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Exponential growth model of weevil populations: a didactic experiment for undergraduate course of Population Ecology

Maria Eduarda de Jesus Bomfim[1], Claudiane de Lima Braz[1], Vanderléia dos Santos Conceição[1], Nayara Oliveira Dias[1], Francielen da Silva Dias[1], Elton dos Santos Freitas[1], Paloma Regina Peixoto de Jesus[1], Verônica Santos de Jesus[1], Roberto da Silva Dourado Junior[1], Vitor Castor Modesto[1], Joanna Karine Gomes de Oliveira[1], Tainara da Silva Pereira[1], Diana Souza Trindade Rocha[1], Stefane de Jesus Sacramento[1], Roseane Souza Sampaio[1], Ana Caroline de Souza Santos[1], Glaucio dos Santos Silva[1], Joseane Conceição da Silva[1], Stheffy Hevhelling Vila Verde Souza[1] and Guilherme de Oliveira[2*]

[1]Centro de Ciências Agrárias, Ambientais e Biológicas, Universidade Federal do Recôncavo da Bahia, Cruz das Almas, Bahia, Brazil. [2]Laboratório de Biogeografia da Conservação, Centro de Ciências Agrárias, Ambientais e Biológicas, Universidade Federal do Recôncavo da Bahia, R. Rui Barbosa, 710, 44380-000, Cruz das Almas, Bahia, Brazil. *Author for correspondence. E-mail: guilhermeoliveira@ufrb.edu.br

ABSTRACT. Exponential model for population growth (exponential model) is a foundation to evaluate population dynamics in Population Ecology field. Here, we used a didactic experiment to teach exponential model for an undergraduate course of Population Ecology. We built nine populations of weevils with three different initial population sizes: eight, 16, and 32 individuals with three replicates each. We provided equal food resource availability, and counted their population sizes weekly for 12 weeks. We estimated the intrinsic growth rate (i.e., r parameter), by trials and errors with an exponential model build in an Excel spreadsheet. The population growth rate (i.e., dN/dt parameter) was estimated using r values. Replicates with eight and 16 individuals reached the highest values of r and dN/dt, while replicates with 32 individuals reached the lowest values. Beyond of exponential model, two density dependency issues acting in populations were observed. First, in the lowest initial population sizes we observed the effect of demographic stochasticity acting in both r and dN/dt in one of the three populations. Second, we observed the intraspecific competition reducing r values in largest initial populations. Therefore, we highlight the importance of didactic experiment into learning exponential model in Population Ecology course, both for teaching and learning practices.

Keywords: problem-based learning; intrinsic growth rate; density dependency; demographic stochasticity; intraspecific competition.

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Introduction

Exponential model for population growth (hereafter exponential model) was deeply studied by Thomas Robert Malthus in the end of eighteenth century to evaluate human population growth in the context of Industrial Revolution (Seidl & Tisdell, 1999). It is a simplistic model where population growth depends only on birth and death rates. Consequently, exponential model takes the assumptions of (following Gotelli, 2008; textbook): i) a single closed population (i.e., no events of migration between populations); ii) birth and death rates are constant (i.e., no influence of environmental instability affecting the environmental conditions and resource availability); iii) no influence of genetic structure; and iv) age structure into birth and death rates. However, despite being a simplistic model, exponential model is a foundation for population ecology field, recognized as a general law to derive more realistic population growth models (e.g., logistic growth model, competition, and predation models) (Turchin, 2001).

Following the derivations of exponential model (Turchin, 2001), the intrinsic rate of growth (i.e., r: the Mathusian parameter), which is the difference between birth and death rates, is proportional to the population size. Consequently, population growth rate (i.e., dN/dt), under an exponential growth, is larger in larger population sizes. This linear relationship between population growth rate and population size (i.e., dN/dt x N) highlights the influence of the number of individuals of a population in both intrinsic rate of growth and population growth rate (i.e., r and dN/dt) in an exponential model.

Taking into account the importance of exponential model in population ecology, its teaching must be emphasized in undergraduate population ecology courses (Lehman, Loberg, Clark, & Schmitter, 2020). Thus, problem-based learning (PBL) approach is recognized to be an interesting tool for undergraduate courses to make students self-directed learners (Allen, Donham, & Bernhardt, 2011). In this sense, didactic experiments, as a PBL methodology, can be a facilitator into teaching exponential model for students of undergraduate population ecology courses, improving their active learning (Waree, 2019; Zendler, 2019). Here, we are considering a didactic experiment, a pattern that can be easily observed without complex analyses and methodologies.

