Journal of Mammalogy, 86(4):677–682, 2005

SPATIALLY EXPLICIT POPULATION DYNAMICS IN A DECLINING POPULATION OF THE TROPICAL RODENT, *BOLOMYS LASIURUS*

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We investigated the effects of food availability, fire, and habitat structure on population rates of increase of the rodent *Bolomys lasiurus* in forty 4-ha plots distributed over an area of about 200 km^2 in Amazonian savannas near Alter do Chão, Pará, Brazil. Mean rodent density over the entire study area declined by about one-half during the study period, despite largely independent density fluctuations within plots. Fires had no detectable association with density and population growth rates. Both densities and population growth rates were significantly associated with availability of invertebrate prey and a multivariate index of habitat structure. Invertebrate availability varied temporally within plots, and was not predictable from knowledge of vegetation structure or fire events.

Key words: fire, food availability, habitat structure, habitat suitability, population dynamics rodent

Densities of small mammals vary temporally because of variation in food availability (Johnson and Sherry 2001; Johst et al. 2002; Layme et al. 2004), perturbations such as fire (Vieira 1999), density-dependent processes (Klemola et al. 2002), and potentially many other factors. Densities also vary spatially, and spatial variation in density is used to develop habitat-suitability models based on vegetation structure or other presumed surrogates of habitat quality (Norris 2004). However, if food availability varies spatially independent of changes in habitat structure, habitat suitability models based on vegetation structure will be poor predictors of density.

Behavioral responses of rodents to food availability depend on structural characteristics of the habitat in which the food is found (Yunger et al. 2002). Therefore, species of small mammals whose population dynamics respond to temporal variation in food availability may not be able to respond to spatial variation in food availability. It is difficult to distinguish the effects of structural variation in habitat quality from temporal variation in food availability in most studies of natural populations because spatial and temporal variation in food resources are not studied simultaneously.

Layme et al. (2004) showed that densities of *Bolomys lasiurus*, a small murid rodent, are strongly correlated with invertebrate food availability in the Amazonian savannas near Alter do Chão, Pará, Brazil. Those authors concluded that the effect of food availability was independent of habitat structure or fire in the previous dry season. However, they investigated only a small subset of the potential descriptors of habitat structure, and fire could have a cumulative effect that induces spatial variation in invertebrate abundance largely independent of the presence of fire in the previous dry season.

Studies that relate consumer densities to resource availability have the implicit assumption that changes in the resource are reflected instantaneously in the consumer population. If the rate of increase (or decrease) of the consumer is slower than the rate of increase of the resource, densities of the consumer and resource may show little relationship, even when there is a strong deterministic relationship between resource availability and the rate of increase of the consumer (Caughley 1987). In this study of the same populations studied by Layme et al. (2004), we show that population rates of increase can reveal relationships with factors, such as habitat structure and food availability, that are only weakly or inconsistently associated with density.

Materials and Methods

Study species.—Bolomys lasiurus is a terrestrial rodent common in Cerrado, Caatinga, and Atlantic Forest (Alho 1982; Fonseca et al. 1996).

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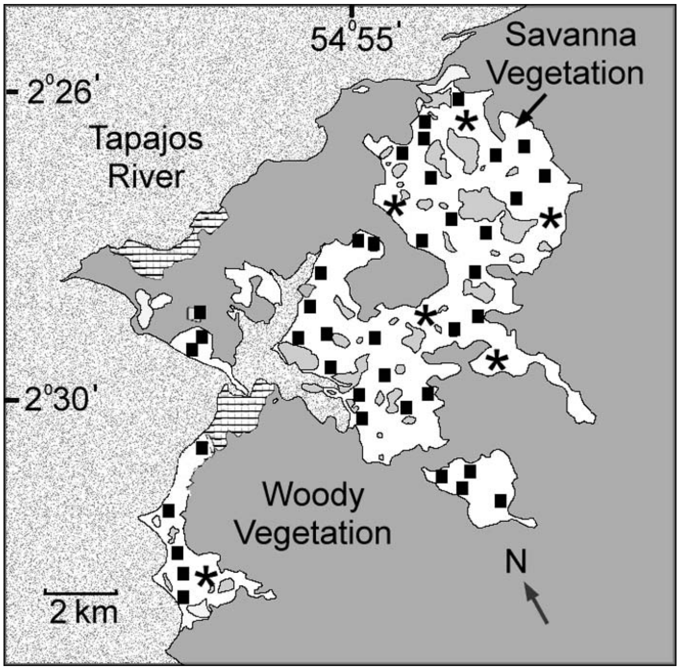

