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Population dynamics of the marsupial *Micoureus demerarae* in small fragments of Atlantic Coastal Forest in Brazil

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ABSTRACT. Patterns of population fluctuation, reproductive activity and age structure were studied in populations of the marsupial *Micoureus demerarae* occupying two small (7.0 and 8.8 ha) fragments of Atlantic Coastal Forest in southeastern Brazil, from 1995 to 1998. Males, but not females, were observed to move between populations. Estimated sizes of the populations in each fragment were very small, usually below 20 individuals. Breeding usually occurred from September to April. Population peaks came mostly by the end of this season, the delay reflecting the time required for the young to become trappable. In August 1997, the area was hit by a fire severely affecting the smaller fragment. Populations were synchronous before the fire, although they became asynchronous after it, possibly in the short term only. Small population sizes, synchrony and presumable male-biased migration are all likely to make the set of populations more vulnerable to extinction than expected for a metapopulation.

KEY WORDS: Atlantic Coastal Forest, demography, fragmentation, metapopulation, *Micoureus demerarae*

INTRODUCTION

The process of habitat fragmentation poses severe threats for tropical biodiversity. The Atlantic Coastal Forest in southeastern Brazil is among the areas most drastically depleted (Fonseca 1985). Mammals are particularly vulnerable to the effects of such process, due to the synergistic effects of their relatively small population sizes, high energetic needs, and sometimes high trophic level

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as well (Wilcox 1980). Therefore, understanding the local dynamics of small mammalian populations is important in order to evaluate the risks of extinction to which they are exposed. However, the vulnerability of a species in a fragmented landscape depends also on how isolated are the populations in each fragment (Fahrig & Merriam 1985, 1994). This degree of isolation, in its turn, is set not only by the structure of the landscape (number of fragments, distances between them and so on) but also by the ability of the species to disperse across the surrounding habitat in which the fragments are immersed (Fahrig & Merriam 1994, Laurance 1991). Unfortunately, such information is not available for most mammalian species, especially in the tropics (Offerman *et al.* 1995).

The wooly mouse opossum, *Micoureus demerarae* (Thomas 1905) (= *Micoureus cinereus*, previously *Marmosa cinerea*) is a medium-sized (weight up to 130 g) didelphid marsupial common in the Atlantic Coastal Forest. It is nocturnal, favours areas of secondary growth with rich understorey (Emmons & Feer 1997), and eats mostly insects and fruit (Carvalho *et al.* 1999, Leite *et al.* 1994). *M. demerarae* is captured mostly up trees, but often on the ground as well (Passamani 1995). Females are territorial and have smaller home ranges than males, which are not territorial (Pires *et al.* 1999). Some populations of *M. demerarae* in small fragments of Atlantic Forest are connected by individuals which move among fragments (Pires & Fernandez 1999).

The present contribution is part of a long-term study on the effects of fragmentation on populations of marsupials and rodents in small fragments of Atlantic Forest in southeast Brazil. The study described herein aimed to understand the dynamics of two connected populations of *Micoureus demerarae* in small nearby forest fragments.

METHODS

Study area

Poço das Antas Biological Reserve (22°30′–22°33′S, 42°15′–42°19′W), 130 km NE of Rio de Janeiro city, is one of the largest reserves of the vanishing lowland Atlantic Coastal Forest in southeastern Brazil. According to the Golden Lion Tamarin meteorological station, which is located within the reserve, average annual precipitation reaches about 1700 mm, with a moderate seasonality in precipitation, as nearly 30% of the annual precipitation falls during the dry season. During the study years the wet season lasted from September to March, and the dry season from April to August.

The study was carried out in two forest fragments (A and D) which are part of a group of eight such fragments known as Ilhas dos Barbados (Islands of the Howler Monkeys), in the southern part of Poço das Antas reserve. The fragments have been isolated for at least three decades, although the history of the area is not well known and it is not sure if the fragmentation was due to human activities in the area. Therefore we preferred to use here the term 'fragments' instead of 'remnants' as the latter seems to imply that the fragmentation had anthropic origin. The areas of the fragments, as well as the distances between them, were estimated from aerial photographs taken in December 1994, at the scale 1:5000. The smallest fragment had an area of 1.4 ha, the six medium ones vary from 7.0 to *c.* 11 ha, and the largest covered just over 15 ha. The straight line distances among fragments varied from 50 to about 800 m (Figure 1). The vegetation of the fragments is typical Atlantic Coastal Forest, and they are surrounded by a matrix composed mostly of grasses, bracken (*Pteridium aquilinum* Sadebeck) and pioneer trees like *Trema micrantha* Blume and *Cecropia pachystachya* Tréc growing on peaty soils.