We aimed in this study to make a didactic experiment for learning exponential model for an undergraduate course of population ecology. Therefore, we used weevil individuals, *Sitophilus sp*. Linnaeus 1763 (Coleoptera: Curculionidae) as the experimental populations. We used this species due to logistical resource in experimental designing and data collect (Vital et al., 2008) for it is: i) easy to find, because it is considered a pest for cereal storage (e.g., Midega, Murage, Pittchar, & Khan, 2016); ii) resistant to environmental changes (Shazali & Smith, 1985); and iii) a species with fast development, taking about four weeks from larva to an adult individual (Gallo et al., 1978).

Our specific aim in the didactic experiment of exponential model was to evaluate the effect of population size into intrinsic growth rate, and consequently, population growth rate (i.e. r and dN/dt parameters). To achieve that we built populations of weevil with different initial population sizes furnishing them equal resource supply and environmental conditions. As expected, result, under exponential model, smaller population sizes will have lower intrinsic growth and population growth rates than larger population sizes.

Material and method

The experiment was carried out during an undergraduate Population Ecology course of Biological Sciences at *Universidade Federal do Recôncavo da Bahia* (UFRB) from September to December, 2022. Classes were made weekly, and lasted, in average, four hours.

Experiment design

We build the experiment at *Laboratório de Biogeografia da Conservação* (Conservation Biogeography Laboratory) of UFRB, using weevil individuals found in a local cereal shop of Cruz das Almas municipality of Bahia state, Brazil. We used nine plastic bowls with lid to simulate single closed weevil populations with 70 g of corn seeds, in each bowl, as resource availability (Figure 1A). Corn seeds, used as food resource for populations were screened to verify if there were no previous weevil individuals, both in larva and adult forms (Figure 1B). As treatments, three initial population sizes were formed, with eight, 16, and 32 weevil individuals, and each population size was replicated three times (i.e., $N8_{I}$; $N8_{II}$; $N8_{III}$; $N16_{I}$; $N16_{II}$; $N16_{III}$; $N32_{I}$; $N32_{II}$; $N32_{III}$). The experiment was built in September 08, 2022, and after two weeks (i.e., September 22, 2022), for acclimatization purpose, we started to count weevil individuals in each population, weekly, during 12 weeks. Weevil individual counts of each population were done in groups of about five individuals.

Figure 1. A) Weighing of corn seeds used as food resource for each weevil population (i.e., the nine bowls); B) Corn seed screening for seeds which had no appearance of consumption by weevils.

Estimation of r and dN/dt

We used Gotelli (2008) (Gotelli, 2006, in Portuguese version) textbook as the main guide for the entire Population Ecology course, including when exponential model was taught. Consequently, we used (1), as the exponential model, to estimate the intrinsic rate of growth of each weevil population.

$$N_t = N_0 e^{rt} \quad (1)$$

where:

N_t is the population size at t time, N_0 is the initial population size, e is a constant, which is the base of natural logarithms (i.e., e ~ 2.717), and r is the intrinsic rate of growth (i.e., difference between birth and death rates).

We estimated r value of each of the nine weevil population following the protocol of: i) the exponential model was built in an Excel spreadsheet, using the population size of the previous week (i.e., N_t was the population size at twelfth week) as the final population size (i.e., t = 12), and, as initial population size, the three different treatments (i.e., N_0 = eight individuals, N_0 = 16 individuals, and N_0 = 32 individuals); and ii) as the r was the only constant which we did not know the value into exponential model (differently of N_t, N_0, e, and, t), we estimate r value by trials and error, trying to reach, as close as possible, the observed final population size of each of the nine populations. Three decimal places were considered in each r value (for each trial and error), for approximation. Following, population growth rate was estimated multiplying r by N (i.e., dN/dt = rN).

We evaluate the differences between r values of the three different initial population sizes using Analysis of Variance (ANOVA) one-way (Gotelli & Ellison, 2011; Andrade, 2019). Nonetheless, one population of initial size of eight individuals reached a very low and discrepant value from the other two populations of the same initial size (see the Results section). Following, we withdraw from the ANOVA one population with lower and discrepant value of r to avoid biases, however, it remained in the graphical building (i.e., Figure 3 and 4). Finally, we observed differences on the population dynamics between initial population sizes in two ways: i) plotting patterns of observed and predicted populations sizes within 12 weeks, according to an exponential model (i.e., N x t); and ii) plotting the relationship between population growth rates and observed population sizes (i.e., dN/dt x N).

