

Use of space by the marsupial *Micoureus demerarae* in small Atlantic Forest fragments in south-eastern Brazil

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ABSTRACT. The spatial patterns presented by the marsupial *Micoureus demerarae* were studied through capture–mark–recapture in two small Atlantic Forest fragments (areas 7.1 and 8.8 ha). The study took place from March 1995 to August 1997. Considering all captures of each individual, males did not have larger home ranges within the fragments than did females. A negative correlation was found between home range sizes and population densities. For males, home ranges overlapped often, and were larger during the breeding season. For females, home ranges did not overlap except for a short period when there were many individuals present, and home range sizes were not significantly larger in the breeding season. Five movements between the two forest fragments were detected, across 300 m of open vegetation. All the movements were performed by males during the reproductive season. *M. demerarae* in the small fragments therefore displays a metapopulation structure, although possibly an atypical one where only males disperse.

KEY WORDS: Atlantic Forest, conservation, dispersal, habitat fragmentation, home range, metapopulation, *Micoureus demerarae*, spatial patterns

INTRODUCTION

With the increasing fragmentation of tropical forests (Whitmore 1997), there is a great need for detailed field data on the responses of tropical species to this process (Bierregaard *et al.* 1997). Fragmentation throws animals into a radically new situation, and how they will cope with the fragmented landscape is critically dependent upon the characteristics of their spatial patterns, such as whether they are territorial within the fragments, and whether they are able to move among different fragments. Mammals are likely to be one of the taxa most vulnerable to the effects of fragmentation (e.g. Wilcox 1980), but most of the available data come from the Amazonian region (Offerman *et al.*

1995). In the biologically rich Atlantic Forest along the Brazilian east coast, fragmentation has already reached a very advanced stage (Dean 1996, Fonseca 1985) and yet detailed information on its mammals' responses to the process is very scarce. Therefore, it is a critical priority to carry out studies on responses of Atlantic Forest mammals to fragmentation.

This paper reports the results of a 30-mo field study on the spatial patterns of the long-furred woolly mouse opossum *Micoureus demerarae* (Thomas 1905) in small fragments of Atlantic Forest. The two fragments studied, with areas below 10 ha, are representative of the modal size class of fragments remaining today in the intensely fragmented forest in south-east Brazil. *M. demerarae* (previously *Marmosa cinerea*, then *Micoureus cinereus*) is a medium sized didelphid: adults weigh up to 130 g, males being slightly larger than females. The species is widely distributed in South America, from Colombia to northern Argentina, Paraguay and eastern Brazil (Emmons & Feer 1997). It is common in Atlantic Forest, where it seems to favour areas of dense forest, rich in vines and palm trees, although it also occurs in open, high forest (Emmons & Feer 1997), or even in *Eucalyptus* forests with a native subcanopy (Stallings 1989). *M. demerarae* is nocturnal, its diet is composed mostly of insects and fruits (Leite *et al.* 1994, 1996; Nowak 1991), and it has arboreal habits (Charles-Dominique *et al.* 1981, Miles *et al.* 1981, Passamani 1995, Stallings 1989, Voltolini 1998).

The main aspects investigated in the present study included home range sizes and patterns of overlap among ranges of different individuals, and the relationships of these patterns with sex, reproductive condition and population density. Use of the matrix of open areas separating the fragments and frequency of movements between fragments were also studied.

STUDY SITE

The study was carried out in two Atlantic Forest fragments which are part of a group of eight such fragments known as 'Ilhas dos Barbados' ('Islands of the Howler Monkeys'), within Poço das Antas Biological Reserve. Poço das Antas is the largest reserve of the vanishing lowland Atlantic Forest in Rio de Janeiro state, south-east Brazil (22°30'–22°33'S, 42°15'–42°19'W). The climate of the region is warm tropical with average annual temperatures above 24 °C. According to the meteorological station of the Golden Lion Tamarin Project, 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 vegetation of the fragments is typical Atlantic Forest, *c.* 20 m tall, rich in palms, mostly *Astrocaryum aculeatissimum* and *Attalea* spp. The forest was disturbed to a moderate degree by selective logging in the past, but otherwise has been protected from any further disturbances since 1975, except for fires which

