Development time and fitness: is there an adaptive development delay in the *Rhodnius prolixus* fifth nymphal stage?

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Abstract

Triatomines (Hemiptera: Reduviidae) are vectors of *Trypanosoma cruzi* Chagas, the etiological agent of Chagas's disease. They display pre-adult development delay – that is, a development time much longer than on average – which usually has been considered as a maladaptive trait. However, this hypothesis has not been tested. We carried out an experiment under controlled laboratory conditions to (1) test whether a development delay exists in the fifth nymphal stage of *Rhodnius prolixus* Stål (Hemiptera: Reduviidae, Rhodniini), and (2) measure any fitness cost related to such delay by estimating the relationship between individual development time and other life-history traits. We analyzed the development time with various continuous statistical distributions (normal, log-normal, Weibull, gamma, Pareto, Burr, and log-logistic). Using goodness-of-fit tests, the best fit was obtained with asymmetrical distributions, with the Burr distribution showing the best fit to the data. We concluded that a development delay exists in stage five of *R. prolixus* without fitness cost. The combination of our results and previous work suggests that such a delay could be viewed as an adaptive response to environmental stochasticity and/or density-dependence rather than as a maladaptive trait. We propose further investigations to provide a conclusive test of adaptive delay in triatomines.

Introduction

Environmental stochasticity may have interesting consequences for optimal life-history strategies, including a delay in development (e.g., Tuljapurkar & Orzack, 1980; Yoshimura & Clark, 1993; Gourbière & Menu, 2009; Luckhart et al., 2010; Rajon et al., 2014). Theoretical studies have shown that, independent of environmental stochasticity, density-dependent mechanisms may select for development delay (Bulmer, 1984; van Dooren & Metz, 1998; Lalonde & Roitberg, 2006). Development delay is one of several adaptive traits of diversified bet-hedging strategies responding not only to environmental

stochasticity (Seger & Brockmann, 1987; Philippi & Seger, 1989; Menu et al., 2010) but also to density-dependent mechanisms (Rand & Wilson, 1991; Rajon et al., 2009, 2014). The interaction between a density-dependent mechanism and environmental stochasticity is known as 'chaotic stochasticity' (Rand & Wilson, 1991; Rajon et al., 2009, 2014). Bet-hedging strategies may act in temporal or spatial ways to spread the risk of complete failure in vital traits, such as survival and reproduction, and variation in development time may be related to adaptive temporal dispersion (Starrfelt & Kokko, 2012; Buoro & Carlson, 2014).

Development delays are a well-studied aspect of evolutionary strategies, and have been analyzed in insect pest species, such as the chestnut weevil (Rajon et al., 2014); however, they have been scarcely investigated in disease vectoring insects (Menu et al., 2010). Recently, Pelosse et al. (2013) showed that bet-hedging strategies in Chagas

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disease vectors potentially affect the epidemiology and evolution of the parasite *Trypanosoma cruzi* Chagas, the etiologic agent of Chagas disease, which ultimately affects the control of Chagas disease transmission. These authors also demonstrated that environmental stochasticity associated with bet-hedging strategies in triatomine development time may increase the prevalence of vector-borne Chagas disease, favoring more virulent strains of parasites in a relatively short evolutionary time scale. Investigations on development delay in Chagas disease vectors may therefore shed light on the evolution and epidemiology of the disease.

Chagas disease insect vectors belong to the subfamily Triatominae (Hemiptera: Reduviidae), comprising more than 140 species (Schofield & Galvão, 2009). Triatomine species are adapted to a diversity of habitats, ranging from sylvatic (e.g., forests and savannahs) to human peridomestic and domestic environments. The main vector of Chagas disease is *Rhodnius prolixus* Stål, a domiciliated species distributed in northern South America (Lent & Wygodzinsky, 1979; Zeledón & Rabinovich, 1981) that feeds on a broad range of hosts (birds, small rodents, opossums, domestic animals, humans).

