

Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study

Rosana Gentile¹, Paulo Sergio D'Andrea², Rui Cerqueira¹ and Luana Santoro Maroja^{1,2}

¹Department of Ecology, Federal University of Rio de Janeiro, Brazil

²Department of Tropical Medicine, Oswaldo Cruz Foundation, Rio de Janeiro, Brazil

Abstract

A five-year mark-recapture study of small mammals was conducted with sampling every two months in a rural area of Sumidouro, State of Rio de Janeiro, Brazil, from June 1991 to July 1996. Population sizes were estimated through MNKA estimator, survivorship and recruitment rates through Jolly-Seber estimator. *Nectomys squamipes* and *Didelphis aurita* were the most abundant species, followed by *Akodon cursor*, *Philander frenata* and *Oligoryzomys nigripes*. Marsupials reproduced from July/August to March, with the highest population sizes and recruitment rates in the end of the rainy periods and beginning of the dry period. Rodents were able to reproduce throughout the year. *N. squamipes*' population size was correlated with survivorship; peaks and the bulk of reproduction occurred during and after the rainy periods. *A. cursor*'s population size increased in dry periods. These species displayed seasonal patterns of population dynamics related to reproduction, with some variations among years chiefly for the rodents.

Keywords: *Didelphis aurita*, *Philander frenata*, *Nectomys squamipes*, *Akodon cursor*, *Oligoryzomys nigripes*; small mammals

Correspondence: R. Gentile, Laboratório de Vertebrados, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, CP 68020, 21941-590 Rio de Janeiro, RJ, Brasil. Fax: +55-21-2903308. E-mail: labvert@biologia.ufrj.br

INTRODUCTION

Most population studies of small mammals in the Atlantic Forest have been carried out in preserved areas (Fonseca & Kierulff, 1989; Stallings, 1989; Olmos, 1991; Pereira et al., 1993; Bergallo, 1994). Some information is also available from short-term surveys conducted in monoculture landscapes (Alencar, 1969; Amante, 1975; Carvalho & Bueno, 1975; Engel & Mello, 1993) but none from rural areas.

This study monitors small mammal communities associated with typical Brazilian rural areas that include mosaics of rotating crops, remnants of logged forests and pasturelands. We report the population dynamics, reproduction and age structure of two marsupials, the common opossum, *Didelphis aurita* and the gray-four-eyed opossum, *Philander frenata* (Didelphimorphia, Didelphidae), and three rodents, the water rat, *Nectomys squamipes*, the field rat, *Akodon cursor* and the rice rat, *Oligoryzomys nigripes* (Rodentia, Sigmodontinae). The data analyzed in this study were part of a long term Brazilian eco-epidemiological program on the role of *Nectomys squamipes* as a natural wild reservoir of schistosomiasis, at Sumidouro, State of Rio de Janeiro, Brazil.

MATERIALS AND METHODS

Study area

The five year mark-recapture study was carried out in a rural area at Sumidouro, State of Rio de Janeiro, Brazil, and included 12250 trap-nights on 7 transects along streams, irrigation channels and flooded areas in a typical rural valley. The study area was situated in the Pamparrão valley (22° 02'S, 42° 41'W), an area of 1.2 km² comprising small rural properties with vegetable plantations, pasture lands, logging forests and small Atlantic Forest fragments on the top of the mountains. Grass cutting, plantation alternation activities and harvesting frequently modified these habitats. The valley has several streams and irrigation channels with some flooded areas. The climate is humid-mesothermic (Nimer, 1989), characterized by a wet season from September to April and a moderate dry season from May to August (Fig. 1). For the five-year period, mean monthly temperature varied from 19.6°C to 27.4°C, and monthly rainfall from 0.6mm to 462.9mm. The normal monthly temperature of the wet season (September to April) varied from 21.3 to 25.2°C and normal rainfall varied from 69.7 to 288.6mm. The normal monthly temper-

ature of the dry season (May to August) varied from 18.3 to 20.3°C and normal rainfall varied from 24.7 to 44.2mm (Instituto Nacional de Meteorologia do Rio de Janeiro - INMET).

Small mammals were captured on seven line transects (A to G) spread along the valley. All transects were up gentle slopes, and except for D, all were placed along small streams following the original design for schistosomiasis study (i.e. trap lines following river sides). Transects A and G were characterized by an open vegetation consisting of sparse thickets, with little or no canopy. Transect B had a well developed understory with grass for cattle feeding and sparse high trees. Transect C had an open vegetation with grass, sparse shrubs and trees. Transect D was placed on a small hill with a secondary forest fragment used for wood extraction, with a disturbed midstory and a high closed canopy. Transect E was placed in another secondary forest fragment with midstory and a high closed canopy. Transect F was characterized by a continuous dense vegetation of *Hedygium choronarium* (Zingiberaceae).

Field methods

A preliminary species inventory was conducted from June 1990 to May 1991. Animals were collected and identified based on morphology and karyotype. Voucher specimens were deposited at the Museu Nacional do Rio de Janeiro.

A capture-mark-recapture study was carried out every other month from June 1991 to July 1996.

