



Morphology, Life Cycle, Environmental Factors and Fitness – a Machine Learning Analysis in Kissing Bugs (Hemiptera, Reduviidae, Triatominae)

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Populations are permanently evolving and their evolution will influence their survival and reproduction, which will then alter demographic parameters. Several phenotypic, life history and environmental variables are known to be related to fitness measures. The goal of this article was to look into the possible types of those relationships in insects of the subfamily Triatominae, vectors of *Trypanosoma cruzi*, the causative agent of Chagas disease. After an exhaustive literature review of 7,207 records of publications referring exclusively to all possible features of the triatomines, using 15 keywords those records were reduced to 2,968 publications, that were analyzed individually; after deleting those publications that did not have the data in quantitative form as needed for the objective of this article, I found that 171 papers were adequate for the present analysis. From them I compiled a dataset of 11 variables and 90 cases from 36 triatomine species. Those variables included four environmental, two life cycle, and four morphological variables, and one demographic parameter: a fitness measure (the population intrinsic rate of natural increase, r_0), used as dependent variable. However, the relationship between *T. cruzi* and its vector host was not included in this analysis despite triatomine-*T. cruzi* interactions constitute an important factor in the evolution of triatomine's life history. I resorted to the Random Forest method as a machine learning approach for the analysis of this dataset, and found that –in addition to the triatomine species themselves– only the two life cycle variables (mean development time from egg to adult, and mean fecundity, expressed as the average number of female eggs laid per female per day) were statistically significant in determining fitness (r_0). The machine learning approach used in the analysis provided a similar but deeper insight into these relationships than classical regression. Except for an analysis on senescence, this is the first study in triatomines addressing these questions. These results will be useful for other theoretical optimization approaches (frequency-dependence, density-dependence, evolutionary game theory, and adaptive dynamics), thus contributing to the theoretical framework for interpreting the succession of stages in insect adaptations, a framework yet to be constructed.

Keywords: kissing bugs, fitness, phenotype, Chagas disease, triatominae, life history, temperature, development time

INTRODUCTION

Populations of different species are permanently evolving and their evolution will influence the survival and reproduction of its members, ultimately influencing demographic parameters (Hendry, 2015). Morphological features (particularly body size in ectotherms), life cycle traits, demographic parameters, and characteristics of the environment, are intricately related, and the evolution of such a relationship is extremely complex. For decades the heritability of life history traits has been investigated, particularly those more directly related to demographic parameters such as fitness. Mousseau and Roff (1987) found that, in wild and outbred animal populations, life history traits generally possess lower heritabilities than morphological traits, while behavioral and physiological traits have a heritability intermediate between life history and morphological traits; thus, high heritabilities seem to be maintained within natural populations even for life history traits, believed to be under strong selection. Importantly, phenotypic selection seems to work differently between wild and captive conditions (Kingsolver et al., 2001), while a significant part of the data available relating morphology, demography, life cycle, and environmental conditions comes from laboratory-reared animals.

The Triatominae (Hemiptera: Reduviidae), commonly known as kissing bugs, are vectors of the parasite *Trypanosoma cruzi* (Chagas, 1909), the causative agent of Chagas disease. This group of insects feeds primarily on vertebrate blood after evolving from predatory reduviid bugs, most likely in the New World; triatomines diversified extensively across the Americas and in parts of Asia and Oceania, being now represented by over 130 species (Araujo Monteiro et al., 2018). In part for this reason (triatomines are the main mode of transmission of *T. cruzi*), they have been studied for over a century, and there is a wealth of information about this insect group. It is reasonable to expect that in triatomines, as in most other animal groups, there is a relationship between some life cycle and demographic parameters and environmental factors. Below I summarize some strongly suggestive evidence of these relationships in triatomines (without intending to make a complete review of the topic). The analysis of these relationships would not only contribute to the theoretical framework of life history evolution, but also provide knowledge useful for the control of Chagas disease transmission: triatomine species have shown to be in permanent adaptation to environmental modifications, evidenced by changes in phenotype, life history, and population dynamics. Thus, I think that a literature review of the plasticity of those features in triatomines is necessary, followed by an inquiry into their possible relationships. This inquiry, because of data availability, was restricted to the adult stages of the triatomines. Despite important relationships between morphometry and demographic parameters exist along the ontogenetic process. E.g., Bello-Bedoy et al. (2019), in the triatomine *Dipetalogaster maximus*, measured and compared among nymphal stages and adults and, between sexes phenotypic traits linked to some functions: the proboscis length and width in feeding; the head length and width in vision; the pronotum width and length in mobility, and the abdomen length in feeding capacity and fecundity. These authors found

sometimes a steady increase and sometimes an abrupt increase in some of those measurements, with some important effects on the functions evaluated. However, as in this analysis the measurements were limited to the adult stage of triatomines, we could not include the element of ontogeny.

I have organized the structure of this article as follows: (a) I review the triatomine bibliography where phenotype, life history, and environmental factors are related; (b) I describe a comprehensive database of life-history traits from that literature review to investigate possible relationships among them; and (c) I apply a Machine Learning approach to search for those relationships.

There is a complex relationship between *T. cruzi* and its vector host that results in mutually induced changes in both the insect and the parasite (demographic, behavioral, physiological, genetic, etc.), that affect virulence and transmission; a true “arms-race” (Pelosse and Kribs-Zaleta, 2012; Pelosse et al., 2013; Cordero-Montoya et al., 2019; Ramírez-González et al., 2019; Córdoba-Aguilar, 2020), and constitute an important factor affecting the evolution of triatomine’s life history. However, because of that same complexity it was not possible to include it a factor in the present analysis (it would have resulted in many more variables, and a proportionately smaller number of case studies).

Overall, this is the first study of triatomines with this comprehensive goal; a previous and similar effort in that direction was the one of Medone et al. (2012), that analyzed the life history traits of 27 triatomine species, but was restricted only to the analysis of mortality and fecundity through several death and reproductive parameters. However, the analysis here presented should not be confused with a meta-analysis; the latter, although combines results of multiple scientific studies as I have done here, usually address the same question, and try to reconcile individual studies reporting different results, each with some degree of error. On the contrary, here we will handle different studies, frequently estimating new variables (as the population growth rate) that were not present in the original studies. Below I present the results of (a), organized in three main aspects: the response of triatomines to temperature, feeding frequency, and food source effects.

Temperature Effects

There has been a growing body of literature showing the effects of temperature on many aspects of the biology of triatomines, particularly from the physiological point of view (molting process, diuresis, protein synthesis, hormone secretion, respiration rate, orientation to radiant heat, shelter selection, performance of flight muscles and flight initiation, electrophysiology of the maxillary stylets, preferred temperatures, rate of weight loss, dispersal, feeding behavior, metabolism, water loss, biting rate, gas exchange patterns and spiracular control, spermiogenesis, heart rate, effects on insecticidal activity, reproductive efficiency, and many others). So below I only review some of the most relevant effects of temperature exclusively related to the triatomines’ life cycle and demographic parameters.

The development time and survival of triatomines eggs as function of temperature began to be studied as early as 1935/36: Clark (1935) showed that the hatching rate of the

eggs of *Rhodnius prolixus* (Stål, 1859) increased with constant temperatures from 15 to 27°C, but that this increase was strongly dependent on relative humidity (hatching rate was higher at higher humidity but the slope of the increase of hatching rate with temperature decreased with humidity); Galliard (1936) determined that exposing triatomines eggs to an increasing and constant temperature from 10 to 35°C, the egg development time (time to hatch) increased by a factor of ≈ 3 in *Triatoma vitticeps* (Stål, 1859) and *Triatoma dimidiata* (Latreille, 1811), and by a factor of ≈ 1.4 in *R. prolixus*; Galliard (1936), applying the Réaumur law, also determined the thermal constant for each species (necessary energy to hatch) as a linear relationship (degree-days). However, the relationship between temperature and development time (a non-linear relationship depending upon complex enzymatic processes), was estimated for the first time for the triatomine eggs of *Triatoma guasayana* (Wygodzinsky and Abalos, 1941) by Rabinovich et al. (2006) (see below the effects of fluctuating temperatures). In *Rhodnius neivai* (Lent, 1953) Cabello (1999) found that egg to adult development times were 118.0, 86.7, and 68.9 days at 22, 27, and 32°C of constant temperatures. Villegas García and Santillán Alarcón (2004) obtained a very small difference in the hatching time of *Meccus pallidipennis* (Stål, 1872) at two constant temperatures: 17 days at 25°C and 15 days at 30°C.

