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Original investigation

Influence of temporal variation and seasonality on population dynamics of three sympatric rodents

Clarisse R. Rocha [a,*], Raquel Ribeiro [b], Jader Marinho-Filho [a]

[a] Dept. Zoologia, Instituto de Ciências Biológicas, Campus Universitário Darcy Ribeiro, Universidade de Brasília, 70910-900, Brasília, DF, Brazil
[b] Instituto de Estudos em Saúde e Biológicas, Universidade Federal do Sul e Sudeste do Pará, Cidade Universitária – Avenida dos Ipês com Rua J, Bairro Cidade Jardim, 68500-000, Marabá, PA, Brazil

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ABSTRACT

Population dynamics of small mammals can be strongly influenced by seasonality. Long-term studies are important in detecting population size variation in small mammals, and understanding the causes of that variation. We performed a six-year study to investigate fluctuations in population parameters (reproduction, recruitment, survival rates, abundance, and capture probability) of three rodent species at the core of the Brazilian cerrado domain. Small mammals were captured monthly within two grids during six years at Aguas Emendadas Ecological Station in the Federal District, Brazil. Model selection for explaining variation in rodent survival rates and capture probability was performed using MARK (Robust Design model). All three rodent species showed highest proportion of reproductive females in wet seasons. *Calomys tener* and *T. lasiotis* are seasonal and population size is higher in dry than in wet seasons, while the most abundant *N. lasiurus* had no seasonal patterns. Annual variation in abundance was also important for these three species. *Thalpomys lasiotis* declined over the six years of the study. These species showed highest survival estimates in the dry season. Our results reinforce the idea that not only climatic (rainfall and drought) events are linked to population numbers, survival rates, and capturability, but also that the life histories of the species can play an important role in their responses to variations in rainfall-productivity events.

Introduction

Fluctuations in population density have been one of the most debated questions in population ecology (Elton, 1924; Bergallo and Magnusson, 1999; Bonecker et al., 2009; Emmons, 2009; Stapp, 2010; Thibault et al., 2010). Why some small mammal populations exhibit multiannual density fluctuations while others present annual cycles that remain stable throughout the years is one of the persisting questions in the field.

In highly seasonal environments, populations of small mammals should be regulated by bottom-up factors (Lima et al., 2003; Merritt et al., 2001). Rainfall acts as an indirect cause that determines not only the amount of food available for the species (Bergallo and Magnusson, 1999; Múrua et al., 1986), but also affects the survival rates through competition for resources, predation rates, epidemics, shelter availability, etc (Alho and Pereira, 1985; Mello, 1980; Vieira, 1997). The factors that determine population dynamics can also vary over the years (McMillan et al., 2005) making it even more difficult to understand these fluctuations.

Abundance values estimated using capture-recapture methods can be affected by the capture probability of a given organism. In the Brazilian cerrado, the highest capture rates observed for rodents during the dry season has been related to a greater bait attractiveness during periods of lower resource availability (Vieira, 1997).

Studies report that reproductive patterns of neotropical cricetid rodents are directly related to resources availability and indirectly related to rainfall (Bergallo and Magnusson, 1999; Cerqueira, 2005; Bonecker et al., 2009; Queirolo and Granzinolli, 2009). Also, for some species, population peaks and high rates of recruitment occur during the dry season (Mello, 1980; Alho and Pereira, 1985; Vieira, 1997). Thus, we believe that the increase in population numbers during the dry season in Cerrado, occurs in response to a previous period of reproduction at the rainy season.

Declines in rodent populations are also documented in cerrado (tropical Brazilian savannas) (Ghizoni et al., 2005; Layme et al., 2004; Mello, 1980), but few studies have had over two years of duration. The decline of *Necromys lasiurus* (Lund, 1840) in cerrado is apparently a consequence of declining invertebrate abundance (Ghizoni et al., 2005; Layme et al., 2004). Long-term studies are

* Corresponding author.
E-mail address: rocha.clarisse@gmail.com (C.R. Rocha).

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important for understanding seasonal patterns and population fluctuations of rodents, in order to determine whether the population is in fact declining, or if variation in population sizes is merely a consequence of cyclic abiotic processes.

To understand the consequences of seasonal demographic changes in rodent populations, we performed a six-year study to investigate fluctuations in population parameters of three sympatric species living in an environment with variable rainfall rates at the core of the Brazilian cerrado domain. Herein, we investigate the influence of seasonality on life history strategies, as reproduction, recruitment, abundance, survival, and capture probabilities. It is expected that populations with faster potential of growth, higher fecundity and shorter life span of individuals have greater capacity to track change in its environment. Thus, small mammals that lives in a high seasonal environment should present fluctuations not only on abundance, but also on reproduction periods, and recruitment rates, accordingly to their environmental conditions.

