Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian savanna

Viviane Maria Guedes Layme, Albertina Pimentel Lima[1] and William Ernest Magnusson

Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia, CP 478, 69011-970 Manaus-AM, Brazil
(*Accepted 12 April 2002*)

Abstract: We investigated the relative influences of vegetation cover, invertebrate biomass as an index of food availability and the short-term effects of fires on the spatial variation in densities of the rodent *Bolomys lasiurus* in an Amazonian savanna. Densities were evaluated in 31 plots of 4 ha distributed over an area of approximately 10×10 km. The cover of the tall grass (*Trachypogon plumosus*), short grass (*Paspalum carinatum*), shrubs and the extent of fire did not explain the variance in densities of *Bolomys lasiurus*. Food availability alone explained about 53% of the variance in *B. lasiurus* densities, and there was no significant relationship between insect abundance and vegetation structure. Fires had little short-term impact on the density of *Bolomys lasiurus* in the area we studied. As the species appears to respond principally to food availability, habitat suitability models based on easily recorded vegetation-structure variables, or the frequency of disturbance by fire, may not be effective in predicting the distribution of the species within savannas.

Key Words: Amazon, grassland, habitat, population, rat

INTRODUCTION

The structure of vegetation is an important component in models of habitat selection by vertebrates (Apollonio *et al.* 1998, Catling & Coops 1999, Jung *et al.* 1999, Roseberry & Sudkamp 1998). At large scales, most vertebrates are restricted to, or more common in, a limited range of habitats (Bos *et al.* 2002, Fitzgibbon 1997). However, at smaller scales, within gross habitat categories, more complex models are needed to distinguish the effects of habitat structure from factors that are more difficult to measure, such as food availability (Beutel *et al.* 1999, Pausas *et al.* 1997).

Burning can affect the short-term population dynamics of vertebrates directly through mortality due to the fire (Cook 1959, Dieni & Anderson 1999, Southgate & Masters 1996, Sutherland & Dickman 1999, Whelan 1995). Or indirectly, due to changes in the structure of the vegetation initiated by the fire (Newsome *et al.* 1975, Zedler *et al.* 1983). Burning can also improve the habitat for some species through effects on the vegetation, resulting in a post-fire succession (Pianka 1996).

In this study, we investigated the effects of the structure of the vegetation, and burning on populations of the rodent *Bolomys lasiurus* Lund 1959 in an area of Amazonian savanna. *Bolomys lasiurus* is the only rodent species captured frequently in the savannas of the area and its biology is relatively well known (Francisco *et al.* 1995, Henriques & Alho 1991, Magnusson *et al.* 1995). The diet of *B. lasiurus* includes fruits and invertebrates (Francisco *et al.* 1995, Magnusson & Sanaiotti 1987). The highest rates of growth and reproduction coincide with the periods of higher invertebrate availability (Francisco *et al.* 1995, Magnusson *et al.* 1995).

Previous studies of *B. lasiurus* in the region investigated habitat selection on a small scale (approximately 0.1 km²; Francisco *et al.* 1995, Magnusson *et al.* 1995). The aim of this study was to determine the relative importance of vegetation cover and food availability on the spatial distribution of *B. lasiurus* on a landscape scale ($\sim 10 \times 10$ km), and to assess the short-term effects of fire on the population density of *B. lasiurus*.

METHODS

Study area

The study was carried out from September 2000 to April 2001 in a region of Amazonian savanna near Alter do
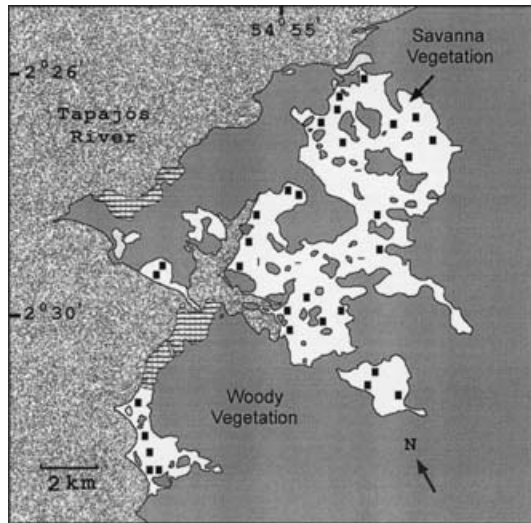
Figure 1. Map of the study area showing sampling plots (black squares), areas with woody vegetation (dark grey), savannas (white), water bodies (stippling) and heavily disturbed areas such as pasture and urban areas (horizontal lines).

