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Original investigation

Population dynamics of small rodents in a grassland between fragments of Atlantic Forest in southeastern Brazil

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Abstract

Population dynamics and reproduction of four species of muroid rodents (*Akodon cursor*, *Bolomys lasiurus*, *Oligoryzomys nigripes*, and *Mus musculus*) were studied through capture-mark-recapture in a grassland between fragments of Atlantic Forest from March 1998 to February 1999. *A. cursor* and *B. lasiurus* accounted together for 93.5% of all captures. *O. nigripes* and *M. musculus* reached highest population sizes by the end of the dry season. *A. cursor* was most abundant during late dry/early wet season, however, its population sizes were higher in the wet season than in the dry season. Populations of *B. lasiurus* were highest during the dry season, although their population levels varied less than those of *A. cursor*. The differences in the pattern of population fluctuations of the two latter species can be explained by differences in their feeding habits, as *B. lasiurus* feeds mostly on grass seeds (most abundant during the dry season), whereas the diet of *A. cursor* includes a high proportion of insects, which are most abundant during the wet season.

Key words: Rodents, grassland, population dynamics, reproduction, Brazil

Introduction

Factors explaining variations in population abundance of neotropical rodents in grassland habitats have been studied mostly in savanna-like vegetations, such as the Venezuelan llanos or the Brazilian cerrado (O'CONNELL 1982; AUGUST 1984; ALHO et al. 1986; FRANCISCO et al. 1995). While population fluctuations of rodents in temperate habitats often follow predictable patterns linked to the seasons of the year (e.g. FLOWERDEW 1987; MILLS et al. 1992; CITTADINO et al. 1994; FERNANDEZ et al. 1996), in tropical rodents population fluctuations have often been linked to temporal variations in precipitation, acting either directly or by affecting the availability of resources (PEARSON 1975; STREILEIN 1982; MURÚA and GONZALEZ 1986; GALANTE and CASSINI 1994; BERGALLO 1995; ADLER 1998; BERGALLO and MAGNUSSON 1999). Populations of neotropical grassland rodents are typically characterized by high densities, low survival and high population turnover (O'CONNELL 1982; ALHO et al. 1986). In many cases, reproduction occurs year-round, with peaks of reproductive activity coinciding with

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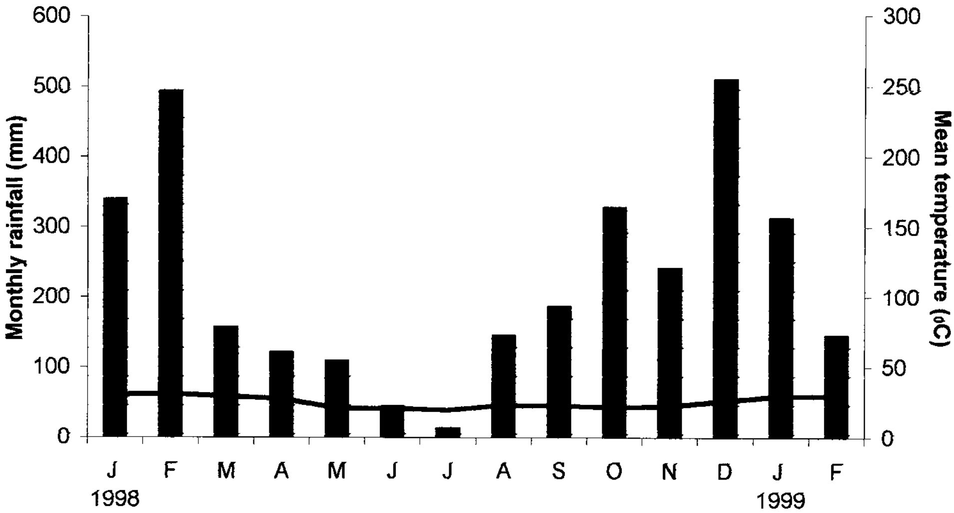


Fig. 1. Variations in rainfall and air temperature of the study area, Poço das Antas Biological Reserve, from January 1998 to February 1999 (bars – monthly rainfall, line – monthly average temperatures).

transitions between seasons (O'Connell 1982; Francisco et al. 1995). The highest population densities are often reached by the end of the dry season, when grass seeds are available to greater amounts on the ground (O'Connell 1982; Dietz 1983; Vivas 1986). However, populations of different species may have different seasonal patterns of fluctuation if they depend on different resources, as the main resources for rodents (arthropods, seeds, other plant parts) may respond in different ways to the variations in precipitation.