Studies on the effects of temperature on the survival and development times of nymphal stages and longevity of adults of triatomines, are more abundant. There is always a decrease in development time with an increase of a constant temperature: the developmental cycle (egg to adult) lasted 602 days at 25°C and 186 days at 30°C in *Triatoma jurbergi* (Carcavallo, Galvão & Lent, 1998) (Gomes and da Silva, 2002); the developmental cycle of *D. maximus* (Uhler, 1894) was 271 and 177 days at constant temperatures of 25 and 30°C, respectively (Da Silva, 1990), a difference of 53.1%; however, for *Triatoma infestans* (Klug, 1834) the difference was smaller (35.9%), also between 25 (271 days) and 30°C (177 days) (Da Silva and Da Silva, 1988). Cabello (1999) rearing *R. neivai* at three constant temperatures (22, 27, and 32°C), found a non-linear relationship of total adult mean longevity (24.6, 36.6, and 16.7 days) and life expectancy when entering adult stage (21, 34, and 20.7 days) as a function of those constant temperatures of 22, 27, and 32°C, respectively. In the triatomine *M. pallidipennis* Villegas García and Santillán Alarcón (2004) found that the average development time from first instar nymph to adult was 171 days at 25°C and 154 days at 30°C (11% reduction), and an adult female longevity of 301 and 379 days (26% reduction) at 25 and 30°C, respectively. Martínez-Ibarra et al. (2008) evaluated the life-cycle of *Triatoma mexicana* (Del Ponte, 1930) with cohorts under constant temperatures of 25°C/50% RH, 25°C/75% RH, and 30°C/75% RH. Development time from egg to adult was 286, 283, and 256 days, respectively, while no difference was found in nymphal mortality (57, 60, and 64%), respectively.

Reproduction is also affected by temperature in triatomines, although Da Silva (1990) found only a small difference (11.4%) in the total number of eggs laid by females of *D. maximus* in their first 30 days of adult life: 29.1 and 26.1 eggs at 25 and 30°C, respectively; however, under the same conditions,

Da Silva and Da Silva (1988) found that in *T. infestans* this difference was twice as large (22.5%). In *R. neivai* Cabello (1999) found that the average number eggs/female/week were 11.1, 14.5, and 17.7, and the average number of eggs per female per lifetime were 264, 724, and 603, for three constant temperatures (22, 27, and 32°C), respectively. In the triatomines *M. pallidipennis* Villegas García and Santillán Alarcón (2004) found that the average number of eggs laid in a 6-month period were 826 at 25°C and 934 at 30°C, both as constant temperatures.

It is well known that there are important physiological effects between regimes of constant and fluctuating temperatures, even with the same mean values; these effects are represented by the so-called Jensen's inequality, that states that for non-linear processes, such as most biological phenomena dependent upon temperature, the effects of fluctuations in environmental temperature cannot be predicted from the mean of an equivalent constant temperature (Ruel and Ayres, 1999). This has been established in the triatomines by experiments carried out by Luz et al. (1999); Damborsky et al. (2005), Rabinovich et al. (2006), and Rolandi and Schilman (2018).

Luz et al. (1999) compared the development time of *R. prolixus* from hatching to the adult stage at constant (15, 20, 25, 28, 35°C) and alternating (16/8 h: 15/28, 20/25, 25/28, and 25/35°C) temperatures. Nymphs of this species reached the adult stage most rapidly (86.7 days) at a constant temperature of 28°C; under alternating temperatures development time was completed within 100 days or less at 25/28 and 25/35°C, while development time was slowest at fluctuating 15/28 and 20/25°C (>185 days), and at constant 20°C (>300 days). Damborsky et al. (2005) compared the life cycle of *Triatoma rubrovaria* (Blanchard, 1843) in a climatic chamber under constant temperature, and under the natural fluctuating temperature of the laboratory; under controlled temperature the average hatching time was 15.6 days and the average egg to adult development time was 10 months, while under the natural fluctuating temperature hatching time was 19.1 days and egg to adult development time was 14 months; no difference was found in the egg hatching rate nor in the total nymphal mortality, but a small difference was found in reproduction, with a mean number of eggs/female per life of 817.6 eggs under controlled conditions and of 837.1 eggs under fluctuating conditions (2.4%). Rabinovich et al. (2006) analyzed the effects of fluctuating temperatures on the development time of the eggs of the triatomine *T. guasayana* using three nonlinear models (Devar, Lactin, and Rueda); these authors found a lower egg development threshold between 15 and 17.5°C, and a thermal death point of eggs at 34.4°C; using a generalized development rate response of *T. guasayana* eggs to increasing temperature was proposed, with three ranges: between 10 and 14.8°C development rate increases in an accelerating way; between 14.8 and 29.2°C development rate increases more or less linearly, and between 29.2 and 34°C development rate decreases. Rolandi and Schilman (2018) studied the effect of daily temperature fluctuation (DTF) of 17–32°C (mean = 24°C) on *R. prolixus*, and found that development time and fertility were not affected by DTF, but that fecundity was lower in females reared at DTF than at constant temperature; considering Jensen's inequality and the species' tropical distribution these authors predicted that living

in a variable thermal environment would have associated higher energetic costs.

Cabello (1999) is one of the few authors to construct a complete life table of a triatomine (in *R. neivai*), and to evaluate the demographic parameters at three constant temperatures (22, 27, and 32°C). The estimation of the demographic parameters showed a non-linear trend: the net reproduction rate (R_0) was 114.6, 374.4, and 142.4, while the intrinsic rate of natural increase (r_0) was 0.14, 0.25, and 0.22, for constant temperatures of 22, 27, and 32°C, respectively.

Feeding Frequency Effects

It has been known in general that the feeding frequency in triatomines affects some life cycle and demographic parameters, although there is not much quantitative data available on these effects. Braga and Lima (2001) manipulated in the laboratory the feeding frequency of *Panstrongylus megistus* (Burmeister, 1835) by creating six groups (GI to GVI) of 15 couples each, with the following feeding schedule: GI, on days 5 and 25; GII, on days 5 and 35; GIII, on days 5 and 45; GIV, on day 20; GV, on day 30; and GVI, on day 40 after the imaginal ecdysis (an additional group of 15 couples, fed on day 5 after the imaginal ecdysis and subsequently fortnightly, were used as a control group). The results indicated a clear reduction in longevity and fecundity: GI produced more eggs, mating and fertile eggs; GII had longer life spans, higher fecundity and hatching rate; GIII had a shorter life span, low fecundity, fertility, and hatching rate; GVI presented the least favorable results for all parameters.

Cabello et al. (1988) got contradictory results in the longevity and life expectancy of adults of the triatomine *R. neivai*, when reared at two feeding frequencies (every 7 and 15 days) depending upon the animal species used as blood source: longevity and life expectancy became longer when fed every 7 days (as compared to being fed every 15 days) when fed on rabbit, but became shorter from 7 to 15 days when fed on chicken. However, several demographic parameters (the intrinsic rate of natural increase, r_0 , among them) were consistently higher at 7 days feeding interval than at 15 days feeding interval, independently of the animal species used as blood source.

Sant'Anna et al. (2001) claimed that the triatomine *R. prolixus* achieves high values of total blood ingestion rate (depending on the host used) due to its high mechanical and salivary efficiency, and that this leads to higher nutritional status, allowing (through shorter development times and higher fecundity) to have a higher population growth rate and reach higher densities.

Blood Source Effects

Being triatomines almost exclusively hematophagous, they are affected not only by the frequency of feeding as shown above, but also by the source of the animal blood ingested. Nattero et al. (2013b) tested the effects of the blood of guinea pigs and pigeons on the fecundity of *Triatoma patagonica* (del Ponte, 1929); although these authors found that females fed on pigeons ingested more blood and needed a higher amount of blood to produce an egg than females fed on guinea pigs, there were no differences in the number of eggs laid and hatched between insects fed on each feeding source. The higher amount of blood

ingested and consumed by *T. patagonica* fed on pigeons did not translate into higher fecundity or fertility, and Nattero et al. (2013b) concluded that the lower amount of guinea pig blood ingested was offset by its high nutritional quality.

