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Local effects of global climate on a small rodent *Necromys lasiurus*

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Global climate drivers often have strong effects on the carrying capacity of animal populations, but little is known about how effects differ between regional and local scales. In this paper we evaluated how climate variables were correlated with regional and local fluctuations of a small rodent, *Necromys lasiurus*, in an Amazonian savanna. Between 2000 and 2019, we evaluated the temporal variation in abundance of *N. lasiurus* in eight 4.0-ha plots separated by 0.8 – 10.6 km. Using generalized linear mixed models, we found that, at a regional scale, the abundance of rodents captured was positively associated with the abundance in the prior year, but had little relationship with the Southern Oscillation Index (SOI), which had been shown to affect rats in a single plot in a previous study. However, variation in densities among years was coordinated among some plots, leading to patchiness in population dynamics. Based on the patterns of density fluctuations, the plots formed three clusters. Analyses based on these clusters indicated that only one was strongly affected by SOI, as in the previous study. The differences in the effects of global climate drivers on populations of a single species in relatively homogeneous habitat indicate that predictions about the effects of climate change should be based on simultaneous studies in a variety of sites or they may lead to spurious relationships.

Key words: Amazon, climate change, metapopulation, population fluctuation, small mammals, Southern Oscillation Index

Os fatores climáticos globais geralmente têm fortes efeitos sobre a capacidade de suporte de populações de animais, mas pouco se sabe sobre como os efeitos diferem entre as escalas regional e local. Neste artigo, avaliamos como as variáveis climáticas foram correlacionadas às flutuações regionais e locais de um pequeno roedor, *Necromys lasiurus*, em uma savana amazônica. Entre 2000 e 2019, avaliamos a variação temporal da abundância de *N. lasiurus* em oito parcelas de 4,0 ha, separadas por 0,8 a 10,6 km. Utilizando modelos mistos lineares generalizados, descobrimos que, em escala regional, a abundância de roedores estava positivamente associada à abundância do ano anterior, mas tinha pouca relação com o Southern Oscillation Index (SOI), que demonstrou afetar roedores em uma parcela única em outro estudo anterior. Entretanto, a variação nas densidades entre os anos foi coordenada entre algumas parcelas, levando a irregularidades na dinâmica populacional. Com base nos padrões de flutuações de densidade, as parcelas formaram três grupos. Análises baseadas nesses grupos indicaram que apenas um foi fortemente afetado pela SOI, como no estudo anterior. As diferenças nos efeitos dos fatores climáticos globais sobre as populações de uma única espécie em habitat relativamente homogêneo indicam que as previsões sobre os efeitos das mudanças climáticas devem basear-se em estudos simultâneos em vários locais ou podem levar a relações espúrias.

Palavras-chave: Amazônia, flutuação populacional, metapopulação, mudança climática, pequenos mamíferos, Southern Oscillation Index

The Southern Oscillation Index (SOI) measures periodic interannual variation in global atmospheric and oceanic circulation patterns, which are known to be correlated with variations in the global pattern of rainfall (Ropelewski and Halpert 1987). SOI and other global climate drivers often have strong effects on animal populations, usually through changes in vegetation productivity (Wright et al. 1999; Letnic et al. 2005; Dunn and Winkler 2010; Duursma et al. 2018). However, many species show cyclical or pseudocyclical variations in population density with little relation to external factors (Krebs et al. 2004; Radchuck et al. 2016). Cyclical patterns may occur over large areas or fluctuations in local populations may not be correlated (Steen et al. 1996; Thibault et al. 2010).

Animal densities depend on both intrinsic and extrinsic factors. Intrinsic factors often are referred to as "density-dependent," but there are many definitions of this term. In principle, all populations that have been in existence for many generations must be subject to density-dependent processes because population regulation by density-independent processes is fragile and unlikely to be observed in practice (Royama 1992). Nevertheless, density-independent processes can produce perturbations that effectively change the carrying capacity of the environment and may have much greater effects on densities than the density-dependent processes that avoid extinction in the long term (Royama 1992; Rees 1996).

There may be a strong spatial component to population dynamics, which in its most extreme form is known as metapopulation dynamics. This can be modeled if information on a large number of independent time periods and locations is available (Royama 1992: table 1.1). However, these analyses require large series of data, which rarely are available in practice (Royama 1992). A first step for such analyses is to determine at what spatial scale density fluctuations in time are uncorrelated.