Mammals were live-caught in wire-mesh live-traps (32 × 18 × 20 cm) spaced 13m apart, baited with peanut butter mixed with banana, oat and bacon on manioc pieces. Transects A, B, C and D had 15 trap stations, transects E and F had 10 trap stations, and transect G had five. Each trapping session comprised five nights for transects A, B, C and D, and four nights for E, F and G. Marsupials were marked by tail tattooing and rodents and pouch young by toe-clipping. All animals were weighed and measured, and their sexual condition and marsupial dental development were rated.

Analysis methods

Population parameters were estimated considering only the captures of transects A, B, C and D, where trapping effort was the same during the entire study. For other analysis, all transects were considered. Population sizes were estimated using Minimum Number Known Alive estimator MNKA (Krebs, 1966) and survivorship and recruitment rates using Jolly-Seber estimators (Jolly, 1965; Seber, 1965) for each trapping session. For *O. nigripes*, survivorship and recruitment rates were estimated using MNKA. Survivorship and recruitment estimates were standardized for a 60-day interval according to Fernandez (1995). Recruitment included individuals incorporated into the population by birth or immigration. We correlated population sizes with survivorship and recruitment, and with rainfall from zero to six months lag using Spearman Correlation (Zar, 1996).

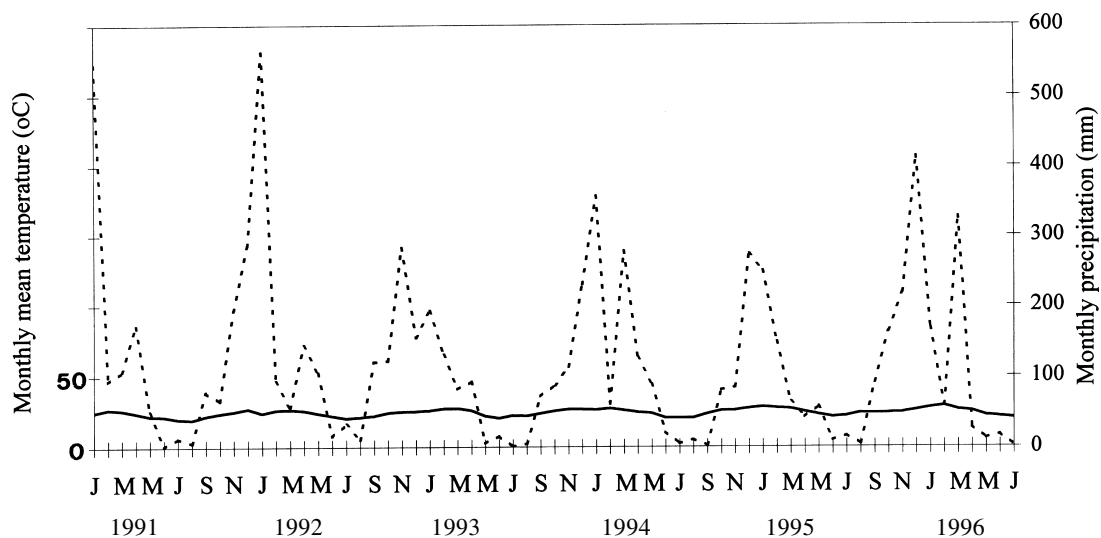


Fig. 1. Climate diagram of the study period from June 1991 to July 1996 (dashed line – rainfall, continuous line – temperature).

The reproductive period of marsupials was determined by the presence of females with young individuals in the pouch or with swollen nipples indicating recently weaning. Population size estimates were correlated with the frequency of reproducing females with two, four and six months lag using Spearman Correlation. Mean litter size of marsupials was compared among breeding periods using an ANOVA (Zar, 1996). Sex ratios of marsupial offspring were compared using chi-square test (Zar, 1996). For rodents, reproduction was detected by the presence of obviously pregnant females or the existence of copulatory plugs and by the birth dates of young individuals. Sexual maturity was assumed as the minimum age and weight of males with scrotal testes and females with open vagina. Of young individuals, age and birth date were estimated using the growth curves of body weight in captivity for each sex of *N. squamipes* (D'Andrea et al., 1996) and of *A. cursor* (Horta & D'Andrea, unpublished data).

Age structure of marsupials was analyzed by separating individuals into three classes according to Gentile et al. (1995), estimating ages by the dental formulas of D'Andrea et al. (1994) for *P. frenata* and using the dental formulas of Motta (personal communication) for *D. aurita*. For *P. frenata* the juvenile class included individuals between 81 and 154 days old, the sub-adult class included individuals from 155 days to 323 days-old and the adult class included all individuals of 324 days or more. For *D. aurita*, juveniles were individuals between 101 and 169 days old, sub-adults were individuals from 170 to 336 days old and adults were all individuals of 337 days or more. For rodents, age classes were defined according to body weights at sexual maturity. Juveniles included only individuals reproductively immature, weighing less than 110g for female *N. squamipes* and 30 g for female *A. cursor*, and 110 g for male *N. squamipes* and 28 g for male *A. cursor*. The sub-adult class included individuals in the maturity transition period in which the individuals weighted from 110 g to 215 g for female *N. squamipes*, from 30 g to 40 g for female *A. cursor*, from 110 g to 190 g for male *N. squamipes* and from 28 g to 45 g for male *A. cursor*. Adults included sexually mature individuals weighing more than 215 g for female and 190 g for male *N. squamipes*, and more than 40 g for female and 45 g for male *A. cursor*.