The main objectives of this study were: (1) to analyse the reproduction and population dynamics of rodents in a grassland area within the Atlantic Coastal Forest biome in Brazil, with emphasis on the species *Akodon cursor* and *Bolomys lasiurus*; and (2) to compare the patterns found among species as well as with patterns described for other neotropical rodent populations in grassland habitats.

Material and methods

Study area

The study area is located within Poço das Antas Biological Reserve, Rio de Janeiro state, southeastern Brazil (22° 30′–22° 33′ S, 42° 15′–42° 19′ W). The climate of the area is warm tropical, with average annual temperatures above 24 °C. The average annual rainfall (measured at the meteorological station from Programa Mata Atlântica, located within the reserve) reaches approximately 2 100 mm, with a moderate seasonality in rainfall (Fig. 1), with 30% of pluviosity recorded along the dry season (April–August) and 70% during the wet season (September–March).

The present study was carried out in an area of anthropic grassland with scattered early successional trees (mostly *Trema micrantha* and *Cecropia pachystachya*). The dominant species were the introduced grasses *Imperata brasiliensis* and *Melinis minutiflora*, bracken (*Pteridium aquilinum*) and the shrubs *Piptocarpha quadrangularis*, *Solanum* spp. and *Lantana* armata. This vegetation grows on peaty soils of the flatland which separates a set of small (1.5–15.0 ha) fragments of Atlantic Forest ("Ilhas dos Barbados") occupying the small hills at the south part of the Reserve, alongside São João River; the area as a whole has been described elsewhere (Pires and Fernandez 1999). The matrix seems to be at least partially of anthropic origin, as there were farms in the area before the Reserve was established in 1974. Later there were changes in the drainage patterns of the whole area due to the building of a dam up the river in the late seventies, which affected the whole vegetation mosaic of the southern part of the Reserve.

Trapping and data recording

Trapping sessions were carried out every month from March 1998 to February 1999. A square 81 point (9×9) trapping grid was used, with 20 m spacing among points. In each point, a Sherman trap (38×10×12 cm) was placed. Two types of bait were used, in alternate points: either cod liver oil on a pineapple slice, or a mixture of oat, banana, bacon and peanut butter on a manioc slice.
Traps were checked in the morning. All animals captured were marked with individually coded Michel ear-tags (LE BOULENGÉ-NGUYEN and LE BOULENGÉ 1986) and/or by toe-clipping. Upon capture the following data were recorded: species, sex, weight, tail length, point of capture and reproductive condition. For males, recorded signs of reproductive condition were scrotal or abdominal testes; for females signs of reproductive condition that were recorded were closed or perforated vaginas, lactation, and late pregnancy determined by palpation.