Rodents often show "boom or bust" dynamics: extremely high—often termed "plague"—densities followed by periods in which the presence of the species may be difficult to detect (Dickman et al. 2010). A study of a small Amazonian-savanna rodent, *Necromys lasiurus*, at the beginning of this century indicated that its population dynamics were closely associated with local rainfall, which was controlled in large measure by the SOI (Magnusson et al. 2010). However, that study was undertaken in a single 4-ha plot. Studies of the population dynamics of rodents often are undertaken in similar-sized or smaller plots (e.g., Rocha et al. 2011; Vieira 2003; Ribeiro et al. 2019), but it is unclear how well such studies capture regional fluctuations.

Studies over a wider area indicated that density fluctuations in *N. lasiurus* in the region studied by Magnusson et al. (2010) also could be related to the availability of invertebrate prey (Layme et al. 2004; Ghizoni et al. 2005). However, the density of *N. lasiurus* at the start of the study by Magnusson et al. (2010) was much higher than in subsequent years, and the species seemed to be suffering a continuous decline in density, which could lead to local extinction (Ghizoni et al. 2005). During the studies by Layme et al. (2004) and Ghizoni et al. (2005) the apparent density of *N. lasiurus* in the plot studied by Magnusson et al. (2010) went to zero, although the species still occurred in other areas. These studies suggested that local density fluctuations of the species may be uncoupled and that drivers of population dynamics of the species could vary spatially and temporally.

To better understand the potential for climate change to impact the species, we extended the studies of Layme et al. (2004), Ghizoni et al. (2005), and Magnusson et al. (2010), for a further 9 years in eight permanent plots distributed over an area of approximately 16,000 ha. Our objective was to determine to what degree fluctuations in different areas were correlated, and to what extent these local fluctuations were related to climatic variables, such as local rainfall and SOI.

Materials and Methods

Our study area is on the outskirts of Alter do Chão (2°30′37″S, 54°57′11″W [WGS84], ~38 m), a village located about 30 km from Santarém, Pará State, in the Brazilian Amazon. The climate is Am following the Köppen classification, characterized as being humid tropical with little monthly variation in temperature (mean of 27.7°C), but with strong seasonal variation in rainfall. Around 75% of precipitation occurs between the months of December and June, with September being the driest month (34 mm average precipitation).

The vegetation is characterized by isolated old-growth or regrowth forest fragments within a savanna matrix (Fig. 1), as well as a large area of continuous native forest (Albernaz et al. 1999). Trees in the savanna are sparse and most of the ground cover consists of herbs and grasses (Magnusson et al. 2008). Natural- and human-induced fires usually burn the savannas at 1- to 3-year intervals and some savanna areas are used as pasture for cattle.

Necromys lasiurus is the only rodent that inhabits savanna environments in our study region, and has a mean home-range size that varies among years and between sexes, with a mean of 2.19 ha for males (Magnusson et al. 1995). Individuals can reproduce at 3–4 months of age, with a litter size of about five individuals (Melo and Cavalcante 1982). In our study region, reproduction and growth patterns are strongly seasonal, with peaks in the wet season (January–May), which appears to be related to availability of fruits and invertebrates, the main food resources for *N. lasiurus* (Francisco et al. 1995; Layme et al. 2004).

We evaluated the temporal variation in abundance of *N. lasiurus* in eight 4.0-ha plots located in savanna environments. The distance among plots varied from 0.8 to 10.6 km. Most of the data were obtained in the months of August or September (dry season) between 2000 and 2019 (with exceptions of 2003, 2007, and 2008), giving data for 17 years. In 2002, we sampled the plots in March; 2006 in July; and 2011 in December. In each plot, 50 Sherman live traps (8 × 9 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were set at 20-m intervals on a trapping grid that covered the plot. The grids had four parallel 250-m lines with 50 m between lines. The traps remained open for 2 days (see Francisco et al. 1995;