Fig. 1.—Locations of 40 plots used to study the dynamics of populations of *Bolomys lasiurus* over 2 years (black rectangles) and 6 control plots (asterisks) surveyed only at the end of the study, in the Alter do Chão region of Brazil. Savanna areas are white, and forested areas are uniform gray. Two other control plots were in savannas on the left bank of the Tapajós River and are not visible on this map.

Local populations of *B. lasiurus* in the Alter do Chão region of Brazil offer an opportunity to study the causes of fluctuations in density and population dynamics in detail because the species is common, it is easily captured (Francisco et al. 1995; Layme et al. 2004; Magnusson et al. 1995), and it has a short life cycle (Magnusson et al. 1995).

In the Alter do Chão region, *B. lasiurus* is found exclusively in savannas and not in forests (Magnusson et al. 1995). In central Brazil, *B. lasiurus* has been recorded in savannas, grasslands, and forests (Alho 1981; Gettinger and Ernest 1995; Macêdo and Mares 1987; Nitikman and Mares 1987). Adults weigh up to 60 g (Fonseca et al. 1996). The species is omnivorous, feeding largely on arthropods, principally during the dry season (June–September), and also on fruits and seeds (Francisco et al. 1995).

Study area.—The study area was located around the Village of Alter do Chão (2°31′S, 55°00′W), bordering the Tapajós River, near its confluence with the Amazon River, approximately 40 km from the city of Santarém, Pará State, Brazil. We studied 40 plots distributed across an area of approximately 20,000 ha, including 5,000 ha of savannas interspersed with forest fragments. The plots were placed to sample all savanna vegetation in the area (Fig. 1). However, not all plots were surveyed in each year because of unexpected fires and other logistical difficulties. We sampled 31, 36, 40, and 39 plots in capture sessions 1 through 4, respectively.

This region is composed of various types of landscapes, including savannas, flooded forests, gallery forests, lakes, rivers, and river beaches. The savannas are covered principally by 2 species of grass, *Paspalum carinatum* and *Trachypogon plumosus*, with some sparsely distributed trees (Magnusson et al. 1999, 2001). Soils in the plots are sandy (Magnusson et al. 2002).

The region is subject to strong seasonal changes in precipitation. The rainy season occurs between December and May, and the dry season between June and November. The mean total annual precipitation is 1,420 mm, and mean temperature is 27.7°C (Azevedo-Ramos et al. 1999).

Sampling procedures for B. lasiurus.—Data were collected in 4 sampling sessions, 2 in the period September–November in 2000 and 2001, and 2 in the period March–May in 2001 and 2002. In each plot, 50 Sherman traps (10 × 10 × 30 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were spaced 20 m apart. The traps were placed along 4 parallel 250-m lines, with 12 traps along the 1st and 3rd lines (220 m between 1st and last trap on each line), and 13 along the 2nd and 4th lines (240 m between 1st and last trap on each line). The plots were located with a global positioning system, and the distances between the plots were calculated as Euclidean distances between the universal transverse mercator coordinates.

All procedures followed guidelines for the capture, handling, and care of mammals published by the American Society of Mammalogists (Animal Care and Use Committee 1998). Each trap was baited with a mixture of peanut butter and oatmeal, and one-half of a Brazil nut (*Bertholletia excelsa*). Each plot was sampled for 2 consecutive days in each capture session. The traps were checked once daily, between 0600 and 1000 h. This protocol was tested in preliminary studies, with no discernable stress or mortality caused by the trapping. More intensive studies (Francisco et al. 1995; Magnusson et al. 1995) indicated that this trapping interval, with this density of traps, is sufficient to capture most individuals whose home ranges overlap the trapping grid within 2 days.