Even morphological traits are being affected by blood source. Although Nattero et al. (2013a) found that in *T. infestans* females exhibited significantly greater head size than males for both food sources (mammals and birds), they also found that the greater head size of *T. infestans* adults fed on guinea pigs is not consistent with variation of body size; these authors claim that although body size seems to respond to food source, phenotypic plasticity in head size was not a simple consequence of allometric plasticity between body and head size, and hypothesized that the diet-induced phenotypic plasticity in head size for bugs fed on guinea pigs might be due to changes in developmental allocation to tissue growth that maintain growth of head size while reducing growth of body size, and that this, in turn, was probably due to the reduced amount of blood ingested when fed on guinea pigs relative to those fed on pigeon. There are other several indications that we should expect a relationship between body measures and feeding in triatomines. Zeledón et al. (1970) found that body length in adult *T. dimidiata* were larger when collected in the field than those reared in the laboratory, and suggested that this was the result of a more frequent feeding rate of those insects caught in the field. Gürtler et al. (2017) investigated the links among individual bug bloodmeal contents in *T. infestans* and body length as well as host blood sources and habitats; body length correlated positively with other body-size surrogates and was modified by habitat type, bug stage, and recent feeding (e.g., bugs from chicken coops were significantly larger than pig-corral and kitchen bugs).

Lunardi et al. (2017) did not find variations in the head centroid size in *Triatoma williami* (Galvão & Col., 1965) related to the blood source, while in *T. infestans* Nattero et al. (2013a) found that the head was greater when fed on mammals, but the body was greater when fed on birds. Furthermore, Nattero et al. (2013a) demonstrated experimentally that adult *T. infestans* showed evidences of phenotypic plasticity in head size.

Guarneri et al. (2000) showed in four triatomines species of the genus *Triatoma* [*T. infestans*, *Triatoma brasiliensis* (Neiva, 1911), *Triatoma sordida* (Stål, 1859), and *Triatoma pseudomaculata* (Erichson, 1848)] that the development time was on average almost twice as long when fed on pigeons (279 days) than when fed on mice (159 days). Similarly, total nymphal mortality (as %) was 1.6 times larger when fed on pigeons (24.2%) than when fed on mice (14.6%). However, the average total body length, for both sexes together, did not differ when fed on pigeons (2.25 cm) than when fed on mice (2.16 cm) for the pool of all four species.

Martínez-Ibarra et al. (2003) tested the response of development time of the triatomine *Triatoma picturata* (Usinger, 1939) to being fed on hens and rabbits and, assuming normality, I carried out a sample *t*-test of their results (mean = 196.8 days; SD = 15.8; $n_1 = 69$ for hens, and mean = 189.6 days; SD = 22.88; $n_2 = 68$, for rabbits) showing that there was a statistically significant effect of the blood source used for feeding ($t = 2.1459$, $df = 135$, p -value = 0.03367). These differences, coupled with survival differences between feeding

types led to Martínez-Ibarra et al. (2003) to show that there was also an effect on demographic parameters: the net reproductive rate (R_0 , estimated as the number of females produced by cohort \times mean eggs laid per female divided by the number of eggs that started the cohort) was larger for rabbits ($R_0 = 148.5$) than for hens ($R_0 = 114.7$).

Cortico Correa Rodrigues et al. (2007) developed a life table of the triatomines species *Triatoma tibiamaculata* (Pinto, 1926), and estimated the longevity of adults and oviposition of females, and found that although there was no difference in the survival from the egg to the adult stage for insects fed on pigeon or on cocks, there was a large difference in the life-time fecundity: 7,832 eggs were laid by the cohort fed on cocks, and about half that number (3,633 eggs) was laid when the cohort was fed on pigeons.

In summary, considering the richness and variety of information on triatomines, I set as a goal for this article the compilation of the quantitative data available to investigate the possible effects of morphology, life cycle, and environment factors on the population fitness in triatomines, through a Machine Learning approach.

MATERIALS AND METHODS

Data Compilation

I carried out an exhaustive review of the literature on triatomines using the BibTri bibliographic database¹, hosted by the Centre for the Study of Parasitology and Vectors of the National University of La Plata, Argentina. This access-free database has 14,164 bibliographic records on Chagas disease, of which 7,207 refer exclusively to all possible features of the triatomines. Those records were then narrowed down by filtering them with the following 15 keywords available as a special field in the database: life cycle, population growth, demography, density effects, diet and foraging, physiology, age, fecundity, longevity, mortality, population parameters, survival, life tables, temperature, and development time. By this procedure I obtained 2,968 records complying with one or more of those 15 fields of interest (see **Supplementary Material 1** for the complete list of those 2,968 publications); I analyzed them individually, and the publications that did not have the data in quantitative form as needed for the objective of this article were discarded, and 171 papers remained as adequate for the present analysis (see **Supplementary Material 2** for a list of those 171 publications). I would like to highlight that all these publications provided results of laboratory experiments (see section “Discussion” about the importance of this feature).

From the final selection of 171 papers a total of 71 triatomine species were found, representing 539 different case studies (many papers had more than one triatomine species under study, and frequently for any given species more than one experiment under different laboratory conditions were carried out, resulting in many more cases than papers). The full information of those 539 study cases were transcribed to an Excel sheet that had 60 headers (see **Supplementary Material 3** for the complete list

of those headers), that represented the following seven types of information (N refers to “nymph”):

1. *Metadata*: case number, publication code, species, genus (text), species (text), genus (code), species (code), geographical origin, observations.
2. *Environmental variables*: mean temperature ($^{\circ}\text{C}$), temperature regime (constant/fluctuating), relative humidity (%), food source (animal blood used), frequency of feeding (in days).
3. *Demographic variables*: population intrinsic rate of natural increase (r_0), net replacement rate (R_0), and generation time (T).
4. *Life cycle variables* (in days): mean development time of eggs, NI, NII, NIII, NIV, and NV, total of egg to adult, total of N1 to adult, and mean and standard deviation of female longevity.
5. *Reproductive variables*: sex ratio, preoviposition period, reproductive period, mean and standard deviation of eggs/female/life, and mean and standard deviation of female eggs/female/day.
6. *Survival variables*: egg, NI, NII, NIII, NIV, and NV mortality, mean and standard deviation of total nymphal mortality, mean and standard deviation of mortality from egg to adult, female mortality, and male mortality.
7. *Morphological variables* (all measurement variables in mm): total length, pronotum length, abdomen width, anteocular-postocular ratio, eye dorsal width/synthlipsis ratio, 2nd to 1st antennal segment ratio, 3rd to 1st antennal segment ratio, 4th to 1st antennal segment ratio, 2nd to 1st rostrum segment ratio, 3rd to 1st rostrum segment ratio, length head/pronotum ratio, length/width of head ratio, ellipsoid short axis of eggs, ellipsoid long axis of eggs, and egg volume (calculated as an ellipsoid). These morphological variables have a unique value for each species, representing the value of the type from the original description (as summarized in Lent et al., 1998); so, they differ from the demographic, life cycle, reproductive, and survival variables in that they have no variability.

A relatively important variable effecting life history traits and fitness is infection of triatomines by *T. cruzi* (Cordero-Montoya et al., 2016), who found that insect hosts infection affects size, number of eggs laid, egg hatching rate, hatching success, and survival. However, despite this study is one of the most relevant to fitness estimation, some life history traits were not in the form adequate to estimate demographic parameters, and additionally development time was not estimated (all experiments were carried out with adult individuals). So, the *T. cruzi* infection factor could not be included in this analysis.

Demographic Parameters' Estimate

As I was interested in finding a possible association between life cycle, morphological and environmental variables with some fitness parameter among the triatomine species, I selected the population growth rate as demographic parameter (r_0 and/or

¹<http://bibtri.cepave.edu.ar>

R_0 , the population intrinsic rate of natural increase, and the net reproductive value, respectively) that are usually considered good indicators of population fitness (Engen and Saether, 2016), and that have been used as such in other triatomine studies (e.g., Pelosse et al., 2013). So, I had to filter again the dataset for those cases that provided some of the demographic parameters directly, or that at least provided enough life cycle information to calculate them. Whenever the demographic parameters were not available and I had to calculate r_0 and/or R_0 from the original data in a publication, I used the Lotka equation ($\sum_{i=1}^{\omega} l_x m_x e^{-r_0 * x}$) (Southwood, 1978), which requires the survival (l_x) and fecundity (m_x) schedules (a quantitative information rarely published); here x is the age (or stage) of the insect, and w is the last reproductive age. Lotka's equation cannot be solved explicitly so the iterative method used by Rabinovich (1980) was applied, implemented in an Excel spreadsheet using the Solver tool. Both growth rate parameters are related by the formula $r_0 = \log_e \frac{R_0}{T}$ (Bengstron, 1969), where T is the cohort generation time (mean age of the females in the cohort at the birth of the female offspring). As both demographic parameters are directly related, I decided to use only one of them: the intrinsic rate of natural increase, r_0 . This new requirement of the r_0 parameter (or l_x and m_x for its calculation), reduced the original 539 case studies and 71 triatomine species to 90 cases and 36 species.

