



Mortality profiles of *Rhodnius prolixus* (Heteroptera: Reduviidae), vector of Chagas disease

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Abstract

Life table data of *Rhodnius prolixus* (Heteroptera: Reduviidae) kept at laboratory conditions were analysed in search for mortality patterns. Gompertz and Weibull mortality models seem adequate to explain the sigmoid shape of the survivorship curve. A significant fit was obtained with both models for females ($R^2 = 0.70$, $P < 0.0005$ for the Gompertz model; $R^2 = 0.78$, $P < 0.0005$ for the Weibull model) and for males ($R^2 = 0.39$, $P < 0.0005$ for the Gompertz model; $R^2 = 0.48$, $P < 0.0005$ for the Weibull model). The mortality parameter (b) is higher for females in Gompertz and Weibull models, using smoothed and non-smoothed data ($P < 0.05$), revealing a significant sex mortality differential. Given the particular life history of this insect, the non-linear relationship between the force of mortality and age may have an important impact in the vectorial capacity of *R. prolixus* as Chagas disease vector, and its consideration should be included as an important factor in the transmission of *Trypanosoma cruzi* by triatomines.

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1. Introduction

Rhodnius prolixus Stål is the main natural vector of *Trypanosoma cruzi* (Chagas) in northern South Amer-

ica and part of Central America. This parasite causes Chagas disease and such situation points out to the relevance of further studies on the life history traits of these insects.

Life table studies in Triatominae have been widely developed, usually under laboratory conditions, to determine population parameters of different species (Rabinovich, 1972; Zeledón, 1981; Feliciangeli and

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Rabinovich, 1985; Cabello et al., 1987; Cabello and Galindez, 1998), or the effects of density-dependence on the growth parameters (Rodríguez and Rabinovich, 1980). Such studies made no emphasis on mortality or longevity, which justifies the present study as those life history traits contribute to the vectorial capacity of an insect that spreads a disease, as the vectorial capacity depends on the mortality rate of an insect species (Garrett-Jones, 1964).

Of the variety of mortality models found in the literature, the Gompertz model is the most widely used (Preston et al., 2000). It states that above a threshold age, sexual maturity or any other important life history event, there is an exponential increase of mortality (μ_x) with age (x), expressed by the equation:

$$\mu_x = ae^{b(x)} \quad (1)$$

where a is the initial mortality rate and b is the “Gompertz parameter”, which represents the slope of the mortality function (Carey, 2001). Another model utilizes the Weibull distribution (Pinder et al., 1978; Gurney and Nisbet, 1998), and is called the Weibull model (Carey, 2001). In this model, mortality is a power function of age:

$$\mu_x = ax^b. \quad (2)$$

A plot of $\log(\mu_x)$ against $\log(x)$ should give a straight line with slope b . In the Weibull model, a is the scale and b the shape parameter (Pinder et al., 1978; Carey, 2001).

There are some evidences that sex mortality differences occur among species and some apparent paradoxes have been reported; e.g., in *Ceratitis capitata* (Wiedemann) mortality is lower in males than in females, but females are usually the last to die (Carey et al., 1995). There is no common pattern of sex mortality differential among species, but differences, when they are present, can have underlying reasons (Carey and Judge, 2001).

In this study, we fitted the Gompertz and Weibull models to the experimental data of *R. prolixus* obtained by Rodríguez and Rabinovich (1980). We compared for adult females and males the slope of the Gompertz model and the shape parameter of the Weibull model, to determine if there is a sex mortality differential.

2. Materials and methods

Mortality parameters of *R. prolixus*, from egg hatching to adult, were estimated from partially published life table data in Rodríguez and Rabinovich (1980). Cohorts of an initial density of 128 individuals per 3.81 jars were reared in the laboratory, at 27 °C and 80% RH. Bugs were fed “ad libitum” once a week on hen. Three replicates were used. Other details can be found in Rodríguez and Rabinovich (1980).

