POPULATION DYNAMICS OF THE CLIMBING MICE *Rhipidomys itoan* (COSTA, 2011) IN THE BRAZILIAN ATLANTIC FOREST

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Abstract: One of the fundamental questions in population ecology is what factors influence size and stability of populations. Rodents are one of the best-studied mammalian species regarding population dynamics, but little knowledge about rodent dynamics in tropical environments is available, especially in tropical rainforests, where special adaptations in behavior and physiology may have evolved. Here, we used a detailed dataset from a long-term monitoring program to identify the feedback structure (density dependence) and determine the effect of local (rainfall and temperature) and large-scale (El Niño events) climate variables on population dynamics of the climbing mice *Rhipidomys itoan* in the Brazilian Atlantic Forest. Individuals were captured and marked (ear tags) from August 2000 to February 2016 and monitored every other month in three trapping grids in trapping sessions of five consecutive nights. Time series diagnostic tools were used to identify the feedback structure and linear models were used to evaluate the relationship between climate and population size. The population was dominated by a first-order negative feedback, possibly as a consequence of intraspecific competition for resources and/or the effect of a generalist predator. Mean maximum temperature with and without one-year time lag acted as the main exogenous factor negatively affecting the population dynamics of this Cricetidae rodent, mainly at low densities. These results have important ecological and conservation implications, since this is the first study elucidating *R. itoan* population dynamics, a new species classified as Data Deficient by the Chico Mendes Institute for the Biodiversity Conservation of Brazil.

Keywords: El Niño; long-term studies; Rodentia; small mammals; tropical forest.

INTRODUCTION

One of the fundamental questions in population ecology is what factors influence size and stability of populations (Royama 1992, Berryman 1999). Rodents are one of the best-studied mammalian species regarding population dynamics, because of their small size, short life span, and fast response to environmental changes (Krebs 2013). Rodent populations have shown a wide variety of dynamics, from stable to highly cyclic (Krebs 2013). One of the first studies on rodent population dynamics was conducted by Elton (1924) and described regular multiannual oscillations in lemming and vole populations. However, this phenomenon, caused mainly (but not only) by the interaction with specialist predators, is less frequent than once imagined (Lima *et al.* 2006).

Rodent population dynamics are often driven by density-dependent effects and population regulation has been related to population self-control and to trophic interactions (food supply, specialist predators, and diseases; Krebs 2013). Overall, interactions between conspecifics or with a second species (*e.g.*, prey, predator, parasite) can have immediate effects by increasing mortality rates, or a lagged effect, by changing the physiology and behavior of individuals, which can affect the demography (survival, reproduction, and migration) and generate population fluctuations. If density dependence operates in a short time period, the population may show numerical stability or seasonal fluctuation, as observed in several tropical forest rodents (Bergallo & Magnusson 1999, López-Arévalo *et al.* 2008, Pacheco 2009). Overall, regular oscillations seem to be the pattern in temperate areas and a consequence of intraspecific interactions independent of local environmental conditions (Lima *et al.* 2006).

Despite the large number of studies on rodent population dynamics, we still lack long-term studies in tropical environments, especially in tropical rainforests, where special adaptations in physiology and behavior may have evolved and influenced the population dynamics (Krebs 2013, Hayes *et al.* 2017). Few long-term studies were carried out in the region (Dickman *et al.* 2001, Lima *et al.* 2003, da Rosa *et al.* 2021, Magnusson *et al.* 2021), and the ones available were conducted mostly in less complex ecosystems such as deserts (Dickman *et al.* 2001, Lima *et al.* 2003). Odum (1971) once suggested that population cycles usually occur in less complex ecosystems, and tropical rainforests are the opposite. In this sense, rodent populations are embedded in a complex network of interactions with other species and with the environment. This leads us to a puzzling question: does the array of biological interactions has direct effects on population dynamics or only one or few dominate the population system?

Populations fluctuations are also partly driven by environmental changes that affect directly or indirectly the reproductive output and survival (Krebs 2013). The influence of local weather on rodent population dynamics has been the focus of several studies in the Neotropics (Bergallo & Magnusson 1999, Lima *et al.* 2008, Previtali *et al.* 2010, Magnusson *et al.* 2021). Overall, rodent reproduction is highly influenced by rainfall regimes (Murúa *et al.* 1986, Cerqueira & Lara 1991, Bergallo & Magnusson 1999, Cerqueira 2004); high rainfall triggers an increase in primary productivity, which is converted into body mass and storage reserves, a major limiting factor for female reproduction (Frisch 1988, Cerqueira & Lara 1991, Cerqueira 2004). Temperature can also affect rodent survival and reproductive rates. However, a considerable small number of studies have focused on its effects on population fluctuations (Bergallo 1996, Magnusson *et al.* 2010).

Variation in local weather can also be a consequence of large-scale climate events such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Jaksic 2001, Stenseth *et al.* 2003). ENSO is one of the best-known large-scale climate phenomena, and one of the most popular indices, the Southern Oscillation Index (SOI), measures the difference between sea-level air pressure of Darwin (Australia) and Tahiti (French Territory) (Chen 1982). During El Niño events (negative SOI), the trade winds along the equator weaken and the equatorial Pacific Sea surface temperature warms, causing changes in atmospheric circulation and, consequently, in rainfall patterns (Stenseth *et al.* 2003). For example, in South America, a combination of ENSO and the Atlantic surface temperature variation (TSA) is thought to be responsible for rainfall anomalies (Kayano & Andreoli 2007); rainfall increases over southeast South America and decreases over northeast South America (Jaksic 2001, Stenseth *et al.* 2003). Disentangling the impact of these different climate variables on rodent population dynamics is not an easy task (Magnusson *et al.* 2021), and for some populations variation in abundance over time may be a response to these large-scale phenomena through changes in local or regional weather (Stenseth *et al.* 2003, Magnusson *et al.* 2021).