Variable Selection for the Final Dataset

Several of the 60 variables of the original dataset (see **Supplementary Material 3**) were redundant or unnecessary because they were included indirectly in other variables (e.g., total of egg to adult development time included the development time of each of the egg, NI, NII, NIII, NIV, and NV stages). Using a parsimonious criterium I selected (in addition to the name of each triatomine species) a subset of the variables available; e.g., the head width and pronotum length were the morphological variables that best differentiated species (Nattero et al., 2017); as a result, the following 11 variables remained in the final dataset to be used in the present analysis:

- (I) *Four environmental variables*: (1) "Temp_Reg" (temperature regime: a categorical variable representing a constant or fluctuating temperature), (2) "Mean_Temp" (average rearing temperature, °C), (3) "Food_source" (a categorical variable representing the blood source fed to the triatomines, with six categories: mouse, pigeon, chicken, rabbit, other mammal, and other birds, and (4) "Freq_feeding_d" (frequency of feeding, in days).
- (II) *Two life cycle variables*: (5) "MEADT_d" (mean egg to adult development time, in days), and (6) "MFEF_d" (mean female eggs/female/day).
- (III) *Four morphological variables* (these are standard morphological traits used routinely in the taxonomy of triatomines; Lent and Wygodzinsky, 1979): (7) "Total_length" (body length, in mm), (8) "Pronotum_length" (also in mm), (9) "Ant_postoc_ratio" (the anteocular-postocular ratio),

and (10) "X4th_1st_ant_seg_ratio" (the 4th to 1st antennal segment ratio).

- (IV) *One demographic parameter* (used as dependent variable): (11) " r_0 " (the intrinsic rate of natural increase, in days).

Although it is well known that population growth rate is affected by fecundity, survival, and development time (Southwood, 1978), both fecundity and development time were included in the analysis (unfortunately not enough data on survival was available) because it would be very informative to learn about the relative importance of those two variables under the variety of species and environmental conditions of the dataset here used. The complete dataset used in the present analysis, plus the triatomine species names, is given in the **Appendix**.

Analysis Procedures

First an exploratory analysis was carried out, using classical box-plot graphics and normal fitting procedures, using the ggplot2 package of R software (Wickham, 2016). Then I selected the Random Forest analysis, using the randomForest (Breiman and Cutler, 2018) and the randomForestExplainer (Paluszynska et al., 2020) packages of the R library (R Core Team, 2019); these packages work by aggregating the predictions made by multiple decision trees of varying depth, with every decision tree in the forest being trained on a subset of the dataset (the bootstrapped dataset). Finally, to verify if the insights gained from the machine learning approach were robust, I compared those results with an ordinary least square (OLS) regression. All analyses were carried out with different packages of the R program (R Core Team, 2019). The R code used for the analyses is given in **Supplementary Material 4**.

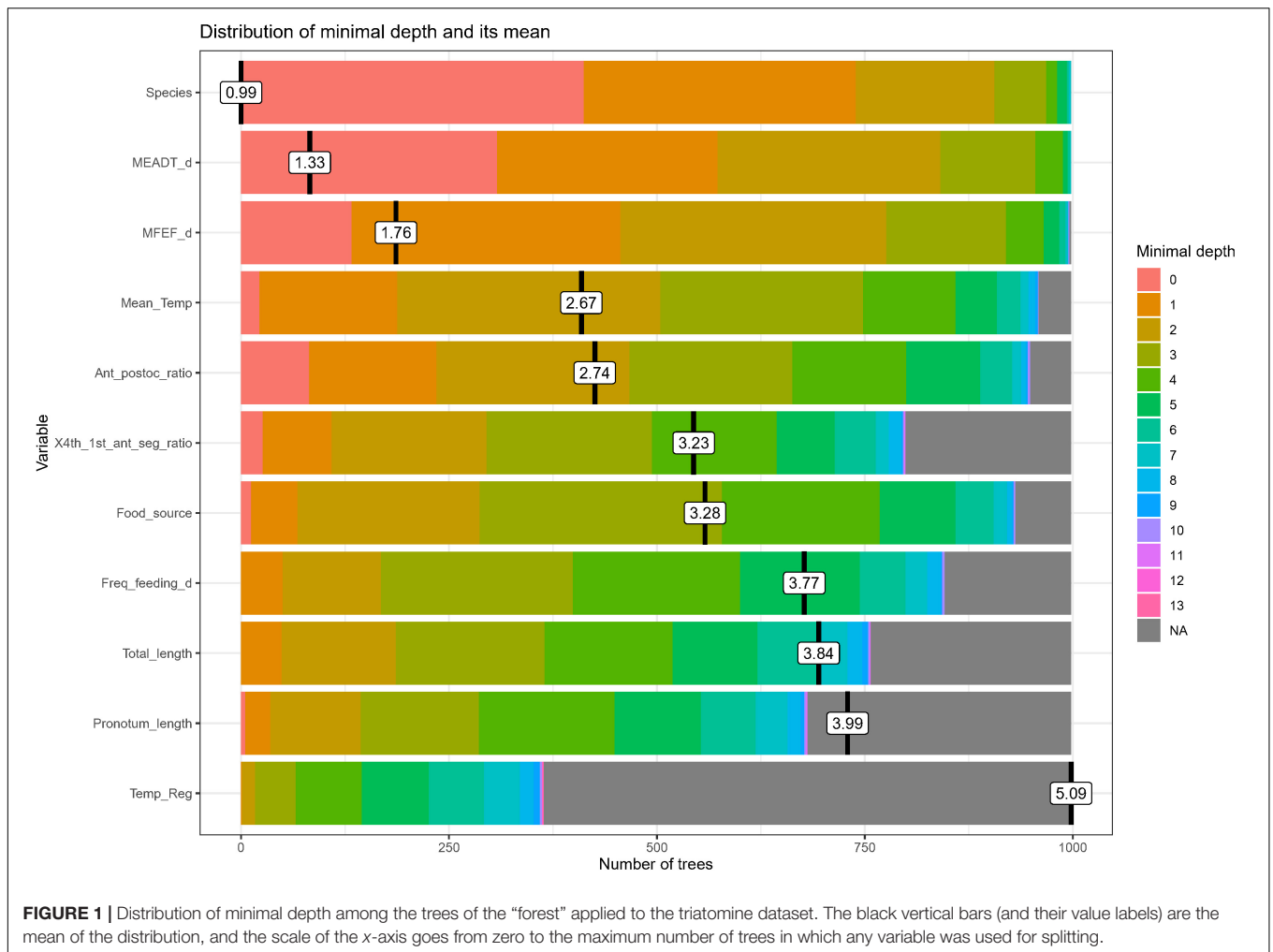
RESULTS

Exploratory Analysis

Supplementary Figure 1 shows the distribution of the dependent variable used in this analysis (r_0 , the intrinsic rate of natural increase). The distribution fits well a normal distribution (the Shapiro test resulted in a p -value = 0.659, so there is no evidence on which to reject the null hypothesis that the variable r_0 is normally distributed). As some species had several estimates of r_0 (sometimes under different environmental conditions), it was also of interest to visualize the distribution of this parameter among species (**Supplementary Figure 2**).

Similar box-plot graphs were prepared with the two numerical environmental variables: mean temperature and feeding frequency (**Supplementary Figure 3**); both variables show an important and useful degree of variation: the range of the mean temperature was 19.5–32°C, and that of the feeding frequency was 2–25 days (see black dots in **Supplementary Figure 3**, that represent the extreme values).

The two life cycle variables used in this analysis (egg to adult development time in days, and fecundity, expressed as average female eggs produced per female per day) show similar variability to the numerical environmental variables (**Supplementary Figure 4**); the range of the egg to adult development time was



69–570 days, and that of the fecundity was 0.17–2.42 female eggs/female/day (the black dots in **Supplementary Figure 4**, represent the extreme values).