The overall capture rate declined by $>$50% during the study period. To assess whether this might have been due to our interference during the 2 years, sampling was also conducted at the end of the study in 8 plots that had not been previously studied. Six of these were located 1–4 km from the other plots in the study. The other 2 plots were located in savanna vegetation on the other side of the Rio Tapajós (about 16 km wide at this point).

Each animal captured was sexed, weighed, and marked by toe clipping. The marking codes indicated the plot where the individual was captured and served to demonstrate if individuals moved among plots; animals were not marked individually. All animals were released immediately after marking. Toe clipping was done with sharp, sterilized surgical scissors. The procedure appeared to cause little distress to animals because individuals were frequently recaptured the following day. None showed signs of infection or impaired movement. In previous, more intensive studies (Magnusson et al. 1995), individuals frequently reentered traps on the same day that they were marked. *B. lasiurus* has small delicate ears so we did not use ear tags, and no other long-term marking system was considered appropriate for the species.

The number of individuals captured during each sampling period was used as an index of population density of *B. lasiurus* in each plot. The exponential rates of population growth (r) were estimated as the difference between the natural logarithm of the density index (d_1) in the 1st capture period and the logarithm of the density index (d_2) in the 2nd capture session ($\ln d_1 - \ln d_2$). Rates of increase were estimated for 3 periods that covered seasonal changes (September–October 2000 [dry season] to March–April 2001 [wet season], March–April 2001 [wet season] to September–October 2001 [dry season], and September–October 2001 [dry season] to March–April 2002 [wet season]).

Invertebrate-prey availability.—Availability of invertebrate prey was estimated with pitfall traps. Each trap consisted of a 2-liter plastic bottle cut transversely across the top to make an opening 10 cm in diameter. The trap was buried 15 cm in the ground, so that the top was flush with the soil surface. A total of 24 pitfall traps were installed in each plot, spaced 50 m from each other, in 4 transect lines with

6 pitfall traps per line. The bottom of each trap was covered with 2–3 cm of water mixed with detergent to reduce the surface tension. Pitfall traps were installed for 24 h, after which all captured invertebrates were sorted to order. *B. lasiurus* at Alter do Chão feeds primarily on Coleoptera, Chilopoda, Araneae, Hemiptera, and Isoptera (Francisco et al. 1995). The combined wet mass of invertebrates from these orders captured in the pitfall traps was used as an index of invertebrate food availability in each plot during each capture session. Invertebrates were not sampled during the 1st collection period (dry season of 2000), so data on invertebrate availability were available only for capture sessions 2–4.

Extent of fires.—The extent of fire was estimated by calculating the proportion of burn zones in each plot. To estimate the extent of burns, a measuring tape was placed along the same transects used to place the pitfall traps, and the length of each transect covered by burnt vegetation was measured in each plot. Estimates of extent of fires were conducted from January to May in 1999, 2000, and 2001, after the start of the wet season and the end of the fires in the annual burn cycle in the region.

Vegetation structure.—Vegetation structure was measured in the plots in 1997 (Magnusson et al. 2001). Vegetation cover up to 2 m in height was estimated by using the point-quadrat method (Mantovani and Martins 1990). A measuring tape was laid along each of the four 250-m-long transects. A 2-mm-diameter metal rod was placed perpendicular to the ground every 2 m, to calculate the percentage cover of the structural categories (shrubs, tall-grass species, short-grass species, and open soil) by the point-intercept method. A visual estimate was made of whether there was a tree canopy over the sampling point (Magnusson et al. 2001).

Principal components analysis (PCA) with the correlation matrix was used to summarize the major gradients in vegetation structure among plots. Models of ecosystem function in savannas generally consider dichotomies between grasses and other plant life forms, or between the herb–shrub layer and the tree layer (e.g., Gignoux et al. 1996; Jeltsch et al. 1998). The variables used in the PCA included the proportion of the following categories: open ground, trees, shrubs, tall grasses (*T. plumosus*), and short grasses (mainly *Paspalum* and *Axonopus*). The 2 classes of grasses were analyzed separately because Layme et al. (2004) speculated that the density of *B. lasiurus* might be related to the cover of *T. plumosus*.