occasionally burned the matrix (open areas around the fragments) and damaged mostly the edge of the fragments themselves. The vegetation of the matrix is composed of grasses, bracken (*Pteridium*) and pioneer trees like *Trema micrantha* and *Cecropia* spp. growing on peaty soils. The areas of the fragments and distances between them were estimated from aerial photographs taken in December 1994, just before the start of the study, on a scale of 1:5000. The area of the forest fragments varied from 1.4 to *c.* 15 ha. The two fragments we studied, 'A' and 'D', had areas of 7.1 and 8.8 ha, respectively, and the shortest distance between them was *c.* 300 m. Distances to other fragments varied from 115 m to *c.* 1200 m.

METHODS

A trapping session was carried out every second month from March 1995 to July 1997 in fragment A and from April 1996 to August 1997 in fragment D, each trapping session comprising five consecutive nights of capture. The study was abruptly cut short when a fire on 18 August 1997 destroyed the matrix and damaged fragment A, and, to a lesser degree, fragment D. Although the trapping programme was resumed, the spatial patterns are likely to have been affected by this strong disturbance, and therefore we limit our analysis to the patterns shown by the animals before the fire.

Trapping lines were marked transversely to the greatest length of each fragment. Lines were 50 m apart and within each line trapping points were 20 m apart. Our goal was to cover the whole area of each fragment rather than sampling just a part of it. At each capture point a live-trap (either Tomahawk, Sherman or wire-mesh Movarti traps) was set on the ground; at every second point an additional Sherman trap was set on tree branches or vines at breast height (*c.* 1.5 m). This design resulted in 94 traps being set each trapping night in fragment A (64 on the ground and 30 in trees) and 116 in fragment D (78 on the ground and 38 in trees). All traps were baited with a mixture of oat, banana, bacon and peanut butter placed on a manioc slice.

Additional trap lines, with 20 m trap spacing, were set in the matrix half way between the two fragments to determine if *M. demerarae* uses it, either as a regular habitat or just crosses it in transit between the woodlots. In August 1995 and January, March and May 1996, traps were set around fragment A (a total of 508 trap-nights). From May to August 1997 traps were set between A and D (a total of 560 trap-nights).

The animals were marked using individually numbered Michel ear-tags (Le Boulengé-Nguyen & Le Boulengé 1986) placed at both ears to prevent the loss of a tag hindering identification. The following data were recorded: sex, reproductive condition (pouch young and swollen mammae for females, position of testes for males), measurements (weight, tail length and internal ear length) and teeth eruption pattern. After recording the data each individual was released at the point of capture.

Home range areas were estimated through the minimum convex polygon method (Jennrich & Turner 1969), using the program MCPAAL, from the U.S. Fish and Wildlife Service. As minimum convex polygon estimates are dependent on the number of captures per individual, all estimates of home range sizes were based on individuals with five or more captures, for which estimates were more reliable; this criterion follows Lidicker (1966) and Murúa *et al.* (1986), among others.

For evaluating the effect of reproductive condition on home range size, home ranges were also calculated separately for reproductive and non-reproductive seasons. Judging from the patterns showed by the females (as adult males' testes remain scrotal even when they are not reproductive), *M. demerarae* reproduced from September to March each year at the Ilhas dos Barbados during the present study (F. S. Rocha, *pers. comm.*). Home range estimates for the reproductive and non-reproductive seasons were based on all captures of each individual within a given season, provided that they still met the minimum of five captures.

For the analysis of patterns of overlap, the study was divided into periods because there was complete population turnover during the study, and it would not be appropriate to study overlap among individuals that were not alive simultaneously. Periods were separated by times of intense population turnover, so that the identity of the population in each fragment was more similar within periods than between them. However, some individuals survived from one period to the next and therefore are represented in both. As the population turnover is not instantaneous, in spite of seasonal reproduction of *M. demerarae*, the choice of the periods had to be arbitrary to some extent. The periods used were: March 1995 to May 1996, June 1996 to January 1997, and February to August 1997. For analysing overlap within each of these periods, only the captures of each individual actually obtained within the period were used.