RESULTS

Population parameters

Nectomys squamipes and *D. aurita* had the most abundant and stable populations, followed by *A. cursor*, *P. frenata* and *O. nigripes* (Table 1). The Population sizes were correlated with both survivorship and recruitment rates for *D. aurita* ($r_s=0.324$, $P<0.05$, $r_s=0.442$, $P<0.01$, respectively), for *P. frenata* ($r_s=0.525$, $P<0.001$, $r_s=0.636$, $P<0.001$, respectively), for *A. cursor* ($r_s=0.398$, $P<0.05$, $r_s=0.451$, $P<0.05$, respectively) and for *O. nigripes* ($r_s=0.357$, $P<0.05$, $r_s=0.762$, $P<0.001$, respectively). For *N. squamipes*, population sizes were correlated only with survivorship rates ($r_s=0.570$, $P<0.001$). The population size of *D. aurita* was correlated with the preceding rainfall in lags of four, five and six months ($r_s=0.512$, $P<0.01$; $r_s=0.647$, $P<0.001$; $r_s=0.565$, $P<0.001$, respectively), and *P. frenata* only with six months lag ($r_s=0.366$, $P<0.05$).

Marsupials had high population numbers towards the end of their breeding periods (July/August to March), reaching the highest number in March or May for *D. aurita* (Fig. 2A) and in May or July for *P. frenata*, except for the first and last years (Fig. 2B). Most of the individuals were born in the previous breeding period, and for *P. frenata* there was a complete population turnover between breeding periods. Highest recruitment rates for *P. frenata* occurred at the end of breeding periods and beginning of non-breeding periods. *N. squamipes* had high population sizes and recruitment rates at the end of the rainy period and beginning of the dry period, except for the last year (Fig. 2C). The peaks of 1993 and 1995 were preceded by long periods of high survivorship rates. The highest population numbers for *A. cursor* (Fig. 2D) and *O. nigripes* were always during and after dry periods, and for the latter species, mostly related to recruitment. *O. nigripes* disappeared from the study area after September 1994. Only *A. cursor* and *O. nigripes* had a significant correlation between their population sizes ($r_s=0.595$, $P<0.001$, $N=31$). There was a high turnover in the population of all rodents between years.

Reproductive patterns - Marsupials

According to estimated birth dates of pouch-young individuals, the breeding periods of *D. aurita* began in July 1991, 1993, 1995 and 1996 and August 1992 and 1994. For *P. frenata*, reproduction began in

TABLE 1. Population size in number of individuals and survivorship and recruitment rates (in frequencies of individuals) of the small mammals in the Pamparrão valley, Sumidouro, Brazil, from June 91 to July 96. (\bar{x} – mean of the entire study, SD- standard deviation, CV- coefficient of variation).

Species	Population size			Survivorship		Recruitment	
	\bar{x}	SD	CV	\bar{x}	SD	\bar{x}	SD
<i>Didelphis aurita</i>	6.67	2.94	44.1	0.54	0.27	0.33	0.31
<i>Philander frenata</i>	2.42	2.43	100.5	0.39	0.44	0.23	0.37
<i>Nectomys squamipes</i>	7.65	5.23	68.4	0.54	0.34	0.41	0.30
<i>Akodon cursor</i>	7.00	5.35	76.4	0.54	0.39	0.33	0.36
<i>Oligoryzomys nigripes</i>	0.68	1.30	191.1	0.21	0.42	0.44	0.48

July or August 1991, July 1993 and 1996 and August 1994 (for 1992 and 1995 it was not possible to determine the beginning of breeding periods for *P. frenata*). From August to January, almost all adult females were reproducing. In all breeding periods the last weaning occurred in March, except for two females of *P. frenata* which weaned their litters in April. No female reproduced in May or June (Fig. 3A, 3B).

The end of the breeding period of *P. frenata* occurred later than *D. aurita*. Young marsupials born at the end of a breeding period could reproduce at the beginning of the following breeding period. In *P. frenata*, the first offspring could reproduce within the same breeding period in which they were born, this could possibly delay the latest recruitment of *P. frenata*.

Population size was positively correlated with the frequency of lactating females, with a four-month lag ($r_s=0.439$, $P<0.01$) and six-month lag ($r_s=0.471$, $P<0.01$) in *D. aurita*, and with a two-month lag ($r_s=0.404$, $P<0.05$), a four-month lag ($r_s=0.327$, $P<0.05$) and a six-month lag ($r_s=0.446$, $P<0.001$) in *P. frenata*.

Considering the five years, the mean litter size was 7.3 young (SD=1.96, $n=45$) for *D. aurita* and was 5.4 young (SD=0.78, $n=18$) for *P. frenata*. Among breeding periods mean litter size varied from 7.2 individuals (SD=2, $n=5$) to 9.1 individuals (SD=1.8, $n=7$) for *D. aurita*, without significant difference ($F=1.980$, $P=0.103$, $n=45$). For *P. frenata* it varied from 5 individuals (SD=1, $n=3$) to 6 individuals (SD=1, $n=3$), without significant difference ($F=0.840$, $P=0.524$, $n=18$). Sex ratio of the offspring did not differ from 1:1 in both species ($P>0.05$). The females of both species captured throughout an entire breeding period had only two litters. In *D. aurita*,

mortality of lactents appeared to occur generally at the beginning of lactation.