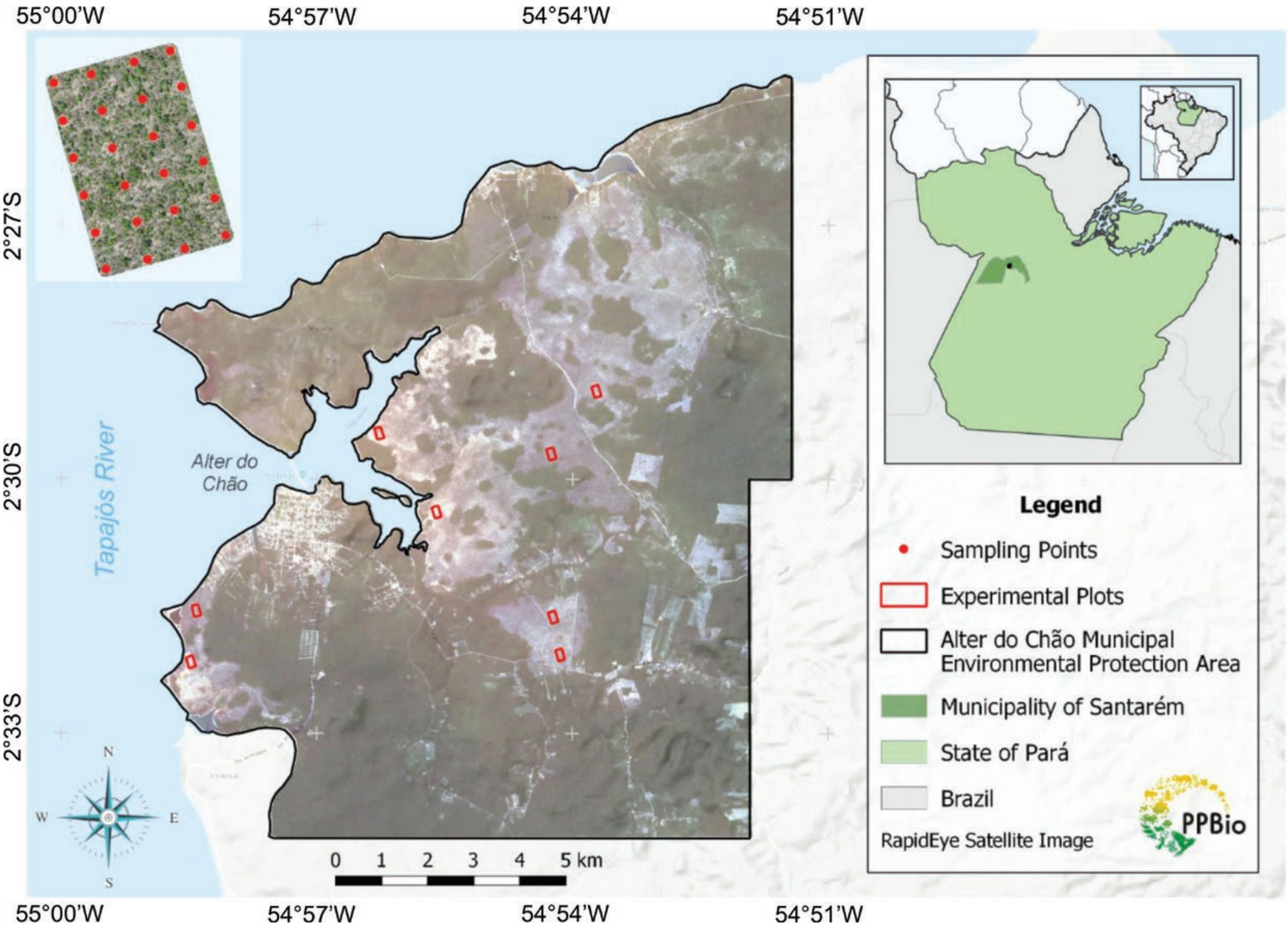

Fig 1.—Sampling areas of *Necromys lasiurus* in Alter do Chão, Santarém, Pará.

Magnusson et al. 1995). A mixture of rolled oats and peanut butter, together with half a Brazil nut (*Bertholletia excelsa*), was used as bait, and traps checked once a day during the morning. Capture, handling, and marking, procedures followed the guidelines of the American Society of Mammologists (Sikes et al. 2016).

We obtained the SOI from the National Climate Centre (http://www.bom.gov.au/climate/current/soihtm1.shtml) and data on local rainfall from the Instituto Nacional de Meteorologia (INMET) substation of Belterra, Pará (OMM: 82246) located 15 km from the study area, available from the INMET internet site (http://www.inmet.gov.br). We measured fire extent in each plot between 2000 and 2018. After the burning season (July–December), a measuring tape was extended along the four 250-m lines in each plot and the presence or absence of burned vegetation recorded at 2-m intervals along the lines, giving an index of fire extent in each plot each year that varied from 0 to 500.

Analyses.—We used the number of animals captured each year as an index of local abundance. Previous studies (Francisco et al. 1995; Magnusson et al. 1995) indicated that this index was close to the number of animals using the plot in that period. *Necromys lasiurus* populations could double in < 6 months, and numbers in 1 year are potentially largely independent of the number the year before. However, both the number of rodents captured and SOI show long-term apparently cyclic behavior, so statistical tests have to include the number of rodents captured in the previous year to account for the temporal autocorrelation. This reduces the number of years that can be included in tests from 17 to 14. We used climate variables (SOI and precipitation) as the summed monthly values of the data for the year before each survey and the proportion of fire extent (ranging to 0–1) in each plot in the year before each survey.

