

MOVEMENT DISTANCES OF FIVE RODENT AND TWO MARSUPIAL SPECIES IN FOREST FRAGMENTS OF THE COASTAL ATLANTIC RAINFOREST, BRAZIL

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Abstract. Movement distances provide information on diverse population biological parameters and are essential in understanding the ecology of a species. Mean distances moved between successive captures (SD), distribution of movement distances, and the mean maximum distances moved (MMDM) were investigated in five rodent and two marsupial species in forest fragments of the coastal Atlantic rainforest (Mata Atlântica) in the state of São Paulo, Brazil. The investigated species were the rodents *Akodon montensis* (Thomas, 1902), *Oligoryzomys nigripes* (Olfers, 1818), *Delomys sublineatus* (Thomas, 1903), *Oryzomys russatus* (Wagner, 1848), and *Thaptomys nigrita* (Lichtenstein, 1829), and the marsupials *Marmosops incanus* (Lund 1840), and *Gracilinanus microtarsus* (Wagner, 1842). *Akodon montensis* differed significantly from all other species and moved the lowest SD and MMDM. The marsupials differed significantly from most of the rodents and moved the largest SDs. All species showed the highest frequency of movements in a distance class of 0–20 m. Differences between sexes in SD was detected for *O. nigripes*, *O. russatus*, and *G. microtarsus*, males moving significantly longer distances than females. The different study sites had no influence on SD in any of the investigated species. Only the males of *G. microtarsus* showed a seasonal variation in SD, moving longer distances during reproductive activity. Accepted 15 August 2006.

Key words: distance moved between successive captures, marsupials, Mata Atlântica, rodents, small mammals.

INTRODUCTION

Movements of animals are an important element in their ecology (Turchin 1991, Diffendorfer *et al.* 1995, Slade & Russell 1998) and provide essential information about the spatial distribution of species (Stapp & Van Horne 1997). Movement patterns and distances are related to several aspects of the ecology of a species, like genetic structure, feeding habits, food availability, mating systems, and reduction to exposure to predators (Slade & Swihart 1983, Austad & Sunquist 1986, Sunquist *et al.* 1987, Barnum *et al.* 1992, Stapp & Van Horne 1997, Roche *et al.* 1999). Moreover, movements are associated with the social organization and population dynamics of a species (Slade & Swihart 1983, Bowers *et al.* 1996, Mendel & Vieira 2003, Bergallo & Magnusson 2004). The knowledge of distances moved by different species is necessary to calculate basic parameters of the ecology

of a population, such as density estimates, as well as to understand its genetic structure (Mendel & Vieira 2003).

The use of distances moved between successive captures instead of area calculations like minimum convex polygons has several advantages. Movement distances are comparatively easy to assess, easy to calculate, and can be used even for individuals with capture histories too brief for models (Stickel 1954, Slade & Swihart 1983). Studies have indicated that distance measurements are correlated with home range size (Faust *et al.* 1971, Slade & Russell 1998). They provide an average index of the home range for the species (Davis 1953) and can be used for comparison between groups within a species (e.g., age- or sex-specific analyses, Slade & Russell 1998) or between different species (Gentile & Cerqueira 1995). Nevertheless, using trapping distances as an index for spatial use also has some disadvantages. Some individuals might preferentially be caught in one trap or make a trap unattractive for others. The capture probabilities

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between individuals or species might differ because of different behavioral responses or heterogeneity due to age or sex, or to time effects (White *et al.* 1982). Therefore, the use of distances between successive captures to reflect movements of species is not directly comparable to home range size data obtained by direct measurements (e.g., radio-tracking).

The coastal Atlantic rainforest of Brazil (Mata Atlântica) is one of the most diverse but at the same time one of the most threatened environments in the world (Myers *et al.* 2000, Galindo-Leal & de Gusmão Câmara 2003). Only about 8% of its original extent still remains and it harbors a great variety of small mammal species (Emmons & Feer 1997, Stevens & Husband 1998) with an overall high percentage of endemic species (Fonseca *et al.* 1996, Stevens & Husband 1998). For most Mata Atlântica species information about distances moved is limited.

