

Differential use of vertical space by small mammals in the Monte Desert, Argentina

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Space use in deserts usually has been considered only along the horizontal dimension; however, vertical structure could be an important variable for habitat segregation among small mammal species. Our study assessed the use of vertical space by small mammals of the Monte Desert by live-trapping animals at different heights. We recorded 1,336 captures of 4 rodent and 1 marsupial species in 27,600 trap nights. All 5 species were captured on the ground and in tree layers, but only the gray leaf-eared mouse (*Graomys griseoflavus*) and the desert mouse opossum (*Thylamys pallidior*) used vertical space appreciably. *G. griseoflavus* used the arboreal space independently of habitat, plant species, or branch diameter, whereas *T. pallidior* showed a more selective behavior, being present at greater heights and on large-diameter branches of *Prosopis* trees. All rodent species used lower more than higher parts of arboreal strata. They used vertical space more or only during the dry season when resource availability is low. Our study suggests that vertical structure offers greater opportunities to acquire resources when these are scarce and plays a role in the coexistence of small desert mammals.

Key words: arboreal activity, aridlands, marsupials, Monte Desert, rodents, scansorial, space use, vertical strata

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[1] Community structure and composition can be influenced by factors such as predation, competition, and use of space and resources, which could be considered as separate axes or dimensions of a species' niche. When resources are scarce and limited, ecologically similar species should show differentiation in at least one of the main niche dimensions to avoid competition (Chase and Leibold 2003; Hutchinson 1957). Habitat and diet differentiation are proposed to be 2 important mechanisms of coexistence among small mammals (Schoener 1974).

The use of habitat by desert small mammals usually has been considered only 2-dimensionally; however, the vertical dimension of the habitat also could be important for some species (Harney and Dueser 1987; Meserve 1977; Rosenzweig et al. 1975). Habitat segregation on a vertical dimension can reduce competition, allowing a greater overlap in the horizontal plane (Dickman 1989; Harney and Dueser 1987; Schoener 1974). The use of arboreal space thus has been proposed as a characteristic that increases the ecological flexibility of species by enhancing the efficiency of resource exploitation and allows the use of a greater range of environments (Layne 1970), favoring the coexistence of ecologically and/or morphologically similar species.

Despite the marked vertical stratification observed in some desert environments, studies of arboreal activity in South American desert species are rare (but see Gallardo-Santis et al. 2005 and Meserve 1981). Although small-mammal assemblages from a Chilean semiarid scrubland exhibit some arboreal activity (Meserve 1981), the absence of suitable stem diameters for climbing could be a possible explanation for the low use of the arboreal stratum by Chilean mammals (Gallardo-Santis et al. 2005). Branch diameter, angle, and height seem to be major variables affecting the climbing ability of rodents (M'Closkey 1975; Meserve 1977). In particular, small-diameter branches make climbing difficult because they provide a low-traction surface. For this reason North American desert rodents (e.g., *Peromyscus*) might use larger-diameter surfaces more frequently than small ones (Meserve 1977).

The small mammals of the temperate Monte Desert show differential use of food (Campos et al. 2001; Giannoni et al. 2005) and other habitat resources (Albanese 2010; Corbalán



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2006; Gonnet and Ojeda 1998; Tabeni and Ojeda 2005). Although a few studies reported climbing behavior in some species (Corbalán 2004; Corbalán and Debandi 2009), the importance of vertical space for these small mammals is still unknown. Within Monte Desert assemblages the gray leaf-eared mouse (*Graomys griseoflavus*) and the desert mouse opossum (*Thylamys pallidior*) show morphologies for climbing (Hershkovitz 1962; Tate 1933). Traits such as a prehensile tail and opposable thumb in *T. pallidior* and long tail and elongated thumb in *G. griseoflavus* make these 2 species good candidates to exploit the arboreal stratum of the Monte Desert. Furthermore, this biome, composed of habitat patches with different degrees of complexity and structure (Bisigato et al. 2009; Morello 1958), is suitable for comparisons to be made among different vegetation units within it and with other desert systems. The aim of our study was to assess the use of vertical space as a mechanism of coexistence by the small-mammal assemblage of the Monte Desert. Specifically, we analyzed which species used vertical space and whether any differences were detected in the use of vertical structure among habitat types, seasons, and vegetation structures.

MATERIALS AND METHODS

Study site.—The study was conducted from October 2005 to August 2007 at the MaB Reserve of Ñacuñán (34°03'S, 67°58'W), located in the central plain of Mendoza Province, Argentina. This region belongs to the Monte Desert biome (Morello 1958), and the MaB Reserve covers an area of 12,300 ha (Tognelli and Boshoven 2001).

The climate is semiarid and strongly seasonal, with hot wet summers with mean temperatures >20°C and cold dry winters with mean temperatures <10°C (Estrella et al. 2001; Ojeda et al. 1998). Mean annual rainfall is 342.4 mm; wet season rainfall averages 262.56 mm and the dry season 79.20 mm (Ñacuñán Reserve Weather Station—Instituto Argentino de Investigaciones de las Zonas Áridas [IADIZA]; www.cricyt.edu.ar/ladyot/red_iadiza/index.htm). Three main habitat types are found in this area (Roig and Rossi 2001): *Prosopis* woodlands, consisting of 3-layer patches with *Prosopis flexuosa* trees, accompanied by a shrub layer of *Larrea divaricata*, *Condalia microphylla*, *Lycium tenuispinosum*, *Junellia aspera*, and *Capparis atamisquea* and a lower layer dominated by *Pappophorum caespitosum* and *Trichloris crinita*, among other grasses; *Larrea* shrublands, characterized by no or few trees and high coverage of shrubs, mostly *L. cuneifolia*, and grasses such as *T. crinita*; and sand dunes, characterized by low cover of shrubs (*Ximenia americana* and *L. divaricata*) and herbs (*Aristida mendocina*, *Panicum urvilleanum*, and *Portulaca grandiflora*, among others).

