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

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Abstract

We report on the population response of a species of rodent, *Necromys lasiurus*, to southern oscillation index (SOI) and extent of regional fire in an Amazonian savanna. Information on temporal variation in local abundance of *N. lasiurus* in a 4.0 ha savanna plot was obtained from 1985 to 1989, from 1997 to 1998 and 2000–2006, giving data on 14 of the 22 years. Throughout this period, rodent density declined by 90%. Densities were positively associated with SOI and the extent of fire in the region. Rainfall was related to SOI and negatively influenced the extent of fire. However, the amount of rain had no measurable direct effect on rat densities. Thus, small changes in temperature, and consequently fire probability and intensity, may have drastic consequences on the biota of Amazonian savannas, especially in El Niño periods.

Keywords: Amazonia, fire, population decline, rodent, savanna, southern oscillation index

Received 8 May 2009; revised version received 24 October 2009 and accepted 14 November 2009

Introduction

Models of global climate change lead to different predictions about future Amazonian climates (Marengo, 2004). Cochrane & Barber (2009) suggested that, even under some of the worst-case scenarios, forest cover in the Amazon basin will be relatively stable unless human activities contribute directly to deforestation because trees can tap ground water. However, this discussion has focused on the effects of climate change in relatively wet areas in the Amazon. Climate change may have greater effects on the biota in areas that are already water stressed. Even if the frequency and intensity of El Niño southern oscillation (ENSO) events does not increase (Collins, 2005; IPCC, 2007), an increase of 2 °C or more in mean temperatures, predicted by almost all models, will increase water stress in dry areas, and increase the frequency and intensity of fires, especially during El Niño events.

The effects of El Niño on the dynamics of small rodents and their predators have been studied extensively in semi-arid regions of Chile (e.g., Lima *et al.*, 2002; Múrua *et al.*, 2003). However, there are no other studies of the effect of ENSO on small-mammal populations in other South American ecosystems. In tropical and subtropical regions, small-mammal populations are thought to respond principally to rainfall (Francisco *et al.*, 1995; Lima *et al.*, 2006; Brown *et al.*, 2008; Andreo *et al.*, 2009). Rainfall is affected by local factors (Meir *et al.*, 2006) and large-scale climatic factors, such as the North Atlantic Oscillation (NAO) and ENSO phenomena (Jaksic, 2001; Letnic & Dickman, 2006). Although the occurrence of ENSO phenomena is predictable, with pseudocycles of 3–5 years, the intensity and duration are unpredictable, and sometimes catastrophic, causing increases in rainfall in some regions, such as western South America and Africa (Jaksic, 2001; Ogutu & Owen-Smith, 2003), and droughts in others, such as Australia (Letnic *et al.*, 2005). In the Amazon, El Niño is associated with reductions in the spatial and temporal distribution of rainfall (Marengo, 2004).

Climate drivers, such as ENSO and NAO have complex effects on the biota. They not only affect the amount of rainfall, they affect the distribution, intensity and predictability of rainfall, as well as temperature and incident radiation (Cochrane & Barber, 2009). The consequences of some of these for the frequency of fire are predictable, but other factors affect the probability of fire (Whelan, 1995), and complex interactions may have unpredictable consequences on the biota of savanna areas in the Amazon.

Smoke from fires in the Amazon does not disperse quickly (Ataxo *et al.*, 1998; Echalar *et al.*, 1998), and

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smoke plumes can be detected by MODIS and MISR sensors (Andreae, 2001; Koren *et al.*, 2007). Smoke from dry-season fires affect climate and human health (Cochrane 2003; Mendonça *et al.*, 2006; Ignotti *et al.* 2007; Martins & Dias, 2009). Emmons (2009) hypothesized that smoke from fires impedes dew fall, and subsequently water availability for savanna rodents. Although many studies have investigated the immediate local effects of fire, Emmons' study was the first study to suggest a regional effect of smoke on a non-human animal species independent of the local effects of fire on population dynamics and habitat structure.