Finally, the four morphological variables were also graphed (**Supplementary Figure 5**) in the form of box-plots in a single figure (with morphological traits in the x-axis), because each species has only one measurement for each morphological trait; so, in **Supplementary Figure 5** the values of the morphological traits represent the variability among and not within species.

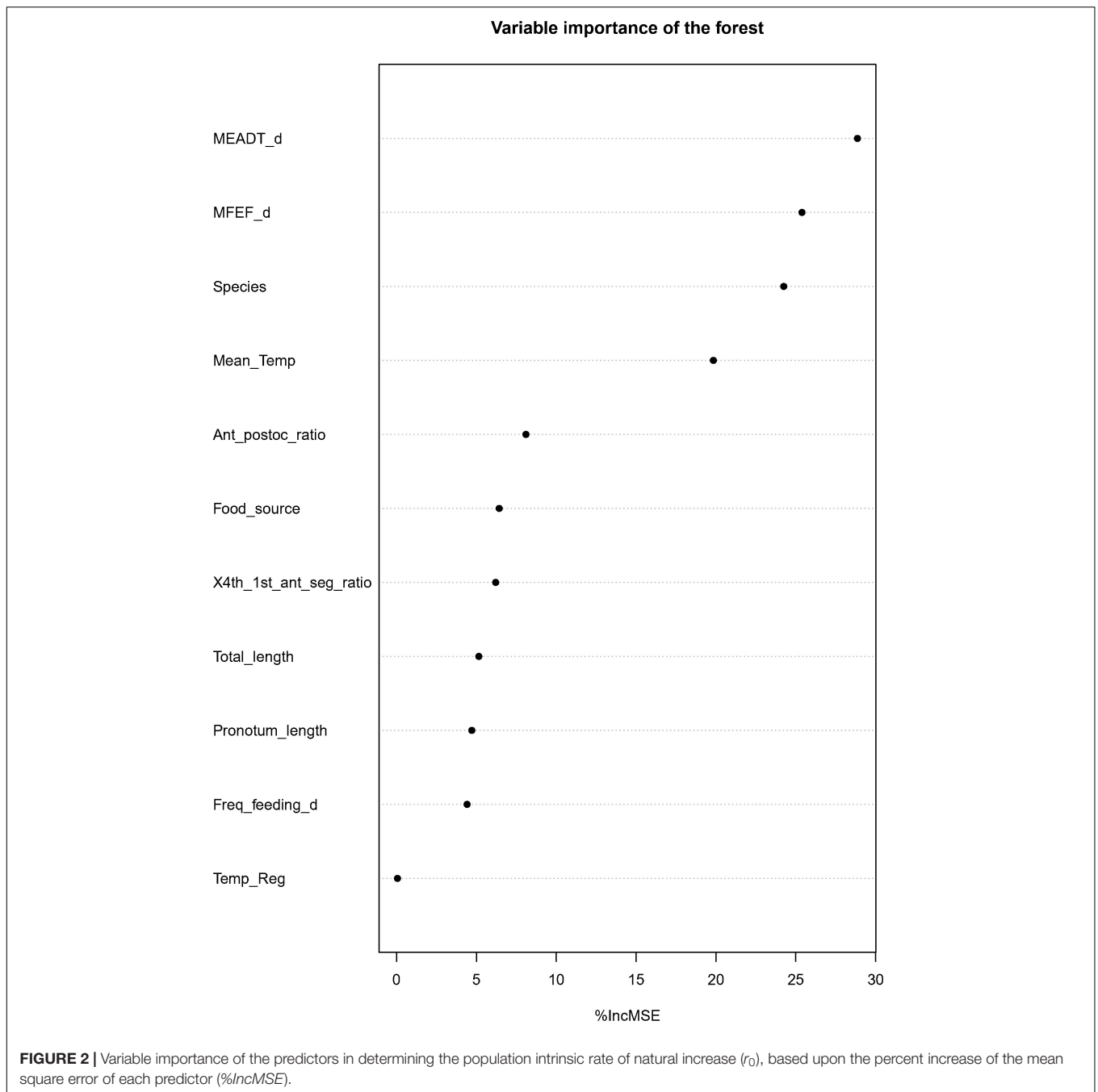
Random Forest Analysis

Why did I select Random Forest for analysis? Regression and classification trees have a very different flavor from the more classical approaches for regression and classification but, unfortunately, trees generally do not have the same level of predictive accuracy as some of the other regression and classification approaches (Gareth et al., 2014). However, methods such as Bagging, Random Forests, and Boosting use trees as building blocks to construct more powerful prediction models. Random forests provide some improvements over bagged trees by a random “de-correlation” of trees: when building the decision trees, each time a split in a tree is considered, a random sample

of m predictors is chosen as split candidates from the full set of p predictors; then that split is allowed to use only one of those m predictors, and a fresh sample of m predictors is taken at each split (technically, the usual procedure is to choose $m = \sqrt{p}$, that is, the number of predictors considered at each split is approximately equal to the square root of the total number of predictors; Gareth et al., 2014). In other words, in building a Random Forest, at each split in the tree, the algorithm is not even allowed to consider a majority of the available predictors.

Before running the Random Forest analysis, I checked for possible collinearity among some of the independent variables, to avoid any degree of strong redundancy. Using the classical criterium of $r > |0.7|$, the only significantly correlated variables were Total length and Pronotum length ($r = 0.846$); I decided to delete Total length from the dataset because the Pronotum length, being a completely chitinized structure, is more reliable.

To run the standard Random Forest method with the dataset (see **Appendix** for the full dataset), I used 1,000 regression trees (the number of bootstrap samples), and r_0 (population intrinsic rate of natural increase) as the dependent variable; I first tried with several values of the parameter $mtry$ (the number of predictors that are randomly sampled as candidates for each