Age structure of *D. aurita* and *P. frenata* are shown in Fig. 3C and 3D. We observed ageing in both species during the year, with a delay in *P. frenata* in relation to *D. aurita*. Individuals reached the greatest ages during dry periods. Juveniles of *D. aurita* were present from November (just after the first weans) to March, and juveniles of *P. frenata* from November to July, indicating that the breeding period finished later in *P. frenata* (Fig. 3C, D).

Reproductive patterns - Rodents

During periods of large population sizes (1992/1993 and 1995/1996 for *N. squamipes*; and 1991/1992 for *A. cursor*) there was a high proportion of females pregnant or with copulatory plug throughout the year (Fig. 4A, B). Birth dates of 24 juveniles of *N. squamipes* and nine juveniles of *A. cursor* were estimated. For *N. squamipes*, 71% of these births occurred in the rainy periods, while 67% of the births of *A. cursor* occurred during the dry periods. *N. squamipes* reproduced throughout the year but predominantly in the rainy periods. *A. cursor* did not present a clear pattern of reproductive activity, but their population increased slightly in the dry periods. Only three females of *O. nigripes* were reproductively active and all of them were captured in the dry months of July 1992, September 1994 and May 1993. For rodents, there was no correlation between population size and frequency of reproductive females ($P>0.05$).

Sexual maturity of *N. squamipes* occurred at 37.8 days old (ranging from 27.7 to 45.5 days old) and 110g for males, and at 44.4 days old (ranging from 31 to 51 days old) and 110 g for females. In *A. cursor*, sexual maturity occurred from 31.6 to 36.7 days old, and 28 g for males, and at 42.3 days