Sampling design.—During the first year we established trapping grids at 18 sampling sites, 6 per habitat type. In the second year we used 12 of these sites, with 4 replicates of each habitat. The other 6 sites were dropped because of consistently poor capture rates. Each grid consisted of 6 × 6 trapping stations, with 20-m spacing of 36 Sherman live traps (7.5 ×

TABLE 1.—Trap heights on the 2 arboreal layers (<90 cm and ≥90 cm) in 3 different habitat types in the MaB Reserve of Ñacuñán, Argentina. *n* = number of traps. 2

	<i>n</i>	Mean	<i>SE</i>	Min.	Max.
Lower layer (<90 cm)					
<i>Prosopis</i> woodland	24	73.15	2.28	52.00	89.50
<i>Larrea</i> shrubland	37	71.49	1.64	39.00	88.00
Sand dunes	37	73.01	2.15	40.50	89.00
Upper layer (≥90 cm)					
<i>Prosopis</i> woodland	36	120.36	3.66	90.00	171.00
<i>Larrea</i> shrubland	23	104.43	2.90	90.00	134.00
Sand dunes	23	125.57	4.83	98.00	189.00

9 × 27 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) on the ground covering a total area of 1 ha. We randomly selected 10 stations per grid where we also placed a small Sherman trap (5 × 6 × 16 cm), fastened with an elastic band, on a shrub or tree branch of a tree at the center of each capture station (hereafter, tree trapping site). The smaller size of the arboreal traps allowed us to attach them to a wide variety of branches and heights. Earlier trapping showed no differences in trapping success between the two trap sizes (S. Albanese, pers. obs.). Within each grid tree traps were placed at different heights so that they were distributed similarly into 2 arbitrary height categories: lower (<90 cm tall) and upper (≥90 cm tall; Table 1). Once traps were removed after each sampling session, their position on the shrub or tree was marked with a flagging tape so heights remained the same throughout the study. All traps were baited with a mixture of rolled oats, apple, moistened cat food, and peanut butter.

Four trapping sessions per year (8 in total) were conducted, 2 in the wet season (November–March) and 2 in the dry season (April–August). Each trapping session consisted of 5 consecutive nights per grid. Captured animals were identified to species, marked with a harmless dye (picric acid), and then released at the capture site. In all our procedures we conformed to the guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

For habitat characterization we set up 2-m × 2-m quadrats on each station and by eye calibration estimated species richness and percent cover of bare soil, litter, herbs and grasses, subshrubs (shrubs < 100 cm tall), shrubs ≥ 100 cm tall, and trees. We also visually estimated percent cover of different vegetation layers at heights of 50, 100, 150, and >150 cm. In addition, at each station we measured trap height, diameter of the branch holding the trap, and basal diameter of the shrub or tree trunk to which the trap was attached (hereafter, branch diameter and basal diameter, respectively). For characterization of habitat complexity we set up 2 perpendicular 50-m transects on each grid. We used the modified point quadrat method (Passera et al. 1983) in which we analyzed the same vegetation variables as in the quadrats.

Data analyses.—Because data did not meet the assumptions of parametric analysis, we used Kruskal–Wallis (*H*) tests to compare trap heights among habitat types in lower and upper arboreal layers.

TABLE 2.—Capture success, trapping effort (trap nights), and number of captures for small mammal species in the arboreal stratum and at ground level in the MaB Reserve of Nacuñan, Argentina.

	Capture success (%)	Trap nights	<i>Thylamys pallidior</i>	<i>Graomys griseoflavus</i>	<i>Calomys musculus</i>	<i>Akodon molinae</i>	<i>Eligmodontia typus</i>
Arboreal	2.35	6,000	20	111	1	4	5
Ground	5.53	21,600	73	673	39	171	239
Total	4.48	27,600	93	784	40	175	244

Using vegetation cover data at different heights we assessed habitat complexity by calculating the Shannon–Wiener index (H') with natural logarithms (MacArthur and MacArthur 1961). We compared habitat complexity among habitats with one-way analysis of variance (Zar 1999). Data were tested to ensure compliance with assumptions of parametric statistical tests by using Shapiro–Wilks to test for normality ($W = 0.89$; $P = 0.0723$) and Levene's test for homoscedasticity ($F_{2,15} = 1.76$; $P = 0.20$). Post hoc comparisons were performed with a Tukey's test.