Home range areas were correlated with population densities, using the average home range sizes in each period as one variable and the average population density in each period as the other. Population density was calculated for each month in each fragment. Density for each period was calculated as the average of the values for the months that comprised the period. Population sizes were estimated by Burnham & Overton's (1979) jackknife method, using the program Jackknife (D. Fuchs, *pers. comm.*). This method is robust to heterogeneity of capture probabilities among individuals, which clearly happens in the populations studied.

We used the non-parametric Mann–Whitney U-test (Zar 1996) throughout when comparing the values of the parameters between the two sexes because in several cases (especially regarding home range areas) either our sample sizes were not enough to allow checking of the normality of data or the homoscedasticity assumption could not be met.

RESULTS

In fragment A, there were 183 captures of 38 *M. demerarae* (nine males, 28 females and one unsexed). In fragment D, 24 individuals (14 males and 10

females) were captured 119 times. *M. demerarae* was the most frequently caught among nine species of small mammals recorded in the fragments during the study, the other species being the marsupials *Caluromys philander*, *Didelphis aurita*, *Metachirus nudicaudatus*, *Philander frenata* and *Gracilinanus microtarsus*, and the rodents *Oryzomys capito*, *Akodon cursor* and *Oligoryzomys nigripes*.

In the matrix, only two captures of a single male *M. demerarae* were recorded, both within a single trapping session. This individual was never captured in the fragments. *M. demerarae* was therefore rare in the open vegetation where the small mammal community was dominated by four species of rodents (*Oligoryzomys nigripes*, *Oryzomys capito*, *Akodon cursor* and *Bolomys lasiurus*).

Although trapping effort with tree traps was less than half the trapping effort with ground traps, most captures were obtained by the former. In A there were 99 captures in trees and 84 on the ground; in D there were 74 and 45 respectively. Frequency of captures was different for tree traps and ground traps (χ^2 with Yates' correction, 74.60 for fragment A and 46.19 for D; both, $P < 0.001$); *M. demerarae* was therefore caught significantly more often in trees at breast height than on the ground.

Home range sizes could be estimated for five males and 13 females in fragment A and for five males and three females in fragment D (Table 1). Two

Table 1. Home range areas of individuals of *Micoureus demerarae* in two Atlantic Forest fragments (1995–1997), as estimated by the minimum convex polygon method. N_{caps} = total number of captures of each individual. HRS = home range size using all the captures. HRS_{rep} = home range size in the reproductive season. $\text{HRS}_{\text{nonrep}}$ = home range size in the non-reproductive season.

Fragment	Sex	Individual	N_{caps}	First-last captures	HRS (ha)	HRS_{rep} (ha)	$\text{HRS}_{\text{nonrep}}$ (ha)
A	M	1	05	Jul 95–Nov 95	1.30	–	–
		2	08	Sep 95–Abr 96	1.75	1.75	–
		3	06	Sep 96–Jan 97	0.65	0.65	–
		4	08	Mar 97–Jul 97	0.15	–	0.15
		5	05	May 97–Jul 97	0.10	–	0.10
A	F	1	13	Mar 95–May 96	0.60	0.20	–
		2	05	Jul 95–Jan 96	0.30	0.30	–
		3	07	Sep 95–Jan 96	0.75	0.75	–
		4	05	Mar 96–May 96	0.40	–	–
		5	07	Mar 96–Jan 97	0.65	–	–
		6	21	May 96–Jul 97	0.50	0.15	0.10
		7	07	Mar 96–Jan 97	0.90	0.75	–
		8	15	Jan 96–Jul 97	0.40	–	–
		9	08	Mar 97–Jul 97	0.25	–	0.25
		10	05	Mar 97–Jul 97	0.20	–	–
		11	06	Mar 97–Jul 97	0.35	–	0.35
		12	05	May 97–Jul 97	0.20	–	0.20
		13	05	May 97–Jul 97	0.15	–	0.15
D	M	6	05	Jun 96–Aug 96	0.40	–	–
		7	22	Aug 96–Aug 97	2.45	2.45	0.40
		8	06	Feb 97–Jun 97	0.40	–	0.40
		9	05	Apr 97–Aug 97	0.50	–	–
		10	06	Feb 97–Aug 97	0.50	–	0.20
D	F	14	08	Apr 96–Oct 96	0.40	–	–
		15	17	Jun 96–Aug 97	1.10	0.40	0.55
		16	05	Apr 97–Jun 97	0.10	–	0.10