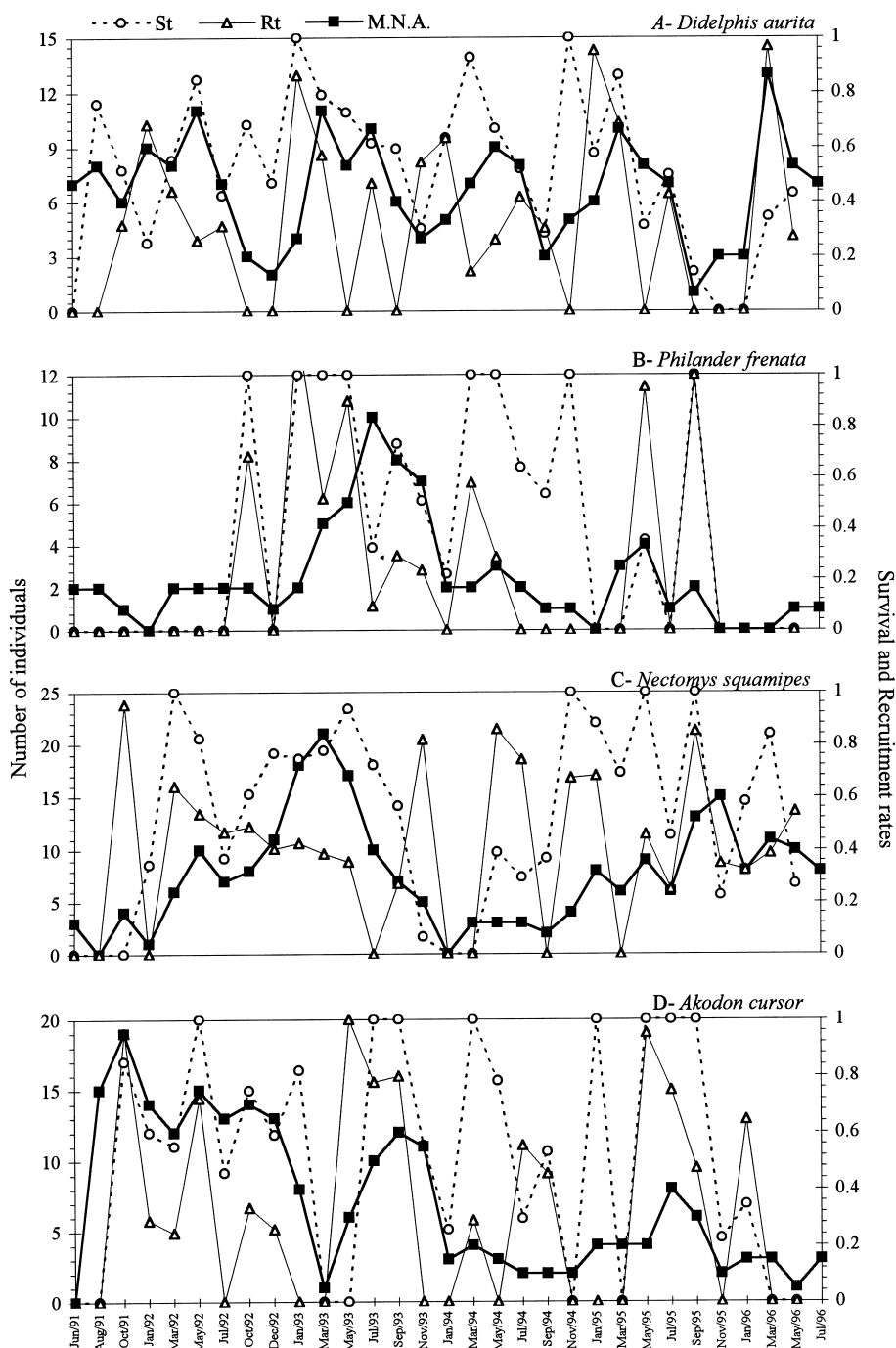


Fig. 2. Population sizes (squares), and survivorship (circles) and recruitment (triangles) rates for the period between the previous session to the session plotted for *Didelphis aurita* (A), *Philander frenata* (B), *Nectomys squamipes* (C) and *Akodon cursor* (D) in the Pamparrão valley, Sumidouro, Brazil, from June 91 to July 96.

old (ranging from 38.8 to 51.2 days old) and 30 g for females. For both species the males first reached maturity. The minimum weight of a mature female *O. nigripes* was 15 g and the maximum weight

of an immature female was 21 g; the maximum weight of a male with abdominal testes was 25 g and the minimum weight of a male with scrotal testes was 14 g.

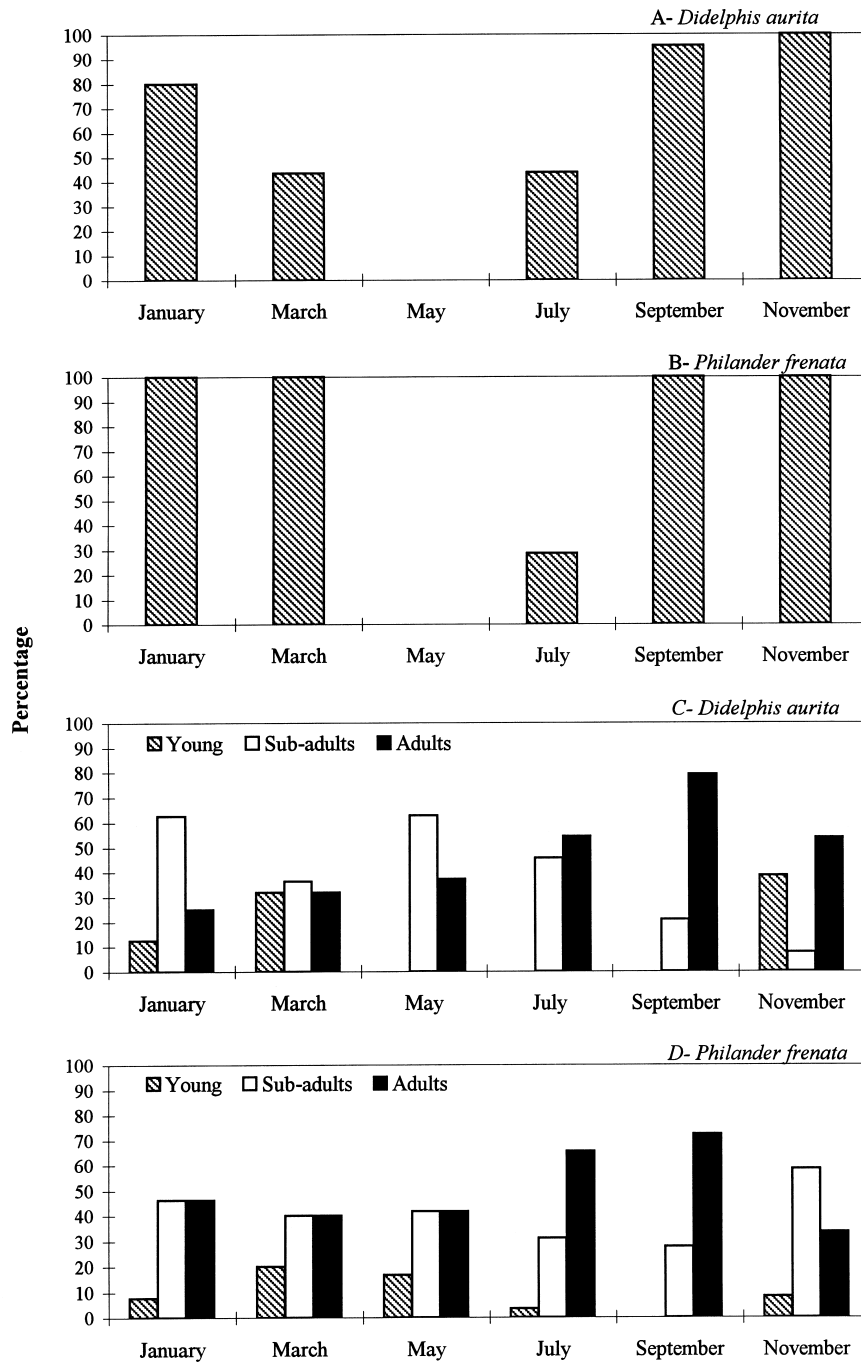


Fig. 3. Accumulated percentage from 1991 to 1996 of reproductive females in relation to total adult females captured for *Didelphis aurita* (A) and *Philander frenata* (B), and accumulated age structure for *Didelphis aurita* (C) and *Philander frenata* (D) in the Pamparrão valley, Sumidouro, Brazil.