Results

The initial population sizes of eight and 16 individuals reached the highest values of r with no significant difference between them (Figure 2, $F_{(2,5)}$ = 22.853, p = 0.003). We have to emphasize that one population of eight individuals of initial size presented a very low and discrepant value of r when comparing to the other two populations (r = 0.191 from the other two values of r = 0.285, and r = 0.263; 33 and 27% lower, respectively). Populations with 32 individuals of initial population size showed the lowest values of r significantly different of the other population sizes (Figure 2, $F_{(2,5)}$ = 22.853, p = 0.003). The values of r of 32 individuals of initial population size reached on average, 34% lower than the r of eight individuals of initial population size, and 25% lower than the r of 16 individuals of initial population size.

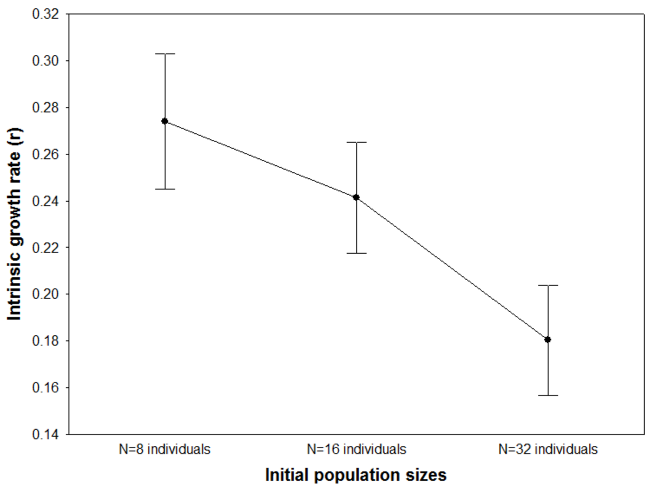

Figure 2. Means (circles) and confidence intervals at 95% level (bars) of the intrinsic growth rates (r) separated by the three different initial population sizes (N) of eight, 16, and 32 weevil individuals.