Although triatomines are adapted to a variety of environmental (climatic, physical, and biological) conditions, those conditions are often quite variable in time and space in an unpredictable manner. Stochastic changes in climatic factors may not only affect triatomines directly through changes in their macro- and micro-habitat, but also through the type and abundance of hosts, which in turn influence their population dynamics and potentially result in selection for a development delay (Menu et al., 2010). The population dynamics of triatomines is also affected by density-dependent mechanisms (Rodriguez & Rabinovich, 1980; Schofield, 1982; Piesman et al., 1983; Gadea, 1984; Ehrenfeld et al., 1998; Pelosse & Kribs-Zaleta, 2012; Márquez & Saldamando-Benjumea, 2013). Adaptive delays are common in many organisms (Rajon et al., 2014); yet, in general development delays in triatomines have been considered as a maladaptive trait (Menu et al., 2010). However, the fitness of individuals with respect to their development time has never been estimated, and no adaptive dynamics approach has studied the long-term outcome of selection in terms of development time. If a development delay in triatomines would be maladaptive, we would expect a low fitness (i.e., negative population growth rate) of those individuals with development delay, whereas the reverse is to be expected (positive population growth rate) if a development delay were adaptive.

Here, we analyze the development time of fifth instar *R. prolixus* because this instar – together with the third and the fourth – displays the highest resistance to fasting

(Feliciangeli et al., 1980). In addition, Colombian data on fifth instar development time indicated bimodality and asymmetry (Figures S1 and S2), suggesting some kind of adaptive (bet-hedging) delay strategy in *R. prolixus* (Sasaki & Ellner, 1995). These authors studied the evolution of quantitative traits and demonstrated, as a general prediction of a bet-hedging model for fitness, that the adaptive (bet-hedging) strategy against fluctuating selection is a discrete phenotype distribution rather than a continuous one. The interpretation of a continuous skewed distribution of development times (e.g., log-normal) is complex. It could be the outcome of constraints on development (i.e., non-adaptive processes). Alternatively, Sasaki & Ellner (1995) showed that it could result from selection for bet-hedging, if the phenotype distribution prior to selection is smooth. We consider the following indicators as supporting an adaptive bet-hedging delay hypothesis: (1) a bimodal distribution of development time, or a skewed continuous distribution, and (2) no survival and fecundity differences among individuals, which would indicate that individuals with the longest development time were not affected by sickness, injuries, etc. Conversely, a symmetric continuous development time distribution with negative growth rate for individuals with the slowest development should be considered as supporting the null hypothesis of a non-adaptive delay in development time. Nevertheless, it is important to note that a decisive conclusion about the adaptive value of the variance in development time needs further investigations as we discuss in detail in the Discussion section.

The aim of this paper was to assess the distribution of development time of fifth instars of *R. prolixus*, looking for individuals with long development time, and subsequently to compare the population growth rates (as a fitness proxy) of individuals in relation to their development time. We conducted an experiment under controlled laboratory conditions, using an ad hoc protocol to analyze the developmental time pattern in relation to survival and adult reproductive traits (fecundity, age of first oviposition, duration of the oviposition period, and female longevity).

Materials and methods

Insects

We started with 1 000 eggs of *R. prolixus*, taken randomly from the colony of the 'Herman Lent' Entomology Laboratory, of the 'Universidad de Los Andes' (Mérida, Venezuela). This colony had been maintained under laboratory conditions for 42 years. From those 1 000 eggs we obtained 400 individuals in the fourth nymphal stage. These individuals were fed weekly on hens, and we selected

individuals that had molted into the fifth instar within 1 day. Within a week of molting into the fifth instar, all individuals were fed on hens and, to have an experimental group as homogeneous as possible, only those individuals that fed to satiation were used in the experiment (206 individuals). Each individual was kept in a separate 10-ml vial at 28 °C and 50% relative humidity, and fed weekly with hens for 30 min. Death or molting from fifth instar into adult was recorded daily, and the fifth instar development time (DT5) was calculated as the difference between the date of molting to adult and the date of entering into the fifth instar. All procedures followed the ethical guidelines of the 'Consejo de Desarrollo Científico, Humanístico, Tecnológico y de las Artes de la Universidad de Los Andes' (CDCHTA-ULA).