To assess the use of vertical space we used the number of individuals caught per 1,000 trap nights. A chi-square goodness-of-fit test with Yates' correction for continuity was used to compare the number of captures in the arboreal and ground-level strata and the number of arboreal captures among or between habitats, height categories (lower and upper), and season (dry and wet) for each species. We also used chi-square goodness-of-fit tests to examine whether the observed frequencies of arboreal captures (o_i) on different plant species were different from what would be expected considering the frequency of their occurrence (availability: π_i). To determine which plant species were drivers of significant differences we calculated 95% confidence intervals ($CI[o_i] = o_i \pm Z_{\alpha/2}SE$) with Bonferroni correction for multiple comparisons (Manly et al. 2002). All data met the assumptions of the chi-square test (Zar 1999). A Mann–Whitney U -test was used to detect differences in vegetation structure among sites used and not used for climbing. We performed one test for each species separately and then another test to compare among species. The vegetation variables analyzed were percent cover of different life forms (i.e., trees, shrubs, forbs, and grasses) and vertical layers and basal and branch diameters.

RESULTS

Trap distribution.—Among habitat types heights of traps were similar on the lower layer ($H_2 = 0.82$; $P = 0.6644$), but in the upper layer of *Larrea* shrubland mean height was lower than in the other habitat types ($H_2 = 11.69$; $P = 0.0029$; Table 1). This was due to different trap attachment possibilities to branches and accessibility in this habitat type.

Characterization of habitat type.—The three habitat types showed differences in their vegetation structure. The *Prosopis* woodland and *Larrea* shrubland were the most complex habitats ($H' = 2.02$ and $H' = 2.07$, respectively), with sand dunes being significantly the least complex ($H' = 1.91$; $F_{2,15} = 5.92$; $P = 0.0127$; Tukey test: $P < 0.05$).

Use of ground versus vertical space.—Of the 27,600 trap nights of effort, 6,000 were in the tree layers (Table 2). We

registered 1,336 captures of 5 species: 4 sigmodontine rodents, the gray leaf-eared mouse (*G. griseoflavus*), the vesper mouse (*Calomys musculus*), the grass mouse (*Akodon molinae*), and the silky mouse (*Eligmodontia typus*); and 1 marsupial, the desert mouse opossum (*T. pallidior*). All species were captured both on the ground and in the arboreal stratum but in different proportions (Table 2). The species most frequently captured in tree traps was *G. griseoflavus*, followed by *T. pallidior*. However, only the latter showed no differences in capture numbers between ground level and arboreal strata ($\chi^2_1 = 0.005$; $P = 0.94$, Fig. 1). Despite nearly one-third of traps being arboreal, all 4 rodents were captured predominantly at ground level (more often than expected by chance): *G. griseoflavus*: 86% of captures at ground level, $\chi^2_1 = 26.04$; $P < 0.0001$; *C. musculus*: 97%, $\chi^2_1 = 7.61$; $P = 0.006$; *A. molinae*: 98%, $\chi^2_1 = 37.79$; $P < 0.0001$; *E. typus*: 98%, $\chi^2_1 = 54.45$; $P < 0.0001$ (Fig. 1). Because of the significantly low capture frequency (<10%) of these last 3 species in the arboreal stratum, all comparisons between ground and arboreal captures were made between *G. griseoflavus* and *T. pallidior*.

Habitat types.—*Graomys griseoflavus* showed no differences in the number of tree captures among different habitats ($\chi^2_2 = 4.13$; $P = 0.12$). Tree capture numbers of *T. pallidior* were significantly lower in sand dunes than in other habitats ($\chi^2_2 = 6.17$; $P = 0.046$; Fig. 2).

Use of different heights.—Captures in both tree layers (lower and upper) were different among species. *T. pallidior* was captured primarily in the upper layer (70% of captures), which was the one selected significantly ($\chi^2_1 = 4.31$; $P = 0.037$; Fig. 3). *G. griseoflavus* showed no selection for either layer ($\chi^2_1 = 2.23$; $P = 0.13$) but tended to be found in lower layers (Fig. 3). However, the highest height recorded was similar for both species: 1.49 m for *G. griseoflavus* and 1.53 m for *T. pallidior*. The other 3 species were captured only in the lower layer (<90 cm).

Characterization of vertical space used.—Sites where *G. griseoflavus* was captured had greater subshrub cover than sites where it was not present (Table 3). Sites used by *T. pallidior* had greater tree cover and larger basal diameter than unused ones. The same pattern occurred when comparing sites used by either *T. pallidior* or *G. griseoflavus*. We also found *T. pallidior* in vegetation with larger branch diameter than recorded for unused sites (Table 3). No significant differences were found for the other vegetation variables.

Plant species used.—The 4 most abundant woody plant species in the study area were *L. divaricata* (41%), *L. cuneifolia* (26%), *P. flexuosa* (18%), and *Geoffroea decorticans* (12%).