During a capture-recapture study, in the course of a study on population dynamics of small mammals inhabiting the coastal Atlantic rainforest, we investigated the distances moved between successive captures (SD, Murie & Murie 1931), the distribution of movement distances, and the mean maximum distance moved (MMDM, Wilson & Anderson 1985) of seven small mammal species in a trapping grid. We focussed on the differences in movement length (SD, MMDM) between species and further investigated differences in SD between gender, study sites, and capture sessions.

METHODS

Study area. The study was conducted in the region of Caucaia do Alto (23°40'S, 47°01'W), situated in the municipalities of Cotia and Ibiúna, São Paulo state, about 80 km south-west of the city of São Paulo, Brazil, in a transition zone between dense ombrophilous forest and semi-deciduous forest classified as "Lower Montane Atlantic rainforest" (Oliveira-Filho & Fontes 2000). The altitude varies between 800 and 1100 m (Ross & Moroz 1997). Monthly mean temperature ranges from a minimum of 11°C to a maximum of 27°C. Annual precipitation equals 1300–1400 mm and fluctuates seasonally with the driest and coldest months between April and August.

The area includes a fragmented area and a large, lower mountainous Atlantic rainforest area (Morro Grande Reserve). The fragmented area consists of secondary forest fragments embedded in an agricultural landscape. Secondary forest covers 31% of the land-

scape, which is dominated by anthropogenic habitat (agricultural fields: 33%; areas with rural buildings or urban areas: 15%; vegetation in early stages of regeneration: 10%; pine and eucalyptus plantations: 7%; others: 4%). The Morro Grande Reserve also consists mainly of secondary forest. Only a minor part of the reserve provides mature forest.

Animals were captured in five forest fragments of different sizes (14–175 ha), and in the Morro Grande Reserve (10 700 ha). All sites are of secondary growth forest and between 50 and 80 years of age (Godoy Teixeira 2005). Two fragments are about 14 ha (S1, S2), another two fragments are approximately twice this size (30 ha; S3, S4), and the fifth fragment (S5) is the largest, embracing 175 ha of secondary forest. The control site (CS) also consists of secondary forest and is part of the Morro Grande Reserve. A more detailed description of the study area can be found in Pardini *et al.* (2005).

Data collection. A regular trapping grid of one hundred trap stations 20 m apart was established in all six study sites. The grid consisted of 10 x 10 trap stations, except in two sites where the shape of the fragments and the general objective of placing all traps within the forest required that the trapping grid be slightly modified. Two live-traps (H. B. Sherman Traps Inc., Tallahassee, USA) were set at each trap station, one small (23 x 9 x 8 cm) and one large (38 x 11 x 10 cm). One of the traps was set on the ground, and the other at about 1.0 to 1.5 m above the ground, alternating the positions of small and large traps between trap stations.

Data were collected during five trapping sessions in each of the study sites from July 2003 to March 2005 (1st session: 23.07.–19.09.2003, 2nd session: 27.09.–7.11.2003, 3rd session: 4.03.–7.04.2004, 4th session: 18.05.–26.06.2004, 5th session: 27.01.–3.03.2005). Each trapping session consisted of six nights of capture, for a total of 6000 trap-nights per study site. Traps were baited with banana and a mixture of peanut butter, oat, and sardines, left open for the night, checked every morning and rebaited if necessary. Captured animals were anesthetized (Forene®, Abbott GmbH, Wiesbaden, Germany) for 1–2 minutes and marked individually by numbered ear tags (Fish and small animal tag size 1, National Band and Tag Co., Newport, Kentucky, USA). In addition to sexing and weighing, the length of their tibia was measured to the nearest 0.5 mm. All individuals were released subsequently at their respective trapping location.

Statistical analysis. All individuals captured more than once were included in the calculations of SD. The SD was compared between species, sexes, study sites, and between sessions (seasonal variation). To investigate the distribution of movement distances, the distances were grouped into classes. The maximum distance moved was calculated for each individual at each capture session, and the mean maximum distance moved (MMDM) was calculated for each species.

Non-parametric statistics were used because distances were not normally distributed. To account for multiple comparisons Bonferroni correction was applied (Sachs 1992). All tests were conducted on SPSS 11.5.1 (SPSS Inc., Chicago, USA) using a significance level of 0.05.