On 18 August 1997, Ilhas dos Barbados was hit by a fire, which destroyed the matrix, and severely affected the edges of the fragments, as well as parts of the interior of fragment A. The interior of fragment D was little affected. As this was a potentially important factor affecting population processes, we have tried to evaluate the effects of this event on the population dynamics of the species.

M. demerarae has been detected in all eight fragments in Ilhas dos Barbados (L. C. Oliveira, *pers. obs.*). The present study was on two populations, the ones in fragments A and D. These fragments are representative of the medium

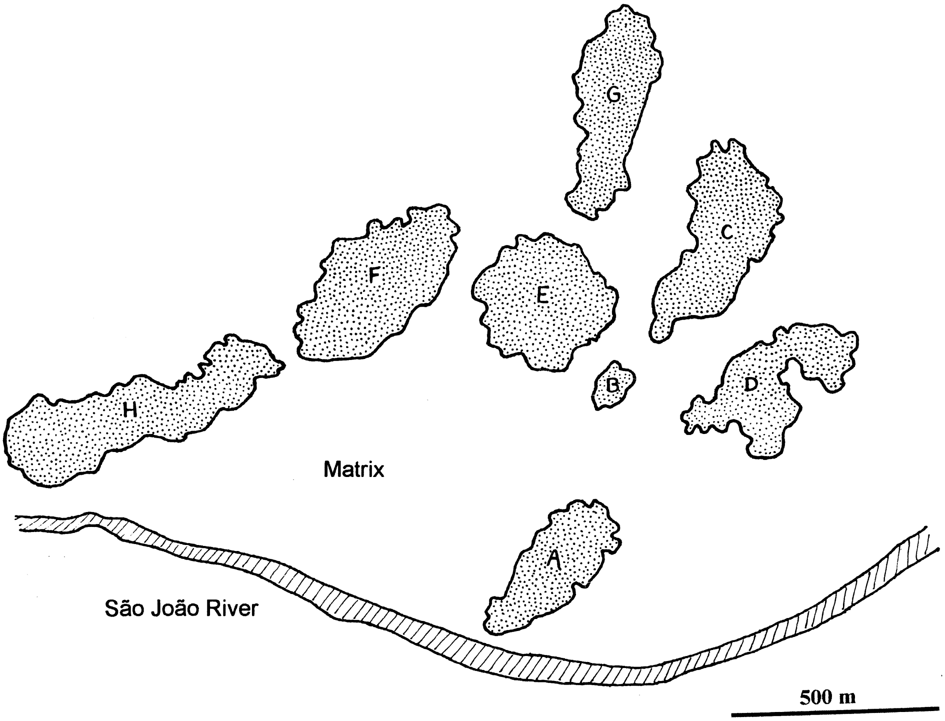


Figure 1. Ilhas dos Barbados, a group of forest fragments in the south part of the Poço das Antas Biological Reserve, Rio de Janeiro, Brazil. Areas of the fragments vary from 1.4 to *c.* 15 ha. Populations of *Micoureus demerarae* were studied in fragments A and D.

sized ones within Ilhas dos Barbados (areas 7.0 and 8.8 ha. respectively), and the minimum distance between them is about 300 m.

Sampling methods

For logistic reasons, fragments were sampled in alternate months. Data collection for the present study was carried out every other month from March 1995 to September 1998 in fragment A, and from June 1996 to August 1998 in fragment D.

Each trapping session comprised five consecutive nights. Traplines were placed 50 m apart and ran perpendicular to the longest axis of the fragment, and trap stations were established at 20 m intervals on these traplines. At every trapping station we placed a single live trap (either Tomahawk, Movarti or Sherman) on the ground. Alternate trap stations were also supplied with an additional Sherman live trap on tree branches or vines at 1.5–2 m. According to this design 94 and 116 traps were set in each trapping night in fragments A and D respectively. All traps were baited with a mixture of oat, banana, bacon and peanut butter placed on a slice of manioc. Animals captured were individually marked using numbered Michel ear-tags (Le Boulengé-Nguyen & Le Boulengé 1986) placed in both ears. Sex, reproductive condition, body measurements and tooth eruption pattern were recorded, and each individual was released at its point of capture.

Data analysis

We followed Pollock's (1982) design combining closed population models to estimate population sizes within trapping sessions with open population models to estimate survival and recruitment between sessions. For population sizes we used Burnham & Overton's (1979) jackknife estimator, which does not assume homogeneity of capture probabilities among individuals. This method was adopted because heterogeneity of capture probabilities was likely to be present in *M. demerarae* populations; many individuals were caught just once and a few were caught 20 times or more. In some trapping sessions the data were not suitable for using the jackknife; in these cases we adopted the following procedure. For every trapping session for which both jackknife and the MNKA (Krebs 1966) estimates could be obtained, we calculated the ratio jackknife estimate / MNKA estimate. This ratio is nearly always above one, as MNKA tends to underestimate population size (Hilborn *et al.* 1976). As the estimates produced by the two methods are correlated, the ratio can be used as a correction factor to multiply the MNKA estimates in the cases where only the latter is available (Gentile & Fernandez 1999). We adopted this procedure instead of using MNKA throughout because we were interested in accurate estimates of absolute population sizes, which are relevant when evaluating the prospects for persistence of the populations.