Species studied and data analysis

The two most abundant species were *Akodon cursor* and *Bolomys lasiurus*, which were analysed in more detail. These two species have been studied previously in several localities in the Neotropics. In *Akodon cursor*, gestation takes on average 22.7 days; females usually have two litters per year, each litter in most cases with three to five young, although as many as 10 were occasionally reported; young are weaned after 1–15 days, and reach sexual maturity after two months (NOWAK 1991). In *Bolomys lasiurus*, females usually have more than one litter per year; each litter may have from one up to 13 young, although litter sizes of 3–6 are most common (NOWAK 1991). In the present study, individuals captured were separated by weight into juveniles (less than 40 g) and adults (more than 40 g), according to GENTILE et al. (2000). Only the reproductive condition of females was used for analyzing reproduction, because for small rodent species testes size is not an accurate indicator of reproductive activity (BERGALLO and MAGNUSSON 1999).
Population sizes were estimated by the Schnabel census (SEBER 1982) for the most common species, and by the Minimum Number Known to be Alive (KREBS 1966) for the remaining ones. For estimating survival and recruitment rates of the most abundant species among consecutive sessions, the Jolly-Seber method (SEBER 1982) was used.
Pearson's correlation (ZAR 1999) was calculated between survival/recruitment rates and proportional variation in population sizes ($\Delta N_{t,\ t+1}$), defined as the difference in consecutive population sizes (N_{t+1}-N_t) divided by N_t. Proportional variation in population sizes was used because, although one would expect any population to vary most (in number of individuals) when it is larger by a simple matter of scale, it would be more informative to analyse how the per capita rates of variation are correlated with the demographic parameters. Additionally, proportional variation in population sizes, recruitment and survival rates and proportion of juveniles were correlated with monthly rainfall for the same month and with a time lag of one and two months. Data were normalized by logarithm transformations (ZAR 1999) when necessary in order to meet the assumptions of parametric correlation.

Results

During the study, with a trapping effort of 3,721 trap-nights, a total of 306 individuals was captured 1,453 times. The community was dominated by the rodents *Akodon cursor* and *Bolomys lasiurus*, which together accounted for 93.5% of the captures. The species caught and the respective numbers of captures are given in table 1. Two introduced synanthropic murid rodents, *Rattus rattus* and *Mus musculus*, which may have come from farms existing in the area prior to the establishment of the Reserve, were found living as wild populations in the study area. Due to small numbers of captures, demographic analyses were not performed for the two marsupial species, or for *R. rattus*.

Age structure and reproduction

For *Akodon cursor*, females in reproductive condition were captured during all months except April, June and September 1998 (Fig. 2 a). Juveniles were recorded in all months except March 1998. The highest frequency of juveniles was recorded in mid dry season and late wet season (Fig. 3 a), but was not related to rainfall either in the same month ($r = -0.132$, $df = 11$, $p > 0.50$), or with a time lag of one ($r = -0.489$, $df = 11$, $p > 0.05$) or two months ($r = -0.395$, $df = 11$, $p > 0.05$).

Table 1. Numbers of different individuals and numbers of captures obtained for seven small mammal species in an area of anthropogenic grassland in Poço das Antas Biological Reserve, from March 1998 to February 1999. M = males, F = females.

Species	Number of individuals		Number of captures	
	M	F	M	F
Marsupialia				
Didelphis aurita (Wied-Neuwied, 1826)	1	–	1	–
Philander frenata (Olfers, 1818)	2	2	5	2
Rodentia				
Akodon cursor (Winge, 1887)	97	61	451	308
Bolomys lasiurus (Lund, 1841)	47	43	315	284
Mus musculus (Linnaeus, 1758)	30	9	44	17
Oligoryzomys nigripes (Olfers, 1818)	10	2	21	2
Rattus rattus (Linnaeus, 1758)	2	–	3	–
Total	306		1,453	

For *Bolomys lasiurus*, females in reproductive condition were captured in April, August, October, December 1998 and February 1999 (Fig. 2 b). Juveniles were recorded in all months except March 1998 (Fig. 3 b); however, the highest frequency of juveniles was recorded by the end of the dry season. The frequency of juveniles was related with rainfall of the previous month ($r = -0.747$, $df = 11$, $p < 0.01$) and of two months before ($r = -0.744$, $df = 11$, $p < 0.01$), but not with rainfall at the same month ($r = -0.464$, $df = 11$, $p > 0.05$).

The reproductive patterns observed for *Oligoryzomys nigripes* and *Mus musculus* were similar. For both species only adults were captured during the study. One single pregnant female of *O. nigripes* was captured in May 1998, and one single reproductive female of *M. musculus* was captured in October 1998, both during the dry season.