Here, we used a detailed dataset from a 16-year small mammal monitoring program to identify the feedback structure (direct or delayed density dependence) and determine the effect of local and large-scale climate variables on population dynamics of the climbing mice *Rhipidomys itoan* in the Brazilian Atlantic Forest. This cricetid rodent was recently described by Costa *et al.* (2011) as a new species and classified as Data Deficient (DD) in a diagnosis of the conservation status of the

Brazilian fauna (ICMBio 2018). Little information regarding its ecology is available in the literature, thus knowledge on the climbing mice population dynamics and trend over time is crucial to inform better management and conservation strategies. Based on previous studies on small mammal populations, we hypothesized that (1) direct density dependence governs the climbing mice population dynamics (Lima *et al.* 2006, Pacheco 2009, Zangrandi 2011, Ferreira *et al.* 2016a), and (2) local weather will explain better the population dynamics than ENSO (Ferreira *et al.* 2016a,b). Rainfall, a proxy for food availability, will have a positive effect on population size by increasing reproductive output (Bergallo & Magnusson 1999, Cerqueira 2004), while temperature extremes (minimum and maximum) will have a negative effect on population size, possibly through a decrease in survival and reproduction, associated with the high energy requirements for thermoregulation.

MATERIALS AND METHODS

Study area

The study was carried out in the southern portion of the Serra dos Órgãos National Park (PARNASO), in the municipality of Guapimirim, state of Rio de Janeiro, Brazil (22º28'28" S, 42º59'86" W). The field site is in a valley locally known as Garrafão, with irregular topography, and in the vicinity of the tributaries of the Inconha River, which is part of the Macacu River basin. Due to the topography, the study area is characterized by a dense hillside mountain rainforest (Rizzini 1979), and has a physiognomy formed by secondary and mature successional stages (Macedo *et al.* 2007). The climate is classified as mesothermal-humid-moderate without a proper dry season (Nimer 1989). The region is characterized by high annual rainfall, which varies from 1,500 to 3,000 mm. The rainy season is from October to March and a less-rainy season (hereafter dry season) from April to September. The rainy season has higher temperatures (26.8 ± 1.0 °C/month; mean minimum = 16.6 °C/month and mean maximum = 28.2 °C/month) and rainfall (232.9 ± 54.9 mm/month), while the dry season is characterized by low temperatures (13.8 ± 1.0 °C/month; mean minimum = 12.7 °C/month and mean maximum = 24.6 °C/month) and reduced rainfall (52.5 ± 10.4 mm/month) (Data source: Instituto Nacional de Meteorologia do Brasil 2016).

Study species

Rhipidomys itoan is a small sized (77 g; Paglia *et al.* 2012) cricetid rodent (Cricetidae, Sigmodontinae), with short and soft pelage, and short to medium tuft at the tip of the tail. It is endemic to Brazil and can be found in the coastal Atlantic Forest of Rio de Janeiro (RJ) and São Paulo (SP), up to Serra da Mantiqueira, including islands such as Ilha Grande and Marambaia, (Costa *et al.* 2011). The climbing mice have arboreal habits, being rarely observed on the forest floor (Macedo *et al.* 2007, Prevedello *et al.* 2008), and a frugivore-granivore diet (R. Cerqueira, unpublished data), potentially acting as seed predator (Paglia *et al.* 2012). The breeding period was suggested to occur between August and December in the study area (Macedo *et al.* 2007), but it was based on few records.

Data collection

This study is part of a long-term monitoring program of small mammal populations, carried out by the Laboratório de Vertebrados of the Universidade Federal do Rio de Janeiro (UFRJ), which began in April 1997 (Gentile *et al.* this issue). For *R. itoan*, individuals were first captured in August 2000, characterizing 16 years of data (February 2000 – February 2016). Small mammal populations were monitored every other month in three live-trapping grids (A, B, and C), established along an elevation gradient (approximately 750, 650, 520 m above sea level, respectively) in trapping sessions of five consecutive nights. Each 5 x 5 trapping grid comprised five parallel lines with five trap stations 20 m apart (total of 25 trap stations), enclosing an area of 0.64 ha (Figure 1). Each trap station had two live traps on the ground (Tomahawk 210, 41 × 14 × 14 cm, Tomahawk Live Trap Co., Hazelhurst, Wisconsin; Sherman XLK, 30.5 × 9.8 × 8 cm, H. B. Sherman Trap Co., Tallahassee, Florida) and, from 2009 onwards, one additional live trap in the understory (≈ 1.5 m height; Sherman XLK). Five larger traps (Tomahawk 105, 50.8 × 17.8 × 17.8 cm) were placed cross-shaped in each grid and, at 13 trap

stations (odd stations), two live traps (Tomahawk 210, Sherman XLK) were placed in the forest canopy at 6–20 m height. Traps were checked and baited every morning with a mixture of oats, banana, peanut butter, and bacon. Individuals were marked with numbered ear tags (National Band and Tag Co., Newport, Kentucky), had their bionomic data collected, and were released at the point of capture.

Population size and capture success

The population size (N_t) was estimated as the minimum number known alive (MNKA; Krebs 1966), an estimate that can be just as robust as any estimate of population size that was a posteriori controlled for detection probability (Pacheco *et al.* 2013, Banks-Leite *et al.* 2014). As the sampling sessions took place in a bimonthly period, initially, the bimonthly MNKA was estimated and, subsequently, the annual average (annual MNKA), starting in April and ending in February of the following year. Population size was later transformed using the natural logarithm to stabilize the variance.

To evaluate if the increase in the sampling effort from 2009 onwards affected the number of captured individuals, we estimated the capture success index, a simple abundance index of the number of individuals captured divided by the sampling effort (*e.g.*, number of trap-nights), proposed by Graipel *et al.* (2014). The degree of correlation between the capture success index and annual MNKA was accessed through the Pearson's correlation coefficient. If a very strong positive correlation is observed ($r > 0.8 – 1.0$), subsequent analyses will be conducted with the MNKA estimates.

The capture success was obtained by multiplying the total number of captures and recaptures by 100 and dividing by the sampling effort. The sampling effort was obtained by multiplying the total number of traps by the total number of trapping nights and the number of sampling months.