RESULTS

Species captured. A total of 1338 individuals belonging to 13 species were captured 3031 times (Table 1), leading to a mean trapping success of 8.4 % in 36 000 trap-nights. Movement distances were calculated for the rodents *Akodon montensis* (Thomas, 1902), *Oligoryzomys nigripes* (Olfers, 1818), *Delomys sublineatus* (Thomas, 1903), *Oryzomys russatus* (Wagner, 1848), and *Thaptomys nigrita* (Lichtenstein, 1829), as well

as for the marsupials *Marmosops incanus* (Lund, 1840) and *Gracilinanus microtarsus* (Wagner, 1842). Only *A. montensis* and *M. incanus* were captured at all six study sites and in every capture session. The didelphid marsupials *Didelphis aurita* (Wied-Neuwied, 1826), *Monodelphis americana* (Müller, 1776), and *Micoureus paraguayanus* (Oken, 1816), and the rodents *Juliomys pictipes* (Osgood, 1933), *Oryzomys angouya* (Fischer, 1814), and *Brucepattersonius aff. iheringi* (Thomas, 1896) were only occasionally captured and therefore excluded from this analysis (Table 1).

Differences between species in movement patterns. The seven species differed significantly in their distance moved between successive captures (SD, Table 2; Kruskal-Wallis-Test, $\chi^2 = 158.07$; $df = 6$; $p < 0.0001$). Pairwise comparison (Mann-Whitney U-Test) showed differences between the movements of *A. montensis* and all other species (all $Z > -3.07$; all $p < 0.002$), between *T. nigrita* and *M. incanus* ($Z = -2.78$; $p = 0.005$), *T. nigrita* and *G. microtarsus* ($Z = -3.19$; $p < 0.001$), *O. nigripes* and *M. incanus* ($Z = -4.21$; $p < 0.0001$), *O. nigripes* and *G. microtarsus* ($Z = -4.43$; $p < 0.0001$), *D. sublineatus* and *M. incanus* ($Z = -2.72$; $p = 0.007$), and *D. sublineatus* and *G. microtarsus* ($Z = -3.56$; $p < 0.0001$). The former species always

TABLE 1. Taxonomy, body mass, locomotion habits, and numbers of individuals captured of each species (males, females, and unsexed individuals in parenthesis). Taxonomy, body mass, and locomotion habits are based on Musser & Carleton (1993), Tyndale-Biscoe (2005), and personal observations.

Species	Family	Subfamily	Body mass	Locomotion	Number of individuals captured
<i>Akodon montensis</i>	Muridae	Sigmodontinae	19-57 g	terrestrial	476 (252/213/11)
<i>Thaptomys nigrita</i>	Muridae	Sigmodontinae	12-30 g	fossorial	79 (44/33/2)
<i>Oligoryzomys nigripes</i>	Muridae	Sigmodontinae	9-40 g	scansorial	158 (99/55/4)
<i>Delomys sublineatus</i>	Muridae	Sigmodontinae	20-75 g	terrestrial	153 (75/73/5)
<i>Oryzomys russatus</i>	Muridae	Sigmodontinae	40-120 g	terrestrial	43 (24/17/2)
<i>Marmosops incanus</i>	Didelphidae	Thylaminae	13-140 g	semi-arboreal	144(72/69/3)
<i>Gracilinanus microtarsus</i>	Didelphidae	Thylaminae	19-29 g	arboreal	140 (75/59/6)
<i>Didelphis aurita</i>	Didelphidae	Didelphinae	700-1500 g	scansorial	42 (15/24/3)
<i>Monodelphis americana</i>	Didelphidae	Marmosinae	23-35 g	terrestrial	14 (8/6/0)
<i>Micoureus paraguayanus</i>	Didelphidae	Marmosinae	80-150 g	scansorial	2 (0/2/0)
<i>Oryzomys angouya</i>	Muridae	Sigmodontinae	40-120 g	scansorial	35 (17/14/4)
<i>Juliomys pictipes</i>	Muridae	Sigmodontinae	11-30 g	arboreal	32 (18/11/3)
<i>Brucepattersonius aff. iheringi</i>	Muridae	Sigmodontinae	11-35 g	terrestrial/ fossorial	20 (13/6/0)
Total					1338

TABLE 2. Number of individuals recaptured, number of captures, mean distance moved between successive captures (SD), and mean maximum distance moved (MMDM), in meters, with standard errors for the different species. In case of significant sexual differences the sexes are separated.