Chão, Santarém, Pará State, Brazil (2°31′S, 55°00′W). The mean temperature in the area is 27.7 °C and varies little throughout the year. The mean annual rainfall of 1420 mm is concentrated in the wet season, which usually occurs from December to May (Azevedo-Ramos *et al.* 1999). The savannas have a high cover of shrubs, such as *Eugenia* cf. *biflora* (L.) DC., *Galactia jussiaena* Kunth, and grasses, such as *Trachypogon plumosus* Flugge and *Paspalum carinatum* Humb. & Bonpl. ex. Flugge (Magnusson e*t al.* 2001).

Data collection

Data were collected in 31 plots of 3.75 ha, distributed as uniformly as possible throughout the 10×10 km of savannas in the area (Figure 1). In each plot, data were collected along four parallel 250-m-long transects spaced 50 m apart.

The relative density of *B. lasiurus* was recorded once per plot (n = 31) during the dry season (September to November), before the fires of 2000, and once in the wet season (March to May 2001), after the fires of 2000. In each capture session, 50 Sherman ($23 \times 8.0 \times 9.0$ cm) live traps spaced 20 m from each other were placed along the transects in each plot. Traps were baited with brazil nuts and a mixture of oatmeal and peanut butter. Traps were opened for 2 consecutive days in each plot, and were checked each day between 07h00 and 10h00. Previous studies have shown that this trapping period was sufficient to capture most of the animals before they became 'trap happy' (Francisco *et al.* 1995, Magnusson *et al.* 1995). The rats were marked by toe clipping with scissors. The method has little effect on other

rodent species (Korn 1987, Wood & Slade 1990) and *Bolomys lasiurus* did not appear unduly stressed by this procedure as many individuals marked were recaptured the following day and none showed signs of infection (Francisco *et al.* 1995, Layme 2002, Magnusson *et al.* 1995). Since the sampled area and capture protocol were the same in all plots, we used the number of individuals captured as an index of relative abundance (Slade & Blair 2000). Records of recaptures within each capture period were not used in abundance estimates.

To compare *B. lasiurus* density with food availability, we measured the abundance of invertebrates in the plots. Invertebrates were captured with 35-cm diameter, 18-cm deep, pitfall traps containing about 150 ml of water mixed with detergent (5%) to break surface tension. Pitfalls were placed at 50-m intervals, giving 24 traps per plot. Traps were left in place for 24 h during the wet-season capture session. Invertebrates captured were separated by order and weighed to 0.0001 g. Food availability for rats was assessed by measuring the biomass (wet weight) of the main orders consumed by *B. lasiurus* (Coleoptera, Hemiptera, Aranae; Francisco *et al.* 1995). Although termites are frequently eaten by *B. lasiurus* (Francisco *et al.* 1995), they were not included in the index of food availability because they rarely fell into pitfall traps.

We measured vegetation cover for several strata that may have provided protection against predators for *B. lasiurus*. We estimated the per cent cover for plant life forms (trees, shrubs and grasses) using the point quadrat method (Bullock 1996). Points were spaced at 2-m intervals along the transect, giving 500 points per plot. At each point we recorded cover by noting the first type of plant in contact with a 2-mm diameter rod held vertically. Plant life forms > 2 m in height were considered part of the tree layer, while plants < 2 m height were classified as shrubs or grasses. We subdivided the grass layer into short grass and tall grass based on dominance of *Trachypogon plumosus* (tall grass) or *Paspalum carinatum* (short grass). More details on vegetation measurement are given in Magnusson *et al.* (1999). Vegetation variables were measured in the wet season of 1998, 3 y before the commencement of the study. Although fire may cause seasonal changes in vegetation structure, vegetative cover in neotropical savannas measured during the wet season is relatively stable and related to soil characteristics (Goodland & Pollard 1973), unless the area is protected from fire and the historical fire regime changed (Coutinho 1990, Miranda *et al.* 2002). Data are not available for other strata, but even 5 y after the initial measurement there was still a correlation of 0.86 between the cover of short grass measured in 1998 and 2002 (P. Pedrosa, pers. comm.).

We used the extent of burns as measures of the fire intensity in each plot. To determine the extent of burns that had occurred in the dry season of the previous year

(2000), we noted the presence or absence of burned vegetation at 2-m intervals along survey lines in each plot between March and May 2001.