Time series diagnostic tools

Stationary time series exhibit some signs of dynamic equilibrium (Berryman 1999). When a time series exhibits changes in the mean population size over the course of the study or discontinuities (non-stationary), it can be split into two or more time
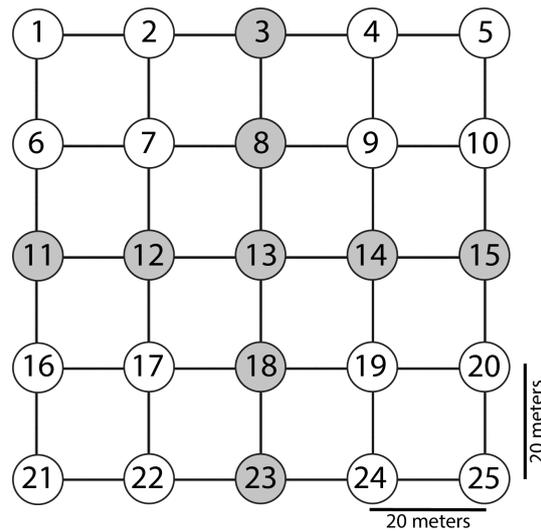
Figure 1. Live-trapping grid scheme of the long-term monitoring program of small mammal populations carried out in the Serra dos Órgãos National Park, southeastern Brazil. Each trapping grid had 25 trap stations (circles) 20 m apart. Each trap station had two live traps on the ground (Tomahawk 210 and Sherman XLK), one in the understorey (Sherman XLK; from 2009 onwards), and five larger traps placed cross-shaped in each grid (gray circles). Additionally, at 13 trap stations (odd stations), two live traps (Tomahawk 210 and Sherman XLK) were placed in the forest canopy.

series and analyzed separately. To test whether there was a trend in the time series, Kendall's rank correlation coefficient (τ) was used (Legendre & Legendre 1998). This analysis was performed in the program BioEstat 5.0 (Ayres *et al.* 2007).

The regulatory processes in the time series of *R. itoan* were analyzed with diagnostic tools following Berryman (1999) and Turchin (2003). We estimated (1) the per capita rate of population growth ($R = \ln N_t - \ln N_t{-}1$), (2) the time series return time, (3) the phase portrait, (4) the autocorrelation function, and (5) the function of partial correlation of the growth rate.

The time series return time (RTM) corresponds to the time a trajectory needs to return to its equilibrium point after a disturbance (Berryman 1999). If the time series is stationary, when some disturbance takes it out of its equilibrium point, there is often a tendency to return to equilibrium (*i.e.*, the mean population size over the course of the study). Mean (MRT) and variance (VRT) was estimated as the sum of the return times, divided by the number of segments of the entire series and its variance:

$$MRT = (\sum_{m=1}^{M} RTM)/M$$
$$VRT = \sum_{m=1}^{M} (RTM-MRT)^2/M-1,$$

where M is the number of years and RT is the number of intervals the series takes to return to its mean after disturbance. In a stationary series, the mean of return time indicates the order of the dynamic population feedback (*i.e.*, the number of components in the system); MRT < 2 implies a first order dynamic (time lag one; one population) in the population, while MRT > 2 implies a higher order dynamic (two or more populations; Berryman 1999). A variance that is slightly longer than the mean indicates an aperiodic or trending series (VRT >> MRT; Berryman 1999).

The Phase Portrait is a plot of the per-capita rate of increase (R) on population size (N_t) at different time lags (Turchin & Taylor 1992). If the connect points in the plot show a relatively narrow orbit, the lag can be calculated by choosing the best correlation with different lag periods, while if a clear orbit (a rounded distribution of the points) is identified, the lag period is too small or too large.

The autocorrelation function (ACF) evaluates the periodicity and whether the time series was generated by endogenous or exogenous dynamics (Turchin 2003). The ACF estimates the correlation of population size (lnN_t) with itself over previous time lags (lnN_t, t = 1, 2 ... i). The partial rate correlation function (PRCF) detects the feedback dimension of the time series (as the MRT), through the correlation between R and the lagged population sizes (lnN_t, t = 1, 2 … i) (Turchin 2003). Significance of ACF and PRCF was assessed by Bartlett's criterion ($\pm 2/\sqrt{n}$, where n is the number of lags—Berryman & Turchin 2001). All analyses were performed in R software version 3.3.2. (R Core Team 2015).

Effect of local and large-scale climatic variables on population size

To determine the influence of local (mean annual rainfall, mean minimum, and mean maximum temperature) and large-scale climate (SOI) on population size, a total of nine exploratory models were formulated. We obtained local weather variables from the climate station at PARNASO, and values of the SOI index from Climate Impacts & Spatial Systems and Queensland Department of Primary Industries (Long Paddock 2016). Each model had only one explanatory variable, due to the relatively small sample size, and effects were evaluated in the current and previous year. An intercept-only model, composed only by the intercept and residual errors as parameters, was also included to compare the explanatory power of independent variable relative to other unaccounted sources of variation in data. Models were compared with a model selection approach (Burnham & Anderson 1998), using the corrected version of Akaike's Information Criteria (AICc), ΔAICc (difference between each model and the one with the lowest AICc value), and AIC weight (w_i - evidence weight that the model is the best model within the set). The lower AICc and ΔAICc, the better the model fits. Model selection was performed with the package MuMIn (Barton 2012) in R environment (R Core Team 2015).

RESULTS

Mean population size ranged from 1 individual in 2006 to 7.17 individuals in 2011, with an average of 2.99 ± 1.66 (mean ± standard deviation) individuals per year (Figure 2a). The per capita rate of population growth ranged from -1.46 in 2012 to 1.03 individuals in 2013, with an average of 0.03 ± 0.75 rate of increase per year. The total sampling effort of 145,440 traps/night resulted in 461 captures of 131 individuals, a total capture success of 0.31%. The correlation between MNKA and the capture success index was high (r = 0.90; p = 0.001) and the population abundance over the years was not affected by the increase in sampling effort (Figure S1).

