectus* was done under a variety of laboratory conditions: temperature and humidity (usually uncontrolled), size of jars, feeding frequency and duration, density of insects per jar, species of host offered for feeding, and other factors were rarely similar to our experimental conditions, and all of them have consequences on the population parameters being estimated. In addition, in evaluating our results, it is important that the following aspects of this cohort study be taken into account.

First, in most cohort studies the individual history of the insects is not known. In triatomines, because of the intensive labor that individual rearing and feeding demands, each cohort is usually followed as a group; thus possible interactions between individuals of a given cohort are not known. Ryckman (1951) notes that in *Triatoma phyllosoma pallidipennis* Stål 1872, older nymphs crowd up to the host to the exclusion of younger members of the colony; and that the considerable amount of warm blood ingested by older nymphs stimulates a thermotropic response in unengorged younger nymphs, elicits a probing reaction that leads to a type of cannibalism he called “kleptohemodeipnonism.” We do not know to what degree, if at all, these two phenomena might have affected our experiments with *R. neglectus*; however, we think that in our study it can be considered negligible because

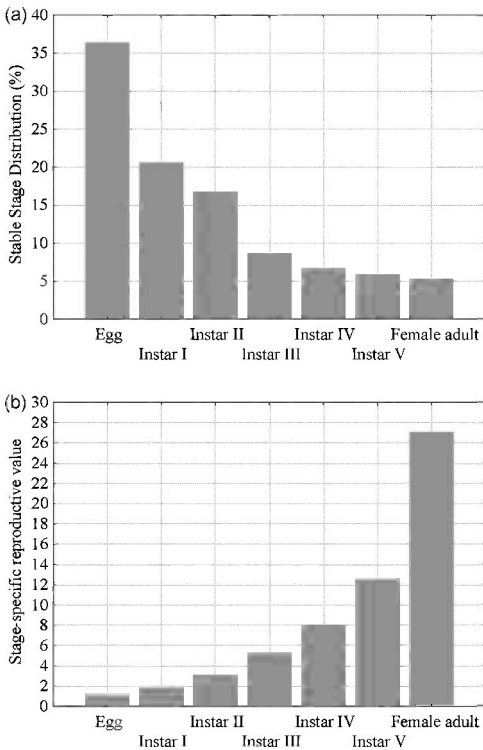


Fig. 2. (a) Stable stage distribution of a *R. neglectus* based on the l_x and m_x average of five cohorts and calculated by considering the average developmental time of each stage. (b) Stage-specific reproductive value of *R. neglectus*, based on the l_x and m_x average of five cohorts and calculated by considering the average developmental time of each stage. The scale represents the number of individuals that each stage will, on average, contribute to the next generation.