Materials and methods

Study area

The cerrado is a savanna-like vegetation lying over the Central Brazilian Plateau, at altitudes from 600 to 1400 m, with two well-defined seasons: a dry and cold period, from May to September, and a hot and rainy period from October to March (Maia and Baptista, 2008; Oliveira-Filho and Ratter, 2002; Ribeiro and Walter, 2001). A number of different types of habitat ranging from open grasslands to semideciduous forests may occur side by side. The study was conducted in Aguas Emendadas Ecological Station (Estação Ecológica de Águas Emendadas – ESECAE), located in the northeastern portion of the Federal District. The Federal District has a tropical climate (Koppen-Geiger Aw), with the annual mean temperature ranging between 21 and 23 °C, and average rainfall between 1400 and 2000 mm (Cardoso et al., 2015). Currently, the ESECAE is practically a remnant island comprising 10,500 ha of native cerrado vegetation surrounded by a matrix of urban and rural land cover (Carvalho, 2008; Lima and Silva, 2008; Lima, 2008). The main habitat types in ESECAE comprise grasslands, palm swamps (*vereda*), and wooded savanna (cerrado *stricto sensu*) (Felfili et al., 2008). The present study was performed in a portion of these grasslands, in the highest part of the reserve, which has a characteristic microrelief, with termite mounds (named *murundus*) around which small trees and bushes grow (Oliveira-Filho and Ratter, 2002; Sano and Almeida, 1998; Silva Júnior and Felfili, 1996). For more detailed information on the study area, see Ribeiro et al. (2011).

Species description

This study focused on the populational parameters of three rodent species of the Cricetidae family (Myomorpha, Muroidea): *Calomys tener* (Winge, 1887), *Necromys lasiurus* and *Thalpomys lasiotis* (Thomas 1916). *Calomys tener* is primarily found in the cerrado of central Brazil, but has also been recorded in areas adjacent to the Atlantic Forest, the Amazon (Bonvicino et al., 2010; Patton et al., 2015) and the southern part of the country (Quintela et al., 2014). It is one of the most abundant species following fire events (Briani et al., 2004). It has a terrestrial, solitary, vesper-nocturnal habit, and is mainly specific to open habitat areas (Alho et al., 1986; Mares et al., 1989; Vieira and Baumgarten, 1995). It has a frugivore-granivore diet (Paglia et al., 2012), although it can occasionally consume animal items (Ramos and Facure, 2009). Individuals are fit for reproduction shortly before turning two months old (Araripe et al., 2006).

Necromys lasiurus presents a wide geographic range, occurring in different biomes, such as the Amazon, Atlantic Forest, Chaco, Cerrado and Caatinga (Redford and Fonseca, 1986). In the cerrado, it occurs in different vegetation formations, and is considered one of the most habitat generalist and abundant species of central Brazil (Alho et al., 1986; Henriques and Alho, 1991; Marinho-Filho et al., 1994; Marinho-Filho et al., 1998). It is a diurnal species, presenting seasonal variation in activity pattern (Vieira et al., 2010). It has a frugivore-omnivore diet (Paglia et al., 2012), and diet variations have been documented in relation to habitat type (Borchert and Hansen, 1983) and climatic seasonality (Couto and Talamoni, 2005).

Thalpomys lasiotis is a terrestrial species (Alho, 1980), found mainly in open grasslands and cerrado *sensu stricto* (Alho et al., 1986; Andrade et al., 2004). Its range is restricted to the cerrado of the states of Minas Gerais, Bahia, Goiás, Mato Grosso and Rondônia (Andrade et al., 2004), and can occur at high densities in some of these localities (Andrade et al., 2004; Ribeiro et al., 2011), as well as in recently burnt areas (Briani et al., 2004). *T. lasiotis* has been recently classified as a threatened species in the 'Endangered' category (EN) following the A2bc criterion, according to the National List of Threatened Fauna Species (MMA, 2014).

Animal capture

Sampling was carried out monthly from March 2004 to April 2010 in two grids including both open grassland and *murundus*, one at 15°32′44,8′′s, 47°36′48,0′′W, which has a lower plant species richness (n = 18) than the other (n = 42) at 15°32′15,3′′s, 47°36′43,3′′W (Ribeiro and Marinho-Filho, 2005). The grids were 135 m × 135 m (1.82 ha), distant 1 km from one another. Grid lines were 15 m apart, forming a 10 × 10 row structure. Fifty traps were placed in each grid simultaneously, at alternating grid line intersections. In order to avoid trap-happy animals, after the third night, the traps were moved to the neighboring intersection until the end of the trapping session. Full moon nights were avoided due to rodent activity decline at that time (O'Farrell, 1974; Price et al., 1984). Monthly trapping sessions lasted for six consecutive nights, and traps were checked each morning. Sherman live traps (250 × 80 × 90 mm) were deployed and baited with a mix of sardine, peanut butter, banana, and corn meal. All captured individuals were identified and marked with numbered ear tags (National Band & Tags Company Newport, KY; Mod. 1005 – 1) or by toe clipping. After capture and treatment, all animals were released at the capture location.

All capture, handling and marking procedures were performed in accordance with American Society of Mammalogists guidelines (Sikes and Gannon, 2011), and were approved by the University of Brasilia Animal Care and Use Committee (CEUA-UNBDOC 47208/2009). All captures and collections were made upon authorization issued by the Brazilian Institute for the Environment (IBAMA No. 15151- 1–6). Trapping methods followed Rocha et al. (2011).

Data analysis

We performed a Linear Model (LM) selection, added the interactions between the variables in the global model, for each species to assess if the proportion of reproductive individuals (reproductive_female–season * study_areas * year), the proportion of juveniles (recruitment–season * study_areas * year), and the abundance estimates (abundance–season * study_areas * year) varied between seasons, years, and grids. The model built to evaluate the factors influencing the abundance of the species took into account three independent variables: 'season' (wet and dry seasons), 'study areas' (Grids 1 and 2) as a binary variable, and 'study year' (six years) as a categorical variable. Data of the proportion of reproductive individuals and the proportion of recruitment were transformed to arcsine prior to the analysis, to satisfy the premises of the tests. We used Robust Design in Mark software to estimate population