Even though Kendall's rank correlation coefficient was not significant (τ = 0.142; p = 0.220), an increase in mean population size (*i.e.*, a trend in the time series) over the course of the study is clear (see MRT and VRT results below). This trend was removed by sequencing (*i.e.*, splitting the series into two stationary segments) and rotating (*i.e.*, linear rotation) the time series around the linear trend. The complete time series and the two detrended series [a low-population sequence from 2000 to 2007 (τ = -0.481; p = 0.965) and a high-population sequence from 2008 to 2015 (τ =-0.285; p = 0.839); Figure 2b and c] were then used to calculate the statistics that led to the following diagnosis.
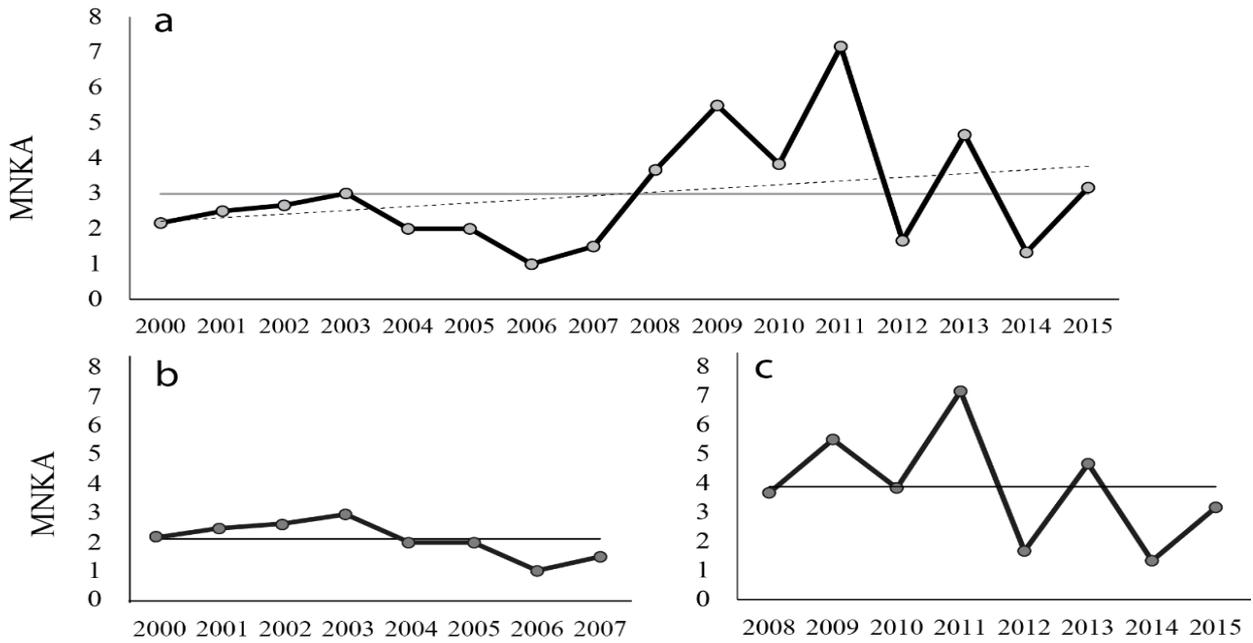
Figura 2. a) Time series of the climbing mice *Rhipidomys itoan* for 16 years in the Serra dos Órgãos National Park, southeastern Brazil. Detrended time series from b) 2000 to 2007 and c) 2008 to 2015. Connected dots indicate the variation in mean population size throughout the study; solid line, the mean population size (complete time series = 2.99; 2000-2007 = 2.10; 2008-2015 = 3.88); and, dashed line, the time series trend.

The complete time series was not stationary (MRT = 0.818 years; VRT = 1.601 years), as well as the low-population sequence (MRT = 0.557 years; VRT = 1.862 years). The high-population sequence was stationary (MRT = 0.580 years; VRT = 0.247 years). The return time indicated a first order dynamic (time lag one) in the population (MRT < 2).

The phase portrait with one-year time lag (N_t-1, R) clearly showed a shift from low- to high population size in the complete time series, indicating a possible change in the feedback mechanism involved in the regulation of *R. itoan* population. Overall, we identified a first-order dynamic at high population sizes, *i.e.*, vectors passing close to the equilibrium point, but with indications of more than one component in the system at low population sizes (Figure S2a-apendice). This is clearer when the low-population sequence was analyzed; a broader, almost circular phase portrait typical of higher-order dynamics was observed (Figure S2b). The phase portrait (N_t-1, R) of the high-population sequence also showed characteristics of a first-order dynamic (Figure S2c).

The autocorrelation function for the complete time series indicated a non-stationary series regulated by endogenous factors (Figure S3a). The ACF for the low-population sequence suggested a non-stationary series affected by exogenous factors (Figure S3b), while the high-population sequence pointed to a stationary series regulated by endogenous factors (Figure S3c). The partial rate correlation function for the complete time series showed a significant negative correlation at one-year lag (PRCF(1) = -0.747; Bartlett's criterion = ± 0.666), indicating a first-order negative feedback in the system (Figure 3a). PRCF for the low-population sequence pointed to a dynamic system characterized by a higher-order negative feedback (PRCF(3) = -0.363; Bartlett's criterion = ± 0.756), with the presence of two or more components in the system (Figure 3b), while the high-population sequence also suggested a first-order negative feedback in the system (PRCF(1) = -0.823; Bartlett's criterion = ± 0.756; Figure 3c).

The most plausible model explaining variation in population size included mean maximum temperature in the previous year (w_i = 0.373), while the second ranked model included mean maximum temperature in the current year (ΔAICc = 0.44; w_i = 0.299) (Figure 4; Tables 1 and S1).
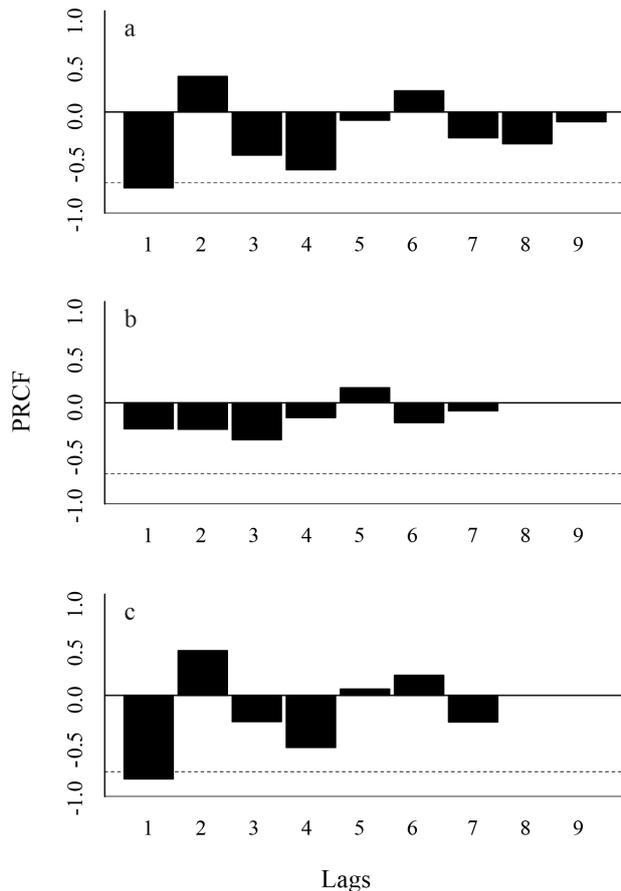
Figura 3. Partial rate of correlation function of the climbing mice *Rhipidomys itoan* for 16 years in the Serra dos Órgãos National Park, southeastern Brazil. a) PRCF of the complete time series; b) PRCF of the detrended time series from 2000 to 2007 (low-population sequence), and c) PRCF of the detrended time series from 2008 to 2015 (high-population sequence). Lags = annual delays. Dashed line = Bartlett's criterion.