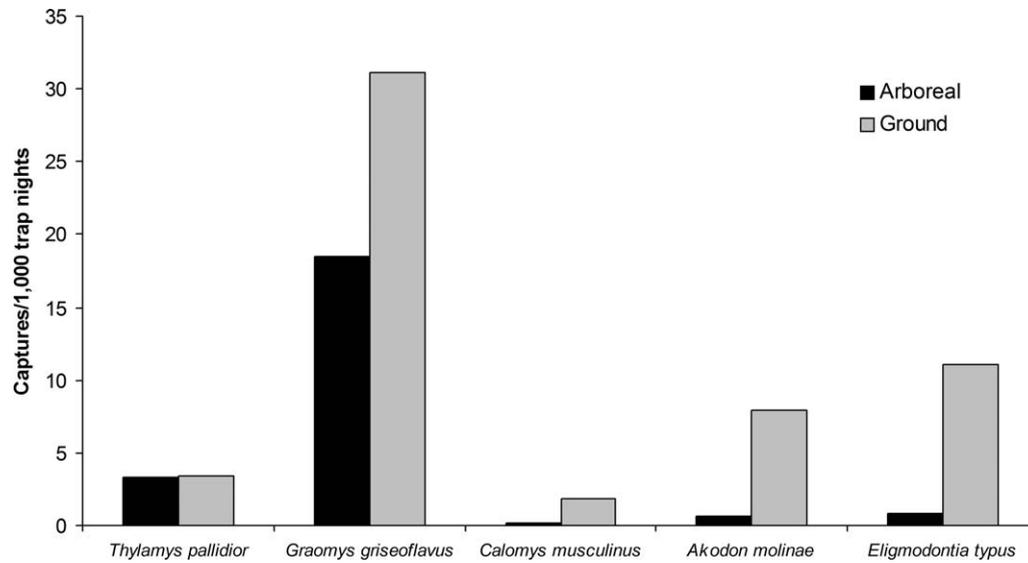


FIG. 1.—Capture rates of species of small mammals in the arboreal stratum and at ground level in the MaB Reserve of Ñacuñan, Argentina.

Graomys griseoflavus did not use all plant species in the same proportion as available ($\chi^2_3 = 12.73$; $P = 0.005$); *L. divaricata* was the only plant used by this rodent in lower proportion than available ($\pi_i = 0.424 > CI(o_i): 0.168-0.392$; Fig. 4). Conversely, *T. pallidior* was associated mainly with *P. flexuosa* ($\pi_i = 0.180 < CI[o_i]: 0.324-0.898$); it was absent in *Geoffroea decorticans* trees and used *Larrea* shrubs in the same proportion as available ($\chi^2_3 = 23.22$; $P = 0.0004$; Fig. 4). Other plant species, such as *Condalia microphylla*, *Atriplex lampa*, and *Capparis atamisquea*, were used by small mammals, but their availability and animal captures were so low that they were not considered in our analysis.

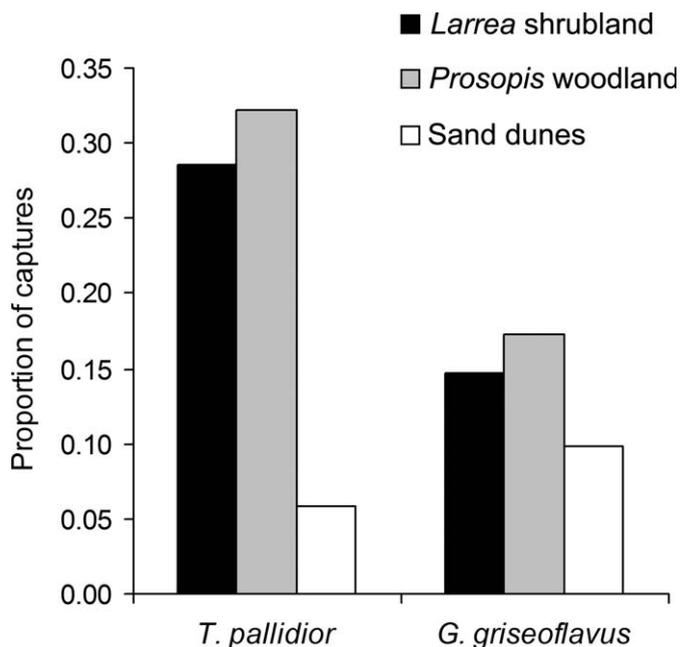


FIG. 2.—Proportion of captures of *Thylamys pallidior* and *Graomys griseoflavus* that were arboreal in each habitat type in the MaB Reserve of Ñacuñan, Argentina.

Seasonality.—*Graomys griseoflavus* used vertical space differently in both seasons, using tree traps mainly during the dry season ($\chi^2_1 = 12.10$; $P = 0.0005$). *T. pallidior*, however, was captured equally in tree layers in both seasons ($\chi^2_1 = 0.93$; $P = 0.34$). Arboreal captures for the other 3 species were too low for statistical analysis, but all of them occurred only during the dry season.

DISCUSSION

Our study indicates that the vertical habitat dimension plays an important role in the coexistence and therefore natural history of some small desert mammals. In Monte Desert assemblages we found that small mammals differed in their degree of arboreality, with the presence of scansorial and ground-dwelling species. We also observed a differential use of arboreal space even among scansorial species. Vertical strata offer an additional way in which space can be

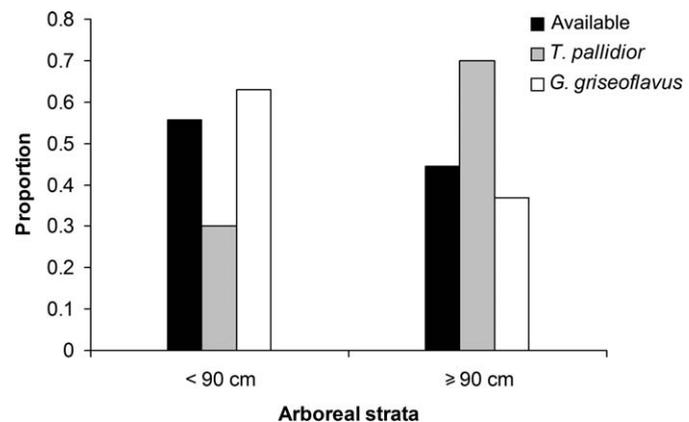


FIG. 3.—Proportion of captures of *Thylamys pallidior* and *Graomys griseoflavus* in lower (<90 cm) and upper (≥90 cm) arboreal strata in the MaB Reserve of Ñacuñan, Argentina. “Available” refers to the proportion of traps in each stratum.