Density and population growth rates of B. lasiurus.—Preliminary tests indicated that the dependent variables (index of density and rates of increase) and some independent variables were spatially autocorrelated, which could invalidate the use of conventional statistical tests (Legendre 1993). However, because distance between plots explained $\leq 1.6\%$ of the variance in the dependent variables, and all conventional regression models explained $>13\%$ of the variance in the dependent variables, we did not include distance in the models.

We used multiple regression analyses to investigate the relationships between environmental factors, densities, and rates of population growth (*r*) of *B. lasiurus* between capture sessions (C1, C2, C3, and C4). The growth rates between transitions from dry to rainy seasons (*r*C1/C2 and *r*C3/C4) and from rainy to dry seasons (*r*C2/C3) were related to mean density (Di), rates of change in availability of invertebrate prey (IAi), extent of burn area in the period between the 2 capture events (EQ), and the 1st (PC1) and 2nd (PC2) principal components of the PCA that summarized vegetation structure. Rate of change in invertebrate availability rather than the absolute quantity of invertebrates was used because changes in rodent numbers are likely to reflect changes in resources. Rate of change in invertebrate availability could not be estimated for the period between the 1st and 2nd capture sessions because invertebrate availability was not estimated in the 1st capture session. Invertebrate availability in the 2nd capture period was used for analysis of this period. Although invertebrate availability in the 2nd period is likely to be positively related to the rate of change in invertebrate availability, this gives a much weaker test (higher probability of type II error) than the analyses of other periods.

Predictor variables are not perfectly orthogonal in regression analyses, and the proportion of the variance associated with each predictor depends on the order the variables are entered into the analysis (Manly 1997). The RT program (Manly 1997) was used to estimate the proportion of variance associated with predictor variables for different orders of entry in the analysis. Coefficients of determination are given as r^2 for simple regressions, and R^2 for multiple regressions.

Because we were interested in the consistency of associations with predictor variables, we ran separate regression analyses for each capture session and period over which population growth rates were measured. However, these represent independent tests of the same hypothesis. Therefore, we used Fisher's log-probability test (Winer 1971:49) to calculate the overall probabilities for the effects of the independent variables on density (All C) and rate of increase (All *r*).

RESULTS

The first 2 axes of the PCA of the vegetation structure explained 84% of the variation of the original data, with 57% and 27% of the variation on the 1st and 2nd axes, respectively. Tree, shrub, and small grass cover had high (>0.82) factor loadings on the 1st axis (PC1). Open ground had high (>0.70) loadings on both axes, and tall grass had a high loading on axis 2 (PC2). Therefore, PC1 represented principally cover of vegetation except tall grasses, and PC2 represented principally cover of tall grasses.

Invertebrate biomass (g/plot) was not significantly associated with vegetation structure (PC1 and PC2) and extent of fire in the previous season during any of the 3 capture sessions (multiple regression: $n = 39$, $R^2 = 0.07$, $d.f. = 3, 35$, $P = 0.50$; $n = 39$, $R^2 = 0.10$, $d.f. = 3, 35$, $P = 0.29$; $n = 36$, $R^2 = 0.02$, $d.f. = 3, 32$, $P = 0.90$). Also, invertebrate availability in 1 capture session was a poor predictor of invertebrate availability in other sessions ($r \leq 0.14$, $P \geq 0.42$ in all cases). The mean biomass of invertebrates (0.23 g) in the rainy season of 2002 (C4) was approximately one-half the mean value (0.50 g) of the rainy season of 2001 (C2).

The extent of fire varied among plots and between years. In 1999, fires passed through 49% of plots, and burned 85% (*SD* = 25%) of the area of affected plots (43% of total area). In 2000, fires passed through 78% of plots, and burned 71% (*SD* = 31%) of the area of affected plots (55% of total area). In 2001, fires passed through 82% of plots, and burned 89% (*SD* = 22%) of the area of affected plots (73% of total area). About one-fourth of the variance in extent of fire in plots was attributable to vegetation structure (PC1 and PC2) in 1999 (multiple regression: $n = 39$, $R^2 = 0.26$, $d.f. = 2, 36$, $P = 0.005$) and 2001 ($n = 39$, $R^2 = 0.28$, $d.f. = 2, 36$, $P = 0.003$), but extent of fire had little relationship to vegetation structure in 2000 ($n = 39$, $R^2 = 0.03$, $d.f. = 2, 36$, $P = 0.57$).