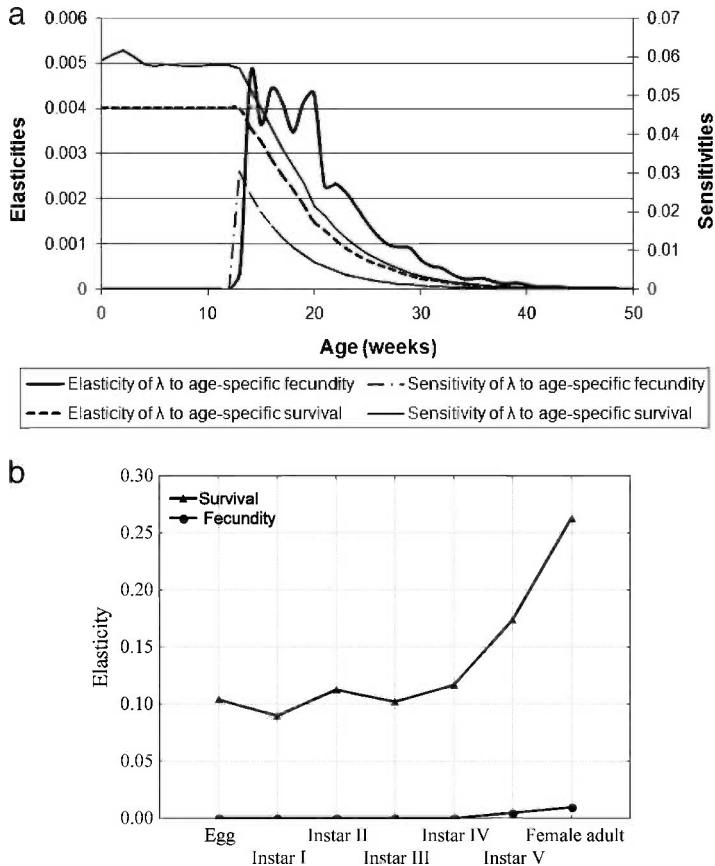


Fig. 3. (a) Sensitivities and elasticities of finite rate of population growth (λ) to age-specific fecundity and survival calculated for the pool of the five cohorts. To visualize the lines of each variable the x-axis (age in weeks) has been drawn up to 50 wk because after that age values are negligible. Sensitivities and elasticities were calculated based on the Leslie matrix; note that they have different scales and are represented on different axes. (b) Elasticities of finite rate of population growth (λ) to stage-specific fecundity and survival also calculated for the pool of the five cohorts but based on the Lefkovich matrix. The fecundity and survival elasticities have reversed their importance between a and b due to the information loss when elasticities are calculated based on stage-specific data.

due to the progression of the development from egg to adults, older nymphs do not coexist with the very younger nymphs. Perlowagora-Szumlewicz (1953) shows the importance of the time of the first meal, and in general it is known that the volume of the blood-meal in successive feedings in different instars drastically affects the process of molting and of production and viability of eggs (Goodchild 1955, Danilov 1968, Perlowagora-Szumlewicz 1969); in our experimental set-up feeding of each individual insect was not recorded, so if this factor also occurred with *R. neglectus* it may have influenced the results of our cohort study. Another disadvantage of treating the cohort as a group is that the reproductive performance cannot be evaluated individually; some information is lost, such as the average individual age of first reproduction and the individual periodicity in oviposition.

Second, as individuals die the density (number of individuals per jar) decreases during the development of a cohort study. Perlowagora-Szumlewicz (1969) demonstrates an apparent density effect upon longev-

ity and fecundity in *T. infestans*. In particular it was shown that *R. neglectus* females which mated only once and were regularly fed had a fertility rate lower than the females that mated several times (Costa et al. 1967); as copulation (by direct observation or by the presence of spermatophores) was not recorded in our study, the consequences of this effect is unknown, although at the initiation of adult life males were abundantly available to females in the cohort jars, particularly in the first half of their adult life when this effect is most important.

Third, calendar age is not the same as physiological age. As a result of the above-mentioned interactions, as well as a result of biological variability, individual triatomines do not molt synchronously even if they developed from eggs laid at the same time. Consequently, as the insects develop into more advanced stages there is increasing overlap between stages, and individuals with the same calendar age may belong to several different instars. It is not known whether these differences affected the results of this study. For ex-