TABLE 3.—Comparisons of vegetation variables measured at sites in the MaB Reserve of Ñacuñan, Argentina, where *Graomys griseoflavus* (Gg) and *Thylamys pallidior* (Tp) were captured in the arboreal stratum (used) and sites where these species were not captured (nonused). Gg vs. Tp indicates comparisons between sites where only 1 species was captured. Values shown are \bar{X} (mean) \pm SE. *P*-values are from Mann-Whitney *U*-tests ($\alpha = 0.05$). See “Materials and Methods” for descriptions of vegetation variables.

Vegetation variables	<i>G. griseoflavus</i>				<i>T. pallidior</i>				Gg vs. Tp	
	Used (n = 57)	Nonused (n = 123)	<i>U</i>	<i>P</i>	Used (n = 20)	Nonused (n = 160)	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
Herbs and grasses (% cover)	23.44 \pm 1.64	22.43 \pm 1.18	3,270.5	0.470	25.74 \pm 3.30	21.87 \pm 1.00	1,358	0.274	532.5	0.666
Subshrubs (% cover)	31.64 \pm 3.24	19.61 \pm 1.51	2,543	0.003	25.15 \pm 4.89	23.12 \pm 1.61	1,500.5	0.653	493.5	0.377
Shrubs (% cover)	61.12 \pm 3.76	55.73 \pm 2.97	3,123	0.239	44.10 \pm 6.97	58.47 \pm 2.48	1,233	0.095	401.5	0.051
Trees (% cover)	26.47 \pm 5.78	25.62 \pm 3.47	3,402.5	0.722	44.88 \pm 9.70	23.24 \pm 3.05	975	0.004	374	0.022
Basal diameter (cm)	27.30 \pm 3.59	24.61 \pm 2.18	3,055.5	0.880	42.11 \pm 7.41	23.65 \pm 1.85	952.5	0.007	365.5	0.041
Branch diameter (cm)	8.08 \pm 0.78	6.44 \pm 0.34	3,116.5	0.231	11.42 \pm 1.86	6.47 \pm 0.31	980	0.004	421	0.084

partitioned to allow species to coexist. A significant degree of vertical space use also has been recorded in some North American deserts; Rosenzweig et al. (1975) and Meserve (1976) found considerable aboveground activity by heteromyid and cricetid rodents. Meserve (1976, 1977) showed the importance of vertical space for cricetid rodents to coexist in California scrubland. He found that some species differ in the use of the 3-dimensional habitat on the basis of structural aspects of the vegetation (such as branch angle, branch diameter, or shrub species), but temporal segregation also was important.

Despite its importance in the Monte Desert and Californian scrubland, use of vertical space is not necessarily relevant in determining niche partitioning between small mammals in other desert systems. For instance, for small mammals of Chilean scrublands low activity was observed in the vertical stratum (Meserve 1981). Differences in arboreal activity have been attributed to different availability of appropriate branch diameters on which to climb (Gallardo-Santis et al. 2005; Meserve 1981); however, the suitable branch diameter for climbing in a small mammal probably depends on its morphology and its consequent climbing ability. Despite large diameters providing more traction surface, thick twigs are not necessarily suitable for climbing for all species. Some rodents move more easily on thin diameters than on large ones, as is the case of *E. typus* (A. G. Orofino, IADIZA, Mendoza, pers. comm.). Thinner sizes might offer a better grip on branches. At our study site woodland patches (mainly composed of

P. flexuosa or *Geoffroea decorticans* trees) are particularly common, offering both a wider variety of diameters and larger branches than reported for Chilean or Californian scrublands (Gallardo-Santis et al. 2005; Meserve 1977, 1981). Therefore, in the Monte Desert availability of appropriate branches might not be a limiting factor for arboreal activity, as it seems to be in Chilean deserts.

Previous research on Monte Desert small mammals suggested some degree of niche differentiation when considering trophic and spatial dimensions (Campos et al. 2001; Corbalán 2006; Gonnet and Ojeda 1998; Tabeni and Ojeda 2005). Specifically, these mammals are mainly omnivorous, with trends toward different food categories, and show preferences for distinct habitat characteristics (Albanese 2010; Ojeda and Tabeni 2009). Our study indicates the existence of another niche dimension by which these mammals can segregate and also supports previous research about their different locomotion habits (Hershkovitz 1962; Ojeda and Tabeni 2009; Taraborelli et al. 2003). *E. typus*, *A. molinae*, and *Calomys musculus* are terrestrial, moving mostly over the ground, whereas *Graomys griseoflavus* and *T. pallidior* can be considered scansorial.

Regarding terrestrial species, previous studies have shown that *C. musculus* consumes large amounts of seeds and prefers habitats with dense vegetation, such as *Larrea* shrublands. *A. molinae* also is associated with these habitats but seems to require high grass cover, and its diet includes a large proportion of insects. *E. typus*, however, is the most omnivorous species of the assemblage and occurs mainly in open habitat, usually being dominant in sand dune environments (Campos et al. 2001; Corbalán 2006; Corbalán and Ojeda 2004; Tabeni et al. 2007). Our results showed that these 3 species, although terrestrial, also occasionally climb in lower layers (<90 cm).