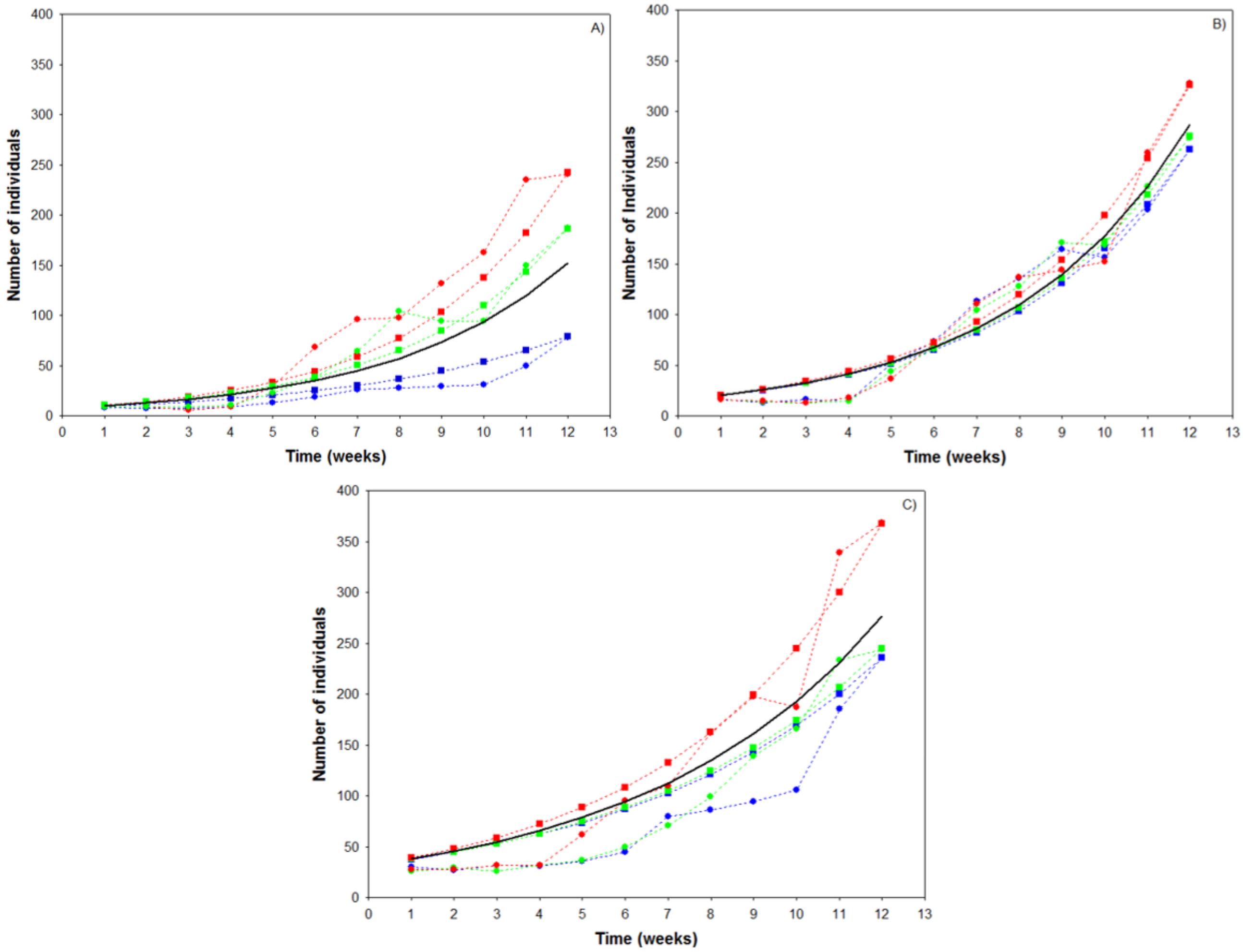

Figure 3. Observed (circles), and predicted (squares) population sizes of weevils within 12 weeks, following an exponential model, for three initial population sizes of A) eight individuals; B) 16 individuals; and C) 32 individuals. Minimum values are marked in blue, intermediary values are marked in green, and maximum values are marked in red. Solid black line is the predicted population sizes under an exponential model from mean values.

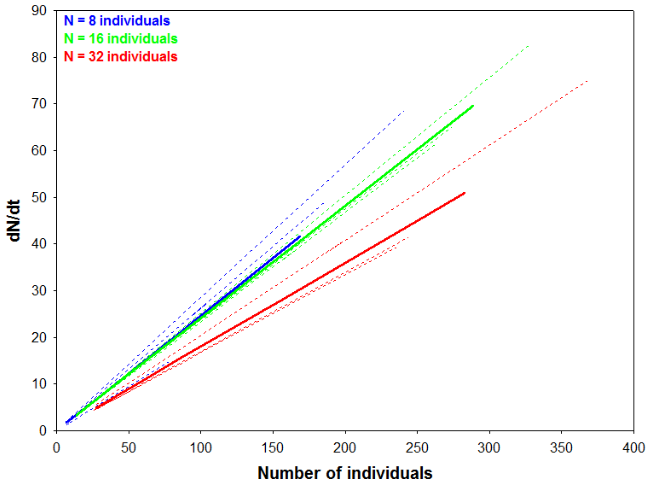

Figure 4. Relationship between population growth rates (dN/dt) and population sizes (N) within three replicates of initial population sizes of eight individuals (blue), 16 individuals (green), and 32 individuals (red). Single replicates are shown in dashed lines, and the mean pattern is shown in solid lines.

Population dynamics within 12 weeks for initial population size of eight individuals presented a highlighted discrepancy between the replicates (Figure 3A) due to the highest values of r between all populations, and one of the lowest values of r. On the other way, population dynamics of initial populations of 16 individuals showed consistency among the replicates (Figure 3B) due to the agreement between the highest values of r within all populations. For populations with initial size of 32 individuals, population dynamics presented intermediary consistency among the replicates (Figure 3C). Such results were obtained, mainly, because the values of r for the replicates of initial population sizes of 32 individuals were intermediary to lower when compared to the sizes of all initial populations.

The results of the dynamics population were reinforced when we see the line slope of the relationship between dN/dt and N for the three different initial population sizes (Figure 4). Where population initial sizes of eight and 16 individuals presented the highest slopes, and initial population sizes of 32 individuals presented the lowest slopes (Figure 4).