In this paper, we report on the relationship between population density, SOI intensity and regional fire intensity for an Amazonia savanna rodent. *Necromys lasiurus* (Lund, 1841) is a small (~60 g) omnivorous rodent common in a variety of open habitats in seasonally dry or arid climates in South America (Karimi *et al.*, 1976; Souza & Alho, 1980; Streilen, 1982a, b; Francisco *et al.*, 1995; Magnusson *et al.*, 1995). In the Cerrado of Central Brazil and the Caatinga biome of Northeastern Brazil, the species shows abrupt population fluctuations, and changes from extremely abundant to rare between seasons or years (Karimi *et al.*, 1976; Souza & Alho, 1980). However, one population in an Amazonian savanna was apparently more stable over a period of 6 years (Francisco *et al.*, 1995; Magnusson *et al.*, 1995). The effect of rainfall on the density of *N. lasiurus* appears to depend on the ecosystem. In the Caatinga, the highest densities were reported in the rainy season (Karimi *et al.*, 1976; Streilen, 1982a, b), whereas the highest densities were recorded in the dry season in the Cerrado (Dietz, 1983) and an Amazonian savanna (Layme *et al.*, 2004; Ghizoni *et al.*, 2005).

We monitored a *N. lasiurus* population on a savanna site intermittently over 22 years, and recorded regional fire frequency during 8 of the last 9 years. The site did not burn during the latter period, so we are able to evaluate the indirect effect of regional fire intensity without the confounding effects of direct local interactions between the rodent population and burning vegetation.

Methods

The study area is close to Alter do Chão (2°31′S, 55°00′W), a village located about 40 km from Santarém, Pará State. The climate is humid tropical with little monthly variation in temperature (mean = 27.7 °C), but with strong seasonal variation in rainfall. During the dry season (July–November), 1 or 2 months may have <60 mm of rainfall and 75% of precipitation occurs between the months of December and June.

There is a diverse mosaic of vegetation types in the region, including old-growth forest, regrowth forest, savannas and agricultural areas. Much of the forest occurs as islands in a matrix of savanna (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 1–3 year intervals and some savanna areas are used as pasture for cattle.

Information on temporal variation in abundance of *N. lasiurus* on a 4.0 ha savanna plot was obtained from 1985 to 1989, from 1997 to 1998 and 2000–2006, giving data on 14 of the 22 years. Capture, handling and marking procedures followed the recommendations of the American Society of Mammalogists Animal Care and Use Committee (1998). Details of the methods are given in Francisco *et al.* (1995) and Magnusson *et al.* (1995). The number of capture sessions per year varied between periods; until 1989 they were carried out at intervals of 2 months, and thereafter they were carried out twice a year.

In this plot, 100 traps were set at 20 m intervals on a trapping grid that covered the plot. The traps remained open for 2 days, after which they were moved forward 10 m and remained open for another 2 days. A mixture of rolled oats and peanut butter, together with half a Brazil nut (*Bertholletia excelsa*), was used as bait, and the traps were checked twice daily. This saturation trapping detected almost all the *N. lasiurus* known to use the grid on each trapping occasion (Magnusson *et al.*, 1995). Rats were marked individually by clipping one or two toes. Animals marked in one trapping session generally re-entered traps on the same or subsequent days (Francisco *et al.* 1995; Magnusson *et al.*, 1995).

The southern oscillation index (SOI) was obtained from the National Climate Centre (http://www.bom.gov.au/climate/current/soihtm1.shtml). Data on local rainfall was obtained from the Agência Nacional de Águas (ANA) substation 254 000 located 28 km from the study area (2°26′35″S, 54°42′27″), available from the ANA internet site (http://www.hidroweb.ana.gov.br). Climatic variables were the summed monthly values between June and July, and the data for the year before each survey were used in regression analyses.

Fire history was measured in 38 plots between 1998 and 2006. The plots were distributed to sample as uniformly as feasible an area of 20 000 ha around Alter do Chão, including 5000 ha of savannas intermixed with forest fragments (Albernaz *et al.*, 1999). In general, the plots were >800 m apart, except two plots that were separated by 100 m. All were more than 50 m from savanna boundaries. After the burning season (July–December), a measuring tape was extended along four 250 m lines in each plot and the presence or absence of burned vegetation recorded each 2 m along the lines, giving an index of fire extent in each plot each year that varied from 0 to 500. The total extent of burned areas in plots the year before the survey was used as a predictor variable in the model.

Analyses

The number of animals captured in June or July (dry season) each year was used 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. Rodent populations can increase rapidly, and many arid-zone species show vast fluctuations. *Necromys lasiurus* can reproduce at 3–4 months of age, with a litter size of about 5 (Melo & Cavalcante, 1982). We recorded annual exponential rates of increase of up to 1.5 (unpublished data). Therefore, the population 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. We estimated parameters using both the full data set (8 years) and data for which the autocorrelation term could be included (6 years) to evaluate sensitivity to the time span and inclusion of the autocorrelation term.