Population size, recruitment and survival rates

For *Akodon cursor*, survival rates did not vary much throughout the year, and recruitment rates peaked at early and mid dry season (May and August respectively) (Fig. 4 a). Adult individuals accounted for 48.5% of the recruitment recorded. The population peak of *A. cursor* was recorded at the transition between the dry and wet seasons (August); however, population sizes in general were higher during the wet than during the dry season (Fig. 4 a). Proportional variation of population size was correlated with recruitment ($r = 0.907$, $df = 8$, $p < 0.001$), but not with survival rate ($r = 0.489$, $df = 8$, $p > 0.10$). None of its population parameters (proportional variation in population sizes and survival and recruitment rates) was correlated with monthly rainfall either in the same month, or with one or two months time lag (all correlations, $p > 0.05$).

Survival rates of *Bolomys lasiurus*, although more variable than for *A. cursor*; also did not show marked peaks; maximum values were reached in the dry season in the months of April, August and September (Fig. 4 b). Although estimated recruitment rates did not show a marked seasonal pattern, juveniles (which accounted for 48.2% of the recruitment recorded) were consistently more frequent during the dry season (Fig. 3 b). Population sizes of *B. lasiurus* fluctuated within a narrow range; its population maximum was recorded at the transition between the dry and wet seasons (Fig. 4 b). Proportional variation in population sizes was not correlated with recruitment ($r = 0.652$, $df = 8$, $p > 0.05$), or with survival rate ($r = 0.509$, $df = 8$, $p > 0.05$). None of its population parameters (proportional variation in population sizes and sur-

