

Scale-dependent habitat selection in three didelphid marsupials using the spool-and-line technique in the Atlantic forest of Brazil

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Abstract: Habitat selection can be detected at different scales. For small mammals, habitat studies normally evaluate micro- or meso-habitat selection, but rarely are multiple scales analysed simultaneously. These studies use quantitative data of structural characteristics around the trap stations to evaluate selection. We test an alternative method to evaluate habitat selection in three didelphid marsupials (*Didelphis aurita*, *Philander frenatus* and *Metachirus nudicaudatus*), using a spool-and-line device, and measure habitat selection at two spatial scales. Habitat was characterized by seven habitat variables measured at ten points of direction change along the path traversed by each individual, and at 25 trap stations distributed in a 1-ha area. Micro-habitat selection was estimated at each point by comparing habitat measures between the direction selected against other directions. Meso-habitat selection was estimated by comparing habitat measurements on the whole path of an individual against habitat measures on the 25 trap stations. Patterns of selection for each species could only be detected at the meso-habitat scale, although a few individuals in each species were selective at the micro-habitat scale. Studies of habitat selection need to address the scale of study quantitatively, if possible comparing two or more scales to determine the scale of selection.

Key Words: *Didelphis aurita*, *Metachirus nudicaudatus*, *Philander frenatus*, scales

INTRODUCTION

Increasing attention has been devoted to understanding how the scale of observation influences our perceptions of ecological dynamics (Kelt *et al.* 1999). Habitat selection appears to be influenced by the scale of study, with the pattern of habitat selection being scale-dependent (Jorgensen & Demarais 1999, Morris 1987). Thus, it is important to explicitly state the scale of analysis in studies of habitat selection, particularly considering the species of study and the questions asked.

For small mammals of the Atlantic Forest of Brazil, the largest scale of study is the Atlantic Forest as a whole, which will be referred to as the macro-habitat. The region occupied by a set of organisms will be the meso-habitat scale, such as a valley, watershed or even smaller areas

(Freitas 1998). The micro-habitat would be the fine-scale subset of environmental conditions preferred by an individual within its home range, usually characterized by variables such as vegetative cover and distance to the nearest tree (Dueser & Shugart 1978). Each species can have particular patterns of preference, depending on their size and behaviour (Monamy & Fox 1999). Considering the size of small mammals, the meso- and micro-scales of habitat seem the most appropriate for evaluation of habitat selection.

Studies that evaluate habitat selection by small mammals at micro-habitat scales generally use quantitative data of structural characteristics around the trap stations. However, live trapping introduces an error of unknown magnitude because baited traps may attract animals away from the preferred microhabitat (Douglass 1989, Otis *et al.* 1978, Tew *et al.* 1994). This error may be negligible if the scale of analysis is the area around traps, where structural variables are measured. However, this resolution cannot distinguish smaller-scale patches of

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micro-habitat types, which may be used preferentially or may otherwise affect behaviour (Todd *et al.* 2000), i.e. selection of micro-habitats may occur at scales smaller than the area around traps.

In the Atlantic Forest, micro-habitat selection has been demonstrated for some marsupials. *Didelphis aurita* was negatively associated with leaf obstruction at 1–1.50 m height (Freitas 1998), *Philander frenatus* was positively associated to litter cover and appears to depend on availability of water (Fonseca & Robinson 1990, Freitas 1998), and *Metachirus nudicaudatus* was negatively associated to rock cover (Freitas *et al.* 1997). These studies used live traps and structural variables measured around the trap stations.

The spool-and-line technique as used by Boonstra & Craine (1986) and Miles *et al.* (1981) is an alternative method but underutilized in habitat-selection studies. This technique allows researchers to accurately map the paths used by small mammals, an accuracy not matched by radio-tracking or live-trapping (Goodyear 1989). Besides, the detailed description of individual paths allows the analysis of individual differences in habitat selection, an aspect that has been neglected in previous studies of habitat selection.

We evaluated habitat selection at two scales – meso- and micro-habitat – of individuals of three neotropical marsupials, *Didelphis aurita* (Wied-Neuwied, 1826), *Philander frenatus* (Olfers, 1818), and *Metachirus nudicaudatus* (Desmarest, 1817) (Hall & Dalquest 1963). Selection will be evaluated for each individual using the spool-and-line technique.

