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The Quest for Immortality in Triatomines: A Meta-Analysis of the Senescence Process in Hemimetabolous Hematophagous Insects

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1. Introduction

There are different views on senescence as a process. In its most general conception it represents the change in the biology of an organism as it ages. However this process may be viewed either at the physiological or at the demographic level. In the former sense senescence deals with changes affecting cells and tissues of the organism and their function and its effect on the organism as a whole (somatic senescence). In the demographic sense (actuarial senescence) the emphasis is in the population's survival decrease as a function of age (Promislow 1991, Tatar et al., 1993); this very general definition does not necessary imply somatic senescence (a physiological deterioration) because the organism may suffer an increased age-specific mortality rate because of an increased reproductive effort (Roff, 2002); the decrease in the reproductive performance with age may be termed reproductive senescence. Williams (1957), based on evolutionary arguments, claims that natural selection will frequently maximize vigor in youth at the expense of vigor later on and thereby he identifies senescence as a declination in vigor during adult life, using the term vigor as associated with a reproductive probability distribution. Here we are interested in this second approach to senescence, and we adhere to the definition of Rose (1991, cited in Roff 2002): "a persistent decline in the age-specific fitness components of an organism due to internal physiological deterioration".

According to Charlesworth & Partridge (1997) there are two main theories trying to explain the senescence process: (1) natural selection is less effective at reducing the frequency of later-acting mutations in populations, and so ageing is expected to evolve, and this is known as the "mutation accumulation" theory of ageing; (2) mutations that increase fitness at younger ages (perhaps because they increase fertility) but at the expense of decreasing

fitness at later ages (perhaps because they increase the death rate) can be incorporated into a population because natural selection will act more strongly on the earlier, beneficial effect. This is the reasoning behind the "antagonistic pleiotropy" or "trade-off" theory of ageing (Williams, 1957).

Abrams & Ludwig (1995), based on an extension of the "disposable soma" model (Kirkwood & Holliday, 1979), provide an explicit realization of the trade-off idea which postulates a conflict between the allocation of resources to reproduction and to the repair of somatic damage. A reduction in damage repair at a given age is assumed to cause an elevated death rate at all subsequent ages. Given a functional relationship between repair allocation and reproductive rate at a given age, the age-specific pattern of allocation to repair versus reproduction that maximizes life-time reproductive success can be determined, yielding a prediction of the age-specific pattern of mortality for the optimal life history (Charlesworth & Partridge, 1997).

Longevity and senescence patterns in mammals and birds are very variable according to the life-history of these organisms (Gaillard et al., 2004), and variation within and between phyla can be expected. Despite phylogenetic similarity is reciprocal to taxonomic level of relatedness (Cheverud et al., 1985) it is also possible that species phylogenetically related show different senescence and/or longevity patterns. So a comparative approach focused on the frequency of senescence in closely related species may contribute to our knowledge of the senescence process. Comparative studies in insects are scarce as compared to mammals and birds; within the insects, demographic analyses of senescence have been carried out mainly for the Diptera (Styer et al., 2007; Curtsinger et al., 1992; Carey et al., 1992, 2005; Fukui et al., 1993), and the Coleoptera (Tatar et al., 1993), and very few studies have considered hemimetabolous species (Dingle, 1966, Chaves et al., 2004a,b, Rabinovich et al., 2010).

In this chapter we investigate the frequency of senescence in a closely related species group of insects: the Triatominae (Hemiptera: Reduviidae). We compiled from the bibliography and resorted to personal data to have phylogeny and life history traits of 27 species reared under laboratory controlled and comparable conditions, and analyzed mortality and fecundity through several death and reproductive parameters. In particular we investigated: (a) species patterns of mortality with respect to age (from cohort studies that followed all individuals from the egg stage until the death of the last individual), (b) the relationship between mortality and different life-history traits (size, reproductive allocation), and (c) the relationship between mortality and environmental factors. Being the 27 selected triatomine species close relatives (they belonged to only five different genera), for our comparative study we included in the analysis a correction for the possible effect of the degree of phylogenetic relatedness.

The advantage of working on laboratory data is that we can estimate intrinsic mortality and fecundity rates without confounding effects resulting from extrinsic factors acting on mortality and fecundity (predation, accidental deaths, starvation, etc.). Even if work with triatomines has the advantage that under natural conditions all life stages occur in a single type of environment and have similar biological requirements, there is always the disadvantage that laboratory data does not reflect natural condition: insects are fed *ad libitum*, and predators, parasites and pathogens are kept out, so that it does not constitute

the best of conditions to detect trade-offs between reproductive effort and mortality. However, we think (in agreement with Mueller et al., 2005) that the identification of which aspects of the environment matter in the evolution of trade-offs can only be obtained by performing experiments in which these environmental variables are carefully manipulated; additionally, if even under such stable and near optimal conditions we are able to detect trade-offs, then our conclusions become much more robust.

Although life history traits such as fecundity, juvenile and adult survival, fasting capacity, developmental time, mortality patterns, and life span have been estimated under controlled conditions in the laboratory for a variety of triatomine species (about 500 scientific articles have been written on these aspects since 1910), very few studies have considered recent evolutionary ecology concepts (although see Menu et al., 2010) to shed some light on the trade-off aspects of life history traits. Understanding the mortality pattern in this group of insects is important both for academic and human health reasons. In the former sense we will provide elements to contribute to the theory of senescence and we discuss our results within of this theoretical background; in particular we will analyze the senescence pattern looking into the relationship between reproductive effort and mortality. In the latter sense, our analyses will provide information about a group of insects that are the vectors of Chagas disease, and represent a health threat estimated in 28 million people, living mostly in Latin America (see WHO, 2007).

2. Materials and methods

2.1 Demographic parameters

The basic information for the demographic parameters was obtained from a database compiled by one of us (JER). The original dataset comprised information on 534 case studies of triatomines representing 71 species; however, many of those cases had only partial information on demographic parameters and were not adequate for the present study. From the ones with complete information (55 cases) we selected 29 species that had relatively homogenous rearing conditions in the laboratory, to render them adequate for meta-analysis. The 29 species were later reduced to 27 species because two of them were not in the phylogenetic tree used for the application of the Phylogenetic Independent Contrast method (see section 2.4). The final list of species is shown in Table 1.

For each species we calculated basic life table parameters following Carey (2001): (i) age-specific survival or fraction alive at age x ($l_x = N_x / N_0$) (where N_x = number of individuals alive at age x), (ii) age-specific period survival or fraction alive at age x surviving to $x + 1$ ($p_x = l_{x+1} / l_x$), (iii) age-specific period mortality (probability of dying over the one-week interval used ($q_x = 1 - p_x$), and (iv) the force of mortality or instantaneous mortality rate ($\mu_x = -\ln(p_x)$). For more details on the definitions and formulae of the life table parameters see Rabinovich & Nieves (2011). The original values obtained from the laboratory (N_x , or number of individuals alive at age x , and M_x or total number of eggs laid by all females of the cohort aged x) were processed with a special program (called TriTV) developed by one of us (JER) that calculates the life table statistics and population growth rate parameters. As it is usual with laboratory cohorts, data of the last time-units of the cohorts are based on a very small number of individuals; thus the mortality rate estimated over the last living individual were excluded from the analysis, due to the unreliability of the mortality rate

estimates (Carey et al., 1992). The TriTV software was programmed in Delphi language, and is available under request to the second author (the interested user should have an adequate command of the Spanish language).

We considered of interest the division of the female's adult life in two, three or four periods of equal length, to analyze possible lag effects between reproductive effort and mortality. For that purpose, the reproductive effort (m_x = number of female eggs per female per unit time) and the instantaneous mortality rates (μ_x) were averaged for each of the periods in which the female's adult life was divided. We also accumulated mortality from the egg to the last adult female ($\sum \mu_x$) and the female's *per capita* fecundity ($\sum m_x$) to look for a relationship of one with respect to the other along the female's adult life (after scaling both between 0 and 1).