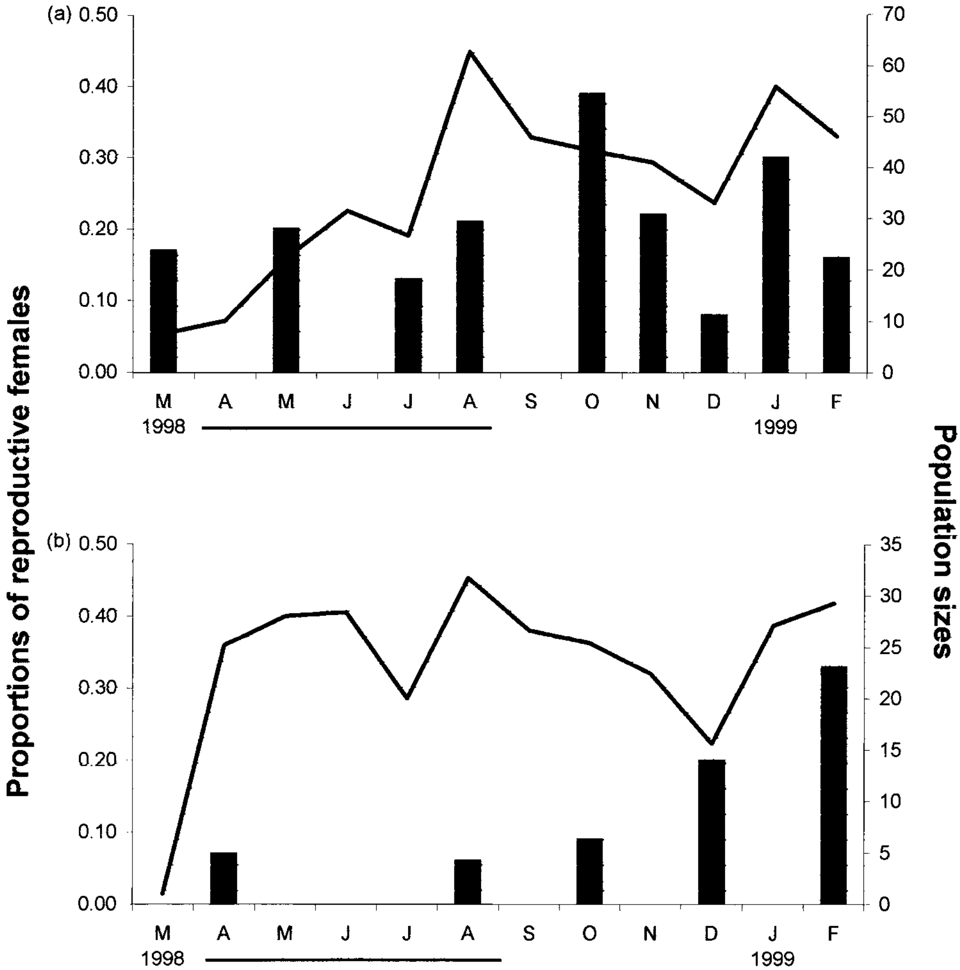


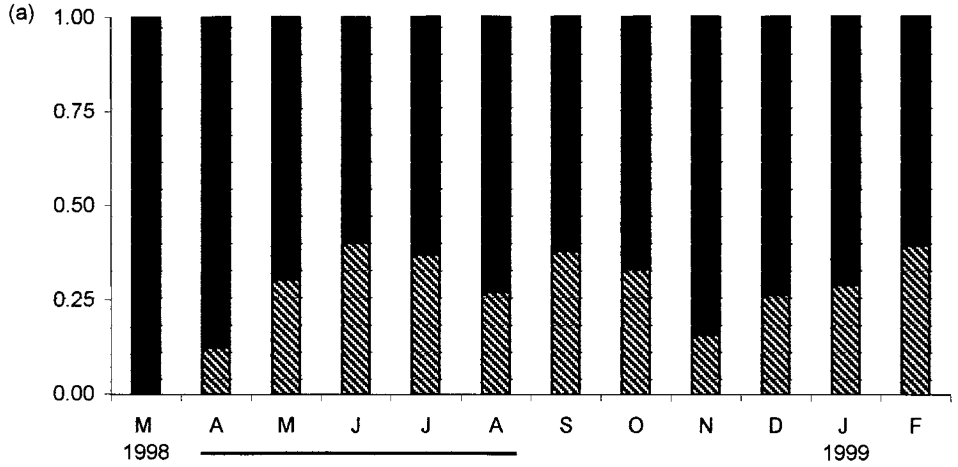
Fig. 2. Population sizes (continuous line) and proportion of reproductive females (bars) of *Akodon cursor* (a) and *Bolomys lasiurus* (b) in an area of anthropogenic grassland in Poço das Antas Biological Reserve, from March 1998 to February 1999. The line under the horizontal axis indicates the months corresponding to the dry season.

vival and recruitment rates) were correlated with monthly rainfall either in the same month, or with one or two months time lag (all correlations, $p > 0.05$).

For *Oligoryzomys nigripes*, higher population sizes were reached during the dry season, with a peak by the end of this season, and a progressive decrease thereafter until no longer being recorded in late wet season (Fig. 5). The pattern found for *Mus musculus* was similar, except that the species ceased being caught earlier than *O. nigripes* (Fig. 5).

Discussion

Muroid rodents show a great degree of variation in their annual patterns of reproduction (Bronson and Perrigo 1987). In natural neotropical grasslands, most rodents show increased reproductive activity and reach higher population densities during the dry season, although some species may reproduce year-round (Alho 1982; O'Connell 1982, 1989; August 1984; Ojasti 1990).