We used Systat 8.0 for all statistical analyses (SPSS Inc.). The relative influence of the environmental factors on *B. lasiurus* distributions were tested with multiple regression models. Variables were tested for multicolinearity before inclusion in models. The proportion of ground without cover was not included in analyses because that variable was strongly correlated with the proportion of area covered by shrubs and short grass (*Paspalum*).

RESULTS

There was a significant reduction in the number of *Bolomys lasiurus* (paired t-test: $t_{30} = 4.2$, $P < 0.001$) captured between the dry (before fire; N = 251, SE = 1.0) and wet (after fire N = 125, SE = 0.6) seasons. However, fires which affected 75% of the plots in 2000 were probably not responsible for this change in abundance, because there was little relationship between extent of burn and reduction in population density between the two sampling periods ($r^2 = 0.13$, $F_{2,28} = 2.1$, $P = 0.15$).

Multiple regression was used to relate the cover of tall grass *Trachypogon plumosus* (TG), short grass *Paspalum carinatum* (SG), shrubs (SH), the extent of burn in 2000 (B2000), and invertebrate biomass (IB) to the number of *Bolomys lasiurus* captured in the wet season (BL). These variables explained about 61% of spatial variation in density of *B. lasiurus* during the wet season (BL = $-5.4 + 0.02$TG $+ 0.02$SG $+ 0.03$SH $- 0.0001$B2000 $+ 8.2$IB, $r^2 = 0.63$, $F_{5,25} = 8.3$, $P < 0.001$). Only invertebrate biomass contributed significantly to the model ($P < 0.001$). The covers of short grass ($P = 0.13$) and shrubs ($P = 0.31$), and the areas burned in 2000 ($P = 0.99$) showed no tendency to vary with *B. lasiurus* density. There was a tendency for tall-grass cover to covary with *B. lasiurus* density ($P = 0.06$). However, a model using only tall-grass cover explained only about 8% of *B. lasiurus* density in the wet season ($r^2 = 0.08$, $F_{1,29} = 2.48$, $P = 0.13$). There was no relationship between vegetation cover (tall grass, short grass and shrubs) and invertebrate biomass (IB = $0.42 + 0.001$TG $- 0.0004$SG $- 0.0005$SH, $r^2 = 0.05$, $F_{3,27} = 0.5$, $P = 0.71$). A model using only invertebrate biomass explained about 53% of spatial variation in *B. lasiurus* density ($r^2 = 0.53$, $F_{1,29} = 32.4$, $P < 0.001$). More *B. lasiurus* were captured in areas with high invertebrate biomass (Figure 2).

DISCUSSION

Fires may have direct short-term effects on densities of animals and/or long-term indirect effects through
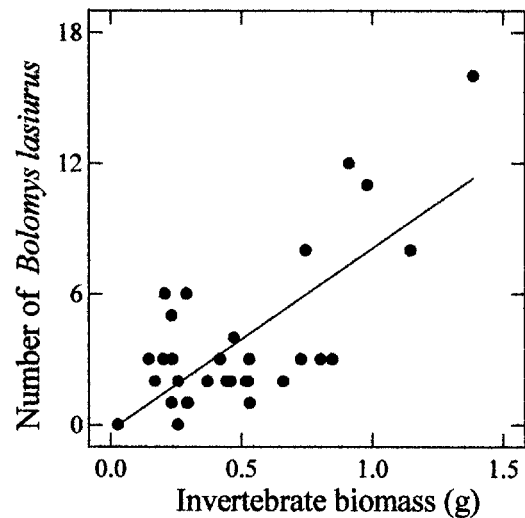

Figure 2. Relationship between number of *Bolomys lasiurus* captured in the wet season and wet weight of invertebrate orders eaten by *Bolomys lasiurus* that were captured in pit-fall traps in 4-ha plots.

habitat modification (Whelan 1995). However, the extent of fire in 2000 did not affect the rate of change in density or spatial variation in density of *Bolomys lasiurus*. This suggests that fire has little direct effect on densities of this species. In addition, we found no dead animals immediately after burns, and several recaptures occurred in the next sampling season providing further evidence for minimal fire impact on *B. lasiurus*. A negligible short-term effect of fire on *B. lasiurus* populations has also been observed in areas of cerrado in Central Brazil (Vieira & Marinho-Filho 1998). Due to the high frequency of fire in the area it is possible that this species uses behavioural mechanisms to survive fires, such as use of underground shelters. Fire, at a local scale, did not influence reproduction or growth of *B. lasiurus* in another study in our area (Francisco *et al.* 1995). The density of *B. lasiurus* declined significantly between the late dry season of 2000 and the wet season of 2001. Either seasonal effects or a long-term population decline could result in this reduction, but only a longer study could distinguish between these hypotheses.