2.2 Mortality pattern models

For several reasons (see Rabinovich et al., 2010) we preferred the use of mortality analysis over survival analysis; in particular because we agree with Carey (2001) in that, despite mortality and survival are intimately related, death can be considered as an event whereas survival is a "non-event", that is, the absence of the mortality event. For the analysis of the age-specific mortality pattern of the 27 triatomine species selected for this study the following two mortality models were used with the formulation proposed by Carey (2001): the Gompertz model

$$\mu_x = a e^{bx}$$

and the Logistic model

$$\mu_x = (n x^{n-1}) / (g^n + x^n)$$

We also used a third model based on reliability theory as proposed by Gavrilov & Gavrilova (2001), but simplified to two parameters, and which, for simplicity, will be called hereafter "Gavrilovs". Its formulation is given as:

$$\mu_x = n k^n x^{n-1}$$

In all models x is the age (in our case in weekly time-units), and for the interpretation of the model's parameters, one of them usually represents the "base" mortality rate, and the other the shape of the function (more directly related to the rate of increase of mortality with age, also called the ageing parameter in the case of the Gompertz model). The reason we selected these three models among about a dozen available models for the analysis of mortality patterns, is that Rabinovich et al. (2010), fitting seven models to the instantaneous mortality rate to another triatomine species (*R. neglectus*), found that these three models offered the best fit to the data.

2.3 Model fitting to the data

We used several tools and procedures to fit the three models to the age-specific instantaneous mortality data (μ_x): (i) the R language (R Development Core Team, 2007), (ii) the Kolmogorov-Zurbenko Adaptive smoothing package (kza) in R language (used with parameter $q = 2$) (Zurbenko et al., 1996), (iii) the Statistica software (StatSoft, 2009),

(iv) the "Online Curve Fitting and Surface Fitting Web Site" (accessible at <http://ZunZun.com/>) (Christopoulos & Lew, 2000), and (v) the Solver utility of the Excel 2007 program. The reason for the variety of procedures resorted to for fitting the data, is that -even after smoothing- the age-specific instantaneous mortality data was quite irregular, and frequently a given software was not able to succeed in fitting the data to the models while another did. This would happen even if the parameter starting values for fitting the data would have been successfully estimated with the Solver utility of the Excel 2007 program. All software products used, if successful in fitting the data, provided the standard deviation of each parameter and the probability for deciding on the significance of the parameters' estimates. When more than one model fitted the data of the same species, the sum of squares ($SSQ = \sum (\mu_{obs} - \mu_{mod})^2$) was calculated and the model with the smallest SSQ was selected. We did not use the Akaike model selection criterion (Akaike, 1974) because the three models tested had the same number of parameters, so the SSQ goodness of fit values would not be affected by any penalty due to the number of degrees of freedom of each model.

2.4 Phylogenetic Independent Contrasts

Comparative studies, either among life-history traits or between those traits and environmental variables, frequently imply resorting to statistical methods such as regressions, correlations and contingency tables, which assume that the data is drawn from a common and independent distribution. However, the comparison among species that are related among each other with different degrees of phylogenetic relatedness does not necessary comply with this assumption. Methods are available to correct for this violation of the assumption of independence. For such purpose we used the Phylogenetic Independent Contrast method (Paradis, 2006) that corrects this violation when derived from phylogeny. The application of this method requires the topology of the phylogenetic tree, and an estimate of the degree of relatedness, generally expressed by the length of the branches of the phylogenetic tree. Calculations were carried out in language R using package "ape".

The phylogenetic tree used for this purpose was the one provided by Silva de Paula et al. (2005), who analyzed the Reduviidae phylogeny by aligning groups of sequences using Clustal-X under gap opening/gap extension penalties, and treating the gaps as missing. For Cladistic analysis Silva de Paula et al. (2005) used the programs PAUP and MacClade to derive trees based both on maximum parsimony (MP) and on maximum likelihood (ML); parsimony bootstrap values were conducted with PAUP employing heuristic search with 100 bootstrap replicates. Decay index for the strict consensus trees (Bremer support) were retained using the decay commands performed by the MacClade software with the heuristic search command activated, and executed with PAUP. This phylogenetic tree covered 57 species of Triatominae, and included 27 species of the 29 species we had selected from the demographic dataset (see section 2.1); thus *Triatoma breyeri* and *Panstrongylus lignarius* were deleted from the analysis, which remained composed by 27 species (Table 1).

3. Results

The following are the main results obtained from our analyses.

3.1 Demographic parameters

Table 1, provides a list of the species analyzed and some of their main environmental information (average annual temperature and precipitation) and provides information about rearing conditions of each species analyzed. In the last column the initial number of eggs (both sexes) with which each cohort was initiated is given; as the sex ratio at the egg stage cannot be established, it was assumed to be 50% for each sex (see Rabinovich et al., 2010 for a justification of this procedure). Initial cohort size was between 35 and 500 eggs (mean: 167 eggs/cohort). Because the senescence analysis was based on female mortality, the initial number for each species was assumed to be one half of original total number of eggs. Feeding frequency of all cohorts was once a week.

Species	Country of origin	Area of distribution (km ²)	Average annual temp. (°C)	Average precipitation (mm/year)	Laboratory rearing conditions			
					Temp. (°C)	R.H (%)	Feeding source	Initial Number of eggs
<i>Dipetalogaster maximus</i>	Mexico	36,074	22.2	198.42	28	70	pigeon	35
<i>Eratyrus mucronatus</i>	Venezuela	6,257,724	25.69	2340.64	26	60	chicken	200*
<i>Panstrongylus geniculatus</i>	Venezuela	12,040,606	24.45	1843.01	26	60	chicken	100
<i>Panstrongylus herreri</i>	Peru	354,387	21.46	1764.42	28	70	pigeon	105
<i>Panstrongylus megistus</i>	Brazil	3,739,358	22.55	1281.21	28	70	pigeon	96*
<i>Rhodnius nasutus</i>	Brazil	403,797	25.49	989.55	26	60	chicken	500*
<i>Rhodnius neglectus</i> ^a	Brazil	2,381,373	23.3	1318.39	26	60	chicken	500*
<i>Rhodnius neivai</i>	Venezuela	155,568	24.73	1347.3	26	60	chicken	100
<i>Rhodnius prolixus</i>	Colombia	5,281,236	25.46	2286.3	28	70	pigeon	102
<i>Rhodnius robustus</i>	Venezuela	3,133,393	25.68	2132.36	26	60	chicken	500*
<i>Triatoma delpontei</i>	Argentina	705,366	20.58	733.59	28	70	pigeon	108*
<i>Triatoma dimidiata</i>	Ecuador	2,176,134	24.26	1807.86	28	70	pigeon	45
<i>Triatoma eratyrusiformis</i>	Argentina	540,347	16.72	407.53	28	70	pigeon	112*
<i>Triatoma garciabesi</i>	Argentina	930,966	19.11	668.67	28	70	pigeon	132*
<i>Triatoma guasayana</i>	Argentina	1,412,079	19.38	747.88	28	70	pigeon	108*
<i>Triatoma infestans</i> ^b	Chile	5,198,083	19.26	957.3	26	60	chicken	500*
<i>Triatoma maculata</i> ^c	Venezuela	152,506	24.26	1421.51	26	60	chicken	50*
<i>Triatoma matogrossensis</i>	Argentina	205,258	22.3	815.29	28	70	pigeon	108
<i>Triatoma mazzotti</i>	Mexico	267,872	20.82	876.65	28	70	pigeon	56
<i>Triatoma pallidipennis</i>	Mexico	1,631,377	16.29	621.44	28	70	pigeon	138*
<i>Triatoma patagonica</i>	Argentina	53,047	20.5	915.06	28	65	pigeon	90
<i>Triatoma platensis</i>	Argentina	1,653,623	18.22	734	28	70	pigeon	126*
<i>Triatoma protracta</i>	USA	2,082,288	16.27	404.55	28	70	pigeon	68*
<i>Triatoma pseudomaculata</i>	Brazil	2,650,721	23.7	1198.89	28	70	pigeon	225*
<i>Triatoma rubrovaria</i>	Argentina	470,659	18.57	1472.36	28	70	pigeon	201*
<i>Triatoma sordida</i>	Brazil	4,408,479	22.25	1170.12	28	70	pigeon	120*
<i>Triatoma vitticeps</i>	Brazil	524,660	21.06	1352.76	28	70	pigeon	135*

Table 1. Natural environmental and laboratory rearing conditions of triatomine species selected for the analysis. R. H.=relative humidity. * Pool of several cohorts. Published sources: ^a Rabinovich & Nieves (2010), ^b Rabinovich (1972), ^c Feliciangeli & Rabinovich (1985); for *T. patagonica* original data from Dr. Elena Visciarelli; the rest of species: original data from this study.

Fig. 1 shows the instantaneous mortality and the fecundity rates of the 27 triatomine species analyzed. The senescence pattern is clear: instantaneous mortality rates stay at extremely low levels during most of the juvenile stages (except in the egg stage for some species) and during the first part of the adult stage, increasing greatly in the old ages (i.e., for old females). Most triatomine species seem to invest more in reproduction during the earlier and intermediate periods (but in general with lower effort) of the female's life. Only three species (*R. nasutus*, *R. neivai* and *D. maximus*) seem to invest more in the intermediate ages. However, six species (*T. eratyrusiformis*, *T. mazzotti*, *T. platensis*, *T. sordida*, *E. mucronatus*, and *P. geniculatus*) invest in reproduction during all periods of the reproductive life of the female. The difference in the reproductive effort pattern seem to be related to particular genera.

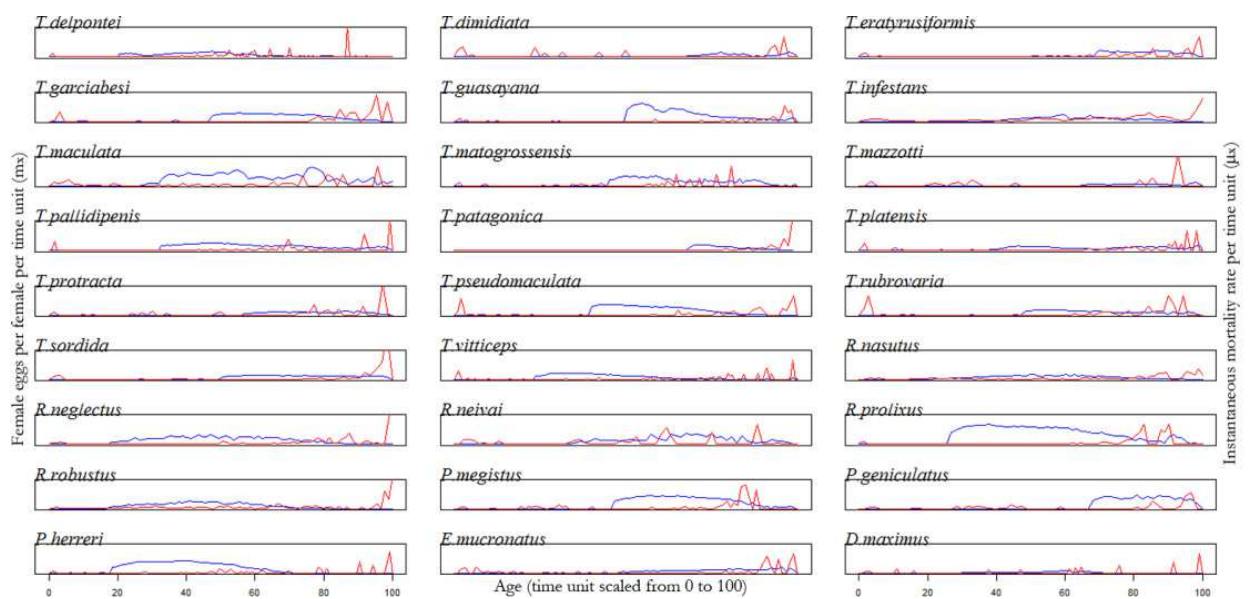


Fig. 1. Age-specific fecundity and instantaneous mortality rates for 27 triatomine species.

Age-specific fecundity (blue lines) and instantaneous mortality rates (red lines) for the 27 species analyzed. All species have a common scale for fecundity and mortality. Fecundity is represented in a scale from 0 to 25 ♀ eggs/♀/unit-time (not shown for better clarity); mortality is represented in a scale from 0 to 1 per unit-time; the x-axis is the age, originally in weeks, but scaled from 0 to 100 to have a common scale for all species.

3.2 Reproductive effort and mortality relationship

Fig. 2 shows the female adult accumulated mortality ($\sum \mu_x$) with respect the female adult accumulated fecundity ($\sum m_x$), both scaled from 0 to 1, in the form of a scatterplot ($\sum \mu_x$ vs $\sum m_x$); to facilitate interpretation of the different patterns, the scatterplots for all species were drawn in the same scale and with a 45° line to be used as a frame of reference. From those graphs we defined six groups with respect of the $\sum \mu_x$ vs $\sum m_x$ observed patterns. Despite the relationships differ among the species of the six groups, the species classed in the first five groups invest strongly in reproduction before a high mortality has been accumulated to a high degree (most of the curves stay below the 45° line) although with increased initial

female adult mortality from Group 1 to Group 5; while Group 6 (*R. neivai*) has a different pattern with a curve that stays above this line during a long period, indicating no significant reproductive accumulation effort in relation to the accumulated mortality rate

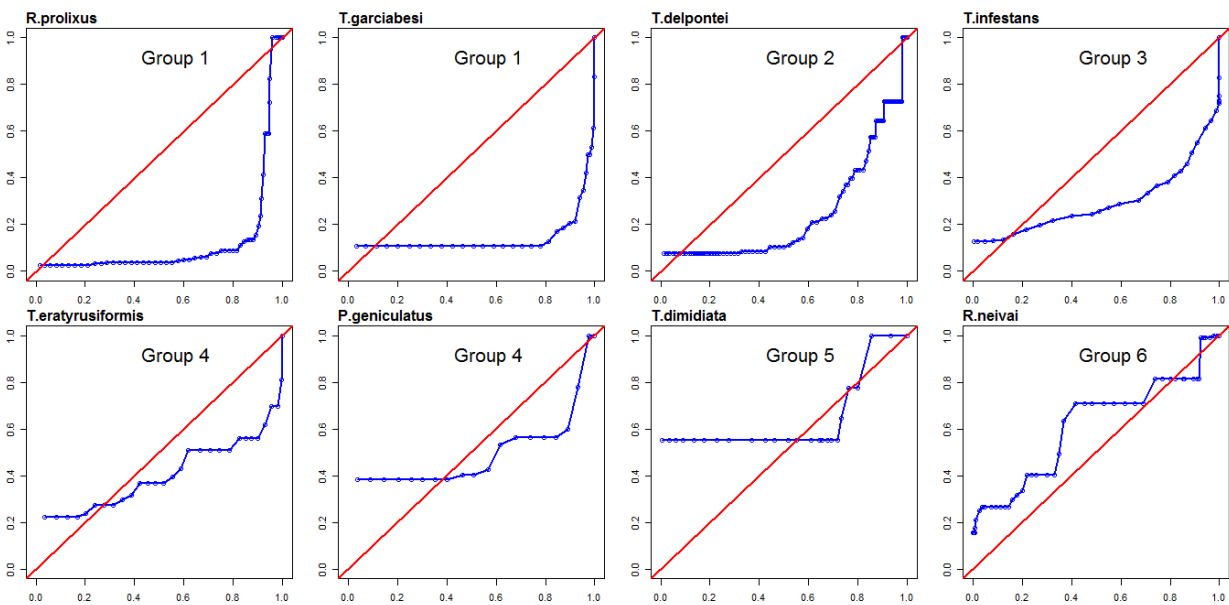


Fig. 2. Grouping of the accumulated mortality and accumulated fecundity relationship

Female adult accumulated instantaneous mortality rate ($\sum \mu_x$) (y- axis) with respect to the female adult accumulated fecundity ($\sum m_x$) (x- axis) (blue line), both scaled from 0 to 1. The 45° line was drawn as a reference (red line). Only selected species representative of each group are shown. For the criteria for grouping and description of the groups see text.

The species classed in first group (n=11) are: *T. garciabesi*, *T. guasayana*, *T. pallidipennis*, *T. vitticep*, *T. pseudomaculata*, *T. sordida*, *R. neglectus*, *R. prolixus*, *E. mucronatus*, *D. maximus* and *P. herreri*; in the second group (n=8): *T. delpontei*, *T. platensis*, *T. rubrovaria*, *T. pallidipennis*, *T. protracta*, *T. matogrossensis*, *T. mazzotti* and *P. megistus*; in the third group (n=4): *T. infestans*, *T. maculata*, *R. nasutus* and *R. robustus*; in fourth group (n=2): *T. eratyrusiformis* and *P. geniculatus*; in fifth group (n=1): *T. dimidiata*, and in last group (n=1): *R. neivai*.