DISCUSSION

Population dynamics of the climbing mice *Rhipidomys itoan* was characterized by two different dynamics over the course of the 16 years. At the first eight years, population numbers were relatively low and strongly influenced by exogenous factors (82%). The last eight years, however, have shown a drastic change in the population dynamics, with an increase of 84% in the mean number of individuals. Diagnostic analyses have shown a system strongly influenced by endogenous factors (71%) and dominated by a first-order negative feedback, *i.e.*, the population self-regulates. The low population size in the first years can be attributed to the high maximum temperature values alone, since no effect of variation in rainfall and SOI was detected,

showing that *R. itoan* was affected by temperature extremes.

The population of *Rhipidomys itoan* was regulated by negative first-order feedback, but with a possible higher-order when the population was at low population size. Generally, in a first-order dynamics, the population can be regulated by intraspecific competition for resources (food, refuge, territorial disputes, or sexually active females), by the action of generalist predators, by territoriality, aggressiveness and spacing or emergence of epidemics and parasites due to population density (Berryman 1999, Lima *et al.* 2006). Regardless of the process involved, it will negatively affect the population by decreasing reproduction and/or survival or increasing emigration (Berryman 1999).

Small mammals, in general, have their dynamics dominated by a first-order mechanism, as is the case of rodents in dry and temperate regions (Berryman 2001, Merritt *et al.* 2001, Lima *et al.* 2006) and rodent and marsupials from tropical forests (Kajin *et al.* 2008, Zangrandi 2011, Ferreira *et al.* 2016a, Santos 2019). The only study that evaluated the feedback structure of a *Rhipidomys* population was conducted with *Rhipidomys mastacalis* for nine years in a tropical savanna ecoregion of Brazil (Rossi & Leiner 2022). Population growth rate was strongly determined by population density in the previous year, also indicating the occurrence of a first-order negative feedback, as in *R. itoan*. As in several other populations, the main process responsible for the population dynamics was identified, but the mechanism that resulted in the fast population response (one-year time lag) was not unraveled. Ferreira *et al.* (2020) identified a direct negative density dependence on survival, not reproduction, for three tropical forest marsupials. This is also a potential mechanism that can drive the population dynamics of *R. itoan*, but this question remains to be answered.

The strong influence of exogenous factors on the dynamics of *R. itoan* in the first monitoring years may have resulted in a higher-order dynamics observed in the system. Second and third order dynamics are often the result of interactions between species, usually consumers and their resources, predators and their preys, or parasites and their hosts (Royama 1992, Berryman 1999, Turchin 2003). We suggest that the diagnosis of
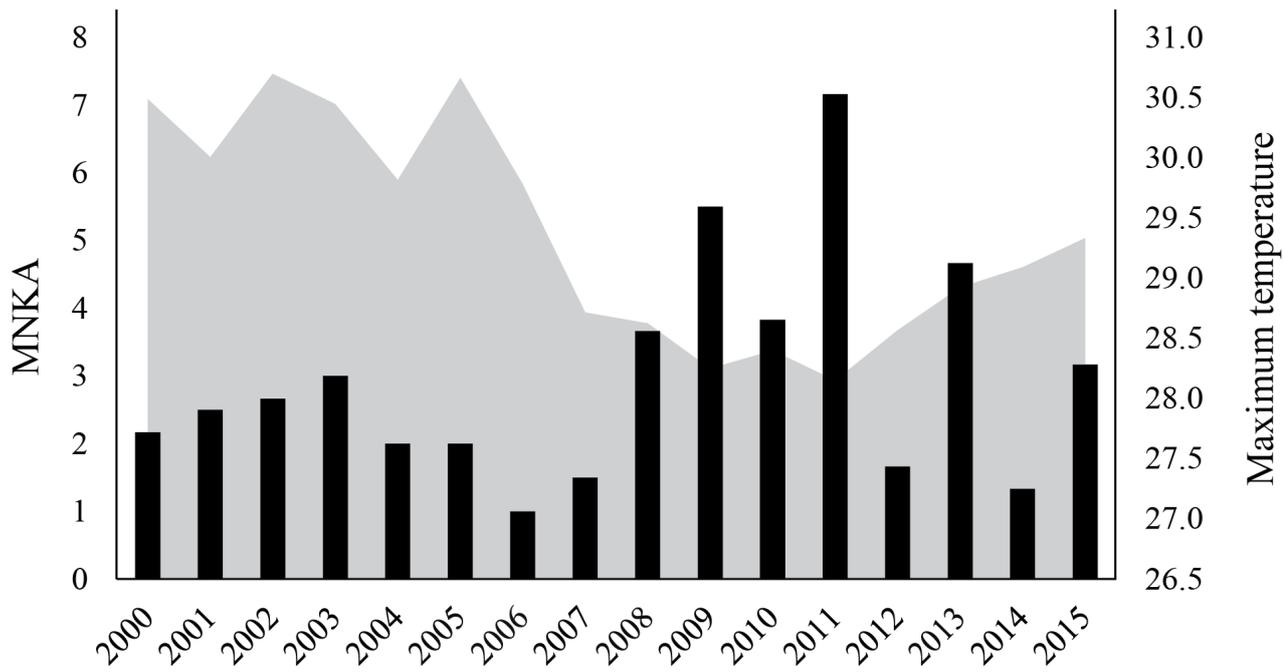
Figure 4. Variation in population size (MNKA; black bars) of the climbing mice *Rhipidomys itoan* and mean maximum temperature (gray shadow) of the study area for 16 years. MNKA is the mean population size each year.