Age structures of rodents are shown in Fig. 4C and 4D. Juveniles of *N. squamipes* predominated in rainy periods, while juveniles of *A. cursor* were more frequent in dry periods.

DISCUSSION

Population dynamics of marsupials were related to the reproductive period, which occurred from July/August to March for *D. aurita* and July/August to

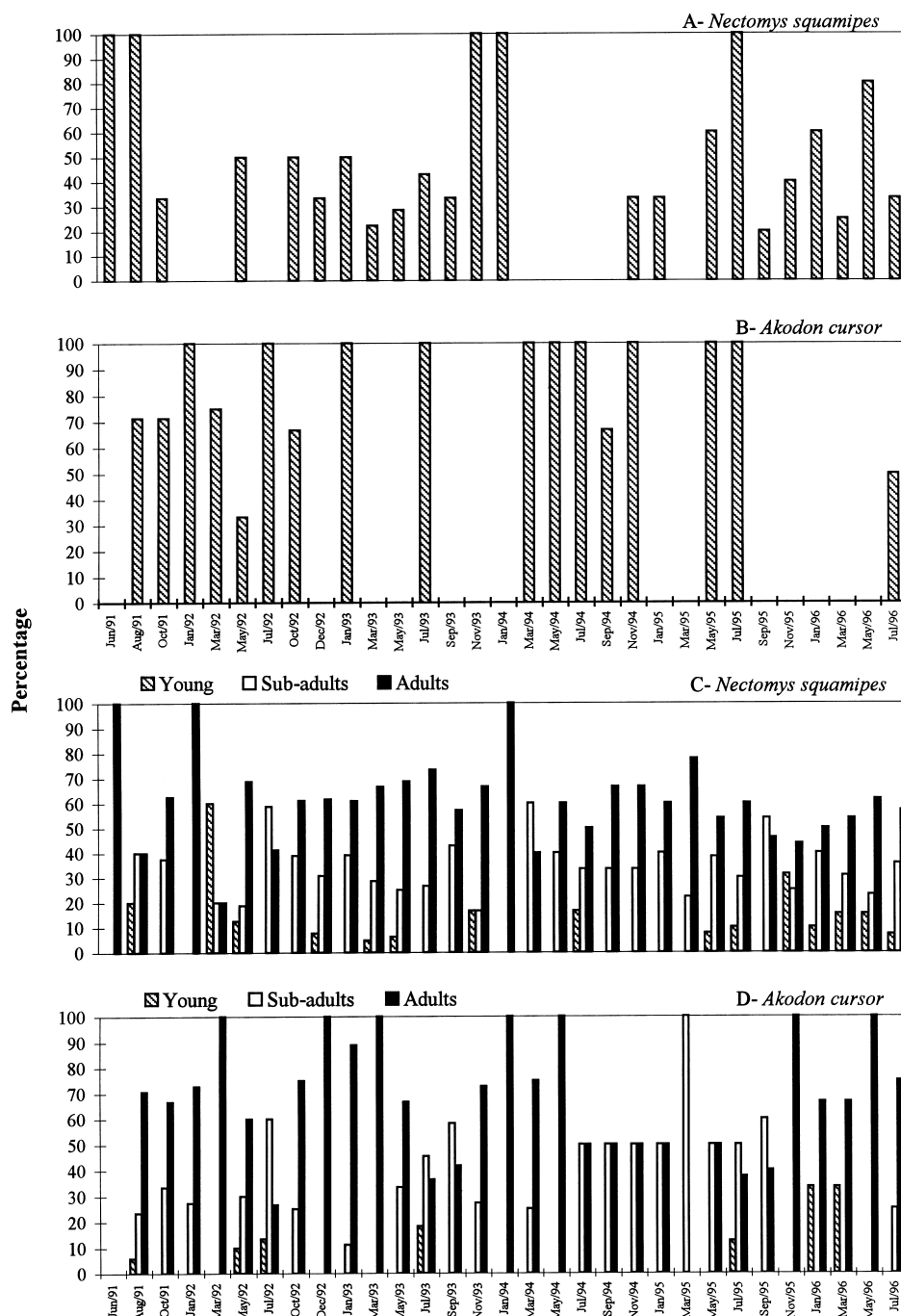


Fig. 4. Percentage of reproductive females in relation to total adult females captured for each session for *Nectomys squamipes* (A) and *Akodon cursor* (B), and age structure of *Nectomys squamipes* (C) and *Akodon cursor* (D) in the Pamparrão valley, Sumidouro, Brazil, from June 91 to July 96.

March/April for *P. frenata*. *D. aurita* and *P. frenata* populations followed the seasonal model of reproduction, like other didelphid marsupials (Cerqueira, 1988). These results are in accordance with other studies on Neotropical marsupials, which also

showed that reproduction begins in dry periods and lasts until the end of the rainy periods (Fleming, 1972; Fleming, 1973; Tyndale-Biscoe & Mackenzie, 1976; O'Connell, 1989; Cerqueira et al., 1993; D'Andrea et al., 1994; Bergallo, 1994). This season-

ality resulted in larger population sizes at the end and after rainy periods, which was more evident for *D. aurita*.