Concerning scansorial species, the marsupial *T. pallidior* uses the ground and vertical space equally. Albanese (2010) observed that although *T. pallidior* occurs in different habitat types (i.e., woodlands, shrublands, and sand dunes), it selects open areas with low vegetation complexity, and has a diet with a large proportion (~70%) of arthropods, being the most insectivorous species of the assemblage. *G. griseoflavus*, although scansorial, shows a greater use of the ground than arboreal level. This species, with a primarily folivorous diet,

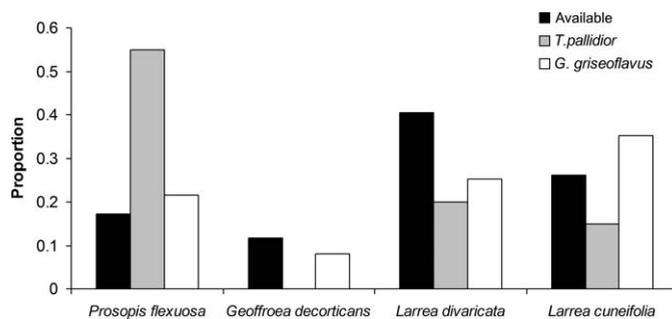


FIG. 4.—Proportion of captures of *Thylamys pallidior* and *Graomys griseoflavus* in different plant species in the MaB Reserve of Ñacuñan, Argentina. “Available” refers to the proportion of traps in each plant species.

uses a wide diversity of habitats, being dominant in *Prosopis* woodlands (Campos et al. 2001; Corbalán and Ojeda 2004; Gonnet and Ojeda 1998).

For this small mammal assemblage segregation in either habitat or food facilitates the coexistence of species. Thus, the use of vertical space can reinforce the segregation of species that overlap in the niche dimensions of habitat and food. This could be the case, for example, in *A. molinae* and *T. pallidior*, which have similar body sizes (~30 g) and diets (mainly insectivorous) but different habits regarding space use, not only in the horizontal but also in the vertical dimension; *A. molinae* is clearly terrestrial and *T. pallidior* scansorial (Albanese 2010; Corbalán 2006; Giannoni et al. 2005; Tabeni et al. 2007; this study). Similarly, in Californian scrublands Meserve (1976) reported a considerable niche overlap between some rodent species due primarily to diet similarities. In this Californian assemblage, however, vertical and horizontal separation are also important mechanisms by which rodents can tolerate high dietary overlap.

In the Monte Desert we observed the differential use of vertical space by scansorial species. Despite *T. pallidior* using the ground and arboreal layers equally, it selected the highest layers and largest branch diameters. That this marsupial selected *P. flexuosa* over *Geoffroea decorticans* for climbing could be related to its dietary preferences. Recent studies have shown that almost 30% of *T. pallidior* diet is leaves, especially those of *P. flexuosa*, whereas it seemingly avoids the leaves of *G. decorticans* (Albanese 2010). In addition, particular microhabitats are created on patches under *Prosopis*, where the arthropod community differs in composition from other sites (Flores et al. 2004; Lagos 2004). These patches provide different prey and probably preferred items for *T. pallidior*, a marsupial that occasionally preys on eggs of birds and then occupies their tree nests for breeding (Mezquida and Marone 2002; M. Santillán, La Pampa University, pers. comm.). Therefore, foraging for food and nesting places could be reasons for *T. pallidior* to use the arboreal stratum.

Our study showed that *Graomys griseoflavus* uses arboreal space independently of habitat type, plant species, or branch diameter. This rodent has been described as capable of occupying a wide variety of habitats (i.e., xeric habitats, cultivated fields, and riparian forest), showing some flexibility in its preferences (Corbalán 2006; Corbalán and Ojeda 2004; Rosi 1983; Tabeni and Ojeda 2005). Therefore, it is not surprising that the same variability was observed with the use of vertical space in our study. Unlike for the anatomically similar species *Phyllotis darwini* (Gallardo-Santis et al. 2005), branch diameter does not seem to affect the aboveground movements of *G. griseoflavus*. This species was found on thin *Larrea* stems and thick *Prosopis* branches, suggesting that its anatomy is not a constraint for climbing. Occasionally, *G. griseoflavus* occupies bird nests during the breeding season, and also was seen using holes in the ground (Rosi 1983; S. Albanese, pers. obs.). Moreover, the diet of *G. griseoflavus* is composed mainly of leaves of *P. flexuosa* and *Geoffroea decorticans* (Campos 1997; Campos et al. 2001), both tree

species in which this rodent was frequently recorded, indicating a potential association between use of vertical space and foraging behavior.

For some small mammals differential use of vertical space is dependent on the season of the year (Buesching et al. 2008; Meserve 1977). In our study *Graomys griseoflavus* used vertical space mostly during the dry season. Moreover, the other rodents were captured in tree traps only in the dry season, when food resources are low and herbs are almost absent or dry in the Monte Desert (Morello 1958; S. Albanese, pers. obs.). Therefore, some species should change their diet or extend their foraging area, if possible, to survive (Stephens and Krebs 1986). Monte Desert rodents have considerable flexibility in their diets, which might be particularly advantageous in arid environments where resources are unpredictable and often scarce (Giannoni et al. 2005). The use of vertical space could provide additional food sources for the small mammals with the ability to exploit them. A similar pattern was observed in the bank vole (*Myodes glareolus*), which displays arboreality only under food shortage and with high population densities (Buesching et al. 2008).