Species	Number of individuals recaptured	Total number of captures (including recaptures)	Mean distance moved between successive captures (SD)	Mean maximum distance moved (MMDM)
<i>A. montensis</i>	392	685	19.54 ± 1.05	26.30 ± 1.37
<i>T. nigrita</i>	28	41	29.98 ± 3.93	38.29 ± 5.65
<i>O. nigripes</i>				
males	46	55	31.81 ± 3.67	32.95 ± 3.96
females	16	26	18.04 ± 4.64	23.39 ± 4.85
<i>D. sublineatus</i>	83	118	32.42 ± 2.33	38.14 ± 3.12
<i>O. russatus</i>				
males	19	30	39.71 ± 5.18	51.71 ± 7.25
females	12	28	23.15 ± 6.13	53.51 ± 19.23
<i>M. incanus</i>	88	158	41.07 ± 2.33	53.75 ± 3.15
<i>G. microtarsus</i>				
males	35	61	65.22 ± 7.54	84.60 ± 8.67
females	30	68	38.86 ± 4.46	59.89 ± 7.67

moved smaller distances than the latter (e.g., *T. nigrita* moved smaller distances than *M. incanus*; all Bonferroni adjusted $\alpha = 0.008$).

The MMDM (Table 2) was smallest for *A. montensis* and differed significantly from other species (all $Z > -2.66$; all $p < 0.008$) except *O. nigripes* ($Z = -1.68$; $p = 0.093$). The two marsupial species *M. incanus* and *G. microtarsus* moved significantly greater MMDM than the rodent species (all $Z > -2.95$; all $p < 0.0001$) except *O. russatus* ($Z = -0.90$; $p = 0.368$ and $Z = -2.13$; $p = 0.034$, all Bonferroni adjusted $\alpha = 0.008$).

Distribution of movement distances. The rodent species *A. montensis* and *O. russatus* were most frequently recaptured at the same station as first capture (Fig. 1). All other species showed the highest frequency of movements in the distance class of 20 m.

All rodent species moved most frequently short distances, and more than 80% of their movements did not exceed 50 m. The distribution of movements was less concentrated for the marsupials *M. incanus* and *G. microtarsus*. Both were rarely recaptured at the same trap station and more than 27% of all movements exceeded 50 m in *M. incanus*. In *G. microtarsus*, almost 50% of the movements were longer than 50 m. It moved long distances more frequently than

the other species, and the longest movement of all, over 200 m, was recorded for this species (Fig 1).

Differences between sexes, study sites, and sessions. Only the movements of *O. nigripes*, *O. russatus*, and *G. microtarsus* differed significantly between males and females (*O. nigripes*: $Z = -2.04$; $p = 0.042$; *O. russatus*: $Z = -2.06$; $p = 0.039$; *G. microtarsus*: $Z = -2.79$; $p = 0.005$). For these species SD was smaller for females than for males (Table 2). The six study sites did not differ significantly in SD for any of the investigated species (all $\chi^2 < 7.76$; $df = 1-5$ because not all species were captured in all study sites; all $p > 0.05$, Fig. 2). For *T. nigrita* this test was not performed because this species only occurred in the Morro Grande Reserve.

A. montensis, *T. nigrita*, *D. sublineatus* and *M. incanus* did not differ significantly between capture sessions in SD. For *O. nigripes*, *O. russatus* and *G. microtarsus*, the test was performed separately for the two sexes because of differences in mean distance moved. Both sexes of *O. nigripes* and *O. russatus* showed no significant difference between capture sessions. Males of *G. microtarsus* could only be compared between three of the capture sessions due to insufficient captures in the other capture sessions ($\chi^2 = 9.20$; $df = 2$; $p = 0.01$). They moved significantly longer distances