Table 1. Comparison of models predicting variation in population size of the climbing mice *Rhipidomys itoan* in an Atlantic Forest area, southeastern Brazil. Explanatory variables were Rain (mean annual rainfall), Tmax (mean maximum temperature), Tmin (mean minimum temperature), and SOI (Southern Oscillation Index); effects were evaluated in the current and previous year (-1). K = number of parameters of the model, AICc = Akaike Information Criteria corrected for small ratio sample size/number of parameters, ΔAICc = $AICc_i$ – minimum AICc, w_i= Akaike weight.

Model	K	Log-likelihood	ΔAICc	w_i
Tmax$_{-1}$	3	-27.588	0	0.373
Tmax	3	-27.809	0.44	0.299
Intercept-only	2	-30.318	2.38	0.113
SOI	3	-29.184	3.19	0.076
Tmin$_{-1}$	3	-29.976	4.78	0.034
Rain$_{-1}$	3	-30.167	5.16	0.028
Tmin	3	-30.235	5.29	0.026
Rain	3	-30.282	5.39	0.025
SOI$_{-1}$	3	-30.283	5.39	0.025

a higher-order dynamics was probably spurious and the consequence of the strong nonlinearity in a first-order endogenous process, as suggested by Berryman & Lima (2007).

Extreme temperatures negatively influenced the population dynamics of *R. itoan*, with and without a one-year time lag. The low population size in the first eight years was a consequence of the increase in the mean maximum temperature. High extreme temperatures can directly affect the population, leading to death, or indirectly by reducing survival and/or reproduction, which will only be observed with a certain time delay (Deitloff *et al.* 2010). In the same study area, extreme temperatures also negatively affected small marsupials, with body mass of less than one kilogram (Ferreira *et al.*

2016b). *Rhipidomys mastacalis* was also affected by temperature in the savanna region, but in an opposite way; a decrease in population growth rate was related to the number of very cold days in the previous year (Rossi & Leiner 2022).

No effect of El Niño (SOI index) was detected on the dynamics of *R. itoan*. However, previous studies have detected changes in population dynamics of marsupials in the study area. *Didelphis aurita* was strongly influenced by ENSO in the first years of the study, probably a consequence of the strong El Niño event of 1997 (Kajin *et al.* 2008). For *Marmosops incanus* and *Philander quica* (formerly *P. frenatus*), ENSO effects were also detected, but it was not clear how it affected these populations (Zangrandi 2011; Ferreira *et al.* 2016b). This is the first study evaluating the effect of ENSO events in a Cricetidae rodent in the study area. Other studies in Brazil have pointed out contrasting results. Direct positive effects of La Niña events were observed in population abundance of *Akodon cursor* and *Necromys lasiurus* in the coastal Atlantic Forest (Restinga; Pacheco 2009) and in the Amazonian savanna (Magnusson *et al.* 2010), respectively, while no effect was recorded for *R. mastacalis* in a Cerrado savanna (Rossi & Leiner 2022).

Rainfall also did not affect the population of *R. itoan*. Overall, rodent reproduction is highly influenced by rainfall, with increase in reproductive activity related to an increase in primary productivity (Cerqueira *et al.* 1989, Cerqueira & Lara 1991, Bergallo & Magnusson 1999, Cerqueira 2004). Several rodent species need a minimum body weight and fat reserve to start reproducing (Frisch 1988, Cerqueira & Lara 1991) and usually an increase in population size is observed after the rainy season as detected in *Rhipidomys latimanus* in a cloud forest (Bosque andino) in Colombia (López-Arévalo *et al.* 1993). However, the mean annual rainfall does not seem to be a limiting factor for this population.

During the study, there was an increase in the sampling effort with the addition of 25 Sherman live traps in the understory of each trapping grid. This increase in the sampling effort could have affected the number of captured individuals, inflating population size estimates. We considered this possibility and estimated an index that controls for the increase (or decrease) in sampling effort suggested by Graipel *et al.* (2014). In this study, the

authors have shown a positive association between the capture success index [a simple abundance index of the number of individuals captured divided by the sampling effort (*e.g.*, number of trap-nights)] and the MNKA, the Cormack-Jolly-Seber, and others. We compared the MNKA and the capture success index and observed a correlation of 0.90. In fact, the population trend over the years was not changed (Figure S3). Thus, we can conclude that the increase in population numbers were indeed a consequence of changes in the environment, not changes in the sampling effort.

As observed in many small mammals, the population of *Rhipidomys itoan* was dominated by a first-order negative feedback, which may be the result of intraspecific competition for resources and generalist predation. At low densities, the population was mainly affected by exogenous factors (mean maximum temperature). The mean maximum temperature with and without one-year time lag acted as the main exogenous factor, negatively affecting the population dynamics of this rodent. These results have important conservation implications, since this is the first study elucidating *R. itoan* population ecology and dynamics, a new species classified as Data Deficient by the Chico Mendes Institute for the Biodiversity Conservation of Brazil.

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REFERENCES

Ayres, M., Ayres Jr. M., Ayres, D., & Santos, A. A. S. 2007. BioEstat: Aplicações estatísticas nas áreas das Ciências Biomédicas. Ong Mamiraua. Belém, PA.

Banks-Leite, C., Pardini, R., Boscolo, D., Cassano, C. R., Püttker, T., Barros, C. S., & Barlow, J. 2014. Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. Journal of Applied Ecology, 51(4), 849–859. DOI: 10.1111/1365-2664.12272

Barton, K. 2012. MuMIn: Multi-model inference. R package, Version 1.7.7.

Bergallo, H. G. 1996 The population dynamics of the spiny rat (*Proechimys iheringi*) and the rice rat (*Orizomys intermedius*) in southeastern Brazil. Ciência e Cultura, 48(3), 193–196.

Bergallo, H. G. & Magnusson, W. E., 1999. Effects of climate and food availability on four rodent species in southeastern Brazil. Journal of Mammalogy, 80(2), 472–486.

Berryman, A. & Turchin, P. 2001. Identifying the density-dependent structure underlying ecological time series. Oikos, 92(2), 265–270. DOI: 10.1034/j.1600-0706.2001.920208.x

Berryman, A. A. & Lima, M. 2007. Detecting the order of population dynamics from time series: nonlinearity causes spurious diagnosis. Ecology, 88(8), 2121–2123. DOI: 10.1890/06-0609.1

Berryman, A. A. 1999. Principles of population dynamics and their application. Cheltenham, U.K: Stanley Thornes: p. 256.