The most critical periods for survivorship of young in marsupials are the end of lactation and the period after weaning (Lee & Cockburn, 1985; Atramentowicz, 1992). In our study the end of lactation and weaning periods always occurred during or after rainy seasons, when resources seemed to be more abundant. Atramentowicz (1986) and Cerqueira (1988) related reproduction to food resource availability (plants and insects), which is related in turn to rainfall (Lee & Cockburn, 1985). Other studies showed that marsupial reproduction is also correlated with photoperiod which would explain how all of the mature females synchronize their reproduction (Cerqueira, 1988; Cerqueira & Bergallo, 1993).

The reproductive pattern observed for *N. squamipes*, occurring throughout the year but mostly during rainy periods, agrees with other studies of this species (Ernest & Mares, 1986; Bergallo, 1994). The rainy period is the most appropriate time for the reproduction and survivorship of neonates and young individuals of this species, considering the close relationship of this semi-aquatic rodent to water resources (Ernest, 1986).

The reproduction of *A. cursor* throughout the year, with greatest activity on the dry period, is in agreement with Fonseca & Kierulff (1989) and Pereira et al. (1993). Pereira et al. (1993) also found predominance of reproduction of *O. nigripes* during dry seasons. Fonseca & Kierulff (1989) attributed the continuous reproduction of rodents in the Atlantic Forest to the stability of food resource accessibility. Reproduction by *A. cursor* and *O. nigripes* at the study site may be related not only to food but also to habitat availability. These species spatially overlapped in the study area and *A. cursor* occurred mostly in dense herbaceous vegetation with abundant litter (Gentile & Fernandez, 1999). During the rainy periods, we observed that the habitat of these rodents was reduced due to the flooding of marshes and streams and scarcity of litter and midstory. As a consequence, these two species showed similar variation in abundance.

Rodents appeared to reproduce opportunistically, such that reproduction is triggered by resource availability according to rainfall pattern, resulting in rapid population increases. This is the most common reproductive strategy of muroid rodents of temperate

regions (Bronson & Perrigo, 1987) and tropical sigmodontines (Cerqueira & Lara, 1991). Such species have a short life expectancy, short gestation time and early maturity (D'Andrea et al., 1996; Horta & D'Andrea, unpublished data), traits that result in a rapid population turnover and rapid responses to environmental variation.

Our study area was often under human influence, which caused reduced numbers of captures of the more unstable populations such as *A. cursor*, *O. nigripes* and *P. frenata*. These species may have been more susceptible to habitat disturbances and *A. cursor* and *P. frenata* are more habitat selective than *D. aurita* (Gentile & Fernandez, 1999).

In contrast to studies in monocultures (Mills et al., 1992; Engel & Mello, 1993), we did not observe outbreaks and crashes in rodent populations, commonly detected in monocultures due to complete harvesting of crops. Though this study was not designed to test for plague formation, no rodent species seemed to behave as a potential agricultural plague, as there were no major increases in population sizes in spite of the relatively constant availability of food (from rotating vegetable cultures). It is not predictable, though, how these populations would respond to complete harvesting as is usual for monoculture landscapes. All species studied during the five years showed seasonal patterns of population dynamics directly related to reproduction, with some variations among years chiefly for the rodents.

ACKNOWLEDGEMENTS

We thank many people who helped us during this study: L. Rey for the opportunity to work on his project and for all the Laboratory facilities, C.E.V. Grelle, C. Horta, J.W.F. Costa and the people from the LBCE/FIOCRUZ and Lab-Vert/UFRJ for help on the field work and several comments, L. Geise and C.R. Bonvicino for rodent identification by karyological analysis, F.A.S. Fernandez for several suggestions on data analysis and discussions, the people of Pamparrão valley, Sumidouro, who allowed us to carry out the field work on their properties, the Sumidouro Municipal Government, in State of Rio de Janeiro for many operational facilities. This work was supported by Instituto Oswaldo Cruz (FIOCRUZ), and grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Amparo à Pesquisa do Rio de Janeiro (FAPERJ), Fundação José Bonifácio (FUJB), and GEF through BIRD for ProBio/MMA.