Mortality values were obtained in two ways (both justified by Carey, 2001). The first is the classical negative logarithmical relationship:

$$\mu_{x1} = -\ln(P_x) \quad (3)$$

and the second results from a smoothing method to reduce noise:

$$\mu_{x2} = -\frac{1}{2}[\ln(P_{x-1}) + \ln(P_x)] \quad (4)$$

where P_x is the survival probability from age x to $x + 1$. The mortality rate (μ_x) was transformed by taking natural logarithms, and a linear fit with age was carried out for the Gompertz model (1), and with the natural logarithm of age for the Weibull model (2), both by the least squares method (Zar, 1998). Figures and statistical analysis were done using the R language (Ihaka and Gentleman, 1996). Data points for regression analyses were taken for ages after initial random mortality happened. Sexual maturity is a threshold age, at least for gompertzian mortality; any previous mortality can be considered random (Carey, 2001). Thus, after a visual inspection, we eliminated isolated data points that account for random deaths before the age of sexual maturity, this is, the eighth week in cohorts of *R. prolixus* (Rodríguez and Rabinovich, 1980). To test sex mortality differentials, a Student's t -test for slope differences, Δb (Zar, 1998) was carried out.

3. Results

Fig. 1 shows the age specific survival curves for both sexes. After an initial age independent random mortality that spans 7 weeks, the curves show a sigmoid decline of survival with age. Fig. 2 shows that semi- and double-logarithmic representations of mortality against age for females, are good candidates

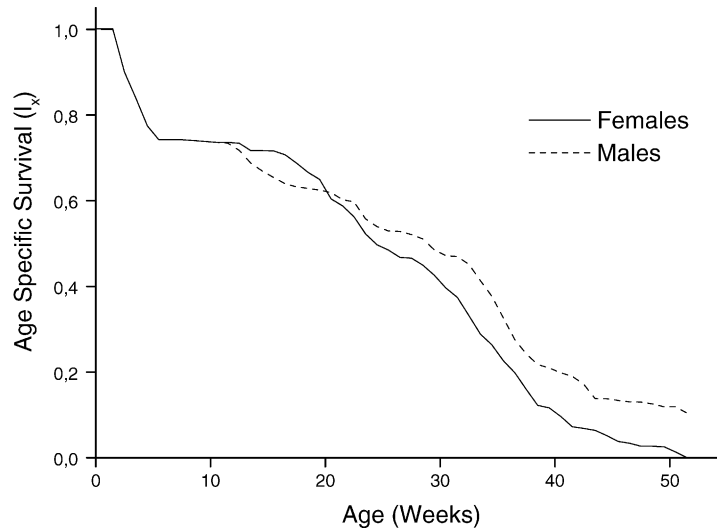


Fig. 1. Age specific survivorship schedules for females and males of *Rhodnius prolixus*.

for linear regression analyses. In Fig. 3, we can see that only smoothed double-logarithmic representation shows an almost linear behaviour. Tables 1 and 2 show the parameter estimates for Gompertz and Weibull models (with non-smoothed and smoothed data) for females and males, respectively. For *R. prolixus* females, the Weibull model fitted with smoothed data gives the highest proportion of explained variation ($R^2 = 0.78$, $P < 0.0005$). For males, the regressions could not explain more than 48% ($P < 0.0005$) of the mortality variation for both models. Independently of the model used and the data being smoothed or not, the mortality parameter is higher in females than in males ($P < 0.05$) (Table 3).

Table 1
Parameter estimates, and their standard errors, of the Gompertz and Weibull mortality models for data of *Rhodnius prolixus* females

Model	μ_{x1} (non-smoothed)	μ_{x2} (smoothed)
Gompertz	$b = 0.10 \pm 0.01$ $\ln(a) = -6.07 \pm 0.37$ $R^2 = 0.66$ $F_{(1,38)} = 73.75$ $P\text{-value} = 1.96 \times 10^{-10}$	$b = 0.11 \pm 0.01$ $\ln(a) = -6.42 \pm 0.36$ $R^2 = 0.70$ $F_{(1,41)} = 93.59$ $P\text{-value} = 3.85 \times 10^{-12}$
Weibull	$b = 2.63 \pm 0.47$ $\ln(a) = -11.76 \pm 0.90$ $R^2 = 0.71$ $F_{(1,38)} = 94.73$ $P\text{-value} = 7.21 \times 10^{-12}$	$b = 2.89 \pm 0.24$ $\ln(a) = -12.70 \pm 0.78$ $R^2 = 0.78$ $F_{(1,41)} = 150.00$ $P\text{-value} = 2.77 \times 10^{-15}$

Table 2
Parameter estimates, and their standard errors, of the Gompertz and Weibull mortality models for data of *Rhodnius prolixus* males