Densities of B. lasiurus.—The mean density of *B. lasiurus* for practically all plots was nearly halved from 2000 to 2002, with most of the decline occurring between 2000 and 2001

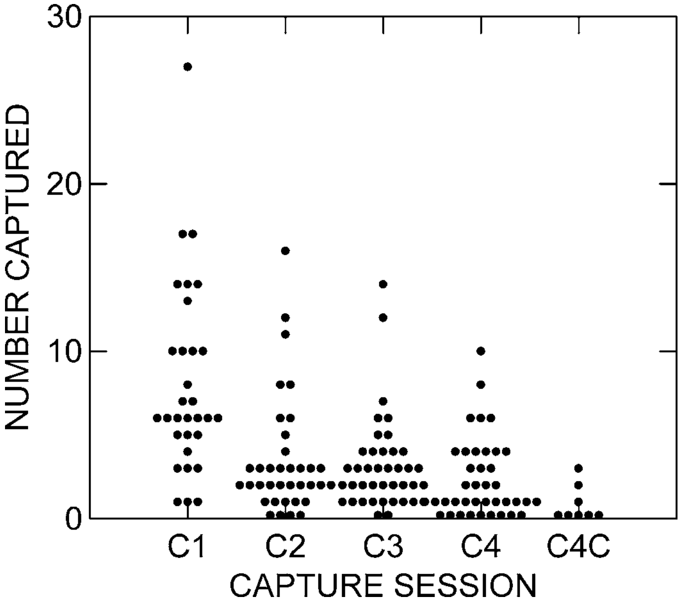

Fig. 2.—Capture rates (number of *Bolomys lasiurus* captured in 50 traps over 2 days) in each plot (50 traps/plot) in the dry season of 2000 (C1), wet season of 2001 (C2), dry season of 2001 (C3), wet season of 2002 (C4), and in control plots surveyed only in the last period (C4C).

(Fig. 2). Although the density of *B. lasiurus* increased in a few plots, density decreased in most. All recaptures of *B. lasiurus* occurred on the same plot where the animals had been originally marked. The 8 control plots that were sampled only during the final period (C4) had mean captures lower than 1 animal per plot (mean = 0.8, median = 0). These capture rates were less than those of other plots (mean = 2.3, median = 1) during the last sampling period (Fig. 2).

The log-probability test indicated low overall probabilities associated with null hypotheses for an association between the index of population density and PC1 (vegetation structure; *d.f.* = 8, $P = 0.055$), and invertebrate availability (*d.f.* = 6, $P = 0.003$). However, when using conventional levels of significance ($\alpha = 0.05$), indices of density of *B. lasiurus* were significantly related to PC1 (vegetation structure) only in capture session 4, and to invertebrate availability only in capture session 2 (Table 1). Little evidence was found for an association with PC2 (*d.f.* = 8, $P = 0.746$) or fire in the previous season (*d.f.* = 8, $P = 0.194$). Invertebrate availability alone explained about 45% ($r^2 = 0.454$) of the variance in density in capture session 2, and habitat structure alone explained about 18% ($r^2 = 0\ .178$) of the variance in density in capture session 4 ($r^2 = 0.67$ including the outlier). Therefore, although statistically significant, the relationships between density and the predictor variables were generally inconsistent.

Table 1.—Results of multiple regression testing of the relationship between rodent densities (Ci) and rates of increase of rodents (*r*Ci/Cj), and the 1st (Veg1) and 2nd (Veg2) axes of a principal components analysis summarizing vegetation structure, the extent of burning of plots (Fire), invertebrate availability (Inv.) for analyses with Ci as the dependent variable, rate of change in invertebrate availability (also Inv.) for analyses with *r*Ci/Cj as the dependent variable, and the mean of the index of rodent density in the period (Den.). The overall probabilities for the effects of the independent variables on density (All C) and rate of increase (All *r*) are based on Fisher's log-probability test (Winer 1971:49).