We use a correlative approach in this study to investigate regional and local fluctuations. Ideally, it would be possible to use a complete population-dynamics model, but breaks in our time series meant that we had a maximum of 11 consecutive years to estimate the autocovariance of the time averages, and for more detailed analyses "the time series must be sufficiently long to ensure the convergence of time averages to a reasonable degree" (Royama 1992). One of us (CR) is continuing the study, and such analyses may be possible in the future.

Variation in abundance of rats is not necessarily independent among plots, so we used principal component analysis (PCA) to summarize spatial patterns in the rat abundance between years and identify plots with correlated fluctuations in abundance. We then used generalized linear mixed models (GLMMs) for Poisson-distributed data (Zuur et al. 2009) to evaluate how rat abundance in the year before, fire, and climatic variables, influenced rat abundance. Plot and year were random effects to control for pseudoreplication in space and time respectively (Millar and Anderson 2004). We constructed the models using both all plots (regional scale) and separately for clusters of plots identified in PCA (local scale).

RESULTS

We captured 437 individuals of *N. lasiurus*, with an average ranging from 0.12 to 10.3 across years. The number of *N. lasiurus* captured fell from 62 in 2000 to 11 in 2019. Numbers peaked in 2000, 2004, and 2013 (Fig. 2). Local rainfall varied considerably throughout the study, with annual totals < 1,600 mm in 2002, 2012, 2015, and 2016, and > 2,200 mm in 2006, 2011, 2013, and 2014; SOI varied from −10.4 in 2014 to 13.6 in 2005.

Variation in densities among years was coordinated among some plots (see Supplementary Data SD1). We identified three spatial clusters; Cluster A: plots 3, 4, and 7; Cluster B: plots 2 and 5; and Cluster C: plots 1, 6, and 8 (Fig. 3). At a regional scale, the abundance of rodents captured was positively associated with the abundance in the year before ($z = 3.042$, $P = 0.00235$) and we did not detect association with climatic variables or fire extent ($P > 0.18$ in all cases; see Supplementary Data SD2). For plot clusters, the abundance in the year before was not associated with rat abundance, and SOI was positively associated with rat abundance only for cluster C (SOI = 0.10586, $z = 2.189$, $P = 0.0286$); there was no statistically significant relationship for the other clusters ($P > 0.09$ in all cases; see Supplementary Data SD2).

DISCUSSION

Rodent populations often respond to El Ninõ Southern Oscillations (ENSO) and predators (e.g., Lima et al. 2002; Múrua et al. 2003; Letnic and Dickman 2005; Letnic et al. 2005) in arid landscapes, and Magnusson et al. (2010) suggested, based on data from a single sampling grid, that *N. lasiurus* shows similar dynamics in Amazonian savanna. However, the effects of global climate drivers may depend on local habitat characteristics (e.g., Shenbrot et al. 2010), and other factors such as predation and social interactions affect rodent population dynamics (Radchuck et al. 2016). The density of *N. lasiurus* in the plot studied by Magnusson et al. went to zero in subsequent years, and no individual of the species has been recorded since 2002, despite the continuous monitoring and consistent captures of the species in neighboring plots.

Many studies show that seasonality driven by precipitation is linked with population patterns of rodent species in arid and semiarid environments, but most of those studies are undertaken at local scales and in no more than 1 or 2 years (e.g., Emmons 2009; Vieira et al. 2010; Rocha et al. 2011; Owen 2013). Similarly, studies in arid and semiarid environments of Australia and Brazil show negative impacts of fire on rodent