For estimating survival and recruitment rates among consecutive sessions (t and t + 1), we used the Jolly–Seber method (Seber 1982). Such values were correlated with proportional changes in population sizes ($\Delta N_{t,\ t+1}$), defined as the difference in consecutive population sizes ($N_t - N_{t+1}$) divided by N_t. For comparisons among parameters we used non-parametric statistics throughout, as either data were impossible to normalize or the homoscedasticity assumption could not be met.

For assessing the reproductive status of the population we used only the proportion of reproductive females, as in adult male marsupials the testes are permanently scrotal. Females were regarded as reproductive either when they had pouched young, were pregnant, or had swollen teats. Age structure was determined using tooth eruption sequence to separate individuals in three classes: juveniles (with deciduous premolars, dP), subadults (with definitive premolars and absent fourth upper molar, P3M3/P3M4) and adults (with complete teeth, P3M4/P3M4).

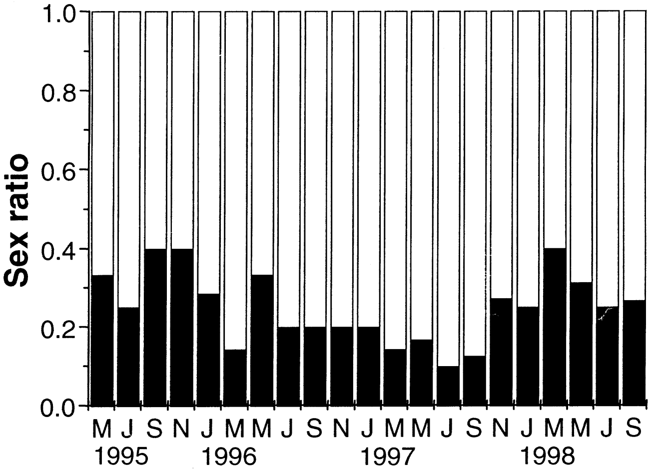
RESULTS

A total of 392 captures of 64 individuals of *M. demerarae* was obtained in fragment A, and 208 captures of 36 individuals in fragment D. Sex ratio (estimated by number of individuals of each sex captured in the whole study) was biased towards females in fragment A (25 males and 45 females, with three individuals unsexed; χ^2 with Yates correction = 5.16, $P < 0.05$); this bias was remarkably consistent along all the study (Figure 2). On the other hand, sex ratios were not biased in fragment D (18 males and 17 females, with one unsexed; χ^2 with Yates correction < 0.01, $P > 0.99$; Figure 2).

Estimated population sizes were very small. In fragment A population sizes averaged 12.25 individuals (SD = 5.83); in fragment D the average was 7.61 (SD = 4.22). Estimated population sizes seldom were as high as 20 individuals in each fragment, and sometimes were less than five (Tables 1 and 2). Given the respective fragment areas, average population densities were significantly higher in fragment A than in D (1.75 and 0.83 individuals ha^{-1} respectively; $U = 246$, $n = 21, 14$, $P < 0.001$).

Variation in population sizes generally followed a seasonal pattern. In fragment A, population sizes were low through most of 1995 (dry season), rose to a peak by the middle of the wet season 1995–1996, fell in the 1996 dry season, then started to rise again in the 1996–1997 wet season (Figure 3). The apparent seasonality was abruptly broken in the 1997 dry season as numbers continued to increase to the highest values in the study in July 1997, one month before the fire. In fragment D, from the start of the study in 1996, the pattern was roughly similar to fragment A in the same seasons, including the population increase just before the fire (Figure 3). Indeed, the population fluctuations in both fragments were synchronous until the fire (Spearman's $r_s = 0.616$, $df = 13$, $0.01 < P < 0.02$). After the fire, populations followed different trends in the two fragments. In fragment A there was a decrease in population levels,