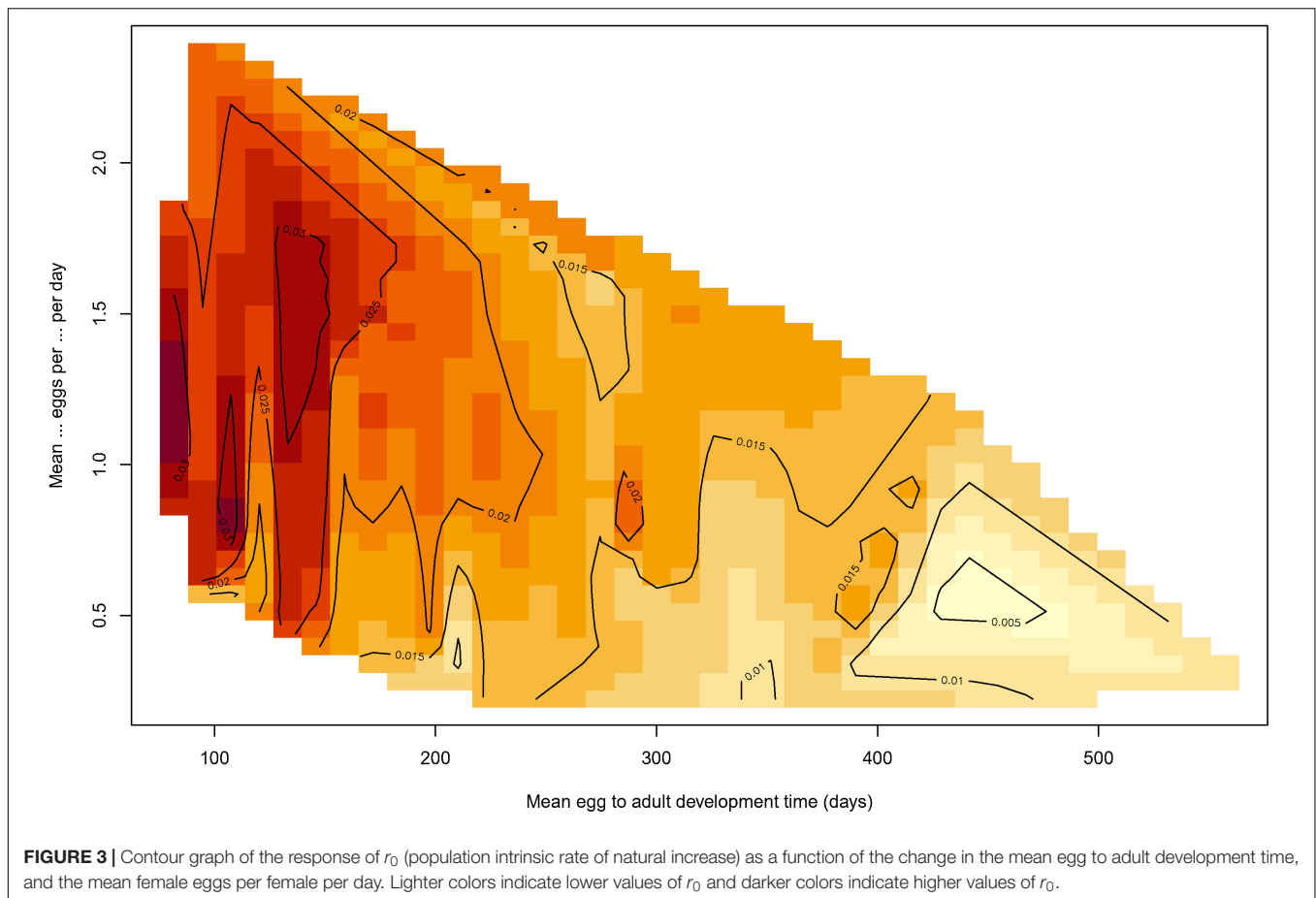


split), and selected the *mtry* value that maximized the percent of the explained variance; as a result I obtained a mean of squared residual of $1.6378e^{-05}$, and a variance explained of 67.6% with *mtry* = 6. I believe that a variance explained of 67.6% is a sensible prediction accuracy.

Figure 1 shows the minimal depth among the trees of the Random Forest applied to the triatomine dataset; the visualization of minimal depth among trees provides an estimate of the importance of each of the variables in the model. There are three “dominant” variables: Species, mean egg to adult development time, and mean female eggs per female per day;

these three variables are the significant predictors given by the “importance measure” function of the Random Forest package. It is illustrative to look not only at the mean but also at the whole distribution of the minimal depths as given in **Figure 1**, that suggests more insights into the role that a predictor plays in a forest.

Two additional common measures of variable importance are given by the indices *IncNodePurity* (the total decrease in node impurities from splitting on the variable, averaged over all trees; i.e., it indicates that a node contains predominantly observations from a single class), and *%IncMSE* (the increase



in the mean square error of predictions as a result of the variables being permuted, i.e., it indicates the extent to which the predicted response value for a given observation is close to the true response value for that observation). *mse_increase* is measured by the well-known Gini index; as *mse_increase* is the most robust and informative measure of importance in Random Forest (Gareth et al., 2014), while *IncNodePurity* is a biased measure, I preferred to present the results of variable importance as *mse_increase* (Figure 2); the higher the value of *mse_increase* associated with a predictor, the more important the role of the predictor in its effect on r_0 .

Table 1 provides the statistical information resulting from the Random Forest analysis, and it is presented with the *p*-values in ascending order, confirming that only Species, mean egg to adult development time, and mean female eggs per female per day are the only significant predictors determining the population intrinsic rate of natural increase (r_0). It was relatively surprising that none of the environmental variables seem to play any role in determining r_0 (see section “Discussion”).

I have also produced the so-called a multi-way importance plot (see Supplementary Figure 6) using the *mse_increase* (in the *x*-axis), and the *IncNodePurity* (in the *y*-axis), and their location on the graph confirms that Species, mean egg to adult

TABLE 1 | Statistics of the dataset variables from the randomForest analysis, with the *p*-values in ascending order.

Variable	Mean minimum depth	Number of trees	<i>p</i> -Value
MEADT_d	1.333	998	1.76E-185
MFEF_d	1.768	996	3.31E-167
Species	0.994	998	2.45E-127
Mean_Temp	2.837	959	4.56E-01
Ant_postoc_ratio	2.942	949	1.00E+00
Food_source	3.524	931	1.00E+00
Freq_feeding_d	4.245	846	1.00E+00
Pronotum_length	4.905	681	1.00E+00
Temp_Reg	6.226	364	1.00E+00
Total_length	4.576	757	1.00E+00

development time, and mean female eggs per female per day are the only significant variables.

The Random Forest package also allows for an estimation of interaction among the predictor variables, by graphing the mean minimal depth (MMD) of the main interactions (Supplementary Figure 7); from the MMD among the main six possible interactions the three interactions between Species and the two life cycle variables (mean egg to adult development time, and mean female eggs per female per day) are the dominant ones,

although the interaction of those variables with the mean rearing temperature was also important; however, as mean rearing temperature was not statistically significant in its effect on r_0 , that means that it is only important as a conditional effect on other variables.

As, in addition to species, the two life cycle variables keep showing to be the ones with the most significant influence on r_0 , it was of interest to look at the empirical response of r_0 as a function of the simultaneous change of the mean egg to adult development time, and the mean female eggs per female per day; this is shown as a contour graph in **Figure 3**. It is clear that the former (mean egg to adult development time) has a stronger effect on r_0 than the mean female eggs per female per day.

Linear Regression Analysis

As a final step, it was of interest to compare the results produced by the Random Forest method with the ones produced by a regular parametric analysis. I resorted to a simple OLS regression, and **Table 2** shows the results of the regression analysis with the same dataset used for the Random Forest analysis, for all species pooled; it was confirmed that only the mean egg to adult development time, and fecundity (mean female eggs per female per day), are the only significant independent variables. However, when the linear regression was carried out with interactions among the independent variables, no effect was statistically significant (results not shown), an important difference with the Random Forest analysis (**Supplementary Figure 7**) and the observed data (**Figure 3**).

DISCUSSION

Historically, there have been two schools of thought in the study of the development of organisms: the “old school” covering mainly the juvenile forms in what is usually called “life cycles,” and a relatively “new school” (developed over the last 50–60 years) concerned largely with adults and their quantitative schedule of reproduction, and usually called “life histories”; the latter was developed in a very different fashion, being highly theoretical from the outset (Bell, 2011). Much of this “life history” theory was based on the principle of optimality, and founded on what has been called “trade-offs,” e.g., the apparent negative association between the rate of reproduction and the probability of survival. Despite some outstanding initial successes, as many exceptions were found as cases following this rule, and it was soon even seen that the correlations between fitness components are usually positive rather than negative; this fact was attributed to environmental variance of productivity among sites when comparisons are made in the field, or to genetic variance of overall fitness among strains when comparisons are made in the laboratory (Bell, 2011).

Within this context, my analysis produced several unexpected results. Despite the evidence of the importance of the source of blood meals and their frequency (see section “Introduction”)

TABLE 2 | Statistics of the linear regression analysis.

	Estimate	Standard error	t-Value	Pr(> t)
(Intercept)	1.81E-02	7.62E-03	2.382	0.01943
Mean_Temp	2.22E-04	2.58E-04	0.86	0.39246
Freq_feeding_d	1.83E-04	1.15E-04	1.585	0.11678
MEADT_d	−4.42E-05	6.11E-06	−7.236	1.90E-10
MFEF_d	4.93E-03	1.30E-03	3.781	0.00029

neither of these factors seemed to influence fitness (as measured by r_0). Similarly, neither temperature nor body size affected r_0 , a surprising result because those factors are considered as the two most important variables affecting nearly all biological rates and times (Gillooly et al., 2002). One possible explanation could be related to the fact that the pool of 36 different triatomine species here analyzed (and identified as significant on its effect on r_0), originated from data coming from quite different environmental conditions. When carrying out the linear regression analysis, I also applied it for each species separately to test if another independent variable would appear as significant, but with no avail (results not shown). However, this lack of results is of little value because when narrowing down the regressions to each species, the number of replicates per species was extremely low (the species with the largest number of observations was *R. neivai*, with $N = 11$, followed by *R. prolixus*, with $N = 6$).

On the other hand, my results that development time and fecundity were the only significant variables (in addition to the species themselves) impinging on fitness are consistent with the known fact that development time (as the time to reach reproductive maturity) is probably one of the life-history variables with the strongest impact on the population growth rates (Cole, 1954). The results are also congruent with the claim of Mousseau and Roff (1987) that in laboratory outbred animal populations traits closely associated with fitness will generally possess higher heritabilities than traits more loosely connected with fitness.