Model	μ_{x1} (non-smoothed)	μ_{x2} (smoothed)
Gompertz	$b = 0.05 \pm 0.01$ $\ln(a) = -5.33 \pm 0.46$ $R^2 = 0.25$ $F_{(1,41)} = 13.50$ $P\text{-value} = 7.00 \times 10^{-4}$	$b = 0.06 \pm 0.01$ $\ln(a) = -5.37 \pm 0.35$ $R^2 = 0.39$ $F_{(1,42)} = 26.42$ $P\text{-value} = 6.00 \times 10^{-6}$
Weibull	$b = 1.44 \pm 0.35$ $\ln(a) = -8.48 \pm 1.16$ $R^2 = 0.29$ $F_{(1,41)} = 16.77$ $P\text{-value} = 2.00 \times 10^{-4}$	$b = 1.60 \pm 0.26$ $\ln(a) = -8.96 \pm 0.85$ $R^2 = 0.48$ $F_{(1,42)} = 39.24$ $P\text{-value} = 1.66 \times 10^{-7}$

Table 3
Differences between the slope parameters for Gompertz and Weibull models

Model	Δb (non-smoothed data)	Δb (smoothed data)
Gompertz	$\Delta b = 0.05 \pm 0.01$ $t_{79} = 7.16$, $P < 0.05$	$\Delta b = 0.05 \pm 0.01$ $t_{83} = 8.74$, $P < 0.05$
Weibull	$\Delta b = 1.19 \pm 0.01$ $t_{79} = 187.71$, $P < 0.05$	$\Delta b = 1.39 \pm 0.01$ $t_{83} = 247.12$, $P < 0.05$

$\Delta b = b_{\text{females}} - b_{\text{males}}$.

4. Discussion

Gompertz and Weibull models seem adequate for the mortality schedules observed in females and males