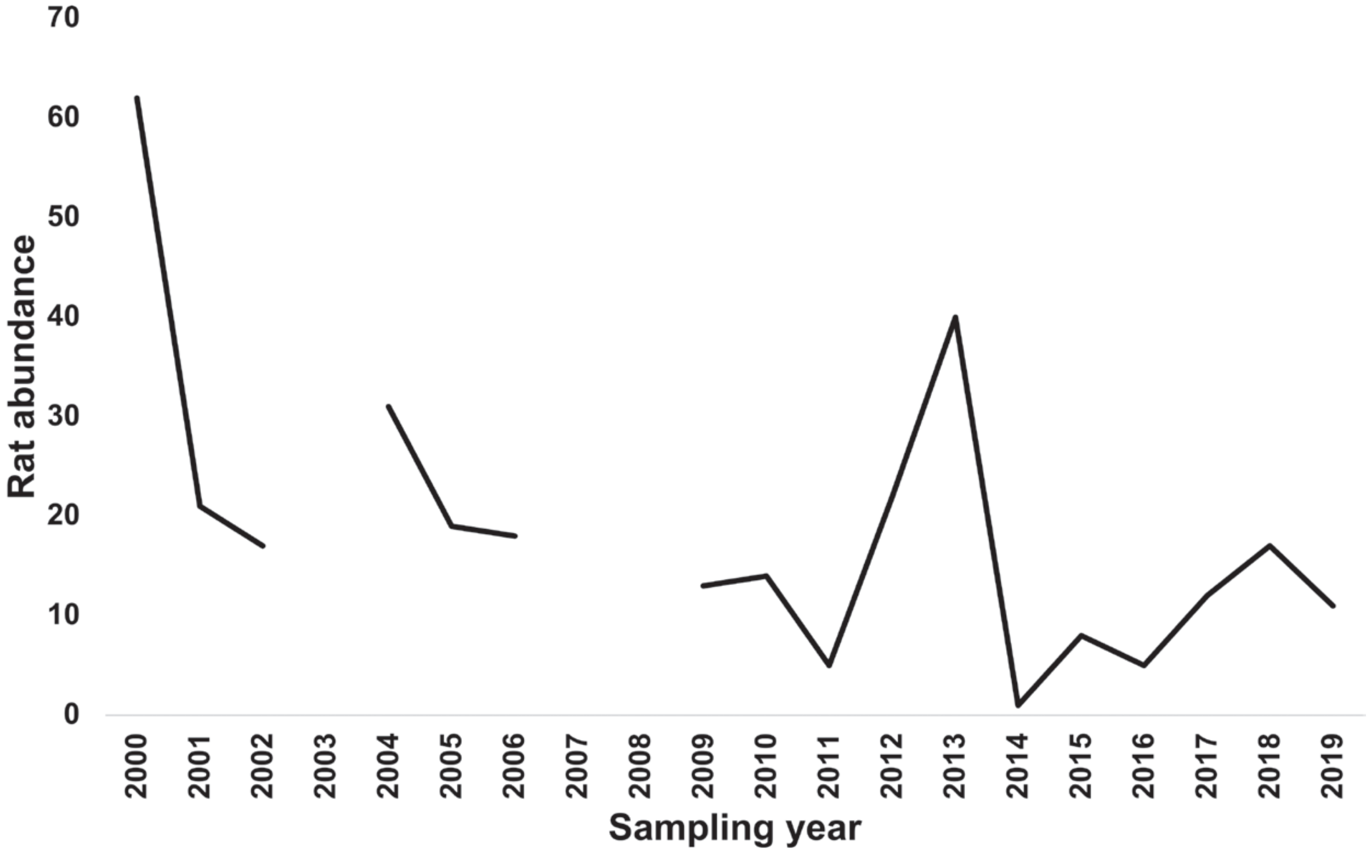

Fig. 2.—Variation in abundance of *Necromys lasiurus* in Amazonian savannas near Alter do Chão, Brazil between 2000 and 2019.