(a) Fragment A



(b) Fragment D

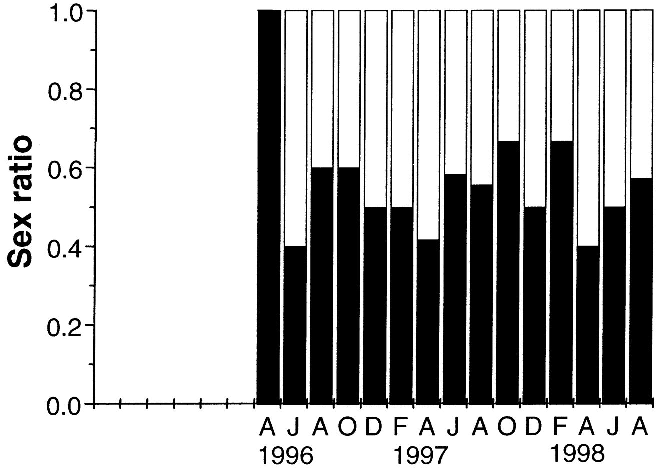


Figure 2. Variation of sex ratios in populations of *Micoureus demerarae* in two Atlantic Coastal Forest fragments: (a) fragment A, from May 1995 to September 1998, and (b) fragment D, from April 1996 to August 1998.

followed by a recovery in the following dry season leading to steady high numbers by the end of the study (Figure 3). On the other hand, in fragment D numbers fell much more abruptly reaching very low levels (an estimated population size of two individuals) before they started to recover, later than the population in fragment A did (Figure 3). Due to this difference, populations became asynchronous after the fire (r_s =0.535, df = 10, $0.05 < P < 0.10$), although there seems to be a trend towards re-establishing synchrony by the end of the study (Figure 3).

Table 1. Demographic parameters for *Micoureus demerarae* in fragment A. Population sizes were estimated using Burnham & Overton's jackknife method, except for the months denoted by *, when the MNKA method was used (see test). In the last column, sample sizes (number of females caught each month) are in parentheses. Traces (-) indicate cases where estimates cannot be obtained due to limitation of the Jolly–Seber method.

Month	Population size (N ± SE) at t	Population density at t (ind. ha^{-1})	Survivial rate from t to t_{+1}	Recruitment rate from t to t_{+1}	Proportion of reproductive females at t (n)
1995 May	4.60 ± 3.33	0.66	0.40	0.93	0.00(2)
July	6.40 ± 2.35	0.91	0.38	0.38	0.00(3)
September*	6.50	0.93	0.71	0.00	0.00(1)
November	6.80 ± 2.35	0.97	0.30	1.55	1.00(4)
1996 January	16.33 ± 9.72	2.33	0.27	0.36	0.33(3)
March	12.54 ± 6.91	1.79	0.40	1.31	0.25(4)
May	11.70	1.67	0.27	0.24	0.00(3)
July	6.60 ± 3.33	0.94	0.35	1.07	0.00(4)
September	4.80 ± 2.35	0.69	0.41	0.29	0.33(3)
November	5.60 ± 3.33	0.80	0.38	0.62	1.00(4)
1997 January*	6.50	0.93	0.13	1.27	0.75(4)
March	12.54 ± 6.91	1.79	0.55	1.16	0.33(6)
May*	15.60	2.23	0.50	1.17	0.20(10)
July	26.00	3.71	0.33	0.59	0.12(17)
September	17.20 ± 4.70	2.46	0.25	0.35	0.00(14)
November	15.00 ± 5.26	2.14	0.26	0.65	0.75(8)
1998 January	13.20 ± 4.70	1.89	0.16	1.36	0.86(7)
March	19.20 ± 5.76	2.74	0.60	0.57	0.22(9)
May	16.40 ± 4.07	2.34	0.33	0.69	0.00(7)
July	16.40 ± 4.07	2.34	—	—	0.00(11)
September	17.40 ± 4.07	2.49	—	—	0.00(11)
Averages (mean ± SD)	12.55 ± 5.83	1.75 ± 0.83	0.37 ± 0.14	0.77 ± 0.45	

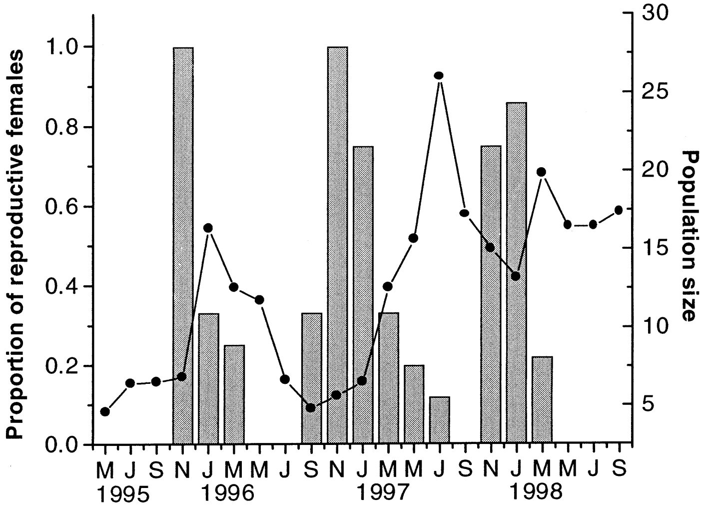
*MNKA method used to estimate population size.