Discussion

The problem-based approach, used in this study of exponential growth model, had the main purpose of including a practical learning of Population Ecology into a professional training of a biologist, beyond teaching ecological concepts only (Lewinsohn et al., 2015). Thus, we presented our discussion below, separating into two ways: 'Ecological concepts discussion', as a formal way to discuss results in purely ecological studies; and, 'Practical use of the ecological concept', as the students' insights and conclusions from our didactic experiment after ecological concepts discussion.

'Ecological concepts discussion': When we see separately the population dynamics within 12 weeks (i.e., N x t graphic), all populations fitted properly into exponential model. Nonetheless, under an exponential model, it was not expected higher r, and consequently dN/dt, values from lower initial population sizes, when comparing the three different initial population sizes (Gregory, Bradshaw, Brook, & Courchamp, 2010; Bowne & Wohlbowne, 2022). This result evidenced the importance of density dependence (Brook & Bradshaw, 2006) for our weevil populations. Density dependence is a process in population ecology which birth rate will decrease when increasing population size, while death rate will increase when increasing population sizes, consequently r will decrease according to increasing number of individuals in the populations (Lande et al., 2002). This happens, mainly, due to individual intraspecific competition for resources (Sibly, Barker, Denham, Hone, & Pagel, 2005). 'Practical use of the ecological concept': In our study, this result can be explained due to the equal food availability across all initial population sizes. Therefore, our study can also be an insight to understand more complex population growth model, beyond exponential model, as logistic population growth model, where limitation of food resources influences in the r and dN/dt parameters.

'Ecological concepts discussion': When we focus only in the lower initial population size (i.e., N = eight individuals), we evidence a huge difference between r, reaching the highest and the top lowest values. Taking into account the influence of density dependence in our populations, the lowest value of r was not expected in the initial population size of eight individuals. Thus, we hypothesized the lowest value of r being a result of demographic stochasticity (Lande, 1993). Demographic stochasticity is recognized as the chance realizations of individual probabilities of death and reproduction in a finite population, being its effect stronger in small populations than in large populations (Shaffer, 1981; 1987). 'Practical use of the ecological concept': Therefore, for the replicate with the lowest r, we assumed the most unbalanced sex ratio in the by chance chosen eight individuals, between males and females, resulting in the lower birth rate (Schacht et al., 2022; Serrano-Davies et al., 2022). This result highlighted the negative effect of population reduction, even though this population is growing under an exponential model.

'Discussion of ecological concepts': On the other hand, when we observe the population dynamics among the initial population sizes of 16 individuals, there is a consistency among r values, being the highest values when compared to all populations. Consequently, all replicates of initial population sizes of 16 individuals reached a marked increase in N within 12 weeks when compared to all replicates. This result can be a sign of absence of density dependency of these populations (Maximov, 2021; Mutshinda, Mishra, Finkel, & Irwin, 2023). That can be explained due to the fact that the initial size populations of 16 individuals did not suffer major effects of neither intraspecific competition (such as the populations of 32 individuals), nor demographic stochasticity (such as the populations of eight individuals). 'Practical use of the ecological concept': Therefore, we indicate, when comparing all replicates, population initial sizes of 16 individuals as the main replicates which fits exponential model.

'Ecological concepts discussion': Lastly, observing the replicates of the largest initial population sizes (i.e., N = 32 individuals), it is evident the density dependency of those populations caused by the intraspecific competition within the replicates, when comparing to the other replicates. In spite of the fact that the exponential model adjusted itself to the initial populations of 32 individuals, the tendency is that more complex models, such as the logistic growth model, will fit better, especially for those populations with bigger initial sizes. (Thibaut & Connolly, 2020). 'Practical use of the ecological concept': This result brings us an insight which no population growth model fits a population dynamic indefinitely. For our three different initial population sizes it was evident that the increasing size of initial population speeds up the transition from an exponential model to a logistic population growth model (i.e., a density dependency growth model).

Conclusion

Beyond the exponential model by itself, our didactic experiment was a pleasant way to understand population dynamics, and factors that could influence it. The most important issues learned as a PBL in our experiment were density dependence effects of low number of individuals in a population, as demographic stochasticity, and high number of individuals in a population, as intraspecific competition. Moreover, we also suggest further didactic experiments with higher number of individuals in populations than of the number of individuals used in our study to evaluate issues about logistic population growth model.

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