However, the results have also to be considered within the context of a certain weakness inherent to the dataset used: the data I analyzed are all derived from laboratory experiments; although it is true that no data of the type needed for this kind of analysis has been obtained in nature (not only in triatomines but in general; Hendry, 2015), some caveats are in order. In a stable environment, evolution maximizes growth rates in populations that are not density regulated, while in a naturally fluctuating environment, evolution maximizes a function of growth rate, carrying capacity, and environmental variance, tending to r -selection and K -selection under large and small environmental noise, respectively (Engen and Saether, 2016). The only analysis made on triatomines related to r - and K -selection (Rabinovich, 1974) showed that the triatomines species *R. prolixus* and *T. infestans* were “intermediate” r -strategists, with *T. infestans* being slightly more r -strategist than *R. prolixus*. This coincides with the high r_0 value of these two species as shown in **Supplementary Figure 2**.

But some caveats still remain associated to another fact: many of the experiments compiled in this review were carried out with specimens of colonies that had been maintained in the laboratory for many generations (sometimes for several hundreds of generations). Kingsolver et al. (2009) have explored, using the tobacco hornworm, *Manduca sexta* (Linnaeus, 1763), the question of the evolution in a constant temperature as altering the adaptation to fluctuating temperature conditions; these authors compared a field population that routinely experiences fluctuating temperatures, and a laboratory population maintained at a constant temperature for more than 250 generations, and showed that diurnal fluctuations significantly alter body size and development time in both populations, and confirmed that these populations differ in their responses to a mean temperature. As a consequence, we could suspect that the results of this analysis might have been different if the experiments would have been carried out in the laboratory with first generation individuals from the field.

Another caveat of the data I used is that there is no variability in the morphological traits; the ideal situation would have been to have the actual body measurements and ratios of the phenotype from same specimens used in the experiments. In triatomines it has been shown that phenotypic traits (including morphological measurements) may differ for the same species when their geographical origin (reflecting modified environmental conditions) is different. E.g., Carmona-Galindo et al. (2020) found that the variation in the size, shape, and coloration of the triatomines species *T. dimidiata* in El Salvador varied in relation to elevation, Holdridge life zone, soil type, and land use, and were able to characterize the local morphological adaptations of *T. dimidiata* with respect to the local ecological, biological, and geographical conditions. The issue of phenotypic plasticity in triatomines is sometimes so serious that leads to the successive splitting or lumping of species. E.g., Nattero et al. (2017) found that the cryptic triatomine species *T. sordida* from Argentina, differed from *T. sordida* from Brazil and Bolivia in all measured shape traits, suggesting that the putative new species may not be cryptic; and recently Dorn et al. (2018), based upon characters found on the pronotum, legs, and abdomen of a population of the triatomine *T. dimidiata* from a cave in Belize, considered those specimens as a new species, *Triatoma mopan*. However, unfortunately no such measurements were ever present in the dataset of the laboratory experiments used in the data I compiled.

Some of the results of my analysis (e.g., that source of blood meals and their frequency did not influence fitness) might seem to invalidate the studies from where the data was obtained. However, this is not the case, for this analysis was carried out using data of 36 species and, as such, the results represent the overall effects among species and do not really invalidate any of the specific studies used as data source, where the opposite effects could be true.

My analysis can be considered as a modest probe in trying to relate life history and evolution in triatomines; I was specifically

looking into a very general types of questions: to see if triatomines follow the evolutionary designs of organisms to achieve reproductive success by some measurement of fitness. Whatever design the triatomines show it will be a solution to the ecological problems posed by the environment and subjected to constraints intrinsic to their “*bauplan*” (Stearns, 2000). In other words, some specific questions addressed by these analyses were of the following type: Why do some triatomines species have a small body size and others a large one? Why do triatomines complete their pre-adult development in a short or in a long time under the same conditions? Why do some triatomines show high fecundity, and others an extremely low one? These types of questions have received here only a very partial answer. Modern methods to answer them resort to non-equilibrium approaches, involving frequency-dependence, density-dependence, evolutionary game theory, adaptive dynamics, and explicit population dynamics that are common in optimization approaches (Stearns, 2000). A more recent methodological approach resorts to genetic mechanisms dealing with challenges such as the genetic correlations between genes or alleles and trade-offs, and how genes interact with the environment to determine life history phenotypes (Flatt and Heyland, 2011). However, these approaches and methods are still being developed, and I hope that the analysis I have presented will contribute to a theoretical framework capable of interpreting the succession of stages in the development of triatomines in terms of morphology, fitness, and environmental factors, a framework that has yet to be constructed.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

JR designed and reviewed the literature, collected the data, analyzed the data, and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.651683/full#supplementary-material>

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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APPENDIX

Complete Dataset Used for the Analysis

Species*	TR	MT	FS	FF	r_0	MEADT	MFEF	TL	PL	APR	4_1AR
<i>Dipetalogaster maximus</i>	Constant	28	Mouse	7	0.019	158	0.809	37.5	8.75	4	2.1
<i>Dipetalogaster maximus</i>	Constant	28	Mouse	7	0.020	158	1.256	37.5	8.75	4	2.1
<i>Dipetalogaster maximus</i>	Constant	28	Pigeon	7	0.016	173.28	0.4	37.5	8.75	4	2.1
<i>Dipetalogaster maximus</i>	Constant	28	Pigeon	7	0.014	173.28	0.37	37.5	8.75	4	2.1
<i>Eratyrus mucronatus</i>	Constant	26	Chicken	7	0.007	205	0.354	26	5.5	3	3.1
<i>Panstrongylus geniculatus</i>	Constant	26	Chicken	7	0.013	280	0.727	25.75	6.75	2	2.6
<i>Panstrongylus geniculatus</i>	Fluctuating	23	Other mammals	7	0.017	297.2	0.845	25.75	6.75	2	2.6
<i>Panstrongylus geniculatus</i>	Fluctuating	23	Chicken	7	0.018	268.8	0.845	25.75	6.75	2	2.6
<i>Panstrongylus geniculatus</i>	Constant	26	Chicken	15	0.017	264.1	0.739	25.75	6.75	2	2.6
<i>Panstrongylus geniculatus</i>	Constant	26	Chicken	7	0.015	290.01	1.204	25.75	6.75	2	2.6
<i>Panstrongylus rufotuberculatus</i>	Constant	24	Mouse	7	0.032	138.82	1.737	26	7.5	3.5	2.1
<i>Rhodnius colombiensis</i>	Constant	28	Chicken	7	0.027	144.4	0.573	18	5.82	2.65	1.5
<i>Rhodnius domesticus</i>	Constant	28	Mouse	7	0.028	93.85	0.62	16.5	4.25	2.75	2.4
<i>Rhodnius nasutus</i>	Constant	26	Chicken	7	0.017	120.3	0.623	15	3.5	3.2	2.5
<i>Rhodnius neglectus</i>	Constant	26	Chicken	7	0.027	105.21	1.541	19	4	3.1	2.8
<i>Rhodnius neivai</i>	Constant	32	Chicken	2	0.029	68.9	1.264	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	26	Chicken	7	0.013	89	0.591	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Rabbit	2.3	0.022	94.06	2.424	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Chicken	2.3	0.032	86.66	1.572	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Rabbit	15	0.024	86.7	0.643	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Rabbit	7	0.029	86.7	0.921	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Chicken	15	0.028	86.7	0.686	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Chicken	7	0.034	86.7	0.721	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	22	Chicken	2	0.019	118	0.912	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	27	Chicken	2	0.032	86.7	1.484	19	4	3	0.5
<i>Rhodnius neivai</i>	Constant	26	Chicken	7	0.014	116.55	0.567	19	4	3	0.5
<i>Rhodnius prolixus</i>	Constant	26	Chicken	7	0.023	118.6	1.002	19.5	4.25	3.5	2.8
<i>Rhodnius prolixus</i>	Constant	26	Chicken	7	0.024	118.6	1.163	19.5	4.25	3.5	2.8
<i>Rhodnius prolixus</i>	Constant	27	Chicken	7	0.038	118.6	0.938	25	4.25	3.5	2.8
<i>Rhodnius prolixus</i>	Fluctuating	23	Mouse	7	0.032	126.1	0.758	19.5	4.25	3.5	2.8
<i>Rhodnius prolixus</i>	Constant	27	Mouse	7	0.035	112.1	0.827	19.5	4.25	3.5	2.8
<i>Rhodnius prolixus</i>	Constant	28	Chicken	7	0.037	117.7	0.938	19.5	4.25	3.5	2.8
<i>Rhodnius robustus</i>	Constant	29	Other mammals	18	0.037	85.51	0.993	23	5.25	3.75	4
<i>Triatoma barberi</i>	Constant	27	Rabbit	4	0.024	286.6	0.8	18	4	2.1	1.6
<i>Triatoma barberi</i>	Constant	27	Rabbit	7	0.019	389.1	0.515	18	4	2.1	1.6
<i>Triatoma brasiliensis</i>	Constant	24	Mouse	7	0.021	160	0.966	23.5	4.75	4	2
<i>Triatoma delpontei</i>	Constant	27	Other birds	15	0.016	225	0.213	25.5	7	3.25	1.5
<i>Triatoma eratyrusiforme</i>	Constant	26	Other birds	15	0.012	367	0.222	21.25	5.5	3	1.7
<i>Triatoma eratyrusiforme</i>	Fluctuating	19.5	Other birds	15	0.009	570	0.257	21.25	5.5	3	1.7
<i>Triatoma flavida</i>	Constant	28	Chicken	7	0.017	230.36	0.496	25.5	6	3	1.5
<i>Triatoma garciabesi</i>	Fluctuating	25	Pigeon	12	0.023	206	0.96	15.4	3.57	2.02	1.26
<i>Triatoma gerstaeckeri</i>	Fluctuating	23	Other birds	7	0.017	361.9	1.185	26	6	2.8	2.2
<i>Triatoma gerstaeckeri</i>	Constant	27	Other birds	7	0.023	213.9	1.044	26	6	2.8	2.2
<i>Triatoma guasayana</i>	Constant	25	Mouse	7	0.010	335	0.614	18.25	3.75	3	2.2
<i>Triatoma guasayana</i>	Constant	25	Pigeon	14	0.022	230	1.038	18.25	3.75	3	2.2
<i>Triatoma infestans</i>	Constant	26	Chicken	7	0.012	189.4	0.253	25	6	3.1	2.3