SOI affects local rainfall, which affects the frequency of fires, and fires potentially affect the number of rodents. The complex interactions among these variables cannot be tested with simple analyses because of the high colinearity. Harris (1975) suggested that it is necessary to have at least 50 degrees of freedom in the residual for multiple regression analyses to be robust in the presence of high colinearity. As we only had 8 years of data in which the extent of fire was measured, we limited the inferential tests to those of the principal variables, SOI and fire. To investigate the magnitude of direct and indirect effects due to local rainfall, we used simple path analyses, but did not include statistical tests of these relationships.

Results

The number of *N. lasiurus* captured fell from 20 in 1985 to two in 2006. The rates of population increase were negative, except for 2000–2001 and 2003–2004. There was no evidence of density dependence because rates of increase were not related to the number of captures in the previous year ($r^2 = 0.20$, $P = 0.20$).

Local rainfall varied considerably throughout the study, with annual totals <1600 mm in 1992–1994 and 1997–1998, and >2800 mm in 1984–1986, 2000–2001 and 2006. Variation in local rainfall (RAIN) was positively associated with the SOI over the whole period (RAIN = 2448 + 3.88SOI, $r^2 = 0.42$, $P = 0.0004$, $N = 25$), and during the years that regional fire extent (FIRE) was measured (RAIN = 2614 + 6.00SOI, $r^2 = 0.79$, $P = 0.003$, $N = 8$). The extent of fires (Fig. 1) was negatively associated with local rainfall (FIRE = 4636-1.00SOI, $r^2 = 0.57$, $P = 0.029$, $N = 8$) and SOI (FIRE = 2002−6.34SOI, $r^2 = 0.50$, $P = 0.05$, $N = 8$).

The number of rodents captured (DENS) was positively associated with the SOI and extent of fires for analyses over the 8 years for which fire data were available (DENS =−4.961 + 0.070SOI + 0.005FIRE, $R^2 = 0.968$ $F = 2,5 = 75.8$, $P < 0.001$, $P_{SOI} < 0.001$, $P_{FIRE} < 0.001$). The partial regressions were positive for