Berryman, A.A. 2001. Functional web analysis: Detecting the structure of population dynamics from multi-species time series. Basic Applied Ecology, 2, 311–321. DOI: 10.1078/1439-1791-00069

Burnham, K. P., & D. R. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. New York, NY: Springer-Verlag: p. 520.

Cerqueira, R. 2004. Fatores ambientais e a reprodução de marsupiais e roedores no leste do Brasil. Arquivos do Museu Nacional, 63(1), 29–39.

Cerqueira, R., Vieira, M. V., & Salles, L. O. 1989. Habitats and reproduction of *Rhipidomys cearanus* (Rodentia, Cricetidae). Ciência e Cultura, 42, 1009–1013.

Cerqueira, R., & Lara, M. 1991. Rainfall and reproduction of cricetid rodents in northeastern Brazil. In: K. Bobek, K. Perzanowaki, & W. L. Regelin, (Eds.), Global trends in wildlife management. pp. 545–549. Cracow, Poland: Swiat Press.

Chen, W. Y. 1982. Assesment of Southern oscillation sea-level pressure indices. Monthly Weather Review, 110, 800–807.

Costa, B. M. A., Geise, L., Pereira, L. G., & Costa, L. P. 2011 Phylogeography of *Rhipidomys* (Rodentia: Cricetidae: Sigmodontinae) and description of two new species from southeastern Brazil. Journal of Mammalogy, 92(5), 945–962. DOI: 10.1644/10-MAMM-A-249.1

da Rosa, C. A., Gananá, P. H. S., Lima, A. P. & Magnusson, W. E. 2021. *Necromys lasiurus*: Lessons from a 38-year study in an Amazonian savanna. Frontiers in Ecology and Evolution, 9, 716384. DOI: 10.3389/fevo.2021.716384

Deitloff, J., Falcy, M. R., Krenz, J. D., & McMillan, B. R. 2010. Correlating small mammal abundance to climatic variation over twenty years. Journal of Mammalogy, 91(1), 193–199. DOI: 10.1644/08-MAMM-A-267R.1

Dickman, C. R., Haythornthwaite, A. S., McNaught, G. H., Mahon, P. S., Tamayo, B., & Letnic, M. 2001 Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. Wildlife Research, 28(5), 493–506. DOI: 10.1071/WR00023

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Journal of Experimental Biology, 2, 119–163.

Ferreira, M. S., Kajin, M., Cerqueira, R., & Vieira, M. V. 2016a. Marsupial population dynamics in a tropical rainforest: intraspecific competition and nonlinear effect of rainfall. Journal of Mammalogy, 97(1), 121–127. DOI: 10.1093/jmammal/gyv161

Ferreira, M. S., Vieira, M. V., Cerqueira, R., & Dickman, C. R. 2016b. Seasonal dynamics with compensatory effects regulate populations of tropical forest marsupials: a 16-year study.

Oecologia, 182, 1095–1106. DOI: 10.1007/s00442-016-3735-x

Ferreira, M. S., Cerqueira, R., & Vieira, M. V. 2020. What are the main drivers of survival and recruitment in tropical forest marsupials? A 16-year study. Journal of Mammalogy, 101(2), 515–525. DOI: 10.1093/jmammal/gyaa013

Frisch, R. E., 1988. Fatness and fertility. Scientific American, 258, 88–95.

Graipel, M. E., Hernandez, M. I. M. & Salvador, C. 2014. Evaluation of abundance indexes in open population studies: a comparison in populations of small mammals in southern Brazil. Brazilian Journal of Biology, 74(3), 553–559.

Hayes, L. D., Ebensperger, L. A., Kelt, D. A., Meserve, P. L., Pillay, N., Viblanc, V. A., & Schradin, C. 2017. Long-term field studies on rodents. Journal of Mammalogy, 98(3), 642–651. DOI:10.1093/jmammal/gyw180

ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade. 2018. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume II - Mamíferos. Brasília: ICMBio: p. 622.

Instituto Nacional de Metereologia do Brasil – INMET. 2022. Normais climatológicas (1991/2020). Brasilia – DF.

Jaksic, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography, 24, 241–250. DOI: 10.1111/j.1600-0587.2001.tb00196.x

Kajin, M., Cerqueira, R., Vieira, M. V., & Gentile, R. 2008. Nine-year demography of the black-eared opossum *Didelphis aurita* (Didelphimorphia: Didelphidae) using life tables. Revista Brasileira de Zoologia, 25(2), 206–213.

Kayano, M. T. & Andreoli, R. V. 2007. Relations of South American summer rainfall interannual variations with the Pacific Decadal Oscillation. International Journal of Climatology, 27(4), 531–540. DOI: 10.1002/joc.1417

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs, 36, 239–273.

Krebs, C. J. 2013. Population fluctuations in rodents. Chicago: University of Chicago Press: p. 320.

Legendre, P., & Legendre, L. 1998. Numerical Ecology. Developments in Environmental Modelling. Amsterdam: Elsevier Science: p. 852.

Lima, M., Stenseth, N. C., Leirs, H., & Jaksic, F. M. 2003 Population dynamics of small mammals in semi-arid regions a comparative study of demographic variability in two rodent species. Proceedings of the Royal Society of London. Series B: Biological Sciences, 270(1528), 1997–2007. DOI: 10.1098/rspb.2003.2448

Lima, M., Ernest, S. M., Brown, J. H., Belgrano, A., & Stenseth, N. C. 2008. Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. Ecology, 89(9), 2594–2603. DOI: 10.1890/07-1246.1

Lima, M., Berryman, A., & Stenseth, N. C. 2006. Feedback structures of northern small rodent populations. Oikos, 112(3), 555–564. DOI: 10.1111/j.0030-1299.2006.14439.x

Long Paddock. 2016. SOI Data Files. The Climate Impacts and Spatial Systems and Queensland Department of Primary Industries. Queensland, AU. (Retrieved on March 3rd, 2016, from https://data.longpaddock.qld.gov.au/SeasonalClimateOutlook/SouthernOscillationIndex/SOIDataFiles/MonthlySOIPhase1887-1989Base.txt).