(Continued)

Continued

Species*	TR	MT	FS	FF	r_0	MEADT	MFEF	TL	PL	APR	4_1AR
<i>Triatoma infestans</i>	Fluctuating	24.3	Chicken	2.5	0.014	189.4	0.622	25	6	3.1	2.3
<i>Triatoma infestans</i>	Fluctuating	21.25	Pigeon	15	0.013	215	0.897	25	6	3.1	2.3
<i>Triatoma infestans</i>	Constant	26	Chicken	7	0.014	160.72	0.342	25	6	3.1	2.3
<i>Triatoma infestans</i>	Constant	27	Other birds	17	0.026	175	0.87	25	6	3.1	2.3
<i>Triatoma infestans</i>	Fluctuating	19.5	Other birds	17	0.023	207	0.989	25	6	3.1	2.3
<i>Triatoma longipennis</i>	Constant	27	Chicken	7	0.024	192.6	0.858	33	7	3.2	1.8
<i>Triatoma longipennis</i>	Constant	25	Chicken	7	0.021	229.7	0.897	33	7	3.2	1.8
<i>Triatoma longipennis</i>	Constant	25	Mouse	7	0.019	259.8	0.819	33	7	3.2	1.8
<i>Triatoma maculata</i>	Constant	28	Chicken	7	0.020	178.89	0.603	19	5	3.5	2.1
<i>Triatoma maculata</i>	Constant	27.6	Mouse	7	0.026	153.8	0.603	19	5	3.5	2.1
<i>Triatoma mazzottii</i>	Constant	27	Rabbit	7	0.020	235.77	0.705	33.5	7.25	3.2	1.8
<i>Triatoma mazzottii</i>	Constant	27	Rabbit	7	0.022	210	1.45	33.5	7.25	3.2	1.8
<i>Triatoma ninioi</i>	Constant	27	Other birds	20	0.022	162	0.362	21.25	5.5	2.7	1.7
<i>Triatoma ninioi</i>	Fluctuating	19.5	Other birds	20	0.016	262	0.404	21.25	5.5	2.7	1.8
<i>Triatoma pallidipennis</i>	Constant	25	Chicken	3	0.022	168	0.923	33	7	3	1.6
<i>Triatoma pallidipennis</i>	Constant	25	Mouse	3	0.029	171	1.5	33	7	3	1.6
<i>Triatoma pallidipennis</i>	Constant	30	Mouse	3	0.031	154	1.5	33	7	3	1.6
<i>Triatoma patagonica</i>	Fluctuating	27.5	Pigeon	15	0.021	228	0.88	19	4	2.5	2
<i>Triatoma patagonica</i>	Constant	26	Pigeon	7	0.002	435.89	0.59	19	4	2.5	2
<i>Triatoma patagonica</i>	Constant	27	Pigeon	7	0.010	326.76	0.259	19	4	2.5	2
<i>Triatoma patagonica</i>	Constant	28	Pigeon	7	0.010	360	0.166	19	4	2.5	2
<i>Triatoma phyllosoma</i>	Constant	26	Chicken	7	0.016	172.55	1.394	33	6.5	2.75	1.7
<i>Triatoma picturata</i>	Constant	25	Chicken	25	0.018	272.3	1	31.5	7	3	1.9
<i>Triatoma picturata</i>	Constant	30	Chicken	18	0.025	175.5	1	31.5	7	3	1.9
<i>Triatoma picturata</i>	Constant	27	Rabbit	7	0.024	189.5	1.719	31.5	7	3	1.9
<i>Triatoma picturata</i>	Constant	27	Chicken	7	0.023	196.8	1.465	31.5	7	3	1.9
<i>Triatoma platensis</i>	Fluctuating	28	Other birds	20	0.020	197	0.412	24	7.5	3	1.6
<i>Triatoma pseudomaculata</i>	Constant	24	Mouse	7	0.019	212	0.829	18.5	4.75	3.1	2.2
<i>Triatoma rubida</i>	Constant	27	Rabbit	7	0.029	119.7	1.8	19.25	5	3	2.5
<i>Triatoma rubrofasciata</i>	Constant	29	Mouse	15	0.027	165.1	1.492	22.25	5.25	2.5	1.8
<i>Triatoma rubrofasciata</i>	Constant	29	Mouse	7	0.019	256.1	1.034	22.25	5.25	2.5	1.8
<i>Triatoma rubrofasciata</i>	Fluctuating	26.75	Mouse	15	0.015	245.5	0.487	22.25	5.25	2.5	1.8
<i>Triatoma rubrofasciata</i>	Fluctuating	26.75	Mouse	7	0.023	204.3	1.382	22.25	5.25	2.5	1.8
<i>Triatoma rubrovaria</i>	Constant	27	Other birds	14	0.027	130	0.444	23	5	3.1	2.6
<i>Triatoma rubrovaria</i>	Constant	28	Chicken	7	0.019	304.5	1.549	23	5	3.1	2.6
<i>Triatoma rubrovaria</i>	Fluctuating	25.7	Chicken	7	0.015	434.1	1.213	23	5	3.1	2.6
<i>Triatoma rubrovaria</i>	Constant	28	Chicken	7	0.013	275.1	1.629	23	5	3.1	2.6
<i>Triatoma sanguisuga</i>	Fluctuating	23	Other birds	7	0.014	387.8	0.605	19.25	4.75	2.2	2.3
<i>Triatoma sanguisuga</i>	Constant	27	Other birds	7	0.016	318.1	0.599	19.25	4.75	2.2	2.3
<i>Triatoma sordida</i>	Fluctuating	26.5	Mouse	8	0.020	196.25	0.635	17	5.5	3.15	1.85
<i>Triatoma sordida</i>	Constant	28	Chicken	7	0.011	319.28	0.398	17	5.5	3.15	1.85
<i>Triatoma sordida</i>	Fluctuating	27.5	Pigeon	16	0.027	146	0.593	17	5.5	3.15	1.85
<i>Triatoma sordida</i>	Constant	28	Chicken	7	0.014908	220.5	0.542	17	5.5	3.15	1.85
<i>Triatoma tibiamaculata</i>	Fluctuating	24.5	Other birds	4	0.021014	199	0.468	31.25	7.25	3.5	1.7

Species, triatomine species; TR, temperature regime; MT, mean temperature ($^{\circ}$ C); FS, food source; FF, feeding frequency (days); r_0 , population intrinsic rate of natural increase (on a per day basis); MEADT, mean development time from egg to adult (days); MFEF, mean fecundity (female eggs per female per day); TL, total body length (mm); PL, pronotum length (mm); APR, anteocular/postocular ratio; 4_1AR, 4th to 1st antennal segment ratio. *Species names were preserved in the same way they were presented in the original publications (see **Supplementary Material 2** for the publications list). Some of those names may not be presently valid because of later synonym identifications, as well as the recognition of subspecies and complexes of species.