Variable	*P* Veg1	*P* Veg2	*P* Fire	*P* Inv.	*P* Den.	R^2	*n*
C1	0.089	0.725	0.062			0.15	31
C2	0.970	0.222	0.618	0.00002		0.49	36
C3	0.359	0.651	0.815	0.545		0.05	39
C4	0.002	0.394	0.087	0.902[a]		0.26	38
All C	0.055	0.746	0.194	0.003			
*r*C1/C2	0.031	0.722	0.162	0.012	0.194	0.37	31
*r*C2/C3	0.373	0.889	0.578	0.019	0.450	0.20	36
*r*C3/C4	0.034	0.980	0.361	0.619	0.999	0.14	39
All *r*	0.016	0.988	0.342	0.007	0.559		

[a] *P* was calculated after excluding a single outlier with high leverage in the analysis; with inclusion of this plot, $P = 0.026$.

Population growth rates.—The log-probability test indicated low overall probabilities associated with null hypotheses for associations between rates of increase and PC1 (vegetation structure; *d.f.* = 6, $P = 0.016$), and invertebrate availability (*d.f.* = 6, $P = 0.007$). When using conventional levels of significance ($\alpha = 0.05$), rates of increase of *B. lasiurus* were significantly related to PC1 (vegetation structure) in periods between capture sessions 1 and 2, and 3 and 4, and to invertebrate availability in periods between capture sessions 1 and 2, and 2 and 3 (Table 1). Little evidence was found for an association with PC2 (*d.f.* = 6, $P = 0.988$) or fire in the previous season (*d.f.* = 6, $P = 0.342$).

Rate of change in invertebrate availability alone was associated with about 16% ($r^2 = 0.158$) of the variance in rate of change in density index between capture sessions 2 and 3. Habitat structure (PC1) alone was associated with about 11% ($r^2 = 0\ .113$) of the variance in rate of change in density index between capture sessions 3 and 4. Invertebrate availability and habitat structure (PC1) together were associated with about 21% ($R^2 = 0.206$) of the variance in rate of change in the density index between capture sessions 1 and 2. When entered into the regression model after PC1, invertebrate availability was associated with about 14% of the variance in rate of increase, and when entered into the regression model after invertebrate availability, PC1 was associated with about 9% of the variance in rate of increase. Therefore, although generally associated with less than 20% of the variance, associations between rates of change in the density index and the predictor variables PC1 and invertebrate abundance were statistically significant.

DISCUSSION

Densities and rates of population increase of *B. lasiurus* in this study were most strongly related to availability of invertebrate prey. In general, availability of invertebrates is important for omnivorous rodents (Crespin et al. 2002; Lima et al. 2001; Meserve et al. 2001). However, invertebrate availability in a given capture session was not related to vegetation characteristics, fire in the previous dry season, or to invertebrate availability in other capture sessions. Therefore, density could be a misleading indicator of structural habitat quality in this species. Density is a poor indicator of habitat in many wildlife species (Van Horne 1983).

There was a general decline in the population of *B. lasiurus* over the whole area during the study period. The mean population density of *B. lasiurus* for all plots dropped by more than one-half between 2000 and 2002. Layme et al. (2004) considered that the decline between the dry season of 2000 and the rainy season of 2001 could have been due to seasonality, but the decline continued during subsequent surveys, indicating that the agent causing the decline had a long-term effect. The decline in density of *B. lasiurus* did not appear to be an artifact of the monitoring itself. Plots sampled for the 1st time during the last sampling period, near the general area of study, and plots separated from other plots by the Tapajós River, exhibited densities similar to the plots sampled over 2 years.

A reduction in invertebrate biomass to approximately one-half the initial value between the rainy seasons of 2001 and 2002 occurred over the entire study area, and coincided with a decrease in the mean density of *B. lasiurus* over the entire study area to about 30% of initial values. This indicates that invertebrate prey availability, possibly related to climate fluctuations (Jaksic 2001; Murúa et al. 2003), could have caused the overall decline. However, short-term fluctuations in rodent density and invertebrate availability were not synchronized among subpopulations.