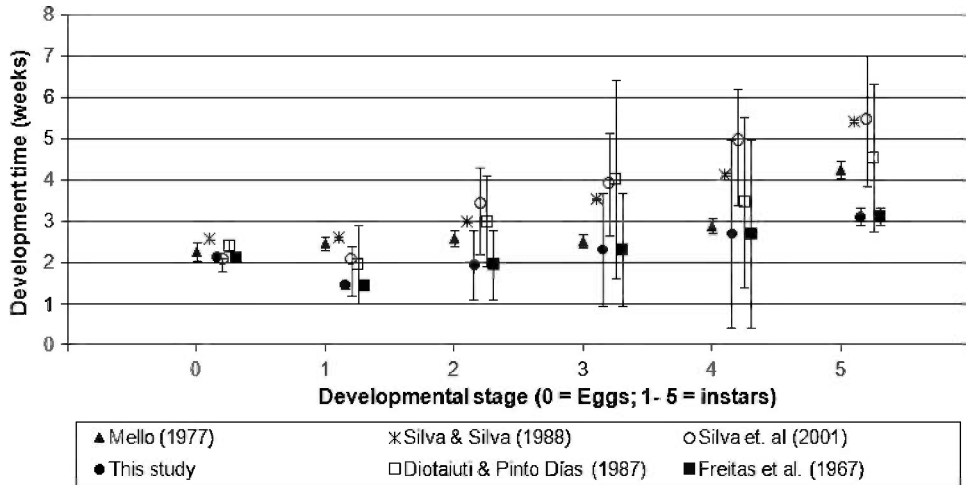


Fig. 4. Mean developmental time (weeks) of the eggs and the instars of *R. neglectus* from Freitas et al. (1967), Mello (1977), Diotaiuti and Días (1987), García da Silva and da Silva (1988), Rocha et al. (2001), and this study. Vertical bars are 1 SD; in the García Silva and Silva (1988) data they are extremely small (0.000, 0.036, 0.000, 0.055, 0.071, and 0.103) and vertical bars do not show clearly. Data values are shown slightly shifted to avoid symbol overlapping.

ample, the probability of dying may differ between a fifth-instar nymph 25 d old and a fifth-instar nymph 40 d old.

With these reservations in mind, however, our results can be compared with results found in the literature and analyzed demographically. Mello (1977), Diotaiuti and Días (1987), and Rocha et al. (2001) studied the developmental time of *R. neglectus* and mortality by stages. García da Silva and da Silva (1988) also studied the developmental time for this species but not mortality (except egg mortality). Figure 4 compares the results of those studies with our own results. Differences with Mello (1977) were significant ($P = 0.01$ for eggs and $P = 0.000$ for all instars, *t*-test); the differences with García da Silva and da Silva (1988), although small, were also significant. However, they proved to be consistent as a function of the feeding conditions: although García da Silva and da Silva (1988) used environmental conditions similar to ours ($25 \pm 0.5^\circ\text{C}$ and $70 \pm 5\% \text{RH}$), and also fed with hens, the feeding was less frequent: every 12, 15, 20, and 25 d for nymphs of instars II, III, IV, and V, respectively. So, it is not surprising to find longer developmental times in their results. The mean developmental times of all stages of *R. neglectus* obtained by Diotaiuti and Días (1987) show significant differences to our study; their developmental times are longer than ours, although we would have expected a shorter developmental time because although the feeding conditions were similar, the rearing temperature was higher ($28 \pm 1^\circ\text{C}$). Similarly, the developmental times obtained by Rocha et al. (2001) (with the exception of instar I, $P = 0.089$) differed from those observed here. But when comparing the total developmental times from egg to adults, our results (15 wk) are larger than the 12.3 wk obtained by Freitas et al. (1967), but shorter than the developmental time values of 17.1 wk of Mello (1977), 21.3 wk of García da

Silva and da Silva (1988), 22 wk of Rocha et al. (2001), and 19.5 wk of Diotaiuti and Días (1987). Those studies did not provide variance estimates, so no statistical comparison was possible.

Mortality by stages was compared in Fig. 5, and the differences between studies are striking. For most developmental stages few of the other studies compared well with our results (most of the stage mortality values of previous studies fall outside the 1 SD bars of our results). This is also evident from the large differences in the total (accumulated) mortality from egg to instar V: 10.6% (Mello 1977), 68.2% (Rocha et al. 2001), 40.2% (Diotaiuti and Días 1987), at least 46.2% (Freitas et al. 1967; egg mortality was not estimated by the authors), and 31.6% in this study. Either stage mortality is more sensitive than developmental time to small differences in environmental and feeding experimental conditions, or differences in manipulation of the bugs during the cohort experiments greatly affect the chances of survival.

Of the five studies amenable to comparison with our results, only Mello (1977) provided an estimate of the sex ratio (expressed here as $\text{♀} / \text{♀} + \text{♂}$): 0.53, only slightly larger than the sex ratio of our study (0.42) but significantly different ($P = 0.047$). Nevertheless, as the sex ratio in *R. neglectus* does not differ statistically from 0.5, and because in other Triatominae the sex ratio is assumed to be 0.5 at the egg stage (unbiased 0.5 sex ratios have been found in other triatomine species; see Ronderos 1972; Paz Rodríguez 1996), *R. neglectus* females seem to have the same intrinsic mortality risks than males during development. In terms of fecundity our result of 18.1 eggs/♀/wk accords with the 17.1 eggs/♀/wk values obtained by Costa et al. (1967); our egg fertility value of 92.2% also accords with the 95.1% hatching rate Costa et al. (1967), the 90.1% value of García da Silva and da Silva (1988) and the 98.5% value obtained by Mello (1977).