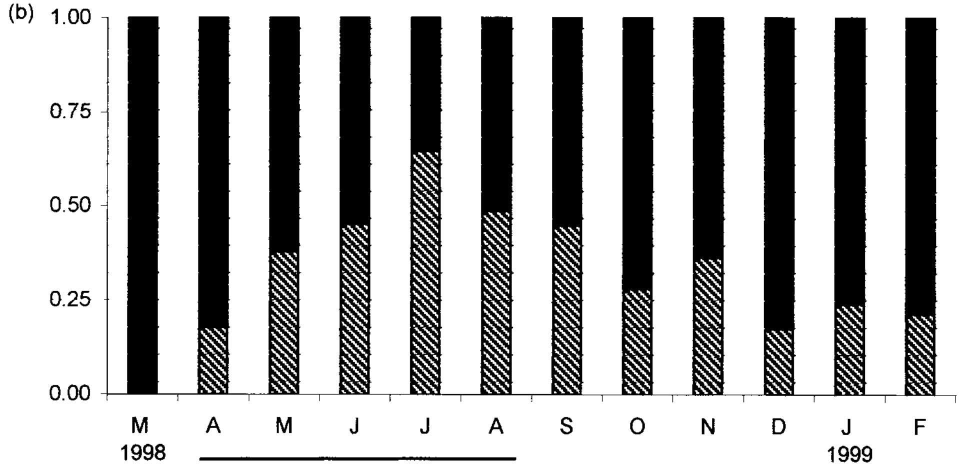


Fig. 3. Variations in age structure of *Akodon cursor* (a) and *Bolomys lasiurus* (b) in an area of anthropogenic grassland in Poço das Antas Biological Reserve, from March 1998 to February 1999. Shading: juveniles (hatched); adults (black). The line under the horizontal axis indicates the months corresponding to the dry season.

As the diet of *A. cursor* is composed mostly of insects and other invertebrates (Alho 1982; Fonseca and Kierulff 1989; Stallings 1989), the higher population sizes of the rainy season can be related to a higher availability of this item. Studies conducted in other neotropical areas showed that insect availability is usually higher during wet months (Wolda 1980; Vivas and Calero 1988; Bergallo and Magnusson 1999). In the study area, *A. cursor* seemed to breed year-round as found in other studies in grasslands (Gentile et al. 2000), coastal shrubland (Cerqueira et al. 1993) and Atlantic Forest (Olmos 1991). Nevertheless, seasonal variation in population sizes of *A. cursor* was explained mostly by variation in recruitment rates, as found for the same species in other studies (Cerqueira et al. 1993; Gentile et al. 2000). This pattern suggests that the marked changes in recruitment are quick responses