We selected the fifth instar because the data we analyzed based on an individually followed cohort of *R. prolixus* (Arévalo et al., 2007) indicated that: (1) egg-to-adult development time had no bimodality nor asymmetry, (2) there was no positive correlation of development times among stages (i.e., individuals that were slow developers in one stage could be normal or fast developers in another stage, and vice versa), and (3) the development time of the fifth instar had a clear bimodality and asymmetry. The results of this analysis are shown in Appendices 1 and 2. Unfortunately, we could not use the data of Arévalo et al. (2007) to test our hypothesis on fitness because the correspondence between adult and pre-adult individuals was not preserved in that study.

The female and male adults that survived from the original batch of 206 fifth instars were randomly paired in 10-ml vials (one pair per vial), and maintained under the same environmental and feeding conditions. Males were exchanged weekly and randomly between vials containing females to guarantee that any male would have the same chance of breeding with any female. The following life-history traits were recorded for each individual female: fecundity (number of eggs laid per female per day), age of first oviposition, duration of the oviposition period, and longevity (lifespan). These procedures were carried out daily, from the day of molting into the adult stage until the death of the last female individual.

Statistical analysis

Development time distribution. We tested the frequency distribution of the DT5 against the normal distribution but, as the observed data suggested a highly skewed (leptokurtic) distribution, we also tested five asymmetric distributions: Weibull, gamma, log-normal, Burr, and log-logistic, with parameters estimated by the log-likelihood method. The Burr distribution, also known as the 'generalized log-logistic distribution', is a flexible continuous probability distribution. We compared the goodness of fit of the various statistical distributions with the Akaike's and Bayesian goodness-of-fit information criteria (AIC and BIC) (Burnham & Anderson, 2002). We used Student's t-test to compare the DT5 between males and females, which is valid even under non-normality if there is a large sample size (>30); however, we also checked normality with the Shapiro–Wilk test. Four life-history traits (female longevity, age at first reproduction, and lifetime and daily egg number per female) were regressed against DT5; for these regressions, some of the continuous variables were first transformed to a decimal logarithmic scale.

Development time and population growth rate. We developed a mathematical model based on a stage-specific female matrix population model, composed of only three stages: adults, fifth instars, and juveniles (i.e., a pool of all stages from egg to the beginning of the fifth instar). This requires the estimation of the following parameters (on a daily time scale): (1) probability of surviving as a juvenile (SJ), (2) probability of passing (i.e., to 'graduate') from juvenile to the fifth instar (G5), (3) probability of surviving as fifth instar, (4) probability to passing (i.e., to 'graduate') from fifth instar to adult female (GA), (5) probability of surviving as an adult female (SA), and (6) fecundity of adult females (F; number of female eggs per female per day). The average values of these parameters were estimated from our experimental results, except for SJ, for which the data were used of Arévalo et al. (2007), a cohort study of the same species, the same environmental conditions, and similar feeding source and regime. The finite rate of population growth (λ) was estimated from the dominant (largest non-negative) eigenvalue of the population matrix model (Caswell, 2001). As we were interested in the possible influence of development time on λ (our fitness metric), we pooled individuals with the same development time, which resulted in nine groups. For each group, we calculated the average values of parameters 1–6 and estimated the finite rate of population growth (λ).

Results

Development time distribution of the fifth instar

The Shapiro–Wilk normality test of DT5 indicated that the data did not follow a normal distribution (W = 0.837, P<0.001). Some individuals displayed extremely slow development, with the largest DT5 value corresponding to a female with 33 days of development, 10 days longer than the mean development time (22.8 days). The goodness of fit of the DT5 to five asymmetric distributions (Weibull,

gamma, Burr, log-normal, and log-logistic) is shown in Table 1 with their corresponding AIC and BIC values. The skewness-kurtosis plots (see Figures 1, 2, S1 and S2) confirmed the high values of skewness and kurtosis of the DT5 variable. The fit to a mixture of two log-normal distributions (data not shown) was the same as the fit of a single log-normal distribution.