Table 2. Demographic parameters for *Micoureus demerarae* in fragment D. Population sizes were estimated using Burnham & Overton's jackknife method, except for the months denoted by *, when the MNKA method was used (see text). In the last column, sample sizes (total number of females caught each month) are given in parentheses.

Month	Population size (N ± SE) at t	Population density at t (ind. ha^{-1})	Survivial rate from t to t_{+1}	Recruitment rate from t to t_{+1}	Proportion of reproductive females at t (n)
1996 June*	6.5	0.74	0.43	0.57	0.00(3)
August	5.80 ± 2.35	0.66	0.27	0.73	0.00(2)
October	5.80 ± 2.35	0.66	0.18	0.22	1.00(2)
December*	2.6	0.3	0.33	2.67	0.00(1)
1997 February	11.85 ± 7.55	1.35	0.66	1.75	0.33(3)
April	15.80 ± 5.76	1.34	0.35	0.48	0.14(7)
June	13.60 ± 3.33	1.55	0.46	0.62	0.00(4)
August*	11.7	1.33	0.08	0.17	0.00(3)
October*	3.9	0.44	0.29	0.38	0.00(1)
December	2.00 ± 0.00	0.23	0.33	1.17	1.00(1)
1998 February	3.80 ± 2.35	0.43	0.29	1.71	1.00(1)
April	6.80 ± 2.35	0.77	0.43	0.75	0.50(2)
June*	7.8	0.89	0.41	0.58	0.00(4)
August	8.60 ± 3.33	0.98	0.42	0.94	1.00(3)
Averages (mean ± SD)	7.61 ± 4.22	0.83 ± 0.42	0.35 ± 0.14	0.91 ± 0.70	

*MNKA method used to estimate population size.

(a) Fragment A



(b) Fragment D

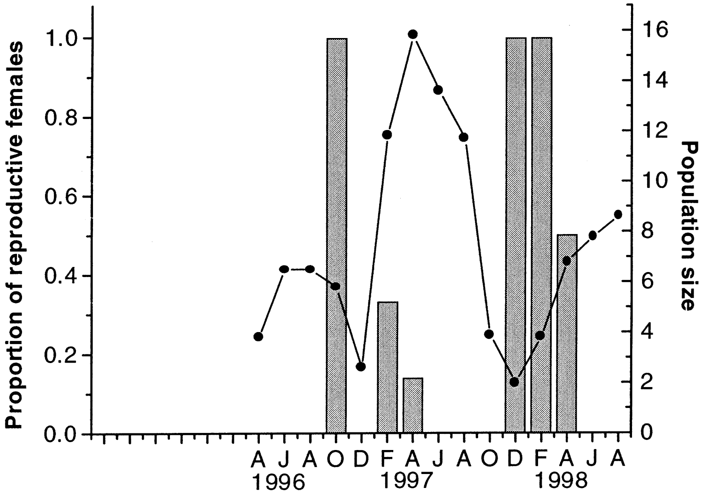
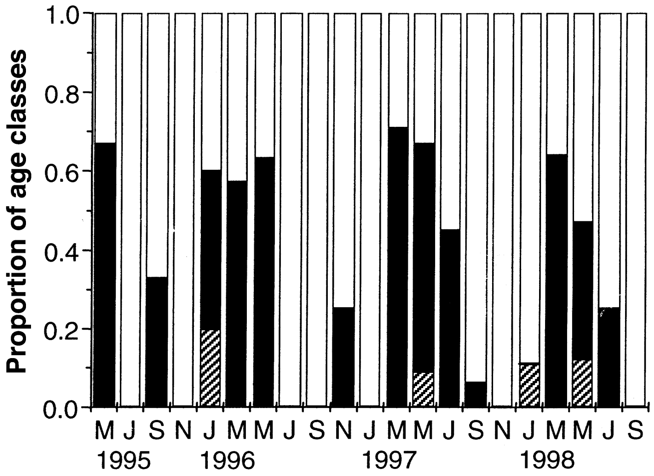


Figure 3. Variations in population sizes (line) and in the proportion of reproductive females (columns) of *Micoureus demerarae* in two Atlantic Coastal Forest fragments: (a) fragment A, from May 1995 to September 1998, and (b) fragment D, from April 1996 to August 1998.

We found seasonality in the reproduction of *M. demerarae*, in both fragments. Most of the reproductive females were found between October and March in all years (Figure 3). There were no reproductive females in October 1997, unlike the other years. In most cases, high population levels in both fragments occurred by the end of the reproductive season, soon after the peak in reproductive activity of the females. The exception was in the 1997 dry season, when the population peak was reached before the reproduction peak. All captures of young individuals were recorded from January to May (Figure 4). No female was observed weaning two litters in the same breeding season.