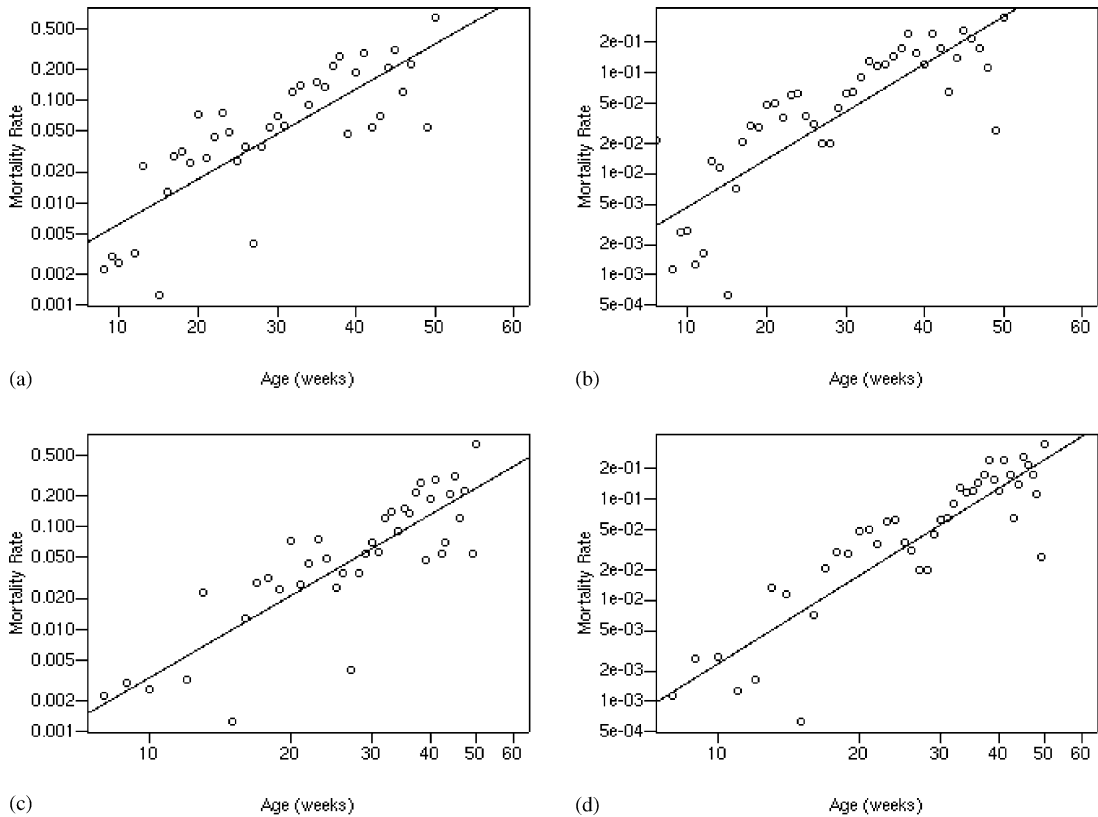


Fig. 2. Plots of mortality rate, in deaths/week, vs. age, in weeks, for *Rhodnius prolixus* females; (a) and (b) use a logarithmic scale for mortality rate as required by the Gompertz model, but (c) and (d) use a double logarithmic scale as required by the Weibull model. Plots (a) and (c) use non-smoothed data, and (b) and (d) use smoothed data. Data used begins at week 7 of the original data, after independent random mortality has acted. Parameters for the regression line are given in Table 1.

of *R. prolixus*. In general, they are better than the assumption of a constant mortality rate that leads to an exponential decrease in l_x instead of a sigmoid one. Although the Weibull model gives the best fit for all data treatments, the Gompertz model has a biological mechanistic background (Carey, 2003; Carey and Judge, 2001), so we think that the fit to the latter could be improved with larger samples, like those of Carey et al. (1992), greater than thousand individuals.

The vectorial capacity of an insect is strongly affected by its longevity. Carey (2001) noted that the longer a vector lives, the greater the expectation that it will become infected, and a higher prevalence of infection in the insect vectors implies a higher probability of transmitting a disease. The probability of *T. cruzi* transmission to the host by fecal contamination during

feeding by a positive *Triatoma infestans* was estimated to be of the order of 0.0005 for humans (Rabinovich et al., 1990) and of the order of 0.06 for opossums (Rabinovich et al., 2001). As the average triatomine longevity, as determined by the mortality rate, plays an essential role in the transmission of Chagas disease, mortality and longevity aspects should be present in transmission studies of *T. cruzi* by triatomines.

Longevity also has to be considered when dealing with the study of bugs as reservoirs of *T. cruzi* infection to other bugs (i.e., horizontal transmission). In triatomines, there are evidences of horizontal transmission of parasites, from older to younger bugs (Ryckman, 1951; Marinkelle, 1965) and of a long lasting vectorial competence in fasting bugs (Takano-Lee and Edman, 2002). As adults of *R. prolixus* are