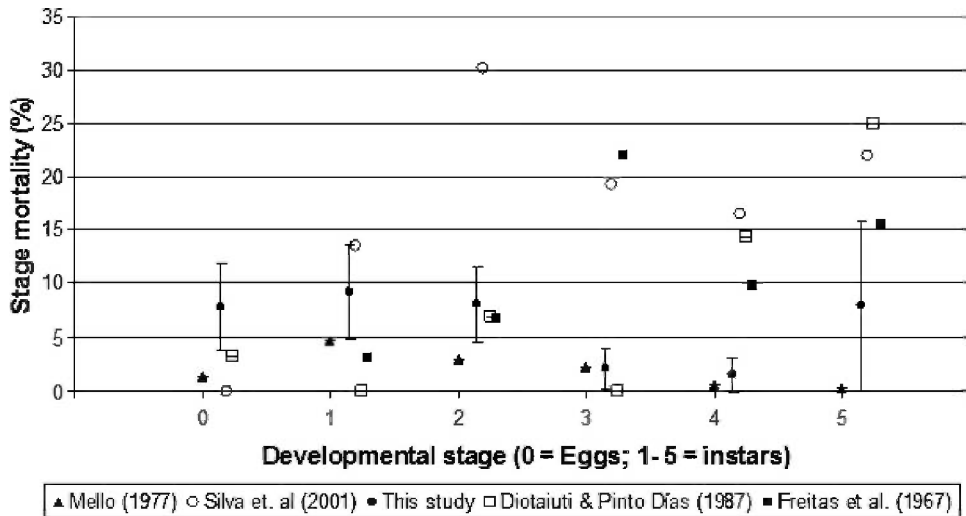


Fig. 5. Stage mortality (percentage) of the eggs and instars of *R. neglectus* from Freitas et al. (1967), Mello (1977), Diotaiuti and Dias (1987), Rocha et al. (2001), and this study. Standard deviations were not provided by previous publications. Vertical bars on data of this study are 1 SD. Data values are shown slightly shifted to avoid symbol overlapping.

Population Parameters. We compared our results with those of two other *Rhodnius* species (*R. neivai* and *R. prolixus*) reared under conditions similar to our experimental settings (constant temperature between 26 and 28°C, relative humidity between 60 and 80%, and fed with hens every 7 d). The instantaneous population growth rate (r_0) of *R. neglectus* (0.209) was smaller than that for *R. neivai* (0.267) and *R. prolixus* (0.286); however, *R. neglectus* had a net reproductive rate ($R_0 = 311.8$) more than twice that of *R. neivai* (118.7) and of *R. prolixus* (133.3). Because there is no important difference between these species in terms of average total length (19, 19, and 19.5 mm for *R. neivai*, *R. neglectus*, and *R. prolixus*, respectively), we conclude that the smaller r_0 and the larger R_0 values of *R. neglectus* must be related to the large differences in generation time ($T = 21.1$ wk) and fecundity ($F = 18.1$ eggs/♀/wk) as compared with *R. neivai* ($T = 14.0$ wk and $F = 10.1$ eggs/♀/wk) and *R. prolixus* ($T = 14.3$ wk and $F = 10.0$ eggs/♀/wk). The high fecundity of *R. neglectus* shows up in a high R_0 value because R_0 is independent of T , but results in a smaller r_0 which is very sensitive to the generation time.

Sensitivity and Elasticity Analysis. Sensitivity analysis provides information about how sensitive the finite population growth rate (λ) is to changes in the specific elements of a demographic transition matrix (Emlen 1970); because λ is an accepted measurement of fitness (Caswell 2009), sensitivity analysis suggests which life-history component should be the main target for population control (Ebert 1999). Because the elements of the demographic transition matrix usually have different units and scales, their contributions to λ are better measured by their elasticity, which is a sort of proportional sensitivity. Sensitivity and elasticity of the life-history traits of *R. neglectus* are given in Fig. 3a as a function of age. Table 3 shows that—in terms of elasticity—there is a clear dominant contribution to λ

by the survival of the adult females, followed by the survival of instar V nymphs (molting into adult females). These dominant traits are on average ≈ 3 and 2 times larger, respectively, than the other life-history traits in their contributions to λ ; the difference is even greater when comparing the fecundity term (≈ 7 and 4 times larger, respectively). From the demographic point of view, any control measure targeting adult survival and/or instar V nymphs would by far be more effective than any other control measure.