3.3 Mortality pattern models

Table 2 shows the coefficients of the fit of the kza- smoothed instantaneous mortality rate (μ_x) to the three mortality models tested (Gavrilovs, Gompertz, and Logistic). Asterisks indicate a statistically significant coefficient with $p < 0.05$. The squared residuals (SSQ) are also shown. Certain mortality models could not be fitted to the instantaneous mortality rate data of some species; additionally, no single model fitted the mortality pattern of all species (Fig. 3, Table 2).

The fit is statistically significant for 14 out of 15 successful fits, for 10 out of 18 successful fits, and for 20 out of 21 successful fits, for the Gavrilovs, Gompertz, and Logistic models, respectively. From the results of the model fitting, Fig. 3 shows three main types of mortality

patterns. A first group (Group I) shows a mortality pattern that we called “Late-spiky senescence” and is defined by a very long period in which the mortality rates are low and stable, with a high increase in the mortality rate at the end of the adult female life. In a second group, called “Gradual-medium senescence” (Group II), the increase in the mortality rate with age is more progressive than in the Group I and the mortality rate values stay at an intermediate level. In these two groups, no stabilization of mortality rate occurs at old age.

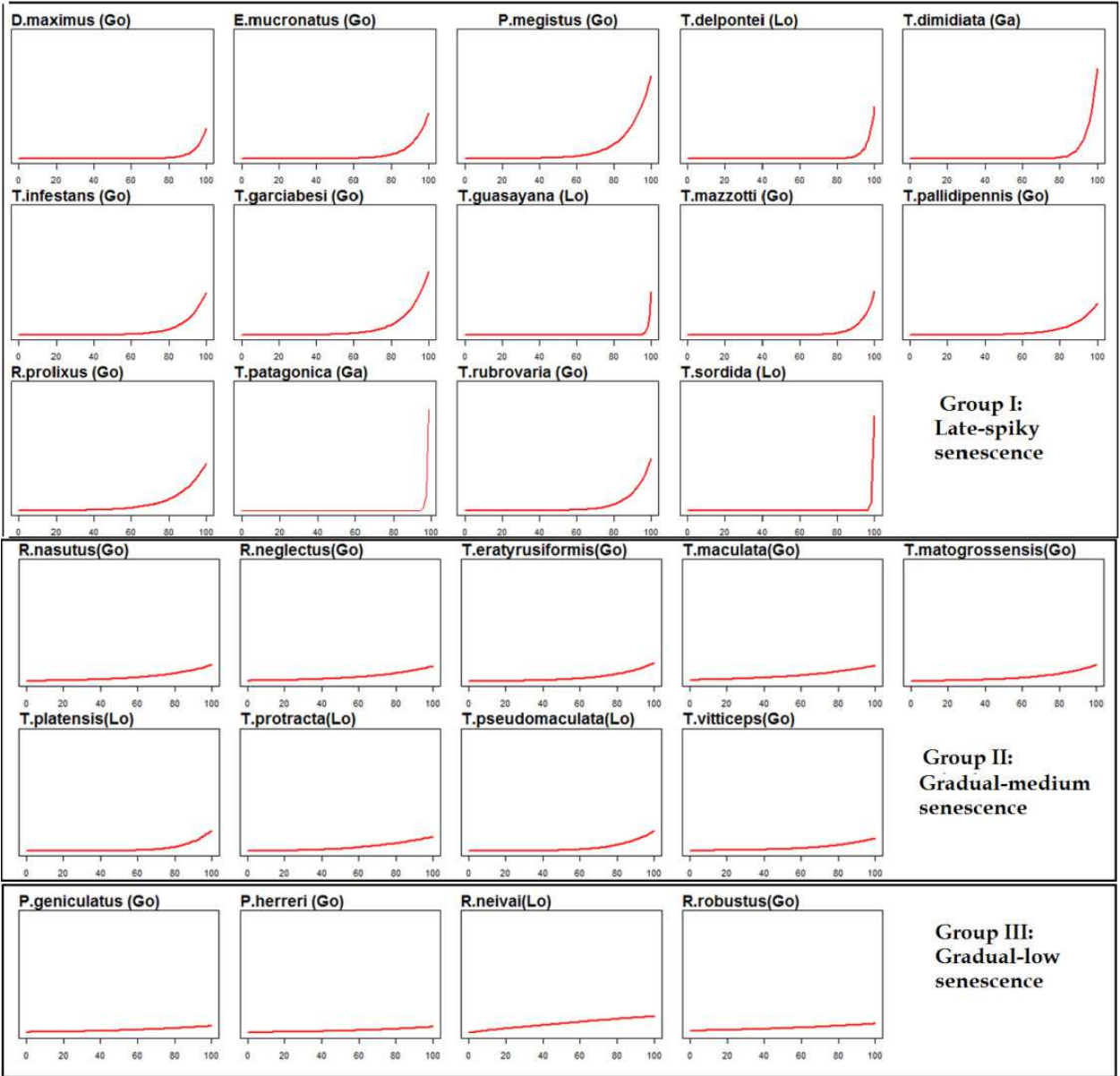


Fig. 3. Age specific mortality patterns of 27 species of triatomines.

The abbreviations in parenthesis indicate the best model that fitted the age-specific instantaneous mortality rate (Go= Gompertz, Lo= Logistic, and Ga= Gavrilovs). Axes have a common scale: from 0 to 1 in the ordinates (not shown) and from 0 to 100 in the abscissa; the latter covers from the egg stage to the last female adult alive.

Species	Gavrilovs model			Gompertz model			Logistic model		
	K	n	SSQ	a	b	SSQ	n	g	SSQ
<i>D. maximus</i>	6.7E-03*	18.78*	1.7E-01	1.5E-09*	1.6E-01*	1.7E-01	18.94*	149.8*	1.7E-01
<i>E. mucronatus</i>	-	-	-	1.6E-06*	1.4E-01*	1.8E-01	11.76*	115.3*	1.7E-01
<i>P. geniculatus</i>	6.7E-03*	18.78*	5.1E-02	1.1E-02*	9.3E+00*	4.8E-02	0.57	3310.3	5.0E-02
<i>P. herreri</i>	-	-	-	7.4E-03*	1.6E-02*	7.2E-02	-	-	-
<i>P. megistus</i>	1.1E-02*	8.18*	3.1E-01	7.9E-05*	1.4E-01*	3.3E-01	8.52*	85.7*	3.0E-01
<i>R. nasutus</i>	4.9E-03*	3.46*	9.4E-02	3.6E-03*	4.5E-02*	8.7E-02	3.56*	200.1*	9.4E-02
<i>R. neglectus</i>	-	-	-	5.0E-03*	3.9E-02*	7.6E-02	2.64*	260.3*	7.1E-02
<i>R. neivai</i>	2.0E-03	0.82	4.6E-01	-	-	-	0.93*	374.1*	4.6E-01
<i>R. prolixus</i>	8.5E-03*	6.32*	7.2E-02	2.6E-04	9.7E-02*	1.7E-01	6.49*	115.8*	1.6E-01
<i>R. robustus</i>	-	-	-	2.1E-02*	1.6E-02*	3.2E-01	-	-	-
<i>T. delpontei</i>	6.1E-03*	29.39*	3.2E-01	-	-	-	29.59*	162.7*	3.2E-01
<i>T. dimidiata</i>	1.2E-02*	28.09*	6.1E-01	-	-	-	-	-	-
<i>T. eratyrusiformis</i>	-	-	-	1.3E-03	5.1E-02*	1.3E-01	3.65*	225.2*	1.4E-01
<i>T. garciabesi</i>	1.2E-02*	8.49*	7.8E-02	4.1E-05	1.5E-01*	8.7E-02	8.72*	85.6*	7.6E-02
<i>T. guasayana</i>	8.9E-03*	88.89*	7.4E-02	-	-	-	89.28*	111.7*	7.4E-02
<i>T. infestans</i>	2.3E-02*	11.85*	5.8E-02	6.0E-06	3.3E-01*	5.4E-02	-	-	-
<i>T. maculata</i>	4.2E-03*	2.10*	1.3E-01	1.0E-02*	4.0E-02*	1.3E-01	2.18*	222.8*	1.3E-01
<i>T. matogrossensis</i>	-	-	-	2.6E-03*	4.1E-02*	7.7E-02	3.07*	270.4*	7.9E-02
<i>T. mazzotti</i>	-	-	-	2.8E-08	3.3E-01*	7.9E-02	15.69*	63.6*	7.7E-02
<i>T. pallidipennis</i>	-	-	-	5.8E-05	7.0E-02*	4.3E-01	-	-	-
<i>T. patagonica</i>	1.3E-02*	137.98*	2.0E-02	-	-	-	-	-	-
<i>T. platensis</i>	5.8E-03*	7.71*	7.9E-02	-	-	-	7.78*	172.5*	7.9E-02
<i>T. protracta</i>	-	-	-	-	-	-	2.96*	192.7*	1.5E-01
<i>T. pseudomaculata</i>	-	-	-	-	-	-	5.64*	163.4*	1.2E-01
<i>T. rubrovaria</i>	1.1E-02*	10.33*	1.8E-01	8.2E-06	1.7E-01*	1.8E-01	10.59*	86.6*	1.8E-01
<i>T. sordida</i>	-	-	-	-	-	-	146.65*	60.1*	4.3E-02
<i>T. vitticeps</i>	-	-	-	1.9E-03	2.8E-02*	2.0E-01	3.29*	406.0*	1.9E-01