As the normal, Weibull, and gamma distributions had the less satisfactory fit, they were discarded from further analysis. The best fit was obtained with the Burr distribution, as illustrated in Figure 1. Similar plots for the log-logistic and the log-normal distributions are given in Figures S1 and S2.

Adult life-history traits and development time

A Pearson's product-moment correlation analysis on the relationship (Figure 2) between DT5 and four life-history traits (based on the arithmetic values) resulted in correlation coefficients of -0.0936 (longevity; $P = 0.37$), 0.2075

(age at first reproduction; $P = 0.045$), 0.0163 (lifetime egg production; $P = 0.88$), and 0.1567 (daily egg production; $P = 0.13$). Apparently the life-history traits do not have a strong relation with DT5.

Development time and population growth rate

The parameters of the population matrix model, estimated from our data (except SJ, which was 0.616; Arévalo et al., 2007), were: SA = 0.9, GA = 0.917, G5 = 0.05, SN5 = 0.8, and F = 1.062, resulting in a finite rate of population growth of $\lambda = 1.0211$ (on a daily basis). Average values of λ as a function of development time, estimated after pooling individuals with the same development time, are shown in Table 2. The last four categories of development time have a low credibility due to their small sample sizes (1–4); nevertheless, $\lambda>1$ for all categories (or almost 1 for DT5 = 23 days) suggesting no fitness cost related to development delay. The average of the nine categories is = 1.0313 (95% confidence interval: 1.0053–1.0572),

Table 1 Akaike and Bayesian information criteria (AIC and BIC) as a measure of the goodness of fit of development time of both sexes of fifth instar *Rhodnius prolixus* (DT5) to the normal distribution and five potentially leptokurtic statistical distributions: Weibull, gamma, Burr, log-normal, and log-logistic

Goodness of fit	Normal	Weibull	Gamma	Burr	Log-normal	Log-logistic
AIC	754.48	821.43	740.29	695.35	733.97	719.32
BIC	760.78	827.73	746.59	704.81	740.28	725.63
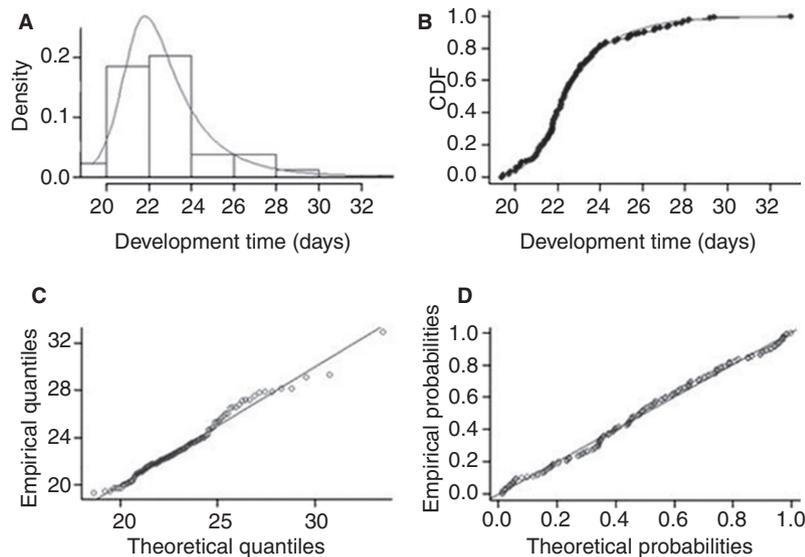
Figure 1 (A) Density function, (B) cumulative density function (CDF), (C) Q-Q, and (D) P-P goodness-of-fit plots of the development time of fifth instar *Rhodnius prolixus* (both sexes; n = 173) as fit indicators to the Burr distribution. The Q-Q plot represents empirical (y-axis) against theoretical quantiles (x-axis); the P-P plot represents the empirical distribution function evaluated at each data point (y-axis) against the fitted distribution function (x-axis). The probability plotting position was defined by default using Hazen's rule, with probability points of the empirical distribution calculated as $(1{:}n - 0.5)/n$, where n = number of observations.
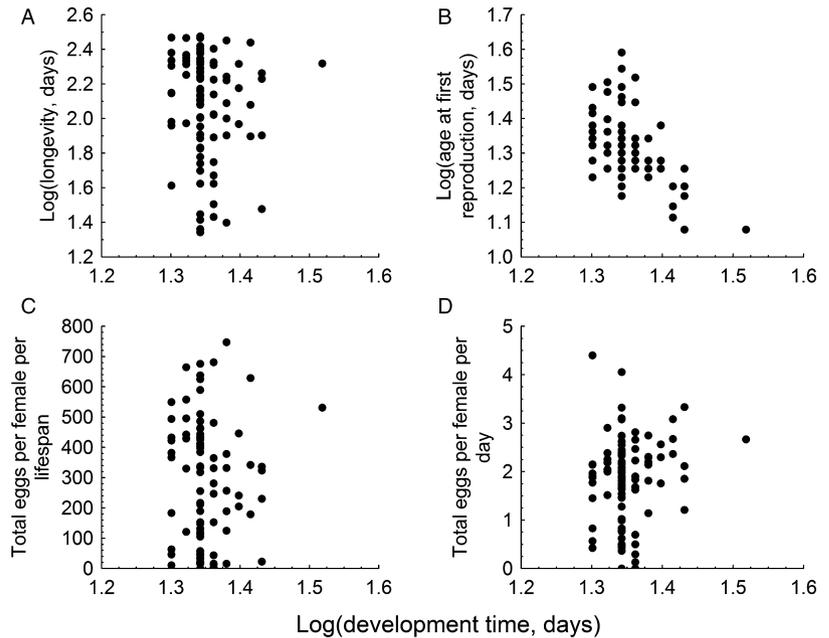
Figure 2 Association patterns among fifth instar development time of female *Rhodnius prolixus* and adult female's (A) longevity, (B) age at first oviposition, (C) lifetime fecundity, and (D) daily egg production, on logarithmic scales. Each point in the graphs represents a single female individual (n = 94).