Damping Ratio and Stable Age and Stage Distribution. The damping ratio (ρ) is related to the period of recovery to a stable age or stage distribution after a population has been disturbed. It can be converted into calendar value by specifying the time required (t_x) for the contribution of the second root (λ_2) of a Leslie or Lefkovich 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} ($x = 1/0.05 = 20$). t_x can be estimated by $t_x =$

Table 3. Results of the elasticity analysis of the life history cycle components of *R. neglectus* on their effect on its finite rate of population growth (λ) based upon the 88 by 88 age Leslie matrix (on a weekly basis and from the pool of the five cohorts) and expressed as stages by accumulating the elasticity values over each stage by using the average developmental time of each instar in weekly time units

Matrix element description	Matrix element value	Matrix element elasticity
Adult female survival (per wk)	0.9779	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 (avg ♀ eggs/♀/wk)	7.224	0.047

Table 4. Stable stage distribution of field studies of *R. neglectus* and that predicted by our study for the dry and wet seasons

% nymphs	Season	Location	Source
56	N/Ap ^a	N/Ap	This study (from vital statistics)
35 (23)	N/Av ^a	Sao Paulo state	Forattini et al. (1977)
77 (51)	Dry	Brasilia	Gurgel-Gonçalves and Cuba Cuba (2007)
60 (245)	Dry	Belo Horizonte	Diotaiuti and Dias (1984)
52 (1,734) ^b	Dry	Sao Paulo state	Forattini et al. (1983a)
75 (1,675) ^b	Wet	Sao Paulo state	Forattini et al. (1983a)
66 (65)	Wet	Curaçá	Das-Lima et al. (2003)
27 (218)	Wet	Belo Horizonte	Diotaiuti and Dias (1984)
58 (33)	Wet	Brasilia	Gurgel-Gonçalves and Cuba Cuba (2007)

Values in parentheses are the total number of insects collected. Only the percentage of nymphs is presented because the complement (100 - [% nymphs]) provides the percentage of adults.

^a N/Ap, not applicable; N/Av, not available.

^b These values are the result of pooling two chicken-coops and averaging for 2 yr of data given by trimesters.

$\ln(x)/\ln(\rho)$ (Caswell 1989), so with $\rho = 1.11$ t_{20} becomes 24.5 wk (≈ 172 d). Assuming a developmental threshold of 16°C in the distribution area of *R. neglectus* the t_{20} value represents ≈ 1780 degree-days (DD), a value within the 1,000–3,000 DD range of a normal growing season for insects in temperate regions. This is a relatively fast recovery period of a SSD, although it depends on the assumption that the vital rates remain constant during that recovery period. Taylor (1979) calculated the t_{20} value of 36 populations of 30 species of insects and mites, and concluded that the time of convergence to the SSD was nearly independent of survivorship and reproductive capacity, but that the higher the age of first reproduction (α) and the larger the variance in m_x the faster the convergence to the SSD.

It is of interest to compare the SSD estimated by the laboratory vital statistics with the field values of the SSD (Table 4). An extradomestic population of *R. neglectus* in Sao Paulo state, Brazil (Forattini et al. 1977), showed that 35% of the insects collected were nymphs; this is almost the reverse of what was expected from a stable stage distribution (our result is $\approx 56\%$ nymphs), indicating that this sylvatic population of *R. neglectus* was either a recent colony or a population that was recently altered and had no time to recover to an SSD. The average proportion of *R. neglectus* nymphs of the field studies was 55.6% ($\pm 15.1\%$ SD) which conforms well with the 54.5% of nymphs from our calculations based on the Lefkovich stage matrix. However, the proportion of nymphs in the field is quite variable in relation to season (Table 4): on average 54 and 75% of the insects were nymphs in the dry and wet season, respectively, a difference statistically significant using a *t*-test. Our result of 54.5% nymphs, although more similar to that of the dry season, cannot be compared with any particular season, for it is the long-term projection of the proportion of nymphs under stable environmental conditions.