both fire extent (Fig. 2a) and SOI (Fig. 2b). With inclusion of density in the previous year, the SOI ($P = 0.003$) and fire extent ($P = 0.013$) continued to contribute significantly to the model. However, density in the previous year did not ($P = 0.163$). The coefficient of density was negative ($−0.129$), indicating that there is no detectable positive influence of density in the previous year. Multiple regression of rodent density on the SOI, fire extent and local rainfall indicated significant effects of the SOI and fire extent independent of local rainfall (DENS = $−0.622 + 0.077$SOI + 0.005FIRE$−0.001$RAIN, $R^2 = 51.5$, $P = 0.001$, $P_{SOI} = 0.001$, $P_{FIRE} = 0.002$, $P_{RAIN} = 0.361$). The lack of significance of rainfall in this model is probably an artifact of its colinearity with SOI and
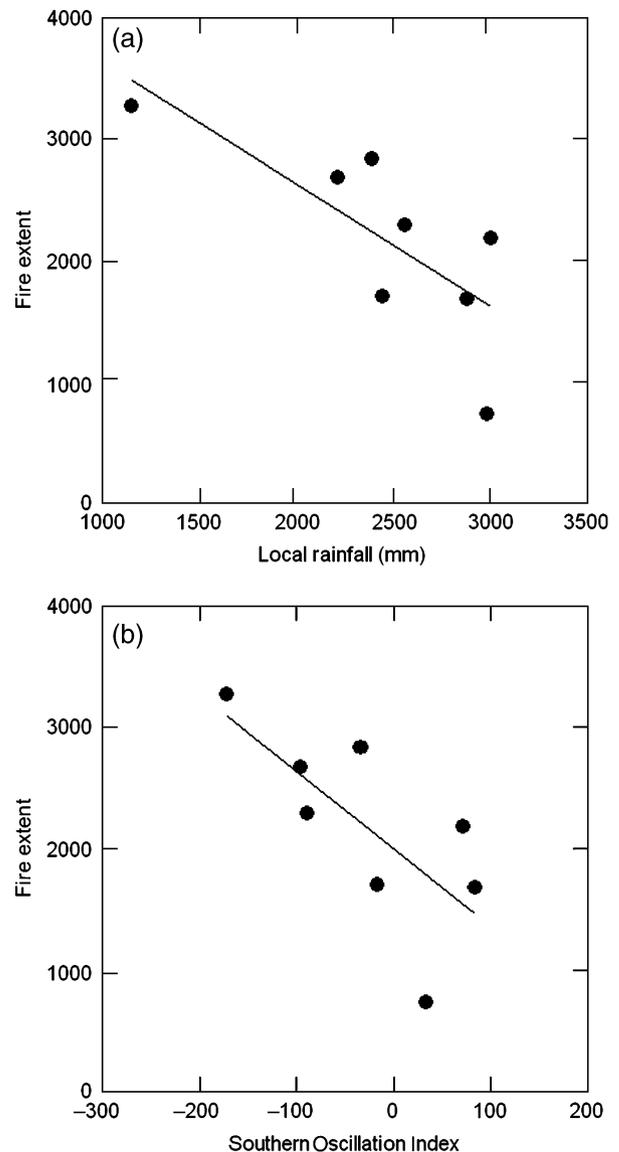
Fig. 1 Relationships between the regional extent of annual fires and (a) local rainfall and (b) southern oscillation index (SOI).
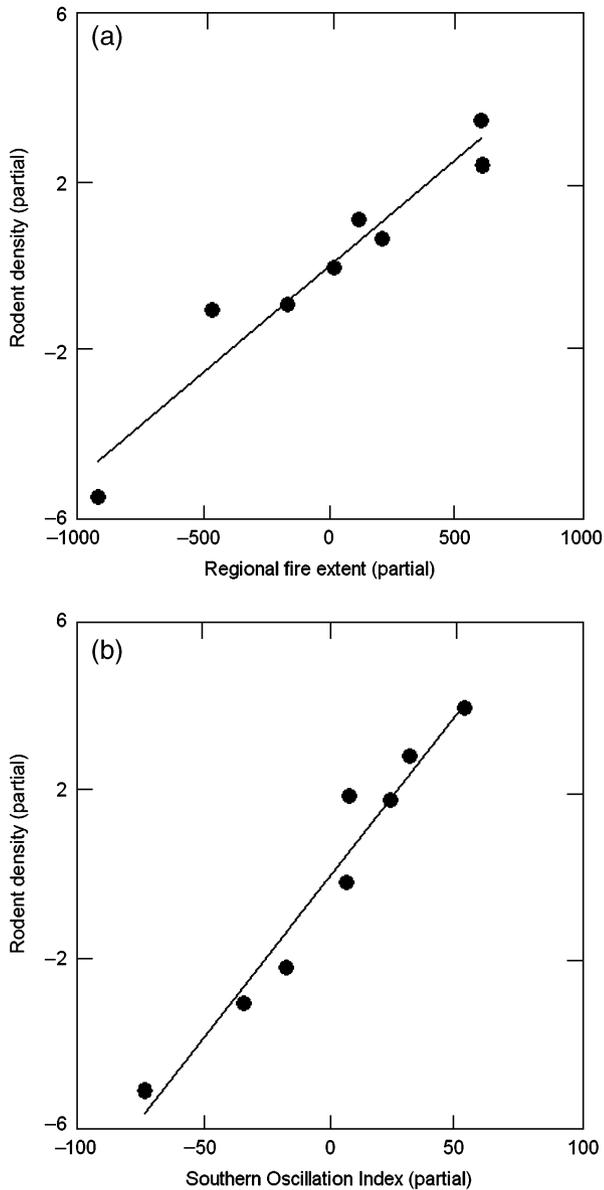
Fig. 2 Relationships between capture rates of *Necromys lasiurus* and (a) the extent of annual fires and (b) southern oscillation index (SOI).

FIRE, and its role in the system has to be evaluated in a path model (Fig. 3).

Path analysis (Fig. 3) indicated that the direct effect of SOI on the density of *N. lasiurus* was positive, and that its indirect effect through its effect on local rainfall was negative, mainly because of its negative effect on the extent of fire. The antagonistic effects of rainfall and fire mean that the overall effect of SOI is relatively small (0.72). This is reflected in the long-term data; the effect of SOI was detectable (DENS = 7.62 + 0.047SOI, $r^2 = 0.32$, $F_{1,12} = 5.54$, $P = 0.037$), but small. Inclusion of data on local rainfall weakened the relationship even
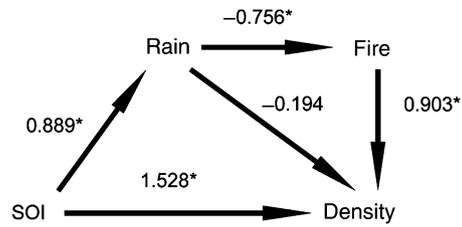
Fig. 3 Path diagram indicating the direct and indirect effects of the Southern Oscillation on the density of *Necromys lasiurus*. The path coefficients are standardized regression coefficients, and the relationships that would be considered statistically significant ($P < 0.004$ in all cases) in simple or multiple regression analyses are indicated by asterisks.