On a large scale, *B. lasiurus* densities are not associated with short-grass *Paspalum carinatum* or shrubs (this study), although there was a slight tendency to capture more individuals in areas with higher cover of tall-grass *Trachypogon plumosus*. However, at scales of tens of metres, in an area with little tall grass, *B. lasiurus* was associated with areas that had a combination of short-grass *Paspalum carinatum* and shrubs (Magnusson *et al.* 1995). Scale dependence in apparent habitat selection has also been reported for the small marsupial *Ningaui yvonneae* (Bos *et al.* 2002).

There was a strong effect of food availability on *B. lasiurus* abundance, despite the fact that we only

evaluated availability of invertebrates for this omnivorous rodent. Many species of rodent have higher densities in sites with more food (Bergallo & Magnusson 1999, Fitzgibbon 1997) and a correlation between the magnitude of population growth and production of seeds has been shown for *Mus musculus* (Choquenot & Ruscoe 2000). Experimental manipulations of food availability often increase rodent densities (Desy & Batzli 1989, Taitt & Krebs 1983, Yunger 2002).

Invertebrate biomass alone explained 53% of the variation in the density of *B. lasiurus* between plots, indicating that food availability is a more important determinant of density for this species than gross habitat structure. This is important for conservation planning, because structural measures are often used as surrogate variables in habitat suitability indices (Beutel *et al.* 1999, Block *et al.* 1994, Roseberry & Sudkamp 1998). This may be a reasonable approach for evaluating suitability of areas with gross structural differences. For example, *B. lasiurus* is not known to maintain viable populations within forests. However, variations in density of this species within savannas were poorly predicted solely by structural characteristics. There was little relationship between vegetation cover (tall grass, short grass and shrubs) and food availability. It appears that direct measures of food resources, a measure of habitat quality (Beutel *et al.* 1999), are necessary to understand the distribution of this omnivorous rodent and that structural habitat variables are poor surrogates.

ACKNOWLEDGEMENTS

LITERATURE CITED

APOLLONIO, M., FOCARDI, S., TOSO, S. & NACCI, L. 1998. Habitat selection and group formation pattern of fallow deer *Dama dama* in a submediterranean environment. *Ecography* 21:225–234.

AZEVEDO-RAMOS, C., MAGNUSSON, W. E. & BAYLISS, P. 1999. Predation as key factor structuring tadpole assemblages in a savanna area in Central Amazonia. *Copeia* 1999:22–33.

BERGALLO, H. G. & MAGNUSSON, W. E. 1999. Effects of climate and food availability on four rodent species in Southeastern Brazil. *Journal of Mammalogy* 80:472–486.

BEUTEL, T. S., BEETON, J. S. & BAXTER, G. S. 1999. Building better wildlife-habitat models. *Ecography* 22:219–223.

BLOCK, W. M., MORRISON, M. L., VERNER, J. & MANLEY, P. N. 1994. Assessing wildlife-habitat-relationships models: a case study with California oak woodlands. *Wildlife Society Bulletin* 22:549–561.

BOS, D. G., CARTHEW, S. M. & LORIMER, M. F. 2002. Habitat selection by the small dasyurid *Ningaui yvonneae* (Marsupialia: Dasyuridae) in South Australia. *Austral Ecology* 27:103–109.

BULLOCK, J. 1996. Plants. Pp. 111–138 in Sutherland, W. J. (ed.). *Ecological census techniques*. Cambridge University Press, Cambridge.

CATLING, P. C. & COOPS, N. C. 1999. Prediction of the distribution and abundance of small mammals in the eucalypt forests of south-eastern Australia from airborne videography. *Wildlife Research* 26:641–650.

CHOQUENOT, D. & RUSCOE, W. A. 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology* 69:1058–1070.

COOK, S. F. 1959. The effects of fire on a population of small rodents. *Ecology* 40:102–108.

COUTINHO, L. M. 1990. Fire in the ecology of the Brazilian Cerrado. Pp. 82–105 in Goldammer, J. G. (ed.). *Fire in the tropical biota: ecosystem processes and global challenges*. Springer Verlag, Berlin.

DESY, E. A. & BATZLI, G. O. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* 70:411–421.

DIENI, J. S. & ANDERSON, S. H. 1999. Effects of recent burning on breeding bird community structure in aspen forests. *Journal of Field Ornithology* 70:491–503.