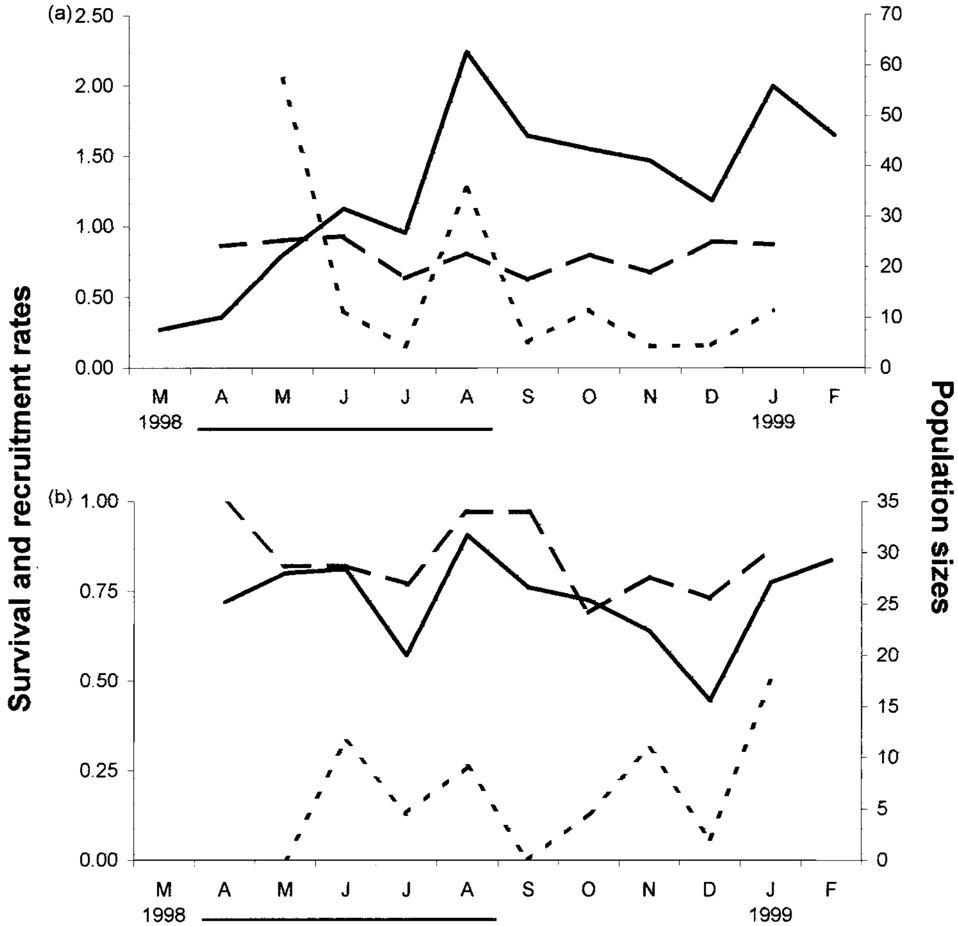


Fig. 4. Population sizes (continuous line), survival (dashed line) and recruitment (dotted line) rates for *Akodon cursor* (a) and *Bolomys lasiurus* (b) in an area of anthropogenic grassland in Poço das Antas Biological Reserve, from March 1998 to February 1999. The line under the horizontal axis indicates the months corresponding to the dry season.

to temporal variation in resource availability. Given gestation and weaning times for *A. cursor*, and its females' ability for having two or more litters in a year, large numbers of juveniles can appear in the population as soon as five weeks after the start of any favourable period. It seems interesting, however, to notice that for this species peaks of recruitment did not coincide with the times of the year when there was the highest proportion of juveniles. This can at least in part be explained by recruitment including not only local births but also immigration, as suggested by adults accounting for a high proportion of the recruitment recorded. Furthermore, recruitment does in fact not only reflect reproduction but also survival in the early stages of life (before the first capture), which is likely to be critically dependent on resource availability, especially during lactation. Independent of what the recruitment rates actually represent, the overall pattern seems consistent with the hypothesis that resource availability could affect population sizes through recruitment. The population fluctuations found for *B. la-*

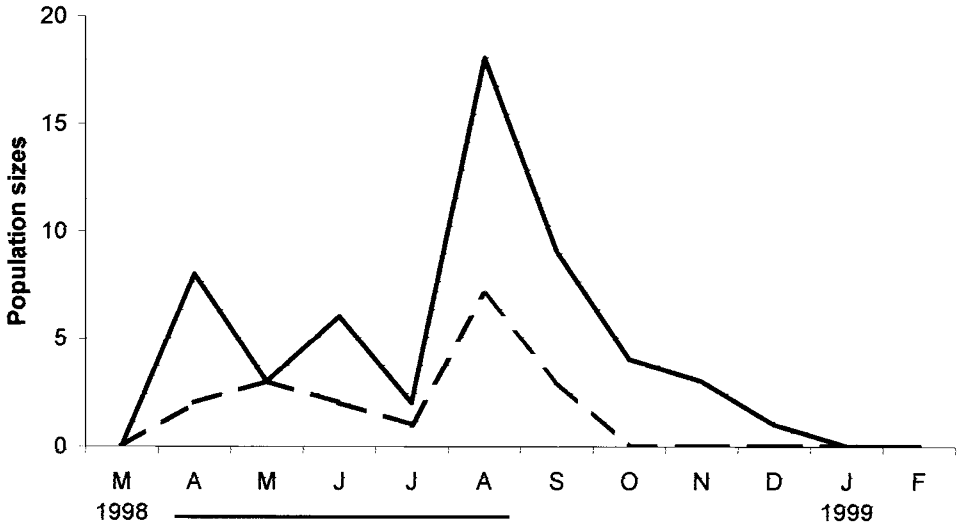


Fig. 5. Population sizes of *Oligoryzomys nigripes* (dashed line) and *Mus musculus* (continuous line) captured in an area of anthropic grassland in Poço das Antas Biological Reserve, from March 1998 to February 1999. The line under the horizontal axis indicates the months corresponding to the dry season.