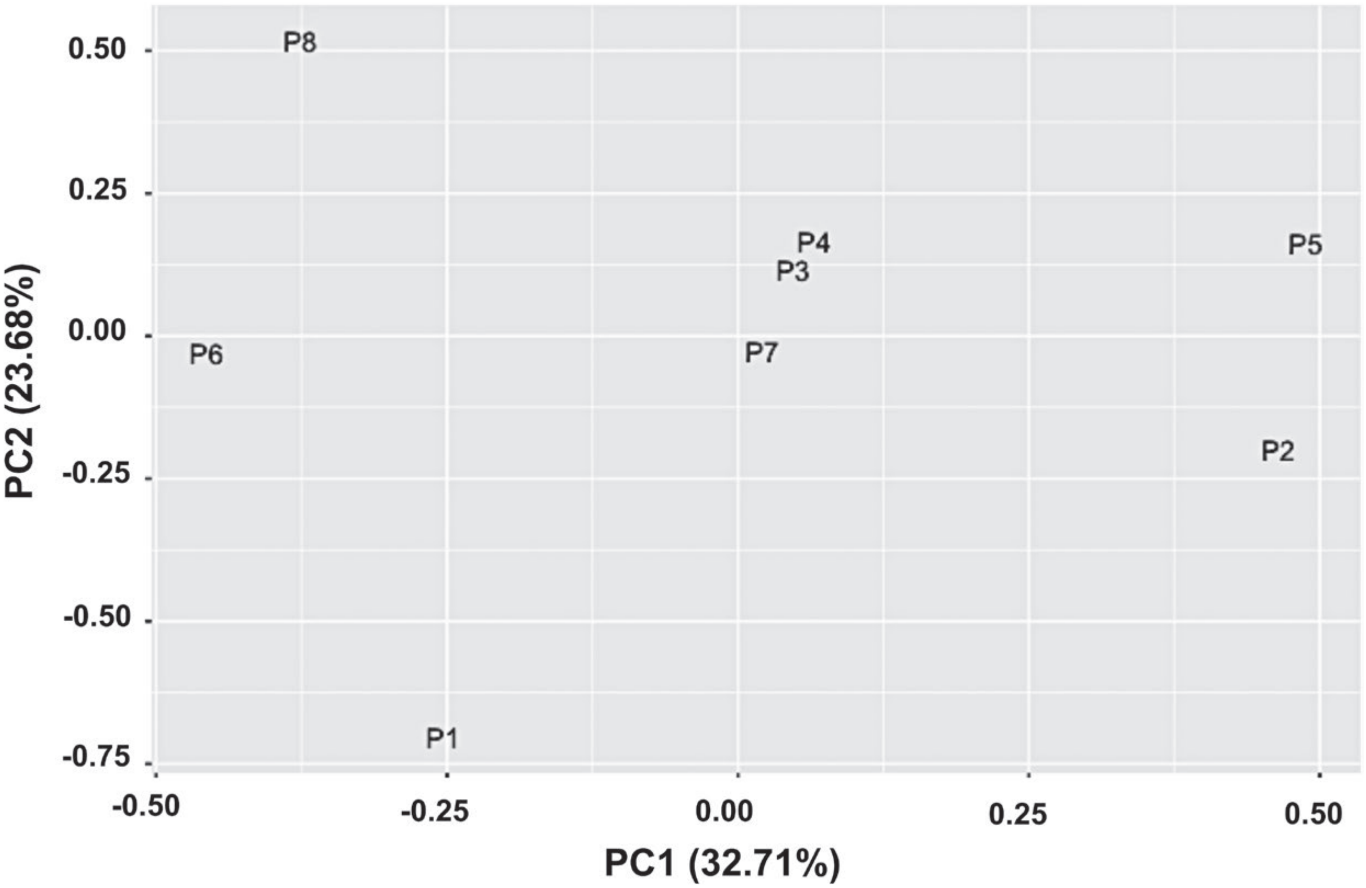

Fig. 3.—Principal component analysis showing spatial clusters in the temporal population variation of *Necromys lasiurus*.

abundance, which is attributed to habitat loss, changes in invertebrate availability, and increased exposure to predation in burned habitats (Briani et al. 2004; Letnic et al. 2005; Vieira and Briani 2013). Predation generally is the most important extrinsic factor regulating rodent populations (Radchuck et al. 2016), and microhabitat explains much of the differences in *N. lasiurus* abundance in Brazilian Cerrado (Briani et al. 2004; Rocha et al. 2011). However, a previous study with *N. lasiurus* in our study area showed that precipitation, vegetation structure, and fire, were not related to growth or reproduction in *N. lasiurus* (Francisco et al. 1995).

The rate of increase of *N. lasiurus* in the Alter do Chão savannas appears to be driven by food availability (i.e., invertebrates) in some years (Layme et al. 2004; Ghizoni et al. 2005) and fluctuations in density of invertebrates have been associated with the SOI (Radnan 2018). However, food availability only could be considered a density-dependent factor (sensu Royama 1992) if it is dependent on rodent densities. *Necromys lasiurus* has a diverse diet that includes both animal and plant matter. Although it is feasible that food availability is reduced at the highest densities we recorded, it is unlikely that a few mice per hectare, which is the density we recorded in most years, could significantly affect it. Therefore, food availability is more likely to be a density-independent factor that can determine carrying capacity at some times, but is not responsible for the long-term stability of the population.

Disease outbreaks can occur following El Niño events, which can eliminate local populations of rodents (Stapp et al. 2004). In Australia, rat population fluctuations were not influenced directly by SOI, which indicates that "boom" or "bust" in rats linked to climate variation is more complex than is commonly assumed (Krebs et al. 2004; Letnic et al. 2005). This complexity probably explains why we have recorded strong effects from the SOI in some localities in some years, but no effect in neighboring localities in the same time interval.

We believe that loss of *N. lasiurus* from our original study site was caused by vegetation changes associated with fire exclusion (i.e., habitat variation). However, there is little obvious habitat variation between the sites for which we have data in the present study, and rat densities were not significantly related to fire extent at either local or regional scales.