STUDY AREA

The study site is located on the edge of Serra dos Órgãos National Park in the municipality of Guapimirim, Rio de Janeiro state, Brazil (22°28'28"S, 42°59'86"W). The area is in the Coastal Forest of the Serra do Mar, a subdivision of the Atlantic Forest Biome (Dinerstein *et al.* 1995). It is surrounded by vacation homes that could have some influence on the structure and composition of the forest (Freitas 1998). The climate of the area is classified as mild-humid mesothermic (Nimer 1989). The soil is shallow, clayey and rocky.

The forest canopy reaches 20–25 m, with diameter at breast height of trees ranging 20–60 cm, sometimes reaching 1 m. A subcanopy and understorey are present, but are not readily distinguishable. The terrain is steep. Rocks are exposed and are more concentrated along small creeks, many with running water only in the wet season, from October to March. Lianas, palm trees, epiphytes, ferns and bromeliads are frequent. Common tree species belong to the genera *Sloanea*, *Ficus*, *Cedrela*, *Cariniana*, *Vochysia*, *Cecropia* among others. Common species of the

subcanopy and understorey include tree ferns of the genera *Alsophila*, *Cyathea* and *Hemitelia*, and the palm tree *Euterpe edulis* (Rizzini 1979).

MATERIAL AND METHODS

Animals were captured in bimonthly trapping sessions of five consecutive nights each, from August 2000 until October 2002, as part of a mark–recapture study of small-mammal populations. Trapping sessions were conducted in three 0.64-ha grids (A, B and C) established at three different elevations (748, 652 and 522 m). Each grid had 25 trap stations, 20 m apart, distributed in five parallel lines. At each station, two traps were placed on the ground: one Tomahawk, model 201 (30.5 × 9.8 × 8 cm) and one Sherman, model XLK (41 × 14 × 14 cm).

Some captured animals were equipped with a spool-and-line device based on Boonstra & Craine (1986). Anaesthetics were not necessary because animals were handled quickly and without harm. Quilting cocoons (no. 5 or no. 10) of nylon thread were used (Culver Textiles Corp., New York) weighing about 1.7 g (175 m of thread) and 4.5 g (480 m of thread), respectively. The size of the cocoon used depended on the size of animal: the small cocoon was used for young, and the large for adults. The large spool weighed less than 1% of the mass of the smallest species, *P. frenatus* and *M. nudicaudatus*. Cocoons of five colours were used to facilitate the identification of threads of different individuals in the field. The cocoon was covered with shrink-wrapped plastic, and wrapped with masking tape to form the spool. The spool was glued to the fur between the shoulders. Any marks of cocoon or glue disappeared in animals recaptured 1 or 2 d later. Most animals were tracked the day after their release, although some were tracked on the same day of release to locate their nest. In these cases, tracking began at least 2 h after release of the animal to avoid disturbance, and continued the next day starting from the nest.

Micro-habitat measurements were initiated at least 20 m away from the trap station where the animal was released. Ten points of change in direction were chosen along the path of each animal, at least 10 m apart. Micro-habitat variables were measured in four directions around each point. These included the direction the animal headed, the second and third were left and right to the chosen direction, and the last was opposite to the direction headed.

Seven variables were measured in each direction, based on Freitas *et al.* (2002), using a 0.25-m² square wooden frame (0.50 × 0.50) with a wire mesh divided in to 100 open squares (Table 1). The number of squares visibly obstructed was a measure of the percentage cover of each variable. We consider as obstructed any square with more than 50% of visual obstruction. The four directions

Table 1. Micro-habitat variables measured around the points of the animal path and at the trap stations.

Variables	Description
PLANT	Plant cover on the ground (%)
LITTER	Litter cover on the ground (%)
ROCK	Rock cover on the ground (%)
CANOPY	Canopy cover
OBSTR1	Obstruction at 0–0.5 m high
OBSTR2	Obstruction at 0.5–1.0 m high
OBSTR3	Obstruction at 1.0–1.5 m high

centred at the point of direction change formed a 3-m-arm cross, which delimited a sample area of 18.8 m² considering a circle of 3 m radius around the point of direction change.

In the trapping grids, each trap station was marked with a central stake and four additional stakes were placed 3 m away in the four cardinal directions, also forming a 3-m-arm cross and a sampling area of 18.8 m². Each measurement consisted of a count of the number of squares visibly obstructed, defined as any square with more than 50% visible obstruction. PLANT, LITTER and ROCK were measured holding the frame horizontally, parallel to the ground near the knees (*c.* 60 cm above the ground) and observing the ground. These variables were constrained to sum to 100%. CANOPY was measured holding the frame in a horizontal position, but over the head, with arms extended. These variables were recorded in each of the four directions, 3 m from the central point. Vertical obstructions (OBSTR1, OBSTR2 and OBSTR3) were measured with the frame held vertically at three heights (0.00–0.50 m; 0.51–1.01 m and 1.00–1.50 m), considering only the vegetation between the observer and a point 3 m away. The observer focused only in the 3-m range between the frame and the lateral point.

Selection of each individual at the micro-habitat scale was determined for each variable, at each point of change in direction along the animal path. The values in the chosen direction were compared against the mean of the three non-chosen directions with the Wilcoxon matched-pairs test (Sokal & Rohlf 1995). The three non-chosen directions do not constitute a random subset of points, but represent habitat that was distinctly selected against. This test provides a measure of habitat selection at this small scale, between four directions around the central point.

Selection at the meso-habitat scale was determined by a bootstrapping procedure, for each variable and individual. First, measurements at each trap station or point of change in direction were summed over the four directions for each variable. Then we compared this set of micro-habitat measurements along each line against an estimate of its availability in the vicinity. Meso-habitat availability in the vicinity was estimated by measuring the same variables at the trap stations of the grids

used to capture the animals. So, at the meso-habitat scale variables were compared between areas of 188 m² measured along the whole path of an individual (the total area of 10 points of 18.8 m²), and equivalent areas of 10 trap stations randomly selected from the nearby trapping grid. For example, the micro-habitat measurements of an individual that was captured and released in grid C were compared to measures of the variables in the 25 trapping stations of grid C. These measurements were taken during the same trapping session when the individual was tracked. Critical regions were determined with 1000 bootstrap samples of 10 stations from the nearby trapping grid. Preference was indicated whenever the mean of measurements on an individual patch fall in the upper 5% of the bootstrap distribution. Likewise avoidance was indicated when the mean measurements on an individual patch fall in the lower part of the bootstrap distribution. In this case the alpha value is 0.10 because we included 5% at each end of the distribution.

RESULTS

From August 2000 to October 2002, we tracked 39 individuals including 17 *Didelphis aurita*, 12 *Philander frenatus* and 10 *Metachirus nudicaudatus*. There was no defined pattern of micro-habitat selection for the three species, but in all species some individuals were selective (Table 2). In some cases, the same individual selected more than one variable. However, it is not possible to affirm whether these individuals were indeed selective or were simply the result of the multiple tests performed for each species and variable. Using a 0.10 significance level implies that significant selection would be detected in 10% of the individuals tested by chance alone.

One individual of *D. aurita* avoided PLANT ($Z = 2.32$, $P < 0.025$), OBSTR1 ($Z = 2.29$, $P < 0.025$) and OBSTR2 ($Z = 2.24$, $P < 0.025$), and four individuals avoided ROCK ($Z \geq 1.88$, $P < 0.05$). Hence, these individuals were preferably heading to places with lower values of these variables. There was also a preference for microhabitats with more litter cover ($Z = -2.31$, $P < 0.025$), and with a closed canopy ($Z = -2.35$, $P < 0.01$). In *P. frenatus* there

Table 2. Percentage of individuals of the three species of marsupial that select micro-habitats. Number of individuals in parentheses.

Variables	<i>Didelphis aurita</i> (n = 17)	<i>Philander frenatus</i> (n = 12)	<i>Metachirus nudicaudatus</i> (n = 10)
PLANT	6 (1)	8 (1)	10 (1)
LITTER	6 (1)	17 (2)	0 (0)
ROCK	24 (4)	0 (0)	20 (2)
CANOPY	6 (1)	16 (2)	0 (0)
OBSTR1	6 (1)	17 (2)	10 (1)
OBSTR2	6 (1)	25 (3)	0 (0)
OBSTR3	0 (0)	8 (1)	0 (0)