Table 2. Fit to the Gavrilovs, Gompertz, and Logistic mortality models.

Parameter values of the mortality models fitted to the laboratory instantaneous mortality rates (μ_x). A “*” indicates a statistically significant coefficient of $p < 0.05$. $SSQ = \sum (\mu_{obs} - \mu_{mod})^2$. A “-” indicates that the model could not be fitted to the data.

The third group (Group III), which we called “Gradual-low senescence”, is defined by a low and progressively increasing instantaneous mortality rate with age. In this group, particularly in *R. neivai*, the mortality rate seems to stabilize at old ages. The senescence pattern variation does not seem to be homogeneous for a given genus: all senescence pattern groups seem to occur in all genera, particularly in the dominant ones (*Triatoma*, *Rhodnius*).

3.4 Phylogenetic Independent Contrasts

The results of a series of phylogenetic independent contrasts among several dependent variables related to mortality and other variables related to the longevity and reproduction of the triatomines are shown in Tables 3-10. For a better illustration about the phylogenetic relationships we present (Fig. 4) the phylogenetic tree provided by Silva de Paula et al. (2005) but restricted to the 27 species used in our analysis. In Fig. 4 numbers close to the

bifurcations identify each node of the phylogenetic tree. Numbers above the branches indicate the length of each branch, estimated by a branch length/decay index (Bremer support); it is proportional to the distance to ancestors. To the right of each species there is a label with a roman numeral corresponding to the Group into which each species has been classified as following a certain age-specific mortality pattern (Group I= “Late-spiky senescence”; Group II= “Gradual-medium senescence”, and Group III= “Gradual-low senescence”; see Section 3.3 for definition of each group).

No significant relationship exists between the female’s post reproductive period (FPRP) and the total length of adults or the age of first reproduction (non scaled, weeks) (Table 3). The relationship is statistically significant and positive between FPRP and the age of first reproduction scaled by total longevity. A statistically significant and negative correlation exists between FPRP and the female’s reproductive period (scaled by longevity), the female reproductive life period (weeks, i.e., not scaled), and fecundity (expressed as ♀ eggs/♀/life).

Independent variables	Coefficient	Std Dev	t value	p
Female’s reproductive period (longevity scaled)	-0.12288	0.05419	-2.26754	0.03226
Total length of adults (mm)	-0.00362	0.00192	-1.88994	0.07042
Female reproductive life period (weeks)	-0.00113	0.00043	-2.61769	0.01481
Fecundity (♀eggs/♀/life)	-0.00007	0.00002	-2.84123	0.00881
Age of first reproduction (weeks) (α)	0.00068	0.00107	0.64255	0.52636
α scaled by total longevity	0.11125	0.04857	2.29050	0.03070

Table 3. Female’s post-reproductive period regressed on several independent variables

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of several independent variables on the female’s post-reproductive period (scaled in terms of lifespan) using 27 species of triatomines.

Therefore, the female’s post reproductive period decreases with reproductive effort, which means that females live less after their last reproduction in those triatomine species in which the reproductive effort is high.

We show in Table 4 a statistically significant and negative correlation between the mean instantaneous mortality rate (called hereafter $\bar{\mu}_x$) and the average total female longevity since the egg stage, but no statistically significant relationship with the female's total length.

Independent variable	Coefficient	Std. Error	t value	p
Total average ♀ longevity (from the egg stage)	-0.00070	0.00014	-4.86	5.0E-05
Total length (mm)	-0.00076	0.00105	-0.73	0.4740

Table 4. Mean instantaneous mortality rate ($\bar{\mu}_x$) regressed on longevity and total length
Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of average female longevity and total body length as independent variables on the mean instantaneous mortality rate ($\bar{\mu}_x$).

Two indicators of mortality, total mean female mortality ($1/e_0$) and the mean female mortality after the first reproduction ($1/e_\alpha$), are significantly correlated to two reproductive effort indicators (total eggs per female per life and reproductive weeks of females), decreasing with higher reproductive effort (Table 5). The mortality indicator $1/e_0$ is statistically significant and negatively correlated with both reproductive effort indicators used. Therefore, the total mean female mortality seems to decrease with the reproductive effort.

Dependent variables: total mean ♀ mortality ($1/e_0$)				
Independent variable	Coeff.	Std. Err.	T value	p
Total eggs/♀/life	-2.7E-05	2.5E-06	-11.05	4.1E-11
Reproductive weeks of ♀	-0.00092	0.00012	-7.96	2.6E-08
Dependent variable: mean ♀ mortality after first reproduction ($1/e_\alpha$)				
Independent variable	Coeff.	Std. Err.	T value	p
Total eggs/♀/life	-3.0E-05	4.5E-06	-6.72	4.8E-07
Reproductive weeks of ♀	-0.00127	9.4E-05	-13.54	5.2E-13

Table 5. Two indicators of mortality rate regressed on two reproductive effort variables

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of reproductive effort indicators as independent variables on two measures of mortality using 27 species of triatomines. The parameter e_0 is the expectation of life at birth (weeks).

Independent variable	Coefficient	Std	t value	p
Average ♀eggs/♀/week	-0.01099	0.07154	-0.15368	0.87979
Average ♀eggs/♀/life	0.00076	0.00133	0.56869	0.57746
α scaled by total longevity	-0.67365	0.89178	-0.75539	0.46099
α scaled by lifespan	-0.98590	0.87855	-1.12219	0.27834
Age of first reproduction (weeks) (α)	-0.01470	0.01375	-1.06885	0.30100
Total female longevity (weeks)	0.00478	0.00692	0.69122	0.49933
Total length (mm)	-0.03625	0.02683	-1.35086	0.19554

Table 6. The parameter b of the Gompertz model regressed on several independent variables

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of several independent variables on the parameter b of the Gompertz mortality model. The phylogenetic tree used was reduced to the 18 species with $\bar{\mu}_x$ data that could be fitted to the Gompertz model. α represents the female’s age (weeks) of first reproduction.

No statistically significant relationship was observed between the parameter b of the Gompertz mortality model (which is related to the shape of the mortality pattern) and the life history traits indicated in Table 6. Additionally, no statistically significant correlation was observed between the parameter b of the Gompertz mortality model and the geographic and/or climatic variables indicated in the table (Table 7).

Independent variable	Coefficient	Std Dev	t value	p
Surface area	-0.02572	0.02877	-0.89415	0.38449
Average annual precipitation (mm)	0.00027	0.00023	1.19358	0.25004
95% Lower precipitation (mm)	0.00029	0.00043	0.66386	0.51623
95% Upper precipitation (mm)	0.00021	0.00014	1.52282	0.14732
Colwell's precipitation index of predictability	2.40489	2.66950	0.90088	0.38101
Precipitation coefficient of variation (%)	0.03058	0.02010	1.52139	0.14768
NDVI coefficient of variation (%)	-0.11072	0.12554	-0.88195	0.39086
Maximum rain of the rainiest month (mm)	0.00405	0.00520	0.77925	0.44721
Minimum rain of the driest month (mm)	0.00204	0.00170	1.20070	0.24734

Table 7. The b Gompertz model parameter regressed on geographic/climatic variables

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of several climatic variables used as independent variables on the parameter b of the Gompertz model. The phylogenetic tree was reduced to the 18 species with $\bar{\mu}_x$ that could be fitted to the Gompertz model. The NDVI is the Normalized Difference Vegetation Index.