The variation of survival rates showed no clear seasonal pattern, whereas recruitment rates were generally higher during the months corresponding to late wet season in both fragments (Tables 1 and 2). Recruitment rates were more variable than survival rates (coefficients of variation: survival, fragment A = 39.4%, fragment D = 39.1%; recruitment, fragment A = 58.7%, fragment

(a) Fragment A



(b) Fragment D

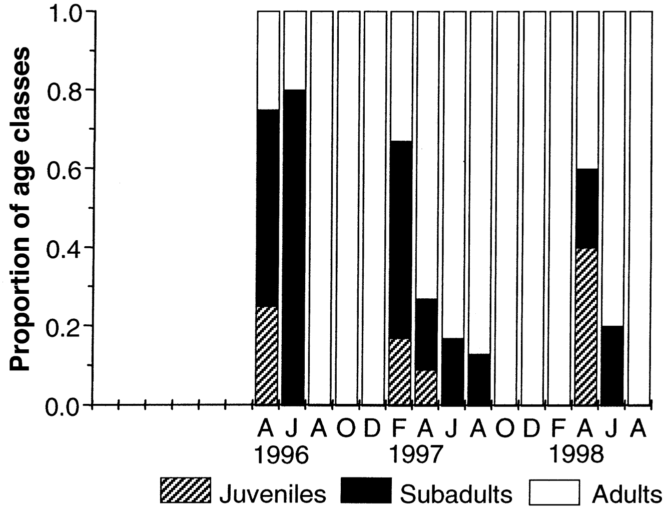


Figure 4. Variation in age structure of *Micoureus demerarae* in two Atlantic Coastal Forest fragments: fragment A, from May 1995 to September 1998 and fragment D, from April 1996 to August 1998.

D = 76.9%). In both populations, there was a positive correlation between changes in population sizes (ΔN) and recruitment rates (fragment A, $r_s = 0.579$, $P < 0.01$, 17 df; fragment D, $r_s = 0.883$, $P < 0.005$, 11 df). On the other hand, survival rates were not significantly correlated with ΔN (fragment A, $r_s = 0.08$, $P > 0.50$, 17 df; fragment D, $r_s = 0.204$, $P > 0.25$, 11 df).

During the study, a total of six movements was detected between the two fragments: four from fragment A to fragment D, and two in the opposite direction. Five were performed by two males before the fire, all between March 1996 and February 1997 (one of the individuals moved just once, from A to D, and the other moved four times back and forth among the two fragments). In January–February 1998, after the fire, one additional movement was carried out by a male from A to D.

DISCUSSION

The seasonal patterns of reproduction of *Micoureus demerarae* were expected, as marsupials in general have a well-defined breeding season (Bronson 1989). Data on the reproductive condition of *M. demerarae* are very scarce. O'Connell (1979) captured only two females during her study in Venezuela, and only one was lactating, in April. Grelle (1996) found only one reproductive female, in August and September, in the Rio Doce Forest Reserve (Minas Gerais State, Brazil). Also in forest areas in Minas Gerais, Fonseca & Kierulff (1989) found lactating females only during the rainy season, which there lasts from September to February. Our data suggest a slightly longer reproductive season than found in previous studies; this difference could be explained by the small numbers of females captured in those studies. The reproduction of marsupials is usually linked to specific factors (e.g. photoperiod) which induce hormonal stimuli, independent of how good the environmental conditions in each particular year are (Bergallo & Cerqueira 1994, Cerqueira & Bergallo 1993, Rigueira *et al.* 1987, Tyndale-Biscoe & Renfreé 1987). This could explain why the reproductive seasons were similar in all years. The only exception was that breeding started later in 1997 than in the other years, which is probably explained by the fire that hit the fragments in August of that year.

Seasonal variation in age structure reflects the seasonal reproductive pattern. Juveniles were captured more frequently towards the end of the reproductive season, from January onwards, probably because juveniles at the early breeding season are too small to be trapped independently. The pattern of population fluctuations, by its turn, reflects these reproductive patterns, as individuals only contribute for estimated recruitment when they become capturable. The seasonality of reproduction accounted for recruitment rates being more variable than survival rates. As the latter were more constant along time while the former varied widely, population fluctuations were driven mostly by the variations in recruitment. Therefore it is not surprising that variations in population sizes were correlated strongly with recruitment rates and not with survival rates.

Typical population densities for neotropical marsupials seldom exceed even one individual per hectare (Offerman *et al.* 1995, Robinson & Redford 1986); average densities estimated in the present study were not far from this range. The reasons why densities were higher in fragment A are unclear. As compared to D, fragment A presented a denser understorey and a higher density of palms. This structural difference may possibly explain the higher densities of *M. demerarae*, as the species seems to favour dense, viny vegetation with many palm trees (Emmons & Feer 1997). As no quantitative habitat description is available, this hypothesis cannot presently be tested. However, it is important to point out that, given typical densities and the areas of the fragments, the very small population sizes estimated for both of them are plausible, and one of the most interesting findings of this study is that these populations are able to persist in fragments isolated for at least several decades. Based on current thinking in conservation biology, one should not expect populations as small as these to be viable (Caughley 1994, Nunney & Campbell 1993, Soulé 1987).