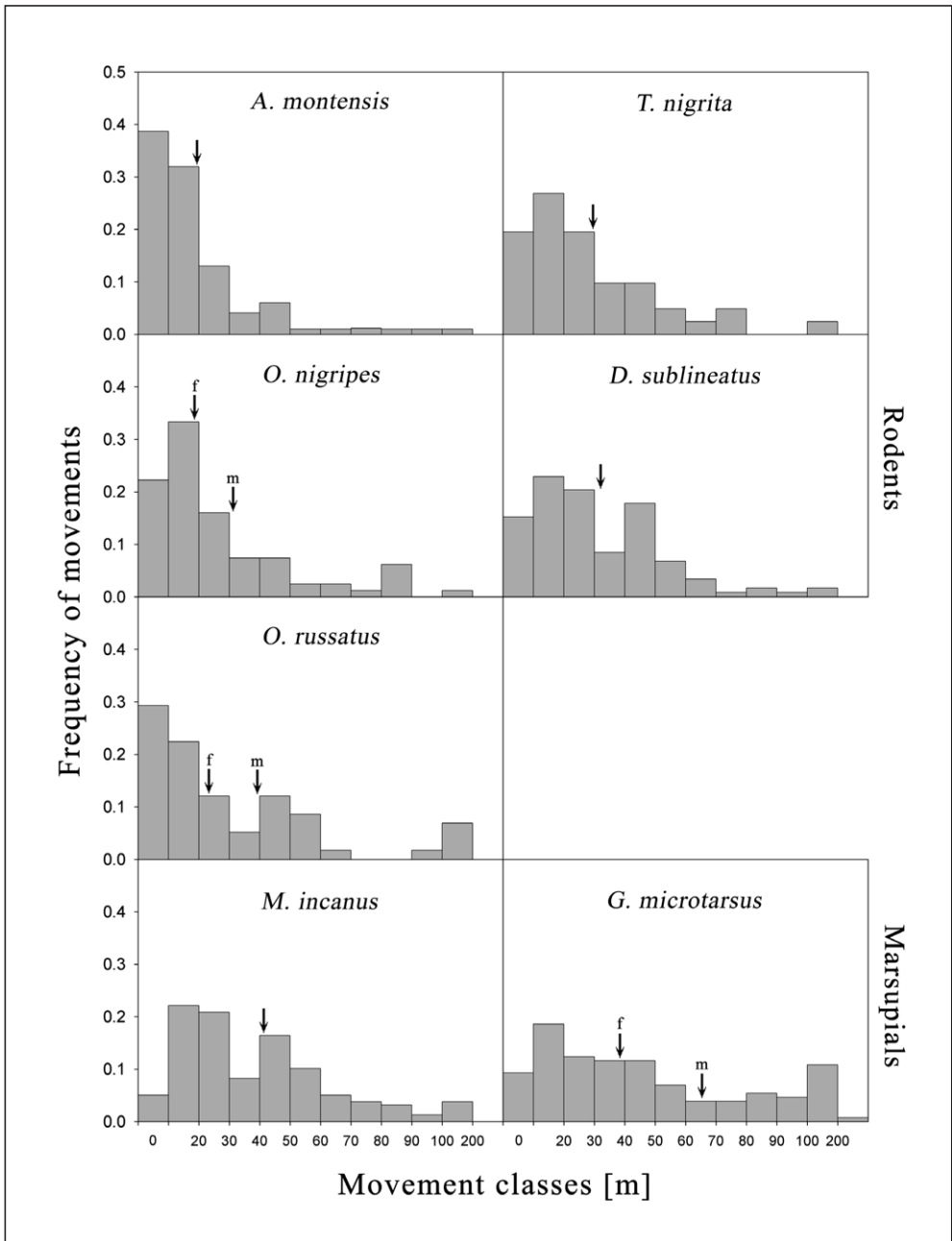


FIG. 1. Distribution of movement distances (in meters) between successive captures for five rodents and two marsupials of the coastal Atlantic rainforest. The arrows mark the mean distance moved between successive captures for the species (m = males, f = females in case of significant difference between sexes). Rodents: *Akodon montensis*, *Oligoryzomys nigripes*, *Delomys sublineatus*, *Oryzomys russatus*, *Thaptomys nigrita*; marsupials: *Marmosops incanus*, *Gracilinanus microtarsus*.