Table 8 shows that from several geographic and/or climatic variables analyzed only the surface area and various precipitation indicators are correlated (negatively) with the mean mortality rate (defined here as $1/e_0$), while with the coefficient of variation (in %) of the Normalized Difference Vegetation Index (NDVI, a common indicator of live green vegetation obtained from satellite data) it was found to be positively correlated. In other words, species' geographical range size and some climatic factors, mainly the ones related to precipitation, seem to be related to mean mortality.

However, mortality ($1/e_0$) is probably not a good estimator of mean mortality because in our data the mortality rate varies greatly with age and this violates the hypothesis underlying this parameter as estimator of mean mortality rate. In consequence, we also used a more reliable estimator of the mean mortality rate from our data: the average for different time periods of the female's adult life ($\bar{\mu}_x$) (see Tables 9 and 10).

Independent variables	Coefficient	Std Err	t value	p
Surface area (km²)	-0.00140	0.00022	-6.43226	9.8E-07
Modal latitude (degrees)	0.00034	0.00022	1.54316	0.13536
Modal longitude (degrees)	0.00025	0.00021	1.20700	0.23900
Average altitude (m)	1.1E-05	1.1E-05	1.05245	0.30266
Average annual temperature (°C)	-0.00060	0.00180	-0.33135	0.74315
Minimum annual temperature (°C)	0.00162	0.00137	1.18693	0.24641
Maximum annual temperature (°C)	0.00225	0.00210	1.07133	0.29425
Average annual precipitation (mm)	-1.5E-05	4.2E-06	-3.56725	0.00149
95% Lower precipitation (mm)	-2.6E-05	7.7E-06	-3.33849	0.00264
95% Upper precipitation (mm)	-9.3E-06	2.7E-06	-3.47074	0.00190
Colwell's rain index of predictability	-0.15913	0.04713	-3.37684	0.00240
Rain coefficient of variation (%)	0.00114	0.00044	2.61404	0.01494
Temperature amplitude (°C)	0.00047	0.00121	0.38703	0.70201
Temperature coefficient of variation (%)	0.00072	0.00055	1.30837	0.20265
Average annual NDVI	-0.05010	0.03350	-1.49561	0.14727
NDVI coefficient of variation (%)	0.00804	0.00263	3.06192	0.00520
Average AET (mm)	-0.00023	0.00015	-1.47877	0.15169
Minim temperature of coldest month (°C)	0.00088	0.00093	0.94976	0.35133
Maximum temperature of the warmest month (°C)	-9.8E-05	0.00272	-0.03617	0.97144
Maximum rain of the rainiest month (mm)	-0.00033	0.00008	-3.99956	0.00050
Minimum rain of the driest month (mm)	-0.00011	3.2E-05	-3.26415	0.00317
Number of dry months/year	0.00197	0.00108	1.83082	0.07907
Number of humid months/year	0.00214	0.00181	1.18209	0.24829
Number of super-humid months/year	-0.00200	0.00089	-2.25957	0.03282

Table 8. Average mortality (1/e₀) regressed on various geographic/climatic variables

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of several climatic variables used as independent variables on the average mortality (1/e₀) using 27 species of triatomines.

The results obtained from the regressed of mean instantaneous mortality rate $\bar{\mu}_x$ were statistically non-significant with respect to the mean reproductive effort (first line in Table 9). However, if we divide the individual female adult life in two, three or four periods of equal length, some correlations between $\bar{\mu}_x$ for a given period and the mean reproductive effort for the same period are statistically significant and positive (Table 9 except the first line). Furthermore, we observe several significant positive correlations between $\bar{\mu}_x$ for a given period and the reproductive effort in the previous period(s) (Table 10). For instance, when divided in two periods, the $\bar{\mu}_x$ value in the second period is significantly and positively correlated to the reproductive effort during the first period (first line in Table

10) or during the first and second ones (second line in Table 10). Similarly, when divided in three periods, the $\bar{\mu}_x$ value of the third period is significantly and positively correlated to the reproductive effort during the all three periods (lines 4 and 6 in Table 10). Similarly for four periods.

Independent variable	Dependent variable	Coefficient	Std Err	t value	p
\bar{m}_x 1/1	$\bar{\mu}_x$ 1/1	0.00021	0.001126	0.187	0.85354
\bar{m}_x 1/2	$\bar{\mu}_x$ 1/2	-0.00556	0.00047	-11.96	7.7E-12
\bar{m}_x 2/2	$\bar{\mu}_x$ 2/2	0.01840	0.00501	3.67	0.00115
\bar{m}_x 1/3	$\bar{\mu}_x$ 1/3	-0.00266	0.00027	-9.75	5.3E-10
\bar{m}_x 2/3	$\bar{\mu}_x$ 2/3	-0.00696	0.00212	-3.29	0.00300
\bar{m}_x 3/3	$\bar{\mu}_x$ 3/3	0.02206	0.00813	2.71	0.01190
\bar{m}_x 1/3	$\bar{\mu}_x$ 2/3	-0.00437	0.00062	-7.00	2.0E-07
\bar{m}_x 2/3	$\bar{\mu}_x$ 3/3	0.01603	0.00327	4.91	4.7E-05
\bar{m}_x 1/4	$\bar{\mu}_x$ 1/4	-0.00216	0.00022	-9.60	7.3E-10
\bar{m}_x 2/4	$\bar{\mu}_x$ 2/4	-0.01076	0.00103	-10.41	1.4E-10
\bar{m}_x 3/4	$\bar{\mu}_x$ 3/4	0.00910	0.00678	1.34	0.37520
\bar{m}_x 4/4	$\bar{\mu}_x$ 4/4	0.02308	0.00877	2.63	0.01438
\bar{m}_x 1/4	$\bar{\mu}_x$ 2/4	-0.00769	0.00066	-11.73	1.2E-11
\bar{m}_x 2/4	$\bar{\mu}_x$ 3/4	0.01196	0.00148	8.07	2.0E-08
\bar{m}_x 3/4	$\bar{\mu}_x$ 4/4	0.00822	0.00607	1.35	0.23480

Table 9. Average mortality and fecundity variables lagged by periods

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of average fecundity (\bar{m}_x) on the average instantaneous mortality rates ($\bar{\mu}_x$) by periods of equal length (see text) using 27 species of triatomines.

Independent variable	Dependent variable	Coefficient	Std Err	t value	p
\bar{m}_x 1/2	$\bar{\mu}_x$ 2/2	0.00528	0.00121	4.38	0.00019
\bar{m}_x 1+2/2	$\bar{\mu}_x$ 2/2	0.01071	0.00197	5.45	1.2E-05
\bar{m}_x 1+2/3	$\bar{\mu}_x$ 2/3	-0.00583	0.00102	-5.73	5.7E-06
\bar{m}_x 1+2/3	$\bar{\mu}_x$ 3/3	0.00960	0.00203	4.73	7.5E-05
\bar{m}_x 2+3/3	$\bar{\mu}_x$ 3/3	0.02390	0.00489	4.89	4.9E-05
\bar{m}_x 1+2+3/3	$\bar{\mu}_x$ 3/3	0.01430	0.00276	5.18	2.3E-05
\bar{m}_x 1+2/4	$\bar{\mu}_x$ 2/4	-0.00903	0.00079	-11.37	2.3E-11
\bar{m}_x 1+2/4	$\bar{\mu}_x$ 3/4	0.00970	0.00128	7.56	6.5E-08
\bar{m}_x 2+3/4	$\bar{\mu}_x$ 3/4	0.02099	0.00267	7.85	3.3E-08
\bar{m}_x 2+3/4	$\bar{\mu}_x$ 4/4	0.00450	0.00436	1.03	0.21760
\bar{m}_x 1+2+3/4	$\bar{\mu}_x$ 3/4	0.01455	0.00176	8.25	1.3E-08
\bar{m}_x 1+2+3/4	$\bar{\mu}_x$ 4/4	0.00231	0.00301	0.77	0.47810
\bar{m}_x 1+2+3+4/4	$\bar{\mu}_x$ 4/4	0.00374	0.00383	0.98	0.31270

Table 10. Accumulated average mortality and fecundity variables lagged by periods

Simple lineal regression results, using the Phylogenetic Independent Contrast method, of the effect of accumulated average fecundity on the accumulated average instantaneous mortality rates by periods of equal length (see text) using 27 species of triatomines.