Of course, classical conservation wisdom would suggest that a metapopulation structure should enhance the persistence of such small local populations (Gilpin & Hanski 1991, Hanski & Gilpin 1997). In Amazonia, Malcolm (1991) verified that *M. demerarae* was able to persist in 10-ha fragments, at least for the short term, as his study was carried out only a few years after the fragments were isolated. He was able to detect movements between continuous forest and an adjacent strip of forest separated from the former area by 350 m. At our study area, according to Pires & Fernandez (1999), the populations of *M. demerarae* form a metapopulation following Hanski & Simberloff's (1997) definition (set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible). As no local extinction or colonization was recorded, there is no evidence that this set of populations fit Levins' classical definition which put emphasis on the extinction/recolonization dynamics. Nevertheless they work as a metapopulation in the genetic sense, as gene flux among the populations is possible.

Six movements were detected between fragments A and D during this study, involving three individuals. After the present study, four additional movements were also detected within Ilhas dos Barbados, performed by two other males and linking three fragments other than the ones we studied (A. S. Pires, *pers. comm.*). It may be worth notice that all 10 movements were carried out by males. In a parallel trapping study within the matrix, a single individual of *M. demerarae* was caught, and it was a male as well (Pires & Fernandez 1999). It is possible that females are also capable of moving, but if they do, the frequency of movements is likely to be smaller for them than for males. Males being the dispersing sex is a common pattern in mammals (Chepko-Sade & Halpin 1987, Ralls *et al.* 1986). However, if the movements are strongly male-biased, this may bring interesting conservation implications as males cannot by themselves recolonize an area originating a new population. Therefore a metapopulation with this structure is likely to be more vulnerable than a metapopulation where both sexes disperse with similar frequencies.

Before the fire, fluctuations of the populations were synchronized. From a conservation point of view, such synchrony is unfortunate, as regionally correlated environmental variation would risk the survival of the whole metapopulation (Hanski 1991, Harrison 1991). The problem would be even worse in a situation where local extinctions could not be replaced. The fire of August 1997 seems to have hit the populations when they were passing through an atypical moment, when numbers of *M. demerarae* in the two fragments were much higher than in the two previous dry seasons. The fire caused different effects in each population, as the synchrony that existed previously was broken. In fragment A the slight population decrease after the fire was short-lived; the population never actually reached levels which would be considered low by pre-fire standards. In fragment D, on the other hand, the population suffered a severe decrease reaching an estimated population size of two, and remained below five individuals for several months; only by the end of the study did this population appear to be recovering, possibly towards re-establishing synchrony with the one at fragment A. Unfortunately, the difference may have been, at least in part, due to a sampling artefact. The fire hit Fragment D precisely when the August 1997 trapping session was being conducted. Three *M. demerarae* died in traps, and two others were released in poor conditions and never recaptured. Regardless of this, it seems certain that the population of *M. demerarae* at fragment D went through a severe bottleneck and probably suffered a high risk of extinction, underlining the vulnerability of populations in small forest fragments.

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LITERATURE CITED

BERGALLO, H. G. & CERQUEIRA, R. 1994. Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in northeastern Brazil. *Journal of Zoology* (*London*) 232:551–563.

BRONSON, F. H. 1989. *Mammalian reproductive biology*. University of Chicago Press, Chicago. 325 pp.

BURNHAM, K. P. & OVERTON, W. S. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936.

CARVALHO, F. M. V., PINHEIRO, P. S., FERNANDEZ, F. A. S. & NESSIMIAN, J. L. 1999. Diet of small mammals in Atlantic Forest fragments in southeastern Brazil. *Revista Brasileira de Zoociências* 1:91–101.

CAUGHLEY, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.

CERQUEIRA, R. & BERGALLO, H. G. 1993. A possible case of photoperiod controlling the reproduction of a South American marsupial. *Ciência & Cultura* 45:140–141.

CHEPKO-SADE, B. D. & HALPIN, Z. T. 1987. *Mammalian dispersal patterns: the effects of social structure on population genetics*. University of Chicago Press, Chicago. 342 pp.

EMMONS, L. H. & FEER, F. 1997. *Neotropical rainforest mammals: a field guide*. (*Second edition*). University of Chicago Press, Chicago. 307 pp.

FAHRIG, L. & MERRIAM, G. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762–1768.

FAHRIG, L. & MERRIAM, G. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.