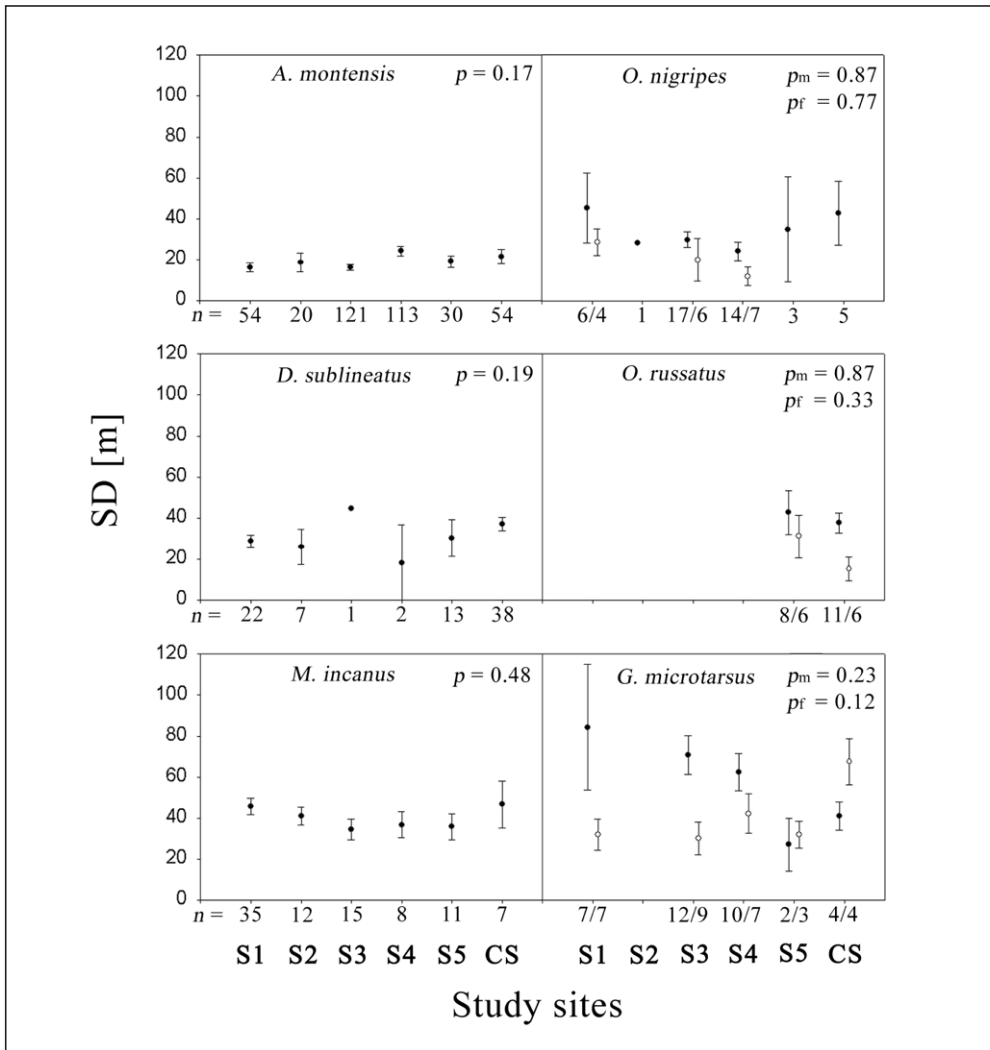


FIG. 2. Differences in distance moved between successive captures (SD) ± SE between study sites. In case of *O. nigripes*, *O. russatus*, and *G. microtarsus* black dots represent males (m) and white dots represent females (f). S1-S5: study sites, CS: control site in the Morro Grande Reserve.

in the fourth capture session ($SD_4 = 80.57$ m, 18. 05.–26. 06. 2004, beginning of dry season) than in the second ($SD_2 = 43.89$ m, 27. 09.–7. 11. 2003, beginning of wet season; $Z = -2.66$; $p = 0.007$, Bonferroni adjusted $\alpha = 0.025$). For females, the number of individuals captured more than once in two of the study sites was too small for statistical analysis.

DISCUSSION

Distinct movement patterns were revealed for the species studied. Hypothetically, the high abundance of *A. montensis* might indicate high resource availability for that species in the study area, which in turn could be a reason for low distances moved, although this can only be tested with additional data on resource avail-

ability in the study area. However, other investigations on closely related species of the genus *Akodon* revealed similar distances moved, such as *A. cursor* in a coastal shrubland in the state of Rio de Janeiro (highest frequency of movements between 0 and 20 m, more than 50% of movements less than 30 m, Gentile & Cerqueira 1995), in Atlantic forest fragments (highest frequency of movements between 0 and 20 m (Pires *et al.* 2002), and in a gallery forest in the *cerrado* of central Brazil (mean distance moved: 32.4 ± 37.2 m, Nitikman & Mares 1987), and *A. montensis* in secondary forest in Rio de Janeiro (over 70% of captures between 0 and 40 m; mean distance moved: 40.1 ± 53.5 m, Davis 1945). Our study does not confirm the general pattern of sexual dimorphism in home ranges in akodontines, males having larger home ranges (review in Gentile *et al.* 1997). We did not find any significant differences in movement patterns between sexes for *A. montensis*.