In summary, both scansorial species used arboreal space but in different ways. *T. pallidior* showed a more selective behavior, preferring the highest layers of *P. flexuosa* and the most complex habitat, whereas *G. griseoflavus* showed more generalist behaviors, exhibiting little preference for habitat characteristics but using the vertical stratum mainly during the dry season. Terrestrial species move on the ground but use low heights in woody plants when resource availability is low. Finally, our study showed that small mammals of the Monte Desert perceive and use their environment in a 3-dimensional way. Therefore, vertical habitat structure could play a role in life histories of small mammals in southern deserts. The use of vertical space can reinforce segregation of species that might overlap in any niche dimension and affords more opportunities to acquire resources when these are scarce in the environment.

RESUMEN

El uso del espacio en pequeños mamíferos de desierto ha sido muchas veces considerado sólo en el plano horizontal, sin embargo el espacio vertical puede también ser importante para la segregación del hábitat entre las especies. Nuestro estudio analizó el uso del espacio vertical por especies de un ensamble de pequeños mamíferos del desierto de Monte a través del trampeo de animales a diferentes alturas. Registramos 1,336 capturas de 4 especies de roedores y un marsupial en 27,600 noches-trampa. Las 5 especies fueron capturadas tanto en el suelo como en el estrato arbóreo, pero sólo el pericote común (*Graomys griseoflavus*) y la marmosa pálida (*Thylamys pallidior*) usaron significativamente el espacio vertical. *G. griseoflavus* usa el estrato vertical independientemente del hábitat, la especie de planta o el diámetro de las ramas. *T. pallidior* en cambio, mostró un comportamiento más selectivo, encontrándose principalmente en el estrato más alto y usando los diámetros de ramas más anchos mayormente de

algarrobos (*Prosopis flexuosa*). Todos los roedores usaron las alturas más bajas del estrato arbóreo y mayormente durante la época seca cuando la disponibilidad de recursos en el ambiente es baja. Nuestro estudio sugiere que la estructura vertical del hábitat cumple un papel importante en la coexistencia de pequeños mamíferos de desierto y ofrecería más oportunidades de adquirir recursos cuando estos son escasos.

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LITERATURE CITED

- ALBANESE, M. S. 2010. Ecología de la marmosa pálida, *Thylamys pallidior* (Marsupialia, Didelphidae), en el desierto de Monte central. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina.
- BISIGATO, A. J., P. E. VILLAGRA, J. O. ARES, AND B. E. ROSSI. 2009. Vegetation heterogeneity in Monte Desert ecosystems: a multi-scale approach linking patterns and processes. *Journal of Arid Environments* 73:182–191.
- BUESCHING, C. D., C. NEWMAN, R. TWELL, AND D. W. MACDONALD. 2008. Reasons for arboreality in wood mice *Apodemus sylvaticus* and bank voles *Myodes glareolus*. *Mammalian Biology* 73:318–324.
- CAMPOS, C. M. 1997. Utilización de recursos alimentarios por mamíferos medianos y pequeños del desierto de Monte. Ph.D. dissertation, Universidad Nacional, Córdoba, Argentina.
- CAMPOS, C., R. OJEDA, S. MONGE, AND M. DACAR. 2001. Utilization of food resources by small and medium-sized mammals in the Monte desert biome, Argentina. *Austral Ecology* 26:142–149.
- CHASE, J. M., AND M. A. LEIBOLD. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois.
- CORBALÁN, V. 2006. Microhabitat selection by murid rodents in the Monte desert of Argentina. *Journal of Arid Environments* 65:102–110.
- CORBALÁN, V. E. 2004. Uso de hábitat y ecología poblacional de pequeños mamíferos del desierto de Monte central, Mendoza, Argentina. Ph.D. dissertation, Universidad Nacional, La Plata, Argentina.
- CORBALÁN, V., AND G. DEBANDI. 2009. Evaluating microhabitat selection by *Calomys musculus* (Rodentia: Cricetidae) in western Argentina using luminous powders. *Mastozoología Neotropical* 16:205–210.
- CORBALÁN, V., AND R. OJEDA. 2004. Spatial and temporal organization of small mammal communities in the Monte Desert, Argentina. *Mammalia* 68:5–14.
- DICKMAN, C. R. 1989. Patterns in the structure and diversity of marsupial carnivore communities. Pp. 241–251 in *Patterns in the structure of mammalian communities* (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). TexasTech University Press, Lubbock.
- ESTRELLA, H., J. BOSHOVEN, AND M. TOGNELLI. 2001. Características del clima regional y de la Reserva de Ñacuñán. Pp. 25–33 in *El desierto de Monte: La Reserva de la Biosfera de Ñacuñán* (S. Claver and S. Roig-Juñent, eds.). Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA)—Comité Argentino Man and Biosphere—United Nations Educational Scientific and Cultural Organization (UNESCO), Mendoza, Argentina.
- FLORES, G. E., S. J. LAGOS, AND S. ROIG-JUÑENT. 2004. Artrópodos epigeos que viven bajo la copa del algarrobo (*Prosopis flexuosa*) en la Reserva Telteca, Mendoza, Argentina. *Multequina* 13:71–90.
- GALLARDO-SANTIS, A., J. A. SIMONETTI, AND R. A. VÁSQUEZ. 2005. Influence of tree diameter on climbing ability of small mammals. *Journal of Mammalogy* 86:969–973.
- GIANNONI, S. M., C. M. BORCHI, M. DACAR, AND C. M. CAMPOS. 2005. Main food categories in diets of sigmodontine rodents in the Monte (Argentina). *Mastozoología Neotropical* 12:181–187.
- GONNET, J. M., AND R. A. OJEDA. 1998. Habitat use by small mammals in arid Andean foothills of Monte desert of Mendoza, Argentina. *Journal of Arid Environments* 38:349–357.
- HARNEY, B. A., AND R. D. DUESER. 1987. Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. *Ecology* 68:1084–1091.
- HERSHKOVITZ, P. 1962. The recent mammals of the Neotropical region: a zoogeographic and ecological review. Pp. 311–431 in *Evolution, mammals and southern continents* (A. Keast, F. C. Erk, and B. Glass, eds.). State University of New York Press, Albany.
- HUTCHINSON, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia in Quantitative Biology* 22:415–427.
- LAGOS, S. J. 2004. Diversidad biológica de las comunidades de artrópodos epigeos en áreas pastoreadas y no pastoreadas del Monte (Argentina). Ph.D. dissertation, Universidad Nacional, Cuyo, Argentina.
- LAYNE, J. M. 1970. Climbing behavior of *Peromyscus floridanus* and *Peromyscus gossypinus*. *Journal of Mammalogy* 51:580–591.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594–598.
- MANLY, B. F. J., L. L. McDONALD, D. L. THOMAS, T. L. McDONALD, AND W. P. ERICKSON. 2002. *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. Kluwer Academic Publishers, Dordrecht, Netherlands.
- M'CLOSKEY, R. T. 1975. Habitat dimensions of white-footed mice, *Peromyscus leucopus*. *American Midland Naturalist* 93:158–167.
- MESERVE, P. L. 1976. Habitat and resource utilization by rodents of a California coastal sage scrub community. *Journal of Animal Ecology* 45:647–666.
- MESERVE, P. L. 1977. Three-dimensional home ranges of cricetid rodents. *Journal of Mammalogy* 58:549–558.
- MESERVE, P. L. 1981. Resource partitioning in a Chilean semi-arid small mammal community. *Journal of Animal Ecology* 50:745–757.
- MEZQUIDA, E. T., AND L. MARONE. 2002. Microhabitat structure and avian nest predation risk in an open Argentinean woodland: an experimental study. *Acta Oecologica* 23:313–320.
- MORELLO, J. 1958. La provincia fitogeográfica del Monte. *Opera Lilloana* 2:1–155.
- OJEDA, R. A., C. M. CAMPOS, J. M. GONNET, C. E. BORCHI, AND V. G. ROIG. 1998. The MaB Reserve of Ñacuñán, Argentina: its role in understanding the Monte Desert biome. *Journal of Arid Environments* 39:299–313.