Table 2 Female *Rhodnius prolixus* population matrix parameters estimated for nine categories of development time and the corresponding finite population growth rate (λ)

Development time (days)	Sample size	Adult ♀ daily survival rate	Fecundity (no. ♀ eggs/♀/day)	Fifth instar ♀ daily survival rate	Probability of graduating from 5th instar to adult	λ
20	11	0.9942	0.8855	0.950	0.04628	1.0091
21	7	0.9952	1.092	0.952	0.04407	1.0308
22	44	0.9930	0.895	0.955	0.04207	1.0012
23	14	0.9917	0.785	0.957	0.04024	0.9900
24	7	0.9926	1.0455	0.958	0.03856	1.0224
25	3	0.9933	1.1035	0.960	0.03702	1.0882
26	3	0.9937	1.353	0.962	0.0356	1.0861
27	4	0.9914	1.0635	0.963	0.03428	1.029
33	1	0.9952	1.334	0.970	0.02805	1.0246

Survival of juveniles (SJ) was kept constant at 0.616, based on Arévalo et al. (2007). All parameters are on a daily time unit basis.

which is not significantly different from either the average finite population growth rate of the population as a whole (1.0211) or from the individual female with the longest development time (33 days, λ = 1.0246; last data point of Table 2).

Discussion

Despite several studies on demography, physiology, epidemiology, genetics, and phylogeny of triatomines (Gourbière et al., 2012; Nouvellet et al., 2015), the evolutionary ecology and population dynamics of this group have been scarcely analyzed (Menu et al., 2010; Rascalou et al., 2012). We studied the distribution of fifth instar

R. prolixus development times, looking for individuals with slow development, and subsequently we related the population growth rate (as a fitness proxy) to the fifth instars development time. Our results confirmed a development delay in the fifth nymphal stage of *R. prolixus* because skewed distributions, such as the Burr and log-logistic distributions, provided a good fit to the extremely leptokurtic distribution of the experimental development time. However, although some individuals were observed with extreme values of development time, the differences between the longest development time and the average development time was about 10 days. As there was no apparent correlation at the individual level in the development time among stages in *R. prolixus*, the asymmetrical

distribution of development time could not be attributed to differences in development time accumulated over all the other pre-adult stages (see Supporting Information).