4. Discussion

The following are our concepts on triatomine senescence in the light of evolutionary ecology.

4.1 Senescence in the triatomines

Since the first attempt to explain evolution of ageing was made by Weismann (1891, cited in Kirkwood & Holliday 1979) senescence has been a major topic of research in evolutionary ecology, both from an experimental and a theoretical approach. Being such a general area of investigation it is not surprising that it has relied strongly on the use of a comparative approach across a wide range of taxa. The phylogenetic variation in rates of senescence has been considered a consequence of a combination of factors that decrease the rate of decline in reproductive probability (and intensifying selection against senescence) and factors that increase this rate (relaxing selection against senescence). We applied a comparative meta-analyses approach within a single subfamily (Triatominae) correcting, for the first time in this group, the regression analyses by the phylogeny.

Williams (1957) has argued that the rate of senescence shown by any species will reflect the balance between a direct adverse selection of senescence as an unfavorable character, and an indirect, favorable selection through the age-related bias in the selection of pleiotropy genes. Thus positive variations in fecundity increase adult mortality rate, and affect other life-history traits (e.g., the shape of the distribution of reproductive effort with age) and thereby influence the evolution of senescence and phylogenetic variation. This theory predicts that (a) rapid morphogenesis should be associated with rapid senescence, (b) that senescence should always be a generalized deterioration of many organs and systems, and (c) that post-reproductive periods should be short and infrequent in any wild population. The latter prediction seems to have been confirmed in the case of triatomines (at least in the laboratory). This is another reason why, despite having selected for our study a relatively low taxonomic level (the species of only five genera, so we can expect a strong degree of phylogenetic relatedness), it is important to have the phylogeny included in these comparisons.

Our study shows that the 27 triatomine species analyzed present a senescence pattern that does not decrease at older ages. Mortality rate stays very low during most of the juvenile stages (except in the egg stage for some species) and during the first part of adult stage, and then increases greatly in the old ages in most species. This senescence pattern observed in triatomine species are in contrast with patterns reported for various Diptera: *Drosophila melanogaster* (Curtsinger et al., 1992; Pletcher & Curtsinger, 1998), *Ceratitis capitata* (Carey et al., 1992, 1998), *Anastrepha ludens* (Carey et al., 2005), and *Aedes aegypti* (Styer et al., 2007).

The mortality pattern of triatomines (Chaves et al., 2004a, Rabinovich et al 2010, and this study) seems to be more similar to that reported in *Oncopeltus fasciatus* (Dingle, 1966), *Dysdercus fasciatus* (Dingle, 1966), and *Callosobruchus maculatus* (Tatar et al., 1993) and is

consistent with models of senescence based on the decline in physiological functions with age (known as the "disposable soma" theory for the evolution of senescence; Kirkwood & Holliday, 1979; Kirkwood & Rose, 1991; Kirkwood & Austad, 2000; Kirkwood, 2002), which can be considered a consequence of the equilibrium predictions of the antagonistic-pleiotropy and mutation accumulation hypotheses (Abrams & Ludwig, 1995).

In our comparative analysis we have used several measures of mortality. Although the use of the Gompertz model to describe the acceleration of mortality with age has been a matter of debate (Nusbaum et al., 1996), for a comparative study this model seems more sound than, e.g., maximum lifespan, particularly because of the sensitivity of maximum lifespan to the initial numbers of a cohort. Nusbaum et al. (1996) have analyzed the evolutionary relationships among several measures of mortality (Gompertz parameters, and average and maximum longevity) in 50 related populations of *D. melanogaster*; they included populations that had been selected for postponed aging and in their conclusions they give credit to a redundancy among these measures of aging, and consider that both the maximum lifespan and the Gompertz equation as adequate indices of aging in evolutionary research. This gives support to their use in our study.

4.2 High variation in senescence pattern

Our results show that the mortality pattern with age varies greatly among triatomine species (showing late-spiky, gradual-medium, and gradual-low senescence) despite our study was based on cohorts reared under very homogeneous environmental conditions; the present challenge is to understand which are the ultimate factors underlying such diversity of mortality patterns in triatomines (Fig. 3). These different patterns are observed in all the species we studied, even in the more phylogenetic related species within any given genus (Fig. 4). We do not dismiss the possibility that the small initial number of eggs of some cohorts may have played a role in the estimation of demographic parameters (e.g. threshold mortality) (Carey, 2001), and thus in the high degree of mortality patterns variability; however, we still think that the variability found is genuine and could reflect multiple underlying causes.

Despite most of the studied species show "late-spiky" (n= 14) or "gradual-medium" senescence (n= 9), the species in the "gradual-low" group (n= 4), particularly *R. neivai*, seem to show a weak late-life mortality plateau. Some demographic findings point to the existence of a late-life mortality plateau in a few dipteran insects (Mueller & Rose, 1996), with both antagonistic pleiotropy and mutation accumulation as driving population genetic mechanisms; this late-life attribute is a switch from accelerating mortality to a relatively stable mortality (Rauser et al., 2006); such plateaus seem to depend on the collection of high numbers of late-life data (Carey et al., 1992). One plausible explanation of the "plateau" behavior was introduced by Vaupel et al. (1979) assuming a life-long heterogeneity in the mortality rates: more robust subgroups survive to later ages, slowing the rate of decline in average survival probabilities at late ages among large cohorts. The older remaining individuals from the cohort are expected to be much more robust so that the mortality rate becomes a very shallow function of age, resembling a plateau. However this demographic heterogeneity model does not seem to be a reasonable explanation of demographic patterns and it has only a weak biological basis (Mueller et al., 2003).

With rare exceptions the Triatominae are exclusively hematophagous, and they also show strict hematophagy across all developmental stages. This may be a potential key to the explanation of the observed mortality pattern: hematophagy from vertebrate blood leads to the digestion of vertebrate hemoglobin resulting in the production of large amounts of heme, a potentially cytotoxic molecule that can exert biological damage (Graca-Souza et al., 2006). The evolution of hematophagy has resulted in many adaptations developed by blood-feeding insects and ticks to counteract those deleterious effects. Antioxidant enzymes and urates are known to play a major role in the protection of cells against free radical damage, and massive amounts of urates have been found in the haemolymph of *R. prolixus* (Souza et al., 1997). Given the strict hematophagy of triatomines these mechanisms that reduce the accumulation of oxidative substances associated with aging (Graca-Souza et al., 2006) may be one of the basic mechanisms that may help explain the senescence patterns observed in the triatomines.

The relationships between average instantaneous mortality rates $\bar{\mu}_x$ and average fecundity by periods show a delay in the effect of the latter on the former, indicating an important reproductive investment before a high accumulated instantaneous mortality rate occurs. The negative relationship between the average instantaneous mortality rate $\bar{\mu}_x$ and average female longevity suggests that species with high longevity can invest in reproduction with a relatively low mean mortality and then a smaller senescence rate than the species with low longevity. This type of relationship between reproductive effort and the effects on age-specific mortality rate is similar to the one found in the beetle *C. maculatus* (Tatar et al., 1993) and confirms the observation of Sulbaran & Chaves (2006) in the kissing bug *R. prolixus*.

Additionally, the female's post reproductive period decreases with reproductive effort indicating that longevity after their last reproduction is shorter in species in which the reproductive effort is high. The above results suggest a trade-off between mortality rate and reproductive effort: a large investment in the reproduction during the first and/or intermediate part of the female adult life that seems to result in an increase in high mortality, and then a high senescence rate at the end of the adult life. Such trade-off could contribute to explain the variation between species in the mean mortality and in the post-reproductive period duration but probably not the difference in the senescence pattern since no significant relationship exists between the parameter b of the Gompertz model and other variables used as indicators of reproductive effort.