females and one male had their capture points in a line, and therefore their home range sizes could not be estimated, although they were plotted to illustrate their position in relation to the remaining ranges (see Figure 1b,c). Considering all captures for each individual, home ranges ranged from 0.10 to 2.45 ha for males ($n = 10$) and from 0.10 to 1.10 ha ($n = 16$) for females (Table 1). Home range sizes did not differ significantly between sexes ($U = 100.5$, $P = 0.286$). The same was true considering each fragment separately (for A, $U = 37$, $P = 0.703$; for D, $U = 10$, $P = 0.571$). Home ranges also did not differ between fragments for males ($U = 13$, $P = 1.00$) nor females ($U = 20$, $P = 1.00$).

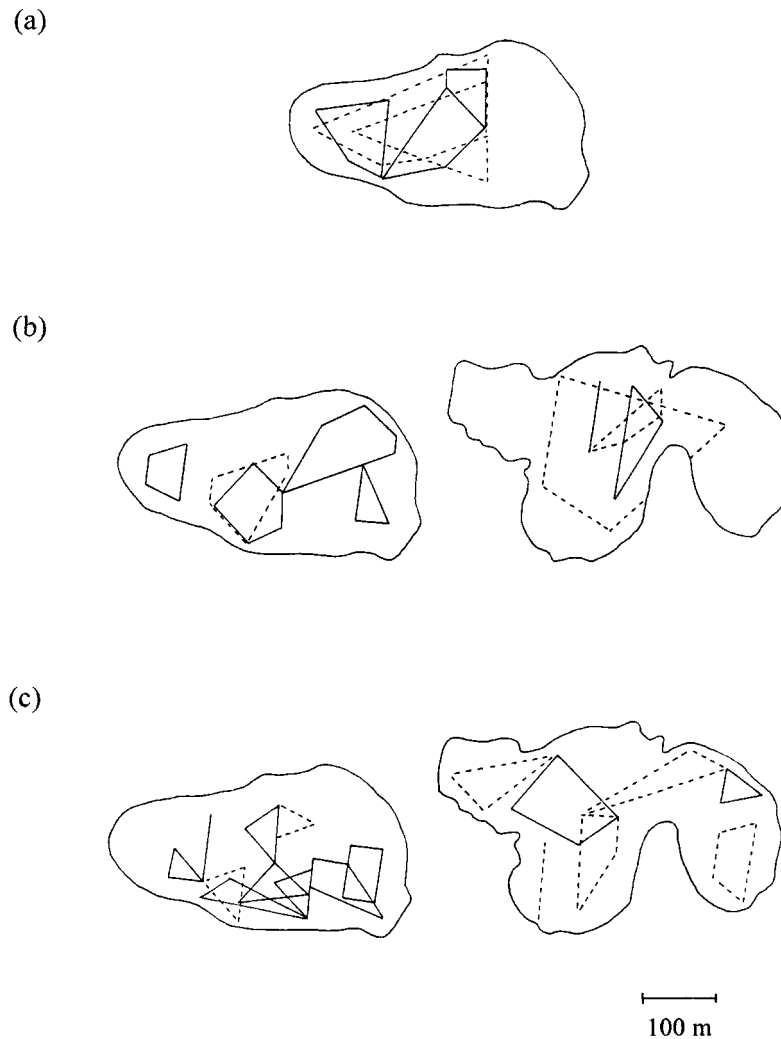


Figure 1. Home ranges of *Micoureus demerarae* in two forest fragments at Poço das Antas Biological Reserve, south-eastern Brazil, as estimated by the minimum convex polygon method, for three different periods: (a) March 1995 to May 1996; (b) June 1996 to January 1997; (c) February to August 1997. Females' ranges are shown by solid lines and males' by broken lines.