FONSECA, G. A. B. 1985. The vanishing Brazilian Atlantic Coastal Forest. *Biological Conservation* 34:17–34.

FONSECA, G. A. B. & KIERULFF, M. C. M. 1989. Biology and natural history of Brazilian Atlantic Coastal Forest small mammals. *Bulletin Florida State Museum, Biological Sciences* 34:99–152.

GENTILE, R. & FERNANDEZ, F. A. S. 1999. A field comparison of two capture-mark-recapture estimators of small mammal populations. *Revista Brasileira de Zoologia* 16:1109–1114.

GRELLE, C. E. 1996. *Análise tridimensional de uma comunidade de pequenos mamíferos*. MSc. Dissertation, Universidade Federal de Minas Gerais. 64 pp.

GILPIN, M. E. & HANSKI, I. 1991. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, San Diego. 336 pp.

HANSKI, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42:17–38.

HANSKI, I. & GILPIN, M. E. 1997. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego. 512 pp.

HANSKI, I. A. & SIMBERLOFF, D. S. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pp. 5–26 in Hanski, I. A. & Gilpin, M. E. (eds). *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego.

HARRISON, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42:73–88.

HILBORN, R., REDFIELD, J. A. & KREBS, C. J. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology* 54:1019–1024.

KREBS, C. J. 1966, Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36:239–273.

LAURANCE, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* 5:79–89.

LE BOULENGÉ-NGUYEN, P. & LE BOULENGÉ, E. 1986. A new ear-tag for small mammals. *Journal of Zoology* (*London*) 209:302–304.

LEITE, Y. L. R., STALLINGS, J. R. & COSTA, L. P. 1994. Partição de recursos entre espécies simpátricas de marsupiais na Reserva Biológica de Poço das Antas, Rio de Janeiro. *Revista Brasileira de Biologia* 54:525–536.

MALCOM, J. R. 1991. *The small mammals of Amazonian forest fragments: pattern and process*. Ph.D. thesis, University of Florida, Gainesville. 217 pp.

NUNNEY, L. & CAMPBELL, K. A. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* 8:234–239.

O'CONNELL, M. A. 1979. Ecology of didelphid marsupials from Northern Venezuela. Pp. 73–87 in Eisenberg, J. F. (ed.). *Vertebrate ecology in the northern neotropics*. Smithsonian Press, Washington.

OFFERMAN, H. L., DALE, V. H., PEARSON, S. M., BIERREGAARD, R. O., JR. & O' NEILL, R. V. 1995. Effects of forest fragmentation on neotropical fauna: current research and data availability. *Environmental Reviews* 3:191–211.

PASSAMANI, M. 1995. Vertical stratification of small mammals in Atlantic Hill forest. *Mammalia* 59:276–279.

PIRES, A. S. & FERNANDEZ, F. A. S. 1999. Use of space by the marsupial *Micoureus demerarae* in small forest fragments in southeastern Brazil. *Journal of Tropical Ecology* 15:279–290.

PIRES, A. S., FERNANDEZ, F. A. S. & FREITAS, D. 1999. Patterns of use of space by *Micoureus demerarae*

(Marsupialia: Marmosidae) in a fragment of Atlantic Coastal Forest in Brazil. *Mastozoología Neotropical* 6:5–12.

POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.

RALLS, K., HARVEY, H. P. & LYLES, A. M. 1986. Inbreeding in natural populations of birds and mammals. Pp. 35–56 in Soulé, M. E. (ed.). *Conservation biology – the science of scarcity and diversity*. Sinauer Associates, Sunderland, USA.

RIGUEIRA, S. E., VALLE, C. M. C., VAREJÃO, J. B. M., ALBUQUERQUE, P. V. & NOGUEIRA, J. C. 1987. Algumas observações sobre o ciclo reprodutivo de fêmeas do gambá *Didelphis albiventris* (Lund, 1841) (Marsupialia, Didelphidae) em populações naturais no estado de Minas Gerais, Brasil. *Revista Brasileira de Zoologia* 4:129–137.

ROBINSON, J. G. & REDFORD, K. H. 1986. Body size, diet, and population density of Neotropical forest mammals. *American Naturalist* 128:665–680.

SEBER, G. A. F. 1982. *The estimation of animal abundance and related parameters*. (*Second edition*). Charles Griffin, London. 654 pp.

SOULÉ, M. E. 1987. *Viable populations for conservation*. Cambridge University Press, Cambridge. 189 pp.

TYNDALE-BISCOE, H. & RENFREE, M. 1987. *Reproductive physiology of marsupials*. Cambridge University Press, Cambridge. 476 pp.

WILCOX, B. A. 1980. Insular ecology and conservation. Pp. 95–117 in Soulé, M. E. & Wilcox, B. A. (eds). *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, USA.