Density fluctuations were correlated between neighboring sites, but we found three clusters of plots with distinct population dynamics despite a maximum distance of 10.6 km between plots. Differences in predation pressure are unlikely over these distances, and the major predators on the species, owls and hawks, could fly easily between and among clusters. Sociability and dispersal can play key roles in regulating rat population dynamics (Radchuck et al. 2016), but densities during most of the study were relatively low in comparison to those we recorded at the beginning, so social factors alone seem unlikely to explain the differences among clusters. Whatever the cause, it is obvious that a spatially explicit population model (Gilpin and Hanski 1991; Royama 1992) is more appropriate for the species at Alter do Chão than one that assumes correlated regional fluctuations.

Metapopulational dynamics have been reported to be responsible for maintaining rodent populations in highly fragmented areas of tropical forests (Adler 1994; Pires et al. 2002) and our data indicate that they may to be important even over short distances in relatively homogeneous savanna, which is consistent with Radford's (2010) assertion that metapopulation studies are necessary to understand the effects of external factors on biodiversity of savannas.

This study illustrates two challenges for predicting the effects of global change on rodent populations. The first is that strong effects on local areas might not translate into regional densities of a species because of complex metapopulation dynamics. The second is that studies of rodents often are undertaken when the species is abundant, which might be due to global climatic events, but these studies may not reflect the processes that maintain the species at low densities for long periods. Identification of density-independent factors that affect carrying capacity are important to understand rodent densities and the food webs that depend on them, but the identification of the density-dependent factors that regulate populations and permit long-term existence requires explicit population models, independent evidence that the factor truly is density-dependent and long time series in a large number of independent locations (Royama 1992). We are a long way from that goal for any species of tropical rodent.

Amazonian savannas have unique faunas and floras, including many endemic species, and are maintained by unknown complex ecological dynamics, but they have been much neglected in comparison with forests (Carvalho and Mustin 2017). Also, with loss of rainforests, knowing the ecological dynamics of tropical savannas is becoming increasingly important both for the conservation of the savanna itself, and for understanding the likelihood of rainforest savannization due to climate change and deforestation.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Animation showing that variation in densities of *Necromys lasiurus* among years was coordinated among some plots.

Supplementary Data SD2.—Detailed results of generalized linear mixed models.

Literature Cited

Adler, G. H. 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. Journal of Animal Ecology 63:903–911.

Albernaz, A. L. K. M., R. C. Soares, T. M. Sanaiotti, A. Lima, and W. E. Magnusson. 1999. Proposta para criação de uma área de proteção ambiental (APA) em Alter do Chão, Santarém/Belterra, Pará. INPA. Santarém, Pará.

Briani, D. C., A. R. T. Palma, E. M. Vieira, and R. P. B. Henriques. 2004. Post-fire succession of small mammals in the Cerrado of central Brazil. Biodiversity and Conservation 13:1023–1037.

Carvalho, W. D., and K. Mustin. 2017. The highly threatened and little known Amazonian savannahs. Nature Ecology & Evolution 1:0100.

Dickman, C. R., A. C. Greenville, C. L. Beh, B. Tamayi, and G. M. Wardle. 2010. Social organization and movements of desert rodents during population "booms" and "busts" in central Australia. Journal of Mammalogy 91:798–81.

Dunn, P. O., and D. W. Winkler. 2010. Effects of climate change on timing of breeding and reproductive success in birds. Pp. 113–128 in Effects of climate change on birds (A. P. Møller, W. Fiedler, and P. Berthold, eds.). Oxford University Press. Oxford, United Kingdom.

Duursma, D. E., R. V. Gallagher, and S. C. Griffith. 2018. Effects of El Niño Southern Oscillation on avian breeding phenology. Diversity and Distributions 24:1061–1071.

Emmons, L. H. 2009. Long-term variation in small mammal abundance in forest and savanna of Bolivian Cerrado. Biotropica 41:493–502.

Francisco, A. L., W. E. Magnusson, and T. M. Sanaiotti. 1995. Variation in growth and reproduction of *Bolomys lasiurus* (Rodentia: Muridae) in an Amazonian savanna. Journal of Tropical Ecology 11:419–428.

Ghizoni, I. R., V. M. G. Layme, A. P. Lima, and W. E. Magnusson. 2005. Spatially explicit population dynamics in a declining population of the tropical rodent, *Bolomys lasiurus.* Journal of Mammalogy 86:677–682.

Gilpin, M., and I. Hanski. 1991. Metapopulation dynamics: empirical and theoretical investigations. Linnean Society of London and Academic Press. London, United Kingdom.

Krebs, C. J., et al. 2004. Can outbreaks of house mice in south-eastern Australia be predicted by weather models? Wildlife Research 31:465–474.