Some striking patterns appeared in the relationship between home range sizes and population densities. For example, females had much smaller home ranges in fragment A when there were more females with established home ranges simultaneously in that fragment. Female home ranges were significantly smaller in the last period, when there were six to eight established females, than during the rest of the time, when there had never been more than four females (Figure 1c; $U = 39$, $P = 0.0031$). More generally, considering both sexes and all study periods, there seems to be a negative correlation between average home range sizes (sexes pooled) and population densities (Figure 2; Pearson's $r = -0.814$; $df = 3$, one-tailed, $P < 0.05$).

Within the reproductive season, male home ranges overlapped extensively with each other and with females' ranges in both fragments (Figure 1a,b). However, out of the breeding season male home ranges were small and did not show overlap with each other, although they showed some overlap with females' ranges (Figure 1c). Males' home ranges were significantly larger in the reproductive than in the non-reproductive season ($U = 15$, $P = 0.0357$).

Home ranges of females showed no overlap with each other in either fragment during most of the time (Figure 1). The exception was in fragment A in the last period, mentioned above, when the many females present showed small home ranges, which overlapped considerably (Figure 1c). For females, home ranges were not significantly greater within the breeding season than out of it ($U = 36$, $P = 0.397$).

Although large in average, male home range sizes in the reproductive season were also very variable, and consequently they were not significantly larger than females' ranges ($U = 19$, $P = 0.067$). The difference between sexes was not significant for the non-breeding periods as well ($U = 19$, $P = 0.683$).

Among the females, the size and shape of home ranges were strongly dependent on the ranges of their neighbours within the population. A typical

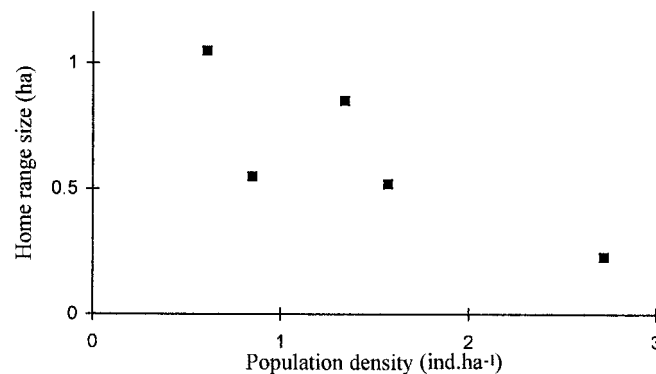


Figure 2. Relationship between average home range sizes and average population densities of *Micoureus demerarae* in each study period. Periods were: March 1995 to May 1996, June 1996 to January 1997, and February to August 1997; one of the two fragments was studied in the two last periods only. Home range sizes were estimated by the minimum convex polygon method, and population densities were estimated by population size (calculated by the jackknife method) divided by fragment area.

case was that after a female stopped being caught, either a neighbour expanded her range using at least part of the area previously used by the one that disappeared, or one or more new female(s) established herself (themselves) in the same area.

Five movements were detected between the two fragments, all carried out by two male individuals. One movement happened between March and April 1996, and the remaining four between August 1996 and February 1997.

DISCUSSION

There are only two previous detailed studies on spatial patterns of *M. demerarae*: the one by Grelle (1996), at a large tract of Atlantic Forest, the Rio Doce Forest Reserve, and the one by Pires *et al.* (in press) in one of the fragments used in the present study (fragment A). Both studies found that males of *M. demerarae* had overlapping home ranges whereas females had smaller, non-overlapping ranges, and suggested that such a pattern was consistent with this species having a promiscuous mating system.

Malcolm (1991) studied responses of *M. demerarae* to fragmentation and found that it seemed to thrive in small, recent (< 10 y isolation) Amazonian forest fragments. Field experiments with radio transmitters also showed that it was able to cross open habitats separating fragments: two out of five individuals homed after being released at the other side of a strip of pasture 150 m to 350 m wide. On the other hand, in Atlantic Forest Fonseca & Robinson (1990) found *M. demerarae* only in their largest forest area (the same Rio Doce Forest Reserve mentioned above), but the species was not found in three smaller fragments (60, 80 and 860 ha).