further (DENS = −3.206 + 0.025SOI + 0.004RAIN, $r^2 = 0.$ 0.37, $F_{1,12} = 3.258$, $P = 0.077$), which is predictable given the collinear positive effects of SOI and local rainfall on rodent densities, but their negative effects on the extent of fire.

Discussion

Predictions about the effects of climate change in the Amazon should not be based only on changes in the amount of rainfall, which may not have large effects on some elements of the biota, such as trees, which can use groundwater in times of low rainfall (Nepstad *et al.*, 1994). Extra insolation associated with reduction in cloud cover may be more important for trees than the reduction in rainfall (Saleska *et al.*, 2007). However, changes in the pattern of rainfall and higher mean temperatures may seriously affect fire frequency, especially in forest adjacent to agricultural areas (Cochrane & Barber, 2009).

Previous studies did not indicate any measurable direct effect of local fire on populations of *N. lasiurus* (Ghizoni *et al.*, 2005). Although fires are known to affect some species directly through increased mortality, or through changes in vegetation structure and productivity (Whelan, 1995), and aerosols may affect cloud formation (Martins & Dias, 2009), regional effects of fires on local microclimate had not been contemplated before Emmons' (2009) dewfall hypothesis. Emmons (2009) predicted a negative effect of regional fires, but we recorded a positive effect. There are many potential explanations for this difference. Perhaps, Emmons (2009) is correct that fires affect dewfall and dewfall affects rodents. Alternatively, fires may be beneficial for rodents because they induce seed production in many species of grasses, and some species of dicotyledons, and higher rodent reproduction could lead to higher rates of migration to adjacent areas. At this point, further speculation is not warranted because we lack data to test the hypotheses. However, the evidence for

the existence of a regional fire effect indicates that further long-term studies will be necessary to evaluate climate change models that imply changes in fire frequency or extent.

In arid or seasonally dry climates, the vegetation, especially herbs and shrubs, responds rapidly to changes in intensity and timing of rainfall (Holmgren *et al.*, 2006). Changes in the intensity of the southern oscillation influence population dynamics of several groups of vertebrates indirectly through effects on primary productivity, and consequently availability of resources for consumers (Jaksic, 2001; Holmgren *et al.*, 2006), which suffer from reduced survival or recruitment (Kiesecker *et al.*, 2001; Ogutu & Owen-Smith, 2003; Waite *et al.*, 2007).

The negative effects of El Niño may extend up to 2 years after return to normal conditions (Lima *et al.*, 2002; Letnic & Dickman, 2006; Holmgren *et al.*, 2006). A single drought event may affect primary productivity in savannas for up to 9 years (Haddad *et al.*, 2002). In contrast, periods of high rainfall (La Niña years in Amazonia) generally have a positive effect on the abundance of small mammals, but the population response varies among species (Yarnell *et al.*, 2007). Also, the higher growth rates of vegetation following dry years may be compensated for by an increase in the intensity of savanna fires (Letnic & Dickman, 2006; Holmgren *et al.*, 2006) or numerical responses of predators to higher abundances of small mammals (Turchin, 2003). We were unable to identify a response of *N. lasiurus* to variation in local rainfall, except through the effect of rainfall on the extent of fires. However, this may be due to the high colinearity between rainfall and the SOI.

We recorded effects of the southern oscillation that were not mediated through differences in the amount of annual rainfall. The southern oscillation affects many aspects of the distribution and intensity of rainfall (Marengo, 2004), and these patterns may change under future climates, even if total rainfall does not. Variations in the patterns of rainfall could affect biological populations, as well as the frequency and intensity of fires (Nepstad *et al.*, 1994). The effects of fire on the earth system are complex (Bowman *et al.*, 2009) and it the strong relationships between rainfall patterns and fire frequency make it difficult to separate the effects of rainfall and regional fire extent. It is possible that the effects we attributed to the extent of regional fires were related to some other unmeasured variable. At this stage, research is generating more hypotheses than answers, so studies in a large number of long-term ecological sites will be necessary to develop models of the effects of climate change before they occur.

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