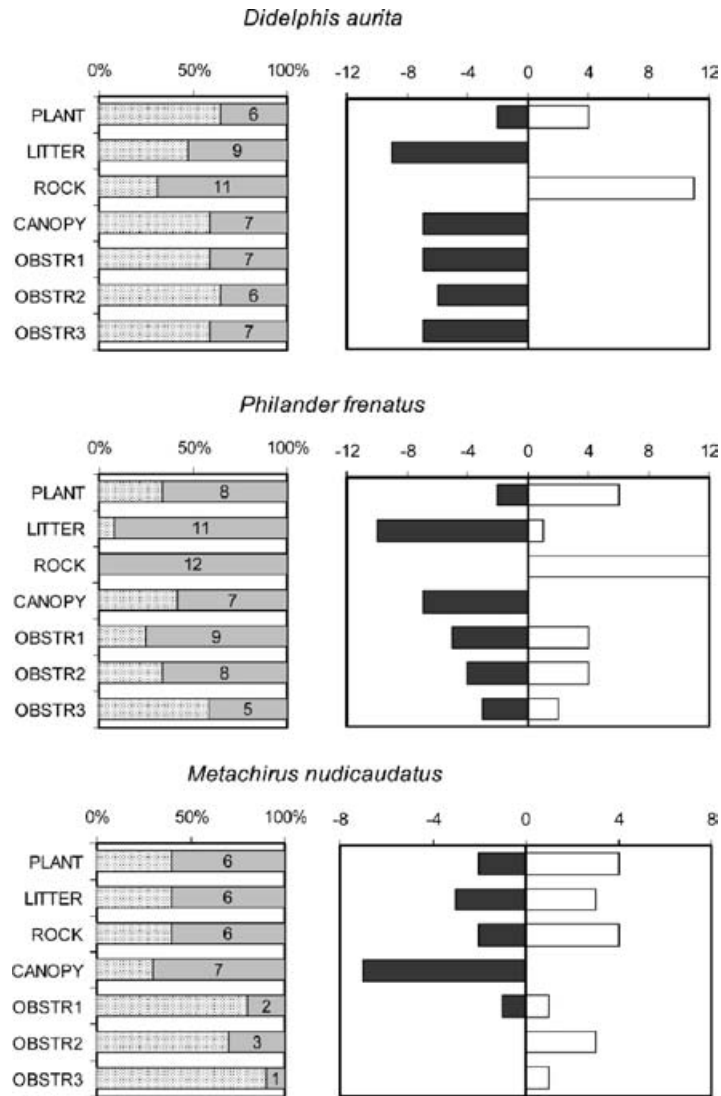


Figure 1. Meso-habitat selection by individuals of the three species of marsupial. The left histogram is the percentage of individuals significantly selective (grey bars, with frequency of selective individuals inside) or non-selective (dotted bars). The right histogram is the frequency of selective individuals that avoided (black bars, negative values) or preferred (white bars, positive values) each meso-habitat variable.

were two cases of selection for more litter cover ($Z \geq -2.70$, $P < 0.05$), one for places with a closed canopy ($Z = -2.15$, $P < 0.03$), and one for places with more OBSTR2 ($Z = -2.19$, $P < 0.04$). There was also a selection for places with less PLANT cover ($Z = 2.21$, $P < 0.02$), CANOPY ($P < 0.03$), and OBSTR3 ($Z = 2.03$, $P < 0.04$), and two selections avoiding OBSTR1 ($Z \geq 1.96$, $P < 0.04$) and OBSTR2 ($Z \geq 2.19$, $P < 0.03$). In *M. nudicaudatus* one individual selected places with less PLANT ($P < 0.04$) and OBSTR1 ($Z = 2.19$, $P < 0.02$), and two individuals selected places with less ROCK ($Z \geq 2.80$, $P < 0.01$).

At the meso-habitat scale, there was a pattern of selection for the individuals of each species. Eleven individuals of *D. aurita* selected places with more rock cover (71%) (Figure 1). In *P. frenatus*, all individuals selected places with more rock cover (100%), and most

selected less litter (84%) (Figure 1). In *M. nudicaudatus* seven individuals selected places with less canopy cover (70%) (Figure 1).

DISCUSSION

Studies comparing two or more scales are necessary to determine to what extent scaling up or down is possible (Schneider 1998). If our results at the micro-habitat scale were extrapolated to meso- or macro-habitat scales, one would wrongly conclude that there is no selection for the variables measured. However, selection was evident at the meso-habitat scale.

Morris (1987) and Jorgensen & Demarais (1999) also found that the small mammals in their study

areas selected habitats at a larger scale. They suggested that micro-habitat partitioning is constrained by macro-habitat, i.e. partitioning of micro-habitat exists only within limits set by as yet poorly understood macro-habitat factors. Our results are similar because selection was detected only at the larger scale. It is possible that for endothermic animals of the size of small mammals movement is not affected by micro-habitat variation in temperature or humidity within the area covered in their nocturnal or daily activities. The risk of encounters with predators or direct competitors also could be more efficiently reduced by selecting meso-habitats with reduced predation rather than selecting more protected micro-habitats within the home range. Exploitative interspecific competition also could be reduced more efficiently by placing the whole home range in areas of reduced abundance of competitors rather than selecting different micro-habitat within the same area of competitors. When competing for resources, the presence of competitors in the same area is likely to depress resource abundance regardless of micro-habitat differences.