The SSD in a field experiment with artificial chicken coops in Minas Gerais, Brazil (Forattini et al. 1983), was calculated after a period of ≈ 2 yr after colonization, but our estimation of the damping ratio for *R. neglectus* ($\rho = 1.11$) resulted in a calendar time to recover an SSD of ≈ 25 wk, much shorter than the chicken coop experiment, suggesting a very high or

permanent perturbation condition in the sylvatic environment that impedes *R. neglectus* populations to reach an SSD. However, this interpretation has to be taken with caution, for there are other possible factors that may result in a non stable stage distribution (sampling artifacts, because small nymphs have a lower catchability than larger nymphs and adults (Rabinovich et al. 1995); and the natural dispersal behavior of individuals in a sylvatic population, with adults sometimes flying away from their natural habitat).

The average stage duration of *R. neglectus* nymphs estimated under the field conditions of the experimental chicken coops by Forattini et al. (1983) (between 8 and 11 wk) was much longer than our experimental cohorts (between 2 and 4 wk) under constant conditions. This important difference should not be surprising for under the field conditions of Forattini et al. (1983) hosts were occasional visitors and the temperature fluctuated along the year.

The population growth of *R. neglectus* after the spontaneous colonization of artificial chicken coops near peridomestic habitats for seven consecutive trimesters obtained by Forattini et al. (1983) in Sacramento, Brazil, was used to fit the continuous logistic model of population growth to estimate the intrinsic rate of natural increase (r_0) and the carrying capacity of the chicken coops (K). Figure 6 shows the observed and predicted values for two chicken coops; in chicken coop *f1* *R. neglectus* colonized by itself, while in chicken coop *a2* it developed a population coexisting with *T. sordida* Stål 1859. In chicken coop *a2* the *R. neglectus* population was growing at a rate of $r_0 = 0.163$ per wk and a carrying capacity (K) value of 226 individuals ($r = 0.945$, $\chi^2 = 1049.7$, $df = 6$, $P = 0.000000$). The r_0 value of 0.163 is lower than the average laboratory value (0.19), indicating that *R. neglectus* populations under natural conditions possibly grow at a rate smaller than under optimal laboratory conditions. In chicken coop *f1* the *R. neglectus* population was growing at a rate of $r_0 = 0.081$ per wk ($\approx 50\%$ lower than in chicken coop *a2*) and with a carrying capacity (K) of 368 individuals ($r = 0.947$, $\chi^2 = 71.73$, $df = 8$, $P = 0.000000$). As both chicken coops were sampled in the same years (1977–78) and simultaneously, the difference between the *R. neglectus* population growth rates of chicken coops *a2* and *f1* can

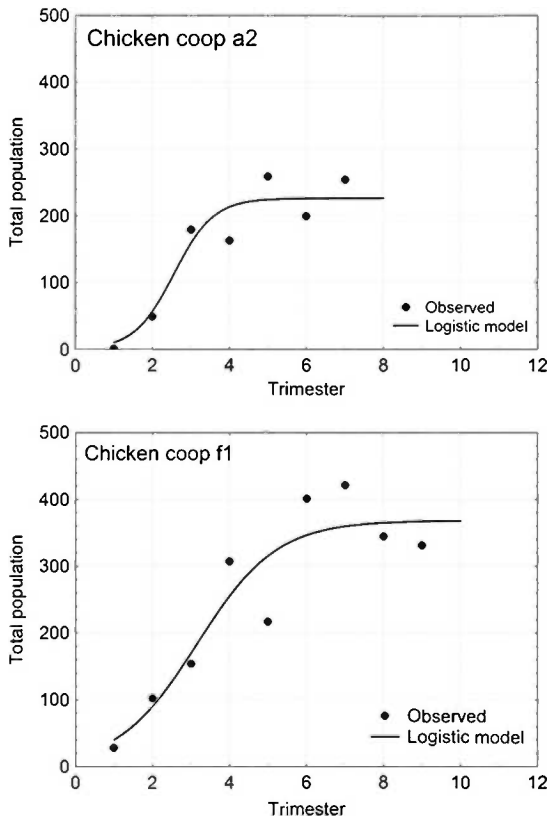


Fig. 6. Fit of the logistic population growth model to natural populations of *R. neglectus* that colonized spontaneously artificial chicken coops placed near peridomestic in Brazil (field data from Forattini et al. 1983). In chicken coop *a2* *R. neglectus* developed in competition with *T. sordida*; in chicken coop *f1* *R. neglectus* developed without competition with other triatomine species.