Neither density nor population growth rate were related to vegetation structure, as represented by the 2nd axis of the PCA, in any period. This component was principally associated with tall grasses, so the hypothesis of Layme et al. (2004) that densities of *B. lasiurus* are associated with tall grasses was not supported. Evidence was found for an effect of vegetation structure (PC1) on density and population growth rates. Longer-term studies are needed to determine whether differences in rates of change are because of lower rates of decline in some vegetation associations, or because some vegetation associations are more attractive to dispersing individuals.

Vieira (1999) noted a decline in a population of *B. lasiurus* after fire in the Cerrado of central Brazil. In contrast, Alho (1981), Gettinger and Ernest (1995), and Magnusson et al. (1995) did not record effects of fire on populations of *B. lasiurus*. The present study did not detect any effect of fire on density of *B. lasiurus*. Either fire generally has little effect, or short-term dispersal between burned and unburned areas masks effects on density. The areas burned were much greater than the normal home ranges of *B. lasiurus*, and females are territorial (Magnusson et al. 1995), so options for movement are probably limited. However, intensive monitoring of marked individuals would be necessary to explain why burned and unburned areas have similar densities of individuals 6 months after the burning season.

The effect of fire also may depend on its frequency. Long periods without fire may result in the accumulation of combustible material, and hence more intense fires (Whelan 1995). Fires are frequent in the savannas of Alter do Chão, and all of our plots burned at least once during the study period.

Numbers of individuals recorded for individual plots were very low in capture periods 2, 3, and 4. This means that random factors could easily mask associations with predictor variables, and associations with food availability and vegetation structure were only detectable because sampling was undertaken in a large number of sites (>30), which covered a wide range of the habitat used by the species in the region.

When factors that affect population dynamics are not spatially consistent, the number of individuals that accumulates in a given site (density) may be a poor indicator of the present suitability of that site (Caughley 1987). By using rates of change in density, rather than density, it is possible to detect deterioration in resource levels associated with a drop in population density, even if the final density is still above that of other sites. We believe that this is why change in food availability was more strongly associated with population growth rates than final density was associated with mean food availability in this study. Also, although we detected no density-dependence, growth rates may be inhibited by high densities (Klemola et al. 2002). Therefore, we recommend the use of a large number of sites and rates of change in density to detect effects of factors, such as food availability, that may change much more quickly than gross habitat structure.

RESUMO

Nós investigamos os efeitos da disponibilidade de alimento, queimadas, e estrutura do habitat sobre a taxa de aumento de uma população do roedor *Bolomys lasiurus* em 40 grades de 4 ha distribuídas em uma área de cerca de 200 km^2 em savanas amazônicas perto de Alter do Chão, Pará, Brasil. A densidade média de roedores em toda a área de estudo declinou para cerca de metade do valor original durante o período de estudo, apesar das flutuações na densidade entre grades serem independentes. Não foi detectável associação das queimadas com densidade ou taxa de aumento populacional. A densidade e a taxa de aumento populacional foram significativamente associadas com a disponibilidade de invertebrados e um índice multivariado da estrutura do habitat. A disponibilidade de invertebrados variou temporalmente entre grades, e não foi previsível através do conhecimento da estrutura da vegetação ou ocorrência de queimadas.

ACKNOWLEDGMENTS

We thank A. Albernaz and the residents of Alter do Chão who made the logistics of the study feasible. For help in the field, we are grateful to W. S. da Costa, W. S. da Costa, M. Castelo, and L. S. de Vasconcelos. M. H. Godfrey carried out the original translation. Financial support was provided by the Programa Piloto para a Proteção das Florestas Tropicais do Brasil—PPG-7—Subprograma de Ciências e Tecnologia—CCE/FINEP/INPA (64.00.0021.00), CNPq postgraduate scholarships to V. Layme and I. Ghizoni, CNPq Produtividade em Pesquisa grants to A. Lima and W. Magnusson, and a CNPq-AI grant to W. Magnusson.

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Submitted 7 October 2004. Accepted 11 January 2005.

Associate Editor was Nancy G. Solomon.