In the present study males did not have consistently larger home ranges than females, and therefore we were not able to confirm previous findings by both Grelle (1996) and Pires *et al.* (in press) on this point. Clearly, the high variability in home range sizes within sexes prevented finding a significant difference between sexes. This is likely to reflect variation of the home range sizes across time, as this study was longer than both previous studies. Incidentally, the 8 mo of Grelle's study (March–October) corresponded mostly to the *M. demerarae* non-reproductive season, and his home range estimates for males are very similar to our estimate for that sex in the non-reproductive season (0.29 ha and 0.25 respectively).

In the present study, home ranges were influenced by two factors that vary across time: reproductive status (at least for males) and population density. Both factors are correlated to some extent, as the population peaks in our study area occurred in the early non-reproductive season (T.B. Quental, *pers. comm.*). Such peaks are due to delayed effect of reproduction late in the previous breeding season, as individuals only begin to be independent and thus trappable when they are a few months old. Although there are reasons to expect

home ranges to be bigger within the reproductive season, especially large overlapping ranges for males to maximize access to females (Ostfeld 1990), on the basis of the data presently available we cannot separate the effects of reproductive status from those of population density *per se*. Nevertheless, a general pattern that arose was a density-dependent variation in home range sizes. Such a pattern is well documented for some small mammals, especially rodents from temperate regions (e.g. Attuquayefio *et al.* 1986, Fernandez *et al.* 1996) and from the neotropics (Adler *et al.* 1997), but we know of no previous study showing this relationship for any neotropical marsupial.

The spatial patterns shown by females confirmed previous studies (Grelle 1996, Pires *et al.* in press) indicating that they are territorial most of the time. The increased overlap in females' home ranges when many females were present in A may be due to fragmentation, as it could be avoided in continuous forest by dispersal to suboptimal patches. Andreassen *et al.* (1986) found that in root voles (*Microtus oeconomus*) fragmentation restricted females' movements more than males' movements; this pattern is consistent with the one found in the present study and with suggestions by Ims *et al.* (1993) and Wolff *et al.* (1997) that voles could be used as a model system to understand responses to fragmentation.

The five movements were performed by just two individuals, but incidentally after the fire two additional movements were detected, performed by two different males. On the other hand, females would not be expected to move due to their territoriality; for a female, to move would imply losing her established home range and taking the risk of not being able to secure a new one in another, unfamiliar, fragment.

The detection of movements between fragments—at least 300 m (straight line distance) crossing open vegetation—corroborates Malcolm's (1991) findings. The higher trapping success of the tree traps in this study confirms that *M. demerarae* is mostly an arboreal species; nevertheless, it is able to cross several hundred metres of grasses and bracken when moving among Atlantic Forest fragments. In the present study *M. demerarae* was very rare in the matrix (only two consecutive captures of the same individual in 1068 trap-nights), suggesting that the animals probably pass through it rather than living there. Unfortunately, the destruction of the open vegetation by the fire at the end of this study prevented a better understanding of how *M. demerarae* uses the intact matrix, as it will take several years until the pioneer trees re-establish.

Whatever the case, what is clear is that the populations of *M. demerarae* we studied are part of a metapopulation, following Hanski & Simberloff's (1997) definition by which a metapopulation is 'a set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible'. This seems to be a valuable result, as a recent review on dynamics of metapopulations of small mammals (Krohne 1997)

shows the scarcity of data on movements of small mammals, especially in the neotropics, from where not a single study is quoted. Besides, the situation described in the present study seems to be an interesting case where the value of connections among populations to enhance the survival of the metapopulation may well be illusory. Only males were shown to disperse and to use the matrix; if this is indeed the case, empty patches cannot be colonized because populations cannot be founded by males alone. Therefore, from the point of view of survival probabilities, this metapopulation is likely to behave more as a series of relict populations than as a typical metapopulation. If females are eventually found to disperse with a much smaller frequency than males, we would have some intermediate pattern but nevertheless very different from the commonly held picture of metapopulation survival being enhanced by dispersal among patches. Therefore, to understand better the structure and dynamics of this metapopulation of a neotropical mammal is a matter of great conceptual interest as well as conservation value.

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