FITZGIBBON, C. D. 1997. Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology* 34:530–539.

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

GOODLAND, R. & POLLARD, R. 1973. The Brasilian Cerrado: a fertility gradient. *Journal of Ecology* 6:219–224.

HENRIQUES, R. P. B. & ALHO, C. J. R. 1991. Microhabitat selection by 2 rodent species in the Cerrado of Central Brazil. *Mammalia* 55:49–56.

JUNG, T. S., THOMPSON, I. D., TITMAN, R. D. & APPLEJOHN, A. P. 1999. Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* 63:1306–1319.

KORN, H. 1987. Effects of live-trapping and toe-clipping on body weight of European and African rodent species. *Oecologia* 71:597–600.

LAYME, V. M. G. 2002. *Influência dos Fatores Ambientais e Antrópicos sobre a Densidade de Bolomys lasiurus (Rodentia: Muridae) em Manchas de Savana de Alter do Chão*. Ms. Thesis, INPA/UFAM, Manaus. 50 pp.

MAGNUSSON, W. E. & SANAIOTTI, T. M. 1987. Dispersal of *Miconia* seeds by the rat *Bolomys lasiurus*. *Journal of Tropical Ecology* 3:277–278.

MAGNUSSON, W. E., ARAÚJO, M. C., CINTRA, R., LIMA, A. P., MARTINELLI, L. A., SANAIOTTI, T. M., VASCONCELOS, H. L.

& VICTORIA, R. L. 1999. Contributions of C$_3$ and C$_4$ plants to higher trophic levels in an Amazonian savanna. *Oecologia* 119:91–96.

MAGNUSSON, W. E., FRANCISCO, A. L. & SANAIOTTI, T. M. 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., LIMA, A. P., FARIA, A. S., VICTORIA, R. L. & MARTINELLI, L. A. 2001. Size and carbon acquisition in lizards from Amazonian savanna: evidence from isotope analysis. *Ecology* 82:1772–1780.

MIRANDA, H. S., BUSTAMANTE, M. M. C. & MIRANDA, A. C. 2002. The fire factor. Pp. 51–68 in Oliveira, P. S. & Marquis, R. J. (eds). *The cerrados of Brazil*. Columbia University Press, New York.

NEWSOME, A. E., MCILROY, J. & CATLING, P. 1975. The effects of an extensive wildfire on populations of twenty ground vertebrates in south-east Australia. *Proceedings of the Ecological Society of Australia* 9:107–123.

PAUSAS, J. G., AUSTIN, M. P. & NOBLE, I. R. 1997. A forest simulation model for predicting eucalypt dynamics and habitat quality for arboreal marsupials. *Ecological Applications* 7:921–933.

PIANKA, E. P. 1996. Long-term changes in lizards assemblage in Great Victoria desert: dynamic habitat mosaics in response to wildfires. Pp. 191–215 in Cody, M. L. & Smallwood, J. A. (eds). *Long-term studies of vertebrate communities*. Academic Press, Sydney.

ROSEBERRY, J. L. & SUDKAMP, S. D. 1998. Assessing the suitability of landscapes for northern bobwhite. *Journal of Wildlife Management* 62:895–902.

SLADE, N. A. & BLAIR, S. M. 2000. An empirical test of using counts of individuals captured as indices of population size. *Journal of Mammalogy* 81:1035–1045.

SOUTHGATE, R. & MASTERS, P. 1996. Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research* 23:289–303.

SUTHERLAND, E. F. & DICKMAN, C. R. 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* 26:405–419.

TAITT, M. J. & KREBS, C. J. 1983. Predation, cover, and food manipulations during spring decline of *Microtus townsendii*. *Journal of Animal Ecology* 52:837–848.

VIEIRA, E. M. & MARINHO-FILHO, J. 1998. Pre- and post-fire habitat utilization by rodents of cerrado from Central Brazil. *Biotropica* 30:491–496.

WHELAN, R. J. 1995. *The ecology of fire*. Cambridge Studies in Ecology. Cambridge University Press, Cambridge. 346 pp.

WOOD, M. D. & SLADE, N. A. 1990. Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. *Journal of Mammalogy* 71:252–255.

YUNGER, J. A. 2002. Response of two low-density populations of *Peromyscus leucopus* to increased food availability. *Journal of Mammalogy* 83:267–279.

ZEDLER, P. H., GAUTIER, C. R. & MCMASTER, G. S. 1983. Vegetation change in response to extreme events – the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818.