López-Arévalo, H., Montenegro-Diaz, O. & Cadena, A. 1993. Ecología de los pequenos mamíferos de la reserva biológica carpanta, en la cordillera oriental Colombiana. Studies on Neotropical Fauna and Environment, 28(4), 193–210. DOI: 10.1080/01650529309360904

Macedo, J., Loretto, D., Mello, M. C. S., Freitas, S. R., & Cerqueira., R. 2007. História natural dos mamíferos de uma área perturbada do Parque Nacional da Serra dos Órgãos. In: C. Cronemberger & E. B. Viveiros de Castro (Eds), Ciência e Conservação na Serra dos Órgãos. pp. 165–181. Brasília: Ibama.

Magnusson, W. E., Layme, V. M. G., & Lima. A. 2010. Complex effects of climate change: population fluctuations in a tropical rodent are associated with the Southern Oscillation Index and regional fire extent, but not directly with local rainfall. Global Change Biology, 16, 2401–2406. DOI: 10.1111/j.1365-2486.2009.02140.x

Magnusson, W. E., Rosa, C., Layme, V. M. G., Ghizoni Jr, I. R., & Lima, A. P. 2021. Local effects of global climate on a small rodent *Necromys lasiurus*. Journal of Mammalogy, 102(1), 188–194. DOI:10.1093/jmammal/gyaa140

Merritt, J. F. Lima, M. A., & Bozinovic, F. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and

climate. Oikos, 94, 505–514. DOI: 10.1034/j.1600-0706.2001.940312.x

Murúa, R., González, L. A., & Meserve, P. L. 1986. Population ecology of *Oryzomys longicaudatus philippii* (Rodentia. Cricetidae) in southern Chile. Journal of Animal Ecology, 55(1), 281–293. DOI: 10.2307/4708

Nimer, E. 1989. Climatologia do Brasil. Rio de Janeiro: Fundação IBGE: p. 421.

Odum, E. P. 1971. Fundamentals of Ecology. Philadelphia: Saunders Co.: p. 574.

Pacheco, M. 2009. Ecologia de Populações de Pequenos Mamíferos em uma Restinga: Comparação de Métodos de Estimativa de Abundância e Dinâmica da População de *Akodon cursor* (Rodentia, Sigmondontinae). Master thesis. Programa de Pós-Graduação em Ciências Biológicas (Zoologia) da Universidade Federal do Rio de Janeiro. p. 138.

Pacheco, M., Kajin, M., Gentile, R., Zangrandi, P. L., Vieira, M. V., & Cerqueira, R. 2013. A comparison of abundance estimators for small mammal populations. Zoologia, 30(2), 182–190.

Paglia, A. P., Da Fonseca, G. A., Rylands, A. B., Herrmann, G., Aguiar, L. M., Chiarello, A. G., Leite, Y. L. R., Costa, L. P., Siciliano, S., Kierulff, M.C.M., Mendes, S. L., Tavares, V. C., Mittermeier, R.A., & Patton, J. L. 2012. Annotated checklist of Brazilian mammals. Occasional Papers in Conservation Biology, 6, 1–82.

Prevedello, J. A., Ferreira, P., Papi, B. S., Loretto, D., & Vieira, M. V. 2008. Uso do espaço vertical por pequenos mamíferos no Parque Nacional Serra dos Órgãos, RJ: um estudo de 10 anos utilizando três métodos de amostragem. Espaço & Geografia, 11(1), 1516–9375.

Previtali, M. A., Meserve, P.L., Kelt, D. A, Milstead, W.B., & Gutierrez, J. R. 2010. Effects of more frequent and prolonged El Niño events on life-history parameters of the degu, a long-lived and slow-reproducing rodent. Conservation Biology, 24(1), 18–28. DOI: 10.1111/j.1523-1739.2009.01407.x

R Core Team 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rizzini, C. T. 1979. Tratado de fitogeografia do Brasil. Volume II. São Paulo: Ed. da Universidade de São Paulo: p. 374.

Rossi, R. C., & Leiner, N. O. 2022. Weather, fire, and density drive population dynamics of small mammals in the Brazilian Cerrado. Journal of Mammalogy, 103(5), 1127–1140. DOI: 10.1093/jmammal/gyac053

Royama, T. 1992. Analytical Population Dynamics. Hong Kong: Springer: p. 371.

Santos, J. R. C. 2019. História de vida e dinâmica populacional do roedor *Delomys dorsalis* (Hensel 1872). Master thesis. Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio de Janeiro. p. 69.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., & Chan, K. S. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. The Royal Society of London. 270, 2087–2096. DOI: 10.1098/rspb.2003.2415

Turchin, P. 2003. Evolution in population dynamics. Nature, 424(6946), 257–258.

Turchin. P. & Taylor, A. D. 1992. Complex dynamics in ecological time series. Ecology, 73, 289–305.

Zangrandi, P. L. 2011. Fatores endógenos e exógenos na regulação populacional: um estudo de caso com o marsupial *Marmosops incanus* (Didelphimorphia, Didelphidae). Master thesis. Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio de Janeiro. p. 112.

SUPPLEMENTARY MATERIAL

Figure S1. Phase portrait of the climbing mice *Rhipidomys itoan* for 16 years in an Atlantic Forest area, southeastern Brazil. a) Complete time series, b) between 2000 and 2007 (low-population sequence), and c) between 2008 and 2015 (high-population sequence). The lines connecting the points represent vectors [Nt-1, R]. (Nt-1 = population size with a lag of one year, R = per capita population growth rate). The blue arrow indicates the beginning of the time series.

Figure S2. Autocorrelation function of the climbing mice *Rhipidomys itoan* for 16 years in an Atlantic Forest area, southeastern Brazil. a) ACF of the complete time series; b) ACF of the detrended time series from 2000 to 2007 (low-population

sequence), and c) ACF of the detrended time series from 2008 to 2015 (high-population sequence). Lags = annual delays.

Table S1. Standardized parameters of the two top-ranked models predicting population size fluctuation of the climbing mice *Rhipidomys itoan* for 16 years in an Atlantic Forest area, southeastern Brazil. Tmax = mean maximum temperature in the current year and $Tmax_{-1}$ = mean maximum temperature in the previous year. Significant code: * 0.05.

Figure S3. Comparison of population dynamics of the climbing mice *Rhipidomys itoan* estimated with a) the capture success index (Graipel *et al.* 2014) and b) the Minimum Number Known to be Alive (Krebs 1966). r = 0,90 (p < 0.001).