siurus were consistent with the patterns found in previous studies with the same species (ALHO et al. 1986; FRANCISCO et al. 1995). The higher population levels during the dry season probably reflect the higher availability of resources for the species, as *B. lasiurus* mostly consumes grass seeds (ALHO et al. 1986), which often are available in greater amounts on the ground of neotropical grasslands during the dry season (O'CONNELL 1982). Therefore, the difference in their diets could explain the opposite patterns of population fluctuation found for the two most common species in this study, *A. cursor* and *B. lasiurus*. *B. lasiurus* also displays a potential for rapid population growth, as females can have more than one litter in a year and litter size can be large, so that its populations quickly react to any changes in resource availability. Additionally, the lower survival rates for *B. lasiurus* during the wet season may also reflect directly the higher rainfall, as MELLO (1980) suggested that strong rains can either destroy shelters or hinder building them, thus reducing survival during the wet season. There seems to be some relationship between recruitment and proportional variation in population sizes; although the result was not significant the correlation was high and the possibility that its non-significance was due to the small number cannot be excluded. As happened with *A. cursor*, peaks of recruitment of *B. lasiurus* did not coincide with the times of the year when there was the highest proportion of juveniles, suggesting that immigration may be important in addition to local births, as a high proportion of the recruitment was accounted for by adults. Again recruitment rates not only reflect reproduction (which was not clearly seasonal for *B. lasiurus*) but also early juvenile survival and its dependence on resource availability.

The population levels of *Oligoryzomys nigripes* were also higher during the dry season, a pattern similar to *B. lasiurus*, which can be explained by *O. nigripes* also having a high proportion of seeds in its diet (EMMONS and FEER 1997). *Mus musculus* also followed a similar pattern; although it is a species with generalist food preferences, which may include arthropods in its diet, *Mus* as wild animals are primarily seed-eaters (NOWAK 1991; EMMONS and FEER 1997), and if this applies to the *M. musculus* population living in the studied grassland, it could explain why its fluctuation followed a pattern so similar to the native seed-eating rodents. As can be noted in both *O. nigripes* and *M. musculus* the peak was reached at the end, not the middle, of the dry season. This was to be expected, since in such short-lived mice two or more generations can be found within the same breeding season and therefore numbers seem to build up quickly over a favorable period reaching the peak by the end of the time period, just before conditions deteriorate. This is similar to what happens in many species of rodents in temperate habitats (e. g. *Apodemus* spp.) where numbers typically peak by late autumn, just before conditions deteriorate in winter (FLOWERDEW 1987).

In summary, the population dynamics of the neotropical grassland rodents seem to be consistent with the view that rainfall is the most important climatic factor affecting rodent numbers indirectly, via the effect of resource availability mostly on recruitment rates. This mechanism tends to produce diverse patterns of population fluctuations, as the main resources for grassland rodents (seeds and arthropods) themselves respond in different ways to variations in rainfall.

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Zusammenfassung

Populationsdynamik von kleinen Nagetieren auf Grasflächen zwischen Fragmenten des atlantischen Küstenregenwaldes im südöstlichen Brasilien

Populationsdynamik und Fortpflanzung von vier muroiden Nagetierarten (*Akodon cursor*, *Bolomys lasiurus*, *Oligoryzomys nigripes* und *Mus musculus*) wurden von März 1998 bis Februar 1999 durch Fang-Markierung auf einer Wiese zwischen Fragmenten des atlantischen Küstenregenwaldes untersucht. *A. cursor* und *B. lasiurus* machten zusammen 93,5% aller Fänge aus. *O. nigripes* und *M. musculus* erreichten die höchsten Populationsgrößen am Ende der trockenen Jahreszeit. *A. cursor* war in der späten trockenen/frühfeuchten Jahreszeit die häufigste Art, obwohl die Populatiosgrößen in der feuchten Jahreszeit höher als in der trockenen waren. Populationen von *B. lasiurus* waren während der trockenen Jahreszeit am höchsten, obgleich ihre Populationsdichten niedriger als die von *A. cursor* waren. Die Unterschiede bezüglich des Musters der Populationsveränderungen der zwei letzten Arten können durch Unterschiede in ihrer Nahrungsgewohnheiten erklärt werden, da *B. lasiurus* meistens Grassamen frisst (reichlicher während der trockenen Jahreszeit), während die Nahrung von *A. cursor* einen hohen Anteil Insekten umfasst, die während der feuchten Jahreszeit reichlicher sind.

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