Thaptomys nigrita is the smallest of the investigated species. It is fossorial and vanished almost always underneath foliage immediately after release. Considering these habits, SD of about 30 m (Table 2) is unexpectedly high. However more than 40% of all movements did not exceed 20 m.

The SD and the distribution of movements of *O. nigripes* are similar to the results of other studies for this species (Nitikman & Mares 1987: 27.3 ± 22.7 m; Pires *et al.* 2002: movements did not exceed 80 m). Males moved larger mean distances than females. To our knowledge, this is the first evidence of sex differences in movement distances in *O. nigripes*. One can speculate that this difference might indicate a promiscuous mating system, with larger male home ranges including more than one female home range, although direct home range data are needed to test this hypothesis.

Davis (1945) captured *D. sublineatus* usually close to the original capture site, with the majority of captures being less than 50 m. This coincides with our results. Over 80% of all movements of *D. sublineatus* were less than 50 m.

Oryzomys russatus showed differences in SD between the two sexes. The values of the SD were significantly smaller for females than for males. In other studies in two different study areas in the Atlantic forest of São Paulo state, no difference was found between home ranges (convex polygon method) of males and females of *O. russatus* (Bergallo 1995, Bergallo & Magnusson 2004), hypothesizing a monogamous mating system in *O. russatus*. In our study, the capture

points of the different female individuals were at least 50 m apart when more than one female was captured during one capture session, implying that there is little overlap at the areas used by different females. In some cases different males were captured close to or in the same capture point of females. These results support the findings of Bergallo (1995), showing little intra-sexual but much intersexual spatial overlap, although more intense data collection is needed for further investigation of the mating system of *O. russatus* in the study area.

The pattern of larger distances moved by marsupials was confirmed in this study (Nitikman & Mares 1987, Fonseca & Kierulff 1989, Pires *et al.* 2002). Fonseca & Kierulff (1989) captured mostly males of *M. incanus* and found a slightly higher SD of 64.7 m compared with our results (41.07 m). We found no significant differences in SD between sexes for *M. incanus*, but did for *G. microtarsus*. The MMDM was also significantly higher for males than for females of this species. This might suggest a sexual dimorphism in movement distances of *G. microtarsus*, probably with larger male home ranges. Larger male home ranges in marsupials in Brazil were recorded for *Micoureus demerarae* (Pires *et al.* 1999). No differences in movements between successive captures could be determined in *Didelphis aurita*, *Philander frenatus*, and *Metachirus nudicaudatus* by Gentile & Cerqueira (1995). On the other hand, Loretto & Vieira (2005) detected seasonal differences between sexes in movements of *Didelphis aurita*. Compared to the mean distance moved by the ecologically similar species *Marmosa agilis* recorded by Nitikman & Mares (1987) in *cerrado* gallery forest (41.1 ± 35.0 m), *G. microtarsus* traveled similar mean distances in our study. *G. microtarsus* was the only species that showed temporal differences in SD. Males moved larger distances at the beginning of the dry season 2004 than at the beginning of the rainy season 2003. The interpretation of this result is difficult. *G. microtarsus* has an insectivorous-omnivorous diet (Martins and Bonato 2004). Further investigation on food availability in the study area is needed to evaluate a possible influence of food abundance on the observed movement distances. In general, arthropod and fruit abundance in the rainy season is higher compared with the dry season (Janzen 1973, Develey & Peres 2000, R. Pardini, pers. comm.). Hence movement distances should be smaller in the rainy season to assure a sufficient food supply. More likely is an influence of reproductive activity. Seasonal reproduction in the rainy season has been observed

for several marsupials in the Neotropics (Fonseca & Kierulff 1989, Bergallo 1994). The males of *G. microtarsus* might travel greater distances in the rainy season in search of females.

We found no evidence that fragment size influences the movement distances of the species. None of the investigated species showed a significant difference between study sites.

The results of this study can help us understand the population ecology of small mammal species in the coastal Atlantic rainforest of Brazil. Additional information will be gained by further investigations into the relationship between population size and the respective movement distance of the different species.

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