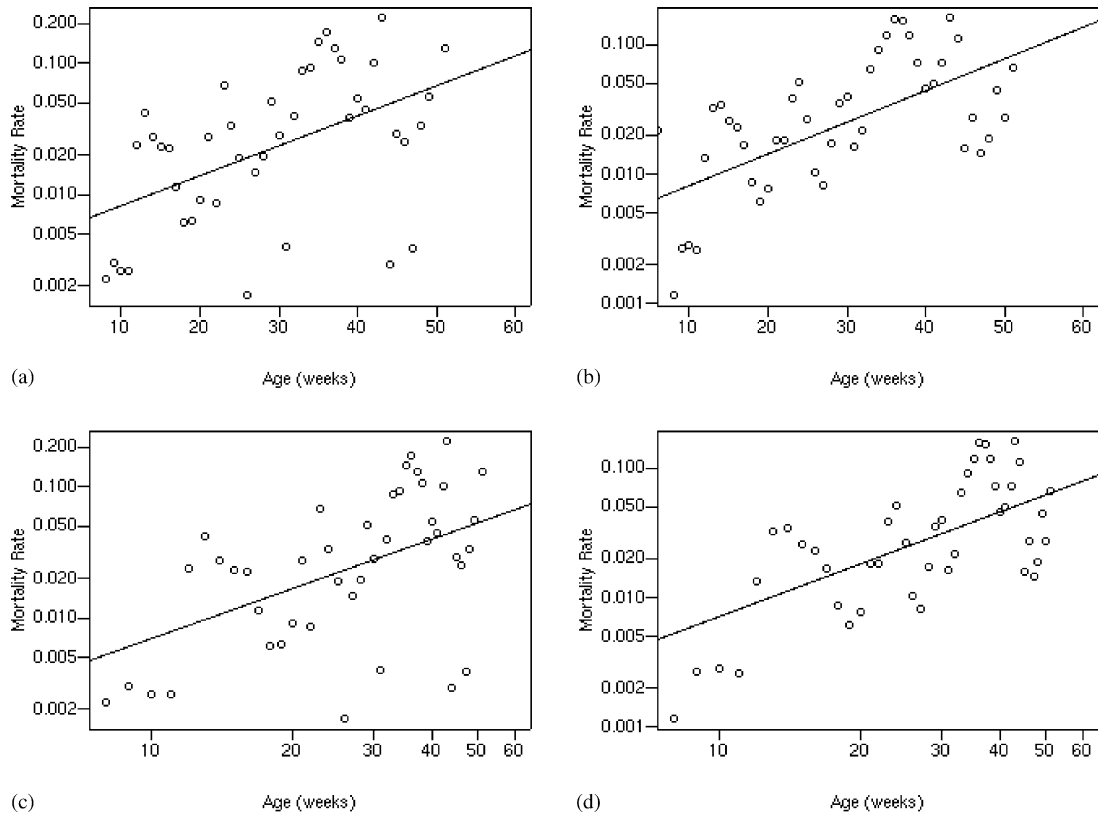


Fig. 3. Plots of mortality rate, in deaths/week, vs. age, in weeks, for *Rhodnius prolixus* males; (a) and (b) use a logarithmic scale for mortality rate as required by the Gompertz model, but (c) and (d) use a double logarithmic scale as required by the Weibull model. Plots (a) and (c) use non-smoothed data, and (b) and (d) use smoothed data. Data used begins at week 7 of the original data, after independent random mortality has acted. Parameters for the regression line are given in Table 2.

not the most abundant stage in domestic populations (Rabinovich et al., 1979) nor in palm trees (Felicangeli and Torrealba, 1977), and as fourth and fifth stage nymphs, the most abundant stages of *R. prolixus*, have greater defecation indices than older individuals (Zeledón, 1981; Takano-Lee and Edman, 2002) apparently adults would not be the main transmitting triatomine stage. However, a detailed knowledge of the relationship between mortality rates and life span extension might assess the potential of *T. cruzi* infection persistence in populations of bugs isolated from infected vertebrates, where parasitic transmission via hygrokleptism (feeding of hungry individuals upon engorged ones; Añez, 1982; Felicangeli de Piñero et al., 1988), might be a common phenomenon.

The mortality rate of an insect vector also has epidemiological importance through the demography of

the insect populations. In the particular case of triatomines, the transmission model of Chagas disease by Velasco-Hernández (1994) shows that the mortality rate of the bugs not only affects the vector population size but also impinges on the value of population density at equilibrium, as well as on R_0 , the basic reproduction ratio of the infection. In this ratio, the mortality rate of the bugs appears in the denominator and, being an instantaneous rate with values usually less than 1 (i.e., below its maximum theoretical value), its effect on the basic reproductive ratio of the infection is an important one. Velasco-Hernández (1994) also calculates a relative index that compares the effectiveness of vector species to transmit parasites using the ratio of the vector numbers to host numbers, before it spreads in the host population and after the steady state is reached. The formula of this index is directly affected by the

vector's mortality rate, which again appears in the denominator, and has been proposed to be used in the evaluation of the effectiveness of control strategies (Dye, 1990).

Sex differences of mortality slopes for each model and data treatment may explain the behaviour that we see in Fig. 1: males live longer than females, because the former have a lower mortality rate. A similar sex differential was found in the milkweed bug *Oncopeltus fasciatus* (Dallas) and the cotton stainer *Dysdercus fasciatus* Sign (Dingle, 1966). However, other studies indicate that mortality trajectories are facultative (e.g., Carey, 2003), because mortality is a life history trait that is affected by environmental conditions (Carey and Judge, 2001), in our case the rearing methods and experimental conditions of the insect laboratory colonies (Rodríguez and Rabinovich, 1980).

The mortality rates and sex differentials here evaluated provide a basic estimate under controlled laboratory conditions, and cannot be extrapolated to field and/or domestic conditions. Most surely the field and possibly also the domestic populations will evidence higher mortality rates than the ones fitted here to the Weibull and Gompertz models. An analysis similar to the one here conducted should also be carried out with sylvatic and domestic populations, particularly with *R. prolixus* and *Triatoma dimidiata* that show interacting sylvatic and domestic cycles, with populations that interchange between sylvatic and domestic biotopes (Gómez-Núñez, 1969; Zeledón, 1981; Dumonteil et al., 2002).

Finally, our results support the claim of Carey (2001) that standard formulae for estimating vectorial capacity should be modified or redefined to account for the age-dependent mortality pattern, providing more realism to these estimates.

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