Our results indicate that no relationship between fitness (measured as population growth rate) and development time exists. The finite rate of population growth of $\lambda = 1.0211$ estimated from our analysis is quite close to the average value of $\lambda = 1.032$ from four cohort experimental studies available in the literature (Pippin, 1970; Rodríguez, 1978; Rodriguez & Rabinovich, 1980; Arévalo et al., 2007). This gives us confidence that the performance of our model is satisfactory, despite the simplification to only three development stages. We conclude that a longer development time of the fifth instar is not related to a higher fitness cost, at least under the favorable laboratory conditions for *R. prolixus* that we have used. However, as we only analyzed completely fed individuals, further studies are needed to assess the variance of development time under different quantity and quality of blood ingested. For this, it would be necessary to analyze individual differences in body size and in development time under restricted feeding conditions.

Because we observed (1) a skewed continuous distribution of development time for the fifth instar and (2) no correlation between growth rate and individual development time, our results indicate that an adaptive development delay exists in *R. prolixus*. In other words, variation observed in the fifth instars may be a response to environmental stochasticity. Female *R. prolixus* lay most of their eggs at the beginning of the dry season (Feliciangeli de Piñero & Torrealba, 1977), so any delay in the onset of rains would imply a high risk for the individuals that emerged from those eggs. In such a context, a development delay in the fifth instars could be advantageous. Furthermore, tropical dry forests and savannahs may occasionally be affected by a delay in the onset of the rainy season, which may be quite critical for a hematophagous insect. The reason is that such a delay may result in a strong (sometimes complete) failure in plant flowering and fructification, with the corresponding nesting failure of common hosts of *R. prolixus*, such as small mammals (Vivas, 1986; Morrison & Hik, 2007; Luis et al., 2010; Krebs, 2013) and birds (Crick, 2004). The weak development delay of *R. prolixus* that we observed may also be due to the long time of laboratory rearing under constant and predictable environmental conditions (>40 generations), which contrast with natural habitat.

To conclude, our results indicate that the development delay found in *R. prolixus* is not a maladaptive trait. Although it seems to correspond to an adaptive process as bet-hedging, we cannot exclude that the observed variation in development time is explained by other underlying mechanisms, such as mixed evolutionarily stable strategies, or a stable genetic polymorphism (Soula & Menu, 2003). Therefore, the existence of an adaptive development delay in triatomines needs further investigation, and we propose that they are based on new ad hoc experiments that should include (1) the estimation of the development time of all pre-adult stages in order to check whether the individuals with cumulative development delay, as in Menu et al. (2010), show a positive fitness value, (2) the consideration of various combinations of sub-optimal conditions (in terms of type of hosts, feeding regimes, etc.), (3) the use of laboratory individuals recently collected from the field (ideally, first generation laboratory individuals), and (4) the density-dependent mechanisms which triatomines experience and the stochasticity of environments in which they live. Also a theoretical investigation of the relative long-term fitness of alternative development strategies with respect to environmental stochasticity and density-dependence via an adaptive dynamics approach would be interesting (e.g., as in Rajon et al., 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (A) Density function, (B) cumulative density function (CDF), (C) Q-Q, and (D) P-P goodness-of-fit plots of the development time of fifth instar *Rhodnius prolixus* (both sexes; n = 173) as fit indicators to the log-logistic distribution. The Q-Q plot represents empirical (y-axis) against theoretical quantiles (x-axis); the P-P plot represents the empirical distribution function evaluated at each data point (y-axis) against the fitted distribution function (x-axis).

Figure S2. (A) Density function, (B) cumulative density function (CDF), (C) Q-Q, and (D) P-P goodness-of-fit plots of the development time of fifth instar *Rhodnius prolixus* (both sexes; n = 173) as fit indicators to the log-normal distribution. The Q-Q plot represents empirical (y-axis) against theoretical quantiles (x-axis); the P-P plot represents the empirical distribution function evaluated at each data point (y-axis) against the fitted distribution function (x-axis).