4.3 Triatominae senescence in the light of evolutionary ecology

The balance between extrinsic and intrinsic mortality rates is an important factor underlying the evolution and the diversity of senescence patterns. Williams (1957) proposed that organisms living in environments with high extrinsic mortality rate may evolve towards high senescence rates. Physiological senescence results from an optimal equilibrium between energy allocation in somatic maintenance and other competitive traits as reproduction (Kirkwood, 2005). In habitats in which life expectancy is short resulting from extrinsic factors (as high predation, starvation, etc.), the maintenance of costly mechanisms to guarantee the reparation of metabolic deterioration is not evolutionary stable.

Conversely, species living in habitats with low extrinsic mortality may increase energy allocation in somatic maintenance until old age and increase longevity by natural selection.

In triatomines no quantitative data exists concerning extrinsic mortality factors in the field. The levels of extrinsic mortality in relation to the habitat (domestic, peri-domestic and sylvatic), is still little known in triatomines. However, our results show a negative relationship between mortality rate and female longevity supporting Williams' (1957) prediction, contrary to other empirical observations that do not support this prediction (Promislow, 1991; Ricklefs, 1998; Reznick et al., 2004), which has also been criticized on conceptual grounds due to the difficulty in separating extrinsic and intrinsic mortality rates (Williams & Day, 2003).

In a recent comparative analysis of mammal and bird survival senescence Jones et al. (2008) arrived to generalizations such as that mammals senesce faster than similarly sized birds. Furthermore, McCoy & Gillooly (2008) developed a model of natural mortality (relating body size and temperature to biological rate processes) and tested it with extensive field data from plants, invertebrates, fish, birds and mammals; their results indicate that much of the heterogeneity in natural mortality rates can be predicted, explicitly and quantitatively, despite the high diversity of extrinsic sources of mortality in natural systems, something that suggests that mortality rates may be governed by common rules.

We show that the geographical range size of species and some climatic factors, mainly the ones related to precipitation, seem to be related to total mean mortality ($1/e_0$). These results suggest that the influence of geographic and climatic factors on the senescence pattern deserves further investigation. However, can the potential senescence that is observed and measured in the laboratory be expressed in natural habitats where extrinsic mortality occurs? In the field, triatomines could die before intrinsic mortality and decreasing fecundity occurs, due to extrinsic factors such as predation, parasitism, extreme climatic conditions, etc. Recent studies in vertebrates (Adams, 1985; Gaillard et al., 1993; Reznick et al., 2002; Rebke et al., 2010) show that senescence is observed under natural conditions, but that kind of information is lacking for triatomines and needs to be investigated. Williams (1957) claimed that greater rates of extrinsic mortality (age- and condition-independent) favored more rapid senescence, but Abrams (1991) showed that the effects of the "extrinsic" mortality affect differentially the rate of senescence as a function of the degree of density-dependence. Abrams (1991) also showed that mortality patterns, contrary to Williams' (1957) predictions, are possible when density-dependence is present, and acts primarily on the survival or fertility of later ages, or when most of the variation in mortality rates is due to variation in non-extrinsic mortality.

There are few laboratory evaluations of the density-dependent processes in triatomines. Rodríguez & Rabinovich (1980) showed that in *R. prolixus* density had a significant effect on the development rate of second, third, and fourth instars, but not on the survivorship of either the first or fifth instars, or even of the adults, nor on the instantaneous population parameters, or the age-specific parameters. Influence of density-dependence on the senescence pattern in triatomines still needs more research.

How organisms distribute their "investment" in reproduction with respect to age is a major question in the senescence theory. It will be optimal for an organism to "invest" more in its reproduction when it becomes old-aged (Williams, 1966). An extension of William's (1966) theory is that old individuals may increase their reproductive effort during their last reproductive occasion(s) because it is their last chance to reproduce. This extension was

called the “hypothesis of terminal investment” (Ricklef, 2000; Coulson & Fairweather, 2001; Ricklefs, 2008). Thus senescent individuals may invest more in reproduction than the non-senescent individuals. Our observations in the triatomines do not support these predictions. Indeed most of the reproductive effort (about 50 to 90%) occurs in the first and intermediate part of the adult life and before the high mortality that takes place at older ages. Furthermore, the duration of the post-reproductive period decreases with reproductive effort suggesting a trade-off between reproduction allocation and future survival. Recently William's (1966) prediction and the concept of terminal investment have been criticized because of scarce empirical support and for resorting to two hypotheses based on quite unrealistic assumptions: (i) organisms must have a fixed longevity, which implies that individual trajectories cannot influence longevity, and (ii) in order to increase their reproductive effort at the end of their life during their last reproductive occasion(s), individuals must be able to anticipate their future, i.e., they have to use cues indicating when their death may occur (Gadgil & Bossert, 1970).

Environmental heterogeneity, and particularly high environmental uncertainty (stochastic effects), affect circumstances that are very important in insects, such as encounter rates associated to suitable oviposition sites, food and refuge availability, physiological state (e.g., reserves for producing oocytes, egg maturation rate, and somatic maintenance costs), and expected reproductive success that can lead to different patterns of behavior and rates of mortality and reproduction (Partridge & Mangel, 1999). Environmental stochasticity and/or density-dependence processes can select bet-hedging dormancy including a development delay in insects (e.g., Menu et al., 2000; Gourbière & Menu, 2009; Rajon et al., 2009). Such a risk spreading strategy has been postulated to exist in triatomines (Menu et al., 2010) and we recommend that this approach be incorporated in future studies for understanding senescence in insects.

Mortality rates of triatomine vectors have epidemiological importance through the demography of its populations (Chaves et al., 2004a). Particularly, it has been shown in these insects that important changes in life-history traits take place when reared under laboratory conditions; for example, in *T. infestans*, *T. pseudomaculata*, *T. brasiliensis*, and *P. megistus* after only four years in the laboratory, the reduction in the number of eggs within the first month of oviposition and the average female life span was in average 37.5 and 45.9%, respectively (Perlowagora-Szumlewicz, 1976). Similar changes, including a reduction in life history traits and population growth parameters, during four successive and separate generations of *T. infestans* of Argentina (reared in the laboratory from a first generation from a sylvatic individual) have also been found (G. Martí, personal communication).

The adaptation to a domestic environment causes similar effects on triatomines as the adaptation to laboratory conditions (Forattini, 1980): indoor conditions of rural houses provide better chances of feeding, and are characterized by smaller predation risks, and smaller fluctuations of temperature and relative humidity that exclude potentially deleterious extreme values. In our study we did not analyze possible adaptations to the laboratory because the precise number of laboratory generations was known for only a few cohorts; however, it is recommended that, when estimating trade-offs, and in particular the senescence pattern, the influence of such changes should be taken into account.

Furthermore, as the data for our comparative analyses did not indicate the mean body length of the individuals used in the experiments we used the estimates provided by Galíndez Girón et al. (1998) based on the types and paratypes of triatomine measurements in museum collections. As the individual's body size distribution can vary with respect to each population, it is recommended that future cohort studies in the laboratory measure the body length of the individuals used. In consequence, we must take with some reservation the lack of a statistically significant correlation between life history traits and total length as obtained in this study and based on 27 triatomine species.

5. Conclusions

Most studies in triatomines have investigated physiology, population genetics, phylogeny (see Gourbière et al., 2011 for a review) and ecology of a given species (e.g., Dumonteil et al., 2002; Gourbière et al., 2008; Barbu et al., 2011) but very few studies have investigated the evolution of life history traits in the light of evolutionary ecology concepts (Menu et al., 2010). Our study is the first comparative analysis to the senescence pattern and its relationship with life history traits in triatomines.

Our results indicate that triatomines show both an actuarial and a reproductive senescence, with a high diversity of mortality patterns, even within a given genus. We believe that the relationship between life history traits, and particularly the trade-off between reproductive effort and future survival, is central to understand this diversity in mortality patterns. In order to identify ultimate and proximate factors underlying this diversity, we need longitudinal studies conducted in the field in order to estimate if the potential senescence observed in the laboratory can be expressed under natural (sylvatic and domestic) conditions. The analysis of senescence in relation to other life history traits in triatomines has not only academic value but also impinges in the areas of vector population management and epidemiology.

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