Layme, V. M. G., A. P. Lima, and W. E. Magnusson. 2004. Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian savanna. Journal of Tropical Ecology 20:183–187.

Letnic, M., and C. R. Dickman. 2005. The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. Austral Ecology 30:24–39.

Letnic, M., B. Tamayo, and C. R. Dickman. 2005. The responses of mammals to La Niña (El Niño Southern Oscillation)–associated rainfall, predation, and wildfire in Central Australia. Journal of Mammalogy 86:689–703.

Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecology Letters 5:273–284.

Magnusson, W. E., A. L. Francisco, and T. M. Sanaiotti. 1995. Home-range size and territoriality in *Bolomys lasiurus* (Rodentia: Muridae) in an Amazonian savanna. Journal of Tropical Ecology 11:179–188.

Magnusson, W. E., V. M. G. Layme, and A. Lima. 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.

Magnusson, W. E., A. P. Lima, A. L. K. M. Albernaz, T. M. Sanaiotti, and J. L. Guillaumet. 2008. Composição florística e cobertura vegetal das savanas na região de Alter do Chão, Santarém – PA. Revista Brasileira de Botânica 31:165–177.

Melo, D. A., and J. P. Cavalcante. 1982. Estudo do ciclo biológico do *Zygodontomys lasiurus* (Cricetidae), em condições de Laboratório. Brasil Florestal 12:57–63.

Millar, R. B., and M. J. Anderson. 2004. Remedies for pseudoreplication. Fisheries Research 70:397–407.

Múrua, R., L. A. González, and M. Lima. 2003. Population dynamics of rice rats (a hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations. Oikos 102:137–145.

Owen, R. D. 2013. Ecology of small terrestrial mammals in an isolated cerrado patch, Eastern Paraguay: communities, species, and effects of ENSO, precipitation, and fire. Mastozoología Neotropical 20:97–112.

Pires, A. S., P. K. Lira, F. A. S. Fernandez, G. M. Schittini, and L. C. Oliveira. 2002. Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. Biological Conservation 108:229–237.

Radchuck, V., R. A. Ims, and H. P. Andreassen. 2016. From individuals to population cycles: the role of extrinsic and intrinsic factors in rodent populations. Ecology 97:720–732.

Radford, I. J. 2010. Fire regimes and regional biodiversity declines in northwest Australian tropical savannas?: review of knowledge and recommendations for future research. Conservation Science Western Australia 7:469–479.

Radnan, G. N. 2018. The effect of changes in landscape and habitat complexity resulting from shrub encroachment and climatic factors (aridity and ENSO) on semi-arid ant communities. Ph.D. dissertation, University of New South Wales. Sidney, Australia.

Rees, W. E. 1996. Revisiting carrying capacity: area-based indicators of sustainability. Population and Environment 17:195–215.

Ribeiro, J. F., A. Guaraldo, G. B. Nardoto, G. Santoro, and E. M. Vieira. 2019. Habitat type and seasonality influence the isotopic trophic niche of small mammals in a neotropical savanna. Hystrix 30:30–38.

Rocha, C. R., R. Ribeiro, F. S. C. Takahashi, and J. Marinho-Filho. 2011. Microhabitat use by rodent species in a central Brazilian Cerrado. Mammalian Biology 76:651–653.

Ropelewski, C. F., and M. S. Halpert. 1987. Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. Monthly Weather Review 115:1606–1626.

Royama, T. 1992. Basic properties and structure of population processes. Pp. 3–46 in Analytical population dynamics (T. Royama, ed.). Springer. Dordrecht, The Netherlands.

Shenbrot, G., B. Krasnov, and S. Burdelov. 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. Journal of Mammalogy 91:776–786.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Stapp, S., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and Environment 2:235–240.

Steen, H., R. A. Ims, and G. A. Sonerud. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. Ecology 77:2365–2372.

Thibault, K. M., S. K. M. Ernest, E. P. White, J. H. Brown, and J. R. Goheen. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy 91:787–797.

Vieira, M. 2003. Seasonal niche dynamics in coexisting rodents of the Brazilian Cerrado. Studies on Neotropical Fauna and Environment 38:7–15.

Vieira, E. M., L. C. Baumgarten, G. Paise, and R. G. Becker. 2010. Seasonal patterns and influence of temperature on the daily activity of the diurnal neotropical rodent *Necromys lasiurus*. Canadian Journal of Zoology-Revue Canadienne de Zoologie 88:259–265.

Vieira, E. M., and D. C. Briani. 2013. Short-term effects of fire on small rodents in the Brazilian Cerrado and their relation with feeding habits. International Journal of Wildland Fire 22:1063–1071.

Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology 80:1632–1647.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media. New York.

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