- OJEDA, R. A., AND S. TABENI. 2009. The mammals of the Monte desert revisited. *Journal of Arid Environments* 73:173–181.
- PASSERA, C. B., A. D. DALMASSO, AND O. BORSETTO. 1983. Método de point quadrat modificado. Pp. 135–151 in *Informe del taller sobre arbustos forrajeros de zonas áridas y semiáridas* (R. Candia and R. Braun, eds.). Food and Agricultural Organization of the United Nations (FAO)–Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina.
- ROIG, F. A., AND B. ROSSI. 2001. Flora y vegetación de la Reserva. Pp. 41–70 in *El desierto del Monte: La Reserva de Biosfera de Ñacuñán* (S. Claver, and S. Roig-Juñent, eds.). Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA)–Comité Argentino Man and Biosphere–United Nations Educational Scientific and Cultural Organization (UNESCO), Mendoza, Argentina.
- ROSENZWEIG, M. L., B. SMIGEL, AND A. KRAFT. 1975. Patterns of food, space and diversity. Pp. 241–268 in *Rodents in desert environments* (I. Prakash and P. K. Gosh, eds.). The Hague, the Netherlands.
- ROSI, M. I. 1983. Notas sobre la ecología, distribución y sistemática de *Graomys griseoflavus griseoflavus* (Waterhouse, 1837) (Rodentia, Cricetidae) en la provincia de Mendoza. *Historia Natural* 3:161–167.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:17–39.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- STEPHENS, D. W., AND J. R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- TABENI, S., L. MASTRANTONIO, AND R. A. OJEDA. 2007. Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. *Acta Oecologica* 31:259–269.
- TABENI, M. S., AND R. A. OJEDA. 2005. Ecology of the Monte Desert small mammals in disturbed and undisturbed habitats. *Journal of Arid Environments* 63:244–255.
- TARABORELLI, P., V. CORBALÁN, AND S. GIANNONI. 2003. Locomotion and escape modes in rodents of the Monte Desert (Argentina). *Ethology* 109:475–485.
- TATE, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*. *Bulletin of the American Museum of Natural History* 66:1–250.
- TOGNETTI, M., AND J. BOSHOVEN. 2001. Localización. Pp. 15–16 in *El desierto de Monte: La Reserva de la Biosfera de Ñacuñán* (S. Claver and S. Roig-Juñent, eds.). Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA)–Comité Argentino Man and Biosphere–United Nations Educational Scientific and Cultural Organization (UNESCO), Mendoza, Argentina.
- ZAR, J. H. 1999. *Biostatistical analysis*. 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

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