Species such as *Didelphis aurita* and *Metachirus nudicaudatus* failed to demonstrate overwhelming patterns of selection, but individuals were clearly selective at the meso-habitat scale. Most studies of habitat selection do not consider individual variation, concluding that a species is opportunistic or non-selective when no general pattern is detected for the species. Our data suggest that much information may be lost when only average values are analysed.

The absence of selection for rock cover at the micro-habitat scale by *Philander frenatus* and for most individuals of *D. aurita* could be explained by the whole path of the animal being in an area of more rock cover compared with other places in the forest (meso-habitat scale). Consequently, at the micro-habitat scale the animal does not need to select the direction with more rock cover because rocks are in all directions. In this sense, micro-habitat selection is indeed constrained by selection at the meso-habitat scale.

Usually, *P. frenatus* headed to places close to running water or dry creeks after release, where rocks are abundant. The nests of this species were always between rocks, close to running water (*pers. obs.*). Hershkovitz (1997) captured *P. frenatus* in dense vegetation along the shores of streams and rivers, and Eisenberg & Redford (1999), Davis (1947) and Fonseca & Robinson (1990) also suggested that this species seems to depend on the availability of running water and of mesic environments. However, this association may not be obligate because *P. frenatus* occurs in places without running water (Freitas *et al.* 1997).

Most individuals of *D. aurita* also preferred places with abundant rock cover at the meso-habitat scale. *Didelphis aurita* is usually considered a generalist species (Fonseca &

Robinson 1990), although preference for places with high litter cover were detected in restinga, a Brazilian coastal shrubby vegetation (Freitas *et al.* 1997). Our study is the first to detect preference for rock cover. One possibility is that rock cover in the Coastal Atlantic Forest provides food sources such as small vertebrates and aquatic insects, less available everywhere. Another possibility is the protection provided by rocks. The combination of food sources and shelter would make rock cover an attractive meso-habitat.

The preference of most individuals of *M. nudicaudatus* for areas with less canopy cover at the larger scale of meso-habitat could be explained by three hypotheses (1) selection for areas with moderate levels of disturbance, (2) with the use of fallen logs or (3) with the use of areas with dense understorey, all associated with lower canopy cover. Indeed, Freitas (1998) detected a negative association between fallen logs and the occurrence of *M. nudicaudatus*. Freitas *et al.* (1997) detected a positive association of *M. nudicaudatus* with a dense understorey, but not with less canopy cover. A dense understorey is usually positively correlated with lower canopy. The association with moderate disturbance cannot be tested with the available data, but studies comparing habitats with different levels of fragmentation or disturbance could provide such a test.

The comparison of our results with Freitas *et al.* (1997) and Freitas (1998) revealed similarities, but also contrasting patterns of selection for the marsupials studied. For example, Freitas (1998) also detected a negative association of *D. aurita* with leaf obstruction, but a negative association with rock cover, contrary to our study. Actually, the micro-habitat selection reported by these studies may refer to different scales of measurement. Freitas *et al.* (1997) and Freitas (1998) analysed habitat selection at a scale intermediate between the micro- and meso-habitat of our study. The micro-habitat scale of Freitas *et al.* (1997) compared variables between areas measured around trap stations, hence between areas of 18.8 m² (wrongly estimated as 36 m² in Freitas 1998, and in Freitas *et al.* 2002). In our study, micro-habitat was measured within 18.8 m² circles, hence measured at a smaller scale. Conversely, our meso-habitat scale compared variables between areas of 188 m² measured along the whole path of an individual with areas of 10 trap stations randomly selected from the nearby trapping grid, hence a larger scale than Freitas *et al.* (1997).

Detection of habitat selection at small scales is only possible with the spool-and-line technique, a major advantage of this method over the traditional use of traps. Traps could be used to detect selection at larger scales, between areas of 18.8 m² or more. At lower scales, traps with bait will tend to attract animals away from the path. Studies comparing habitat selection at different scales would benefit from the combined use of these methods.

The three marsupials studied selected habitat at the larger scale of meso-habitat. At the micro-habitat scale, many individuals were selective, but no general pattern of selection emerged for a species. The selection of rock cover by *Philander frenatus* confirms previous anecdotal observations based on trapping, associating the occurrence of *P. frenatus* with mesic areas. The spool-and-line technique allowed the comparison of habitat selection between areas of 188 m², a scale of analysis larger than usually possible in studies comparing habitats around trap stations. Selection patterns detected in studies using trapping grids revealed similarities and contrasts with our results at the meso-habitat scale. Quantification of the scale of measurement of habitat variables is necessary to determine the scale of habitat selection analysed in different studies.

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