probably be explained by two compounded factors: 1) chicken coop *a2* received a smaller founder population (1 ♀) than chicken coop *f1* (28 individuals: 22 N1, five N2, and one ♀), and 2) in chicken coop *a2* there was competition with *T. sordida* (founder population of 33 individuals) that pressed for a higher population growth rate of *R. neglectus*; on the contrary, in chicken coop *f1* an earlier arrival (third trimester as compared with the fifth trimester in chicken coop *a2*) and larger initial colonizing population lead to an earlier action of the density-dependent population regulation mechanisms, resulting in a lower population growth rate. It is interesting to note that the estimated carrying capacity for *R. neglectus* in chicken coop *f1* was 63% larger (368 individuals) than in the chicken coop *a2* (226 individuals) where it had to compete with *T. sordida*.

In conclusion, the population parameters estimated here for *R. neglectus* will be useful for laboratory and field applications. *R. neglectus* seems to be more efficient than *T. infestans* as a vector of *T. cruzi* (Forattini et al. 1976). In addition, Forattini et al. (1977) found that 47% of 23 insects collected in extradomestic hab-

itats were positive for *T. cruzi* and as *R. neglectus* is in the process of becoming a domestic species (Lent and Wygodzinsky 1979, Forattini et al. 1984, Gurgel-Gonçalves and Cuba Cuba 2009) the application of the population parameters here estimated is important in anticipating control measures, as discussed by Chaves et al. (2004) in relation to *R. prolixus*.

As an SSD implies a well established colony (sylvatic or domestic), it would be useful to evaluate the damping ratio (ρ) of other triatomine species to compare their relative times of convergence to SSD as an indicator of the effectiveness of vector control measures. In view of the global climatic change taking place, and its possible consequences in terms of new geographic ranges of triatomine species, this kind of study gains more importance for the epidemiology of Chagas disease, so we encourage new studies to calculate these parameters in other triatomine species.

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Appendix. Definition of terms and formulae used in the calculation of vital statistics and population parameters of *R. neglectus*

Symbol	Name and/or definition	Calculation
b	Instantaneous birth-rate	$(r_0\beta)/(e^{-r_0} - 1)$
d	Instantaneous death-rate	$B - r_0$
T_x	Number of weeks yet to live to females aged x	$\sum_x L_x$
e^{δ}	Expectation of life or avg future lifetime	T_x/L_x
L_x	No. of weeks lived by the cohort between ages x and $x+1$	$(l_x + l_{x+1})/2$
l_x	Probability of an individual being alive at the end of age x	N_x/N_0
m_x	Age-specific fecundity (eggs/♀/wk)	Observed value
M'_x	♀ age-specific fecundity (♀ eggs/♀/wk)	$m_x p$
N_x	Individuals alive at the end of age x	Observed value
p	Sex ratio	$\varphi / (\varphi + \delta)$
r_0	Intrinsic rate of natural in-crease	Solving for r_0 from $\sum_x l_x m' x e^{-r_0 x} = 1$
R_0	Net reproduction rate	$\sum_x l_x m' x$
T	Generation time	$\log_e(R_0)/r_0$
v_x	Age-specific reproductive value	$\frac{e^{r_0 x}}{\sum_{x=a}^{\infty} e^{-r_0 x} l_x m_x}$
x	Age in weeks	Observed value
a	Female's first age of egg laying	Observed value
β	Finite birth rate	$1/\sum_x l_x e^{r_0+1}$
λ	Finite rate of increase or reproduction rate	e^{r_0}
ω	Female's last age of egg laying	Observed value