REFERENCES

- Alencar FOCC (1969): Notas sobre o rato de cana "*Holochilus sciureus*" Wagner na região do Cariri, Ceará. *Revta Brasil Biol* 29: 567–570.
- Amante E (1975): Prejuízos causados pelo roedor *Clyomys laticeps* (Echimyidae) em *Pinus* spp., em áreas reflorestadas de Sacramento, Minas Gerais. *Ci Cult* 27: 373–374.
- Atramentowicz M (1986): Disponibilités trophiques et rythmes de reproduction chez trois Didelphidés sympatriques de Guyane. *Mus Nac Hist Nat Paris* 132: 123–129.
- Atramentowicz M (1992): Optimal litter size: Does it cost more to raise a large litter in *Caluromys philander*? *Can J Zool* 70: 1511–1515.
- Bergallo HG (1994): Ecology of a small mammal community in an Atlantic Forest area of Southeastern Brazil. *Stud Neotrop Fauna & Environm* 29: 197–217.
- Bronson FH, Perrigo G (1987): Seasonal regulation of reproduction in muroid rodents. *Amer Zool* 27: 929–940.
- Carvalho CT, Bueno RA (1975): Animais causando danos em plantios (Mammalia, Rodentia). *Silvic S Paulo* 9: 39–46.
- Cerqueira R (1988): Modelos de estações reprodutivas em mamíferos. In: Vasconcelos AT, Coimbra C, Koiller J, Iskin M, eds., *Atas do Encontro Interdisciplinar de Ecologia Matemática, Laboratório Nacional de Computação Científica*, Rio de Janeiro, pp. 49–58.
- Cerqueira R, Gentile R, Fernandez FAS, D'Andrea PS (1993): A five-year population study of an assemblage of small mammals in Southeastern Brazil. *Mammalia* 57: 507–517.
- Cerqueira R, Bergallo HG (1993): A possible case of photoperiod controlling the reproduction of a South American Marsupial. *Ci Cult* 45: 140–141.
- Cerqueira R, Lara M (1991): Rainfall and reproduction of cricetid rodents in Northeastern Brazil. In: Bobek B, Perzanowski K, Regelin W, eds., *Global Trends in Wildlife Management*, Swiat Press, Krakow, pp. 545–549.
- D'Andrea PS, Cerqueira R, Hingst ED (1994): Age estimation of the Gray Four Eyed Opossum, *Philander opossum* (Didelphimorphia: Didelphidae). *Mammalia* 58: 283–291.
- D'Andrea PS, Horta C, Cerqueira R (1996): Breeding of water rat *Nectomys squamipes* (Rodentia - Cricetidae) under laboratory setting. *Laboratory Animals* 30: 369–376.
- Engel LA, Mello DA (1993): Rodents in agroecosystems in the Cerrado Province of the Federal District (Brasília/DF, Brazil). *Ci Cult* 45: 128–133.
- Ernest KA (1986): *Nectomys squamipes*. *Mammalian species* 265: 1–3.
- Ernest KA, Mares MA (1986): Ecology of *Nectomys squamipes*, the neotropical Water rat, in central Brazil: home range, habitat selection, reproduction and behaviour. *J Zool* 210: 599–612.
- Fernandez FAS (1995): Métodos para estimativas de parâmetros populacionais por captura, marcação e recaptura. In: Neto PRP, Valentin JL, Fernandez FAZ, eds., *Oecologia Brasiliensis: Tópicos em tratamento de dados biológicos*, Universidade Federal do Rio de Janeiro, Rio de Janeiro, pp. 1–26.
- Fleming TH (1972): Aspects of the population dynamics of three species of opossums in the Panama Canal Zone. *J Mamm* 53: 619–623.
- Fleming TH (1973): The reproductive cycles of three species of opossums and other mammals in the Panama Canal Zone. *J Mamm* 54: 439–455.
- Fonseca GAB, Kierulff MC (1989): Biology and natural history of Brazilian Atlantic Forest small mammals. *Bull Florida State Mus Biol Sci* 34: 99–152.
- Gentile R, D'Andrea PS, Cerqueira R (1995): Age structure of two marsupials in a Brazilian Restinga. *J Trop Ecol* 11: 679–682.
- Gentile R, Fernandez FAS (1999): Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. *Mammalia* 63: 29–40.
- Jolly GM (1965): Explicit estimates from capture-recapture data with both death and immigration - stochastic model. *Biometrika* 52: 225–247.
- Krebs CJ (1966): Demographic changes in fluctuating populations of *Microtus californicus*. *Ecol Monogr* 36: 239–273.
- Lee AK, Cockburn A (1985): *Evolutionary ecology of marsupials. Monographs on marsupial biology*. Cambridge University Press, Cambridge.
- Mills JN, Ellis BA, McKee KT, Maiztegui JI, Childs JE (1992): Reproductive characteristics of rodent assemblages in cultivated regions of central Argentina. *J Mamm* 73: 515–526.
- Nimer E (1989): *Climatologia do Brasil*. IBGE / Departamento de Recursos Naturais e Estudos Ambientais, Rio de Janeiro.
- O'Connell MA (1989): Population dynamics of neotropical small mammals in seasonal habitats. *J Mamm* 70: 532–548.
- Olmos F (1991): Observations on the behaviour and population dynamics of some Brazilian Atlantic Forest rodents. *Mammalia* 55: 555–565.
- Pereira LA, Chagas WA, Costa FE (1993): Ecologia de pequenos mamíferos silvestres da Mata Atlântica, Brasil. I. Ciclos reprodutivos de *Akodon cursor* e *Oryzomys nigripes* (Rodentia, Cricetinae). *Revta Bras Zool* 10: 389–398.
- Seber GAF (1965): A note on the multiple-recapture census. *Biometrika* 52: 249–259.
- Stallings JR (1989): Small mammal inventories in an eastern Brazilian park. *Bull Florida State Mus Biol Sci* 34: 153–200.
- Tyndale-Biscoe CH, Mackenzie RB (1976): Reproduction of *Didelphis marsupialis* and *Didelphis albiventris* in Colombia. *J Mamm* 57: 249–265.
- Zar JH (1996): *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey.

Received: 19 January 1999

Accepted: 7 June 1999

Printed: