

Mammals of the Monte Desert: from regional to local assemblages

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Much of South America consists of diverse arid and semiarid regions characterized by high mammal endemism as a result of a complex interplay between place and lineage histories. In this review we summarize and highlight several biogeographical and ecological features of the small mammals of South America drylands, with special focus on the Monte Desert biome. We provide information on population characteristics, community structure, food and habitat use, and responses to disturbances. Major findings at different scales include the distinctiveness and high species turnover across South American drylands and Monte Desert ecoregions; synchronous population fluctuations with high variability between years; herbivory and omnivory as dominant trophic strategies; community structure organized through habitat and food segregation; and the importance of a landscape mosaic of grazed and ungrazed areas for maintenance of small and medium-sized mammal diversity.

Key words: Man and Biosphere (MaB) Reserve Ñacuñán, macro- and microhabitat utilization, marsupials, rodents, small and medium-sized mammals, trophic ecology

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Desert ecosystems have been a fertile ground for significant advances in evolutionary biology and ecological theory (Brown 1975; Eisenberg 1963; Mares 1980; Noy-Meir 1973; Pianka 1975; Rosenzweig 1973; Schmidt-Nielsen 1964). Substantial research on the ecological, morphological, behavioral, and physiological attributes of North American desert rodents has led to generalizations regarding small mammal communities in other drylands in the world. However, in view of different abiotic and biotic features of desert ecosystems worldwide, caution should be used in generalizing paradigms developed from one region (Morton et al. 1994; Ojeda and Tabeni 2009; Predavec 2000; Reichman 1991; Shenbrot et al. 1999). In particular, in spite of the diverse mosaic of South American drylands (Rundel et al. 2007) and their role in the evolution of a rich and endemic mammal biota (Herskovitz 1972; Mares and Ojeda 1982; Reig 1986), this region has been largely overlooked (Mares 1992). Only in the last 25 years has this trend been somewhat reversed (Jaksic et al. 1997; Lima et al. 2002; Marquet 1994; Marquet et al. 1998; Meserve et al. 1996; Ravetta 2009).

The purpose of this contribution is to present an overview of the South American drylands, with particular emphasis on the Monte Desert and its small to medium-sized mammals (henceforth mammals or mammal assemblages, unless noted otherwise). Our conceptual framework (Fig. 1) encompasses continental to ecoregional and local scales, and seeks to

synthesize and highlight some of the common elements in mammal species composition, distribution, community ecology, and species responses to disturbances.

THE CONTINENTAL SCALE

Place and lineage histories have important influence in the assembly of a particular biota (Brown 1995). They include impacts ranging from geological events and past climatic environments to organismal colonization, speciation, and extinction.

South American landscapes reflect a strong influence from the physical structure of the continent (Orme 2007). For example, the Andes have played a pivotal role in shaping the dispersal and evolution of the South America biota (Antonelli et al. 2009; Meserve 2007; Veblen et al. 2007). The uplift of the Andes changed the course of major river systems and formed the only mountain barrier to atmospheric circulation in the Southern Hemisphere. The rain-shadow effect imposed by this long mountain chain (Orme 2007) has had a major influence on the climate patterns of the continent and favored the development of arid and semiarid landscapes, such as the



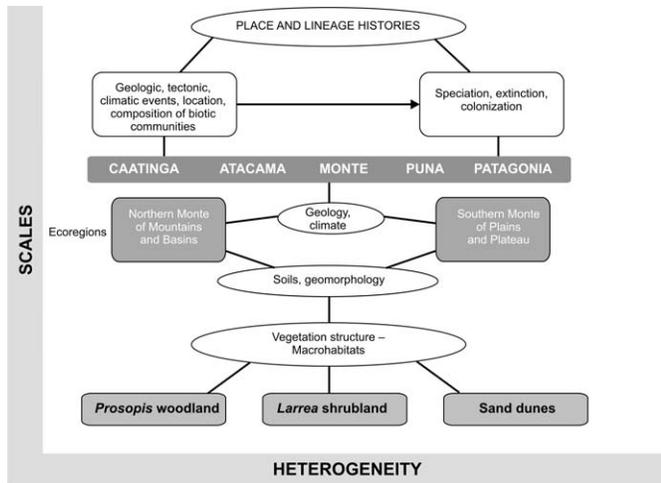


FIG. 1.—Conceptual flowchart showing a hierarchical scale (continental to local) of major drivers of ecoregions, macrohabitats, and species assemblages discussed in the paper.

Peruvian, Atacama, Monte, and Patagonian deserts. The resulting diversity of drylands (Mares 1999; Morello 1985; Rundel et al. 2007) is characterized by high mammal richness and endemism (Mares 1992).

Our assessment of these assemblages (particularly marsupials and rodents) revealed 5 general patterns (Ojeda et al. 2000; Fig. 2). First, the highland Altiplano or Puna is the most species-rich dryland (Fig. 2A). More than 50% of the mammal species are endemic, supporting this area's role as a major evolutionary center of cricetid (i.e., sigmodontine) rodent radiation (Marquet 1994; Ojeda et al. 2000; Reig 1986; R. A. Ojeda, pers. obs.). Second, small mammals of the South American arid and semiarid ecoregions are distinct. A high turnover rate of species (beta diversity) exists among drylands (Ojeda et al. 2000). Approximately 80% of the mammal species occur in only 1 dryland, with a small percentage of species present in 2 or 3 biomes (Fig. 2B). This is a different geographical pattern than among North American desert mammals, whose distribution ranges frequently occupy 2 or more major deserts (Ojeda et al. 2000). Third, herbivores are the main trophic group represented. This can be the result of phylogenetic inertia (i.e., due to the species contribution of caviomorph rodents). Fourth, the Monte and Patagonian deserts show a marked differentiation in species composition from that of the Chilean Mediterranean scrubland and northern semiarid zone, supporting the role of the Andes as a strong biogeographical barrier. Finally, small mammal diversity decreases with distance away from the Andes on both sides. The decrease in richness in the lowland deserts (e.g., Atacama and Caatinga) also could be due to decreased rainfall, sparse vegetation, and climatic unpredictability (i.e., precipitation—Ojeda et al. 2000).

THE BIOME—ECOREGIONAL SCALE

The ubiquity of heterogeneity of desert ecosystems at different spatial scales (Polis 1991) is reflected in the Monte

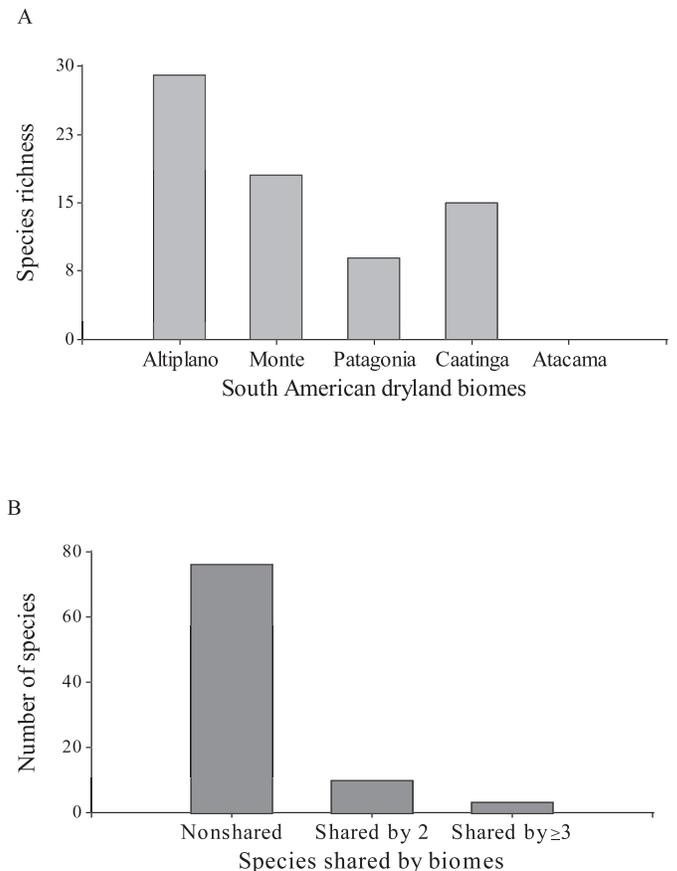


FIG. 2.—Richness and species shared by major biomes. A) Mammal species (<500 g) richness in South American arid biomes. B) Number of shared species by biome.

Desert by its marked variations in topography, climate, precipitation, and vegetation. The Monte is a subtropical to temperate warm desert extending from 24°35'S to 44°20'S in western Argentina (Abraham et al. 2009; Morello 1958; Fig. 3). It is bounded in the west by the Andes, in the north by the high, arid Puna, in the south by the cold Patagonian steppes, and in the east by the arid-semiarid woodlands of the Chaco and Espinal (Roig et al. 2009). The Monte has gradually declining topographic relief and a north to south transition from primarily summer precipitation to a less seasonal pattern. Total precipitation ranges from <100 to 450 mm (Ojeda and Tabeni 2009). Two major ecoregions compose the Monte Desert, the northern Monte dominated by mountains and closed basins (valles y bolsones) between 24°S and 32°S, and the southern Monte with plains and plateau (llanuras y mesetas) between 32°S and 37°S (Fig. 3). Despite the absence of a major barrier between these 2 ecoregions, they share only 36% of a total of 46 mammal species (Appendix I). This high beta (between-habitat) diversity among ecoregions underscores the large spatial variation in the mammal assemblages of the Monte along its latitudinal extension.

The Monte resembles parts of the North American Sonoran and Chihuahuan deserts, with which it shares several plant genera. Major landscape mosaics include the dominant *Larrea*

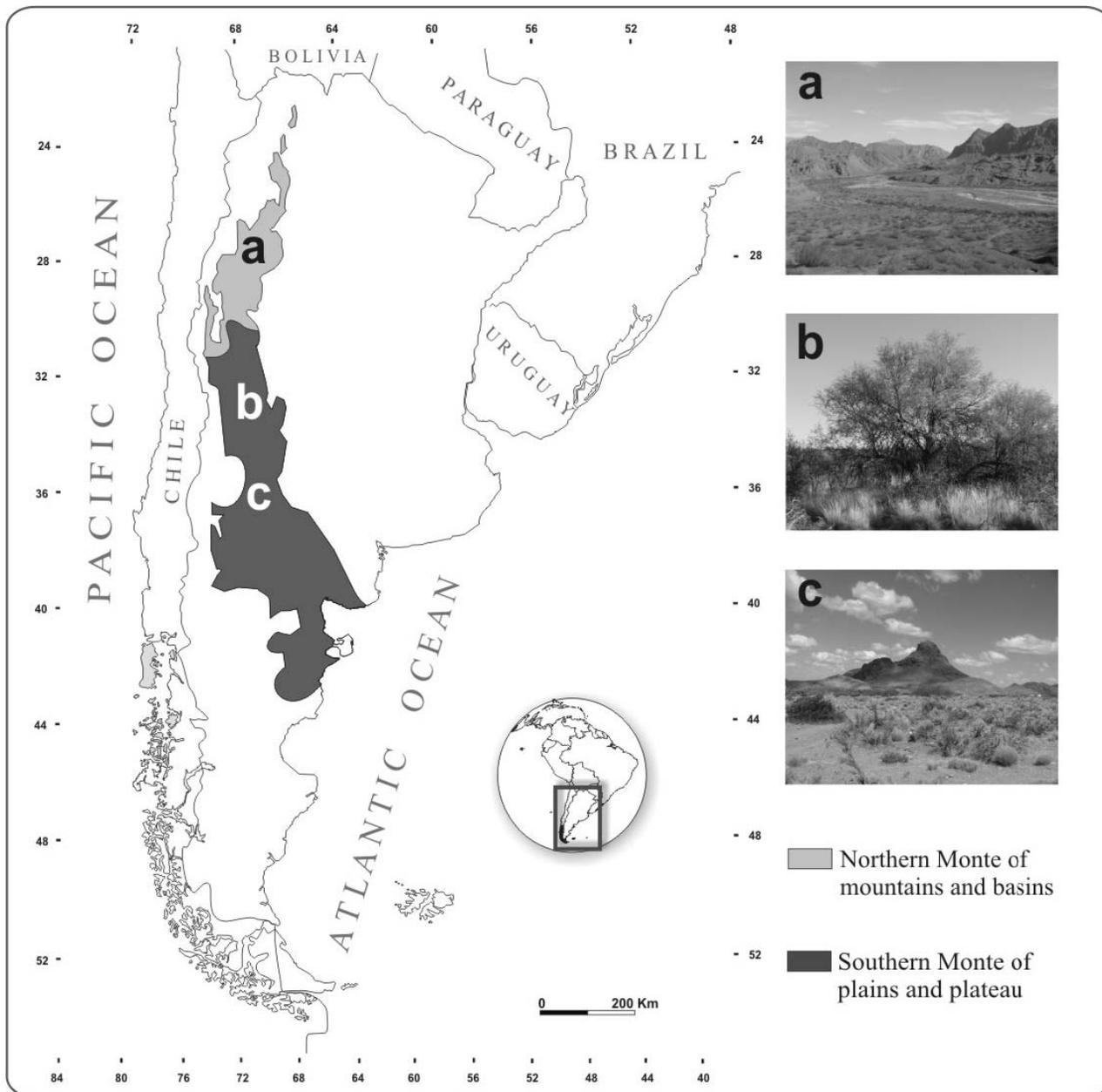


FIG. 3.—Map of the Monte Desert, showing the landscape diversity from mountains and basins in the a) north, and plains and plateau in the b) central and c) southern regions.

shrublands, *Prosopis* woodlands along gullies and alluvial basins, sand dunes (salt basins or salares), rocky outcroppings, and an extensive piedmont desert along the Andean Cordillera, with several species of cacti and bromeliads. Monte Desert mammals include a diversity of niche types, involving differences in diet, habitat use, and life mode. The small mammals here can cope with desert environments through morphological, behavioral, and physiological traits by using major adaptations similar to those found in other deserts, such as concentrated urine, specialized kidneys, dry feces, inflated auditory bullae, long tails, countershading coloration, foot pads, nocturnal activity, and a fossorial habit (Ojeda and Tabeni 2009).

A notable example of these adaptive characteristics is the red vizcacha rat (*Tympanoctomys barrerae*), whose suite of ecological, physiological, morphological, and behavioral adaptations are convergent with the North American chisel-toothed kangaroo rat (*Dipodomys microps*; Heteromyidae), and the African–Asian sand rats (*Psammomys obesus*; Muridae—Giannoni et al. 2000; Mares et al. 1997; Ojeda et al. 1999). A remarkable diversity of ecophysiological adaptations is found among caviomorph and cricetid desert rodents (Bozinovic et al. 2007; Díaz and Ojeda 1999; Díaz et al. 2006). Urine osmolarities >7,000 mOsm/kg for some Monte Desert rodents (e.g., *Eligmodontia*, *Calomys*, *Graomys*, *Salinomys*, and *Tympanoctomys*) and the common desert

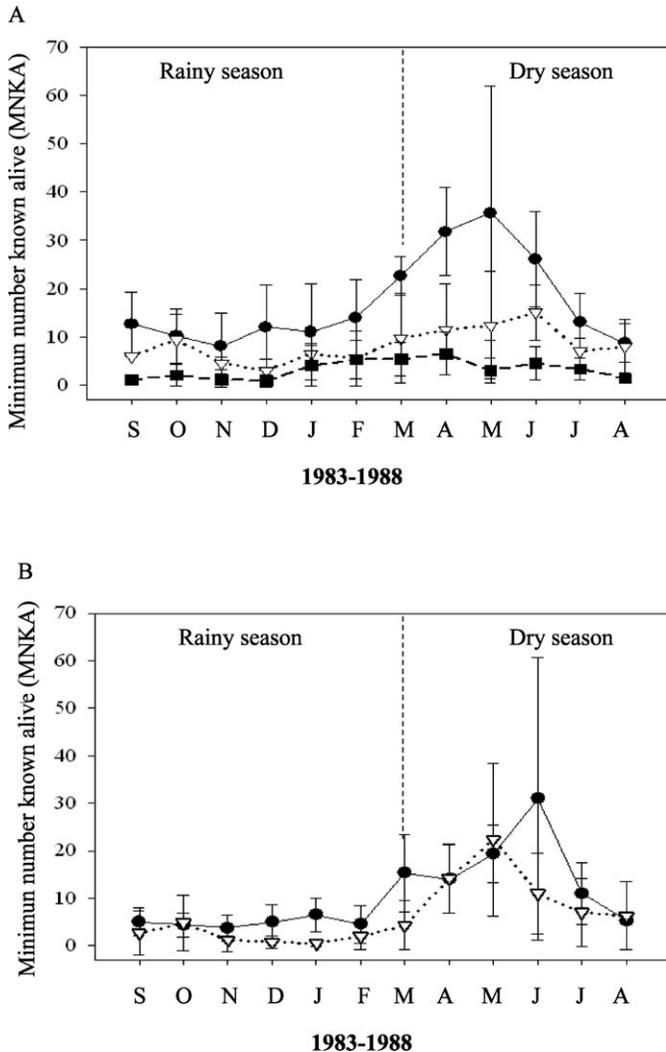


FIG. 4.—Population fluctuation of the small mammal assemblage in the *Prosopis* woodland in the central Monte Desert. Mean and SD of population abundance (minimum number known alive) of monthly records from 1983 to 1988 (R. A. Ojeda, pers. obs.). A) *Graomys griseoflavus* (—●—), *Calomys musculus* (···▽···), and *Thylamys pallidior* (—■—). B) *Akodon molinae* (—●—) and *Eligmodontia typus* (···▽···).

opossum (*Thylamys pallidior*) are among the highest urine concentrations reported for desert small mammals worldwide (Díaz and Ojeda 1999; Díaz et al. 2001).

THE LOCAL SCALE

Population, community structure, habitat, and food utilization.—Much research on Monte Desert mammals in the past 20 years has been conducted in the Man and Biosphere Reserve of Ñacuñán (henceforth Ñacuñán), located in the central Monte Desert (Ojeda et al. 1998). Ñacuñán supports high species richness and a representative number of Monte mammals from both ecoregions (Fig. 3). Common small mammals (<100 g) include the common desert opossum (*T. pallidior*; Didelphimorphia, Didelphidae), and cricetid rodents such as the silky mouse (*Eligmodontia typus*), the vesper

mouse (*Calomys musculus*), the grass mouse (*Akodon molinae*), and the common pericote (*Graomys griseoflavus*). Common medium-sized (>100 g) caviomorph rodents are the Mendocino tuco-tuco (*Ctenomys mendocinus*), the red vizcacha rat (*T. barrerae*), the southern cavy (*Microcavia australis*), the common yellow-toothed cavy (*Galea musteloides*), the plains vizcacha (*Lagostomus maximus*), the Patagonian hare (*Dolichotis patagonum*), and the exotic European hare (*Lepus europaeus*; Lagomorpha, Leporidae).

Temporal fluctuations of small mammal populations are relatively synchronous throughout the year but highly variable between years (Fig. 4). Changes in density (i.e., population peaks) during the dry autumn season (April–June) show a significant association with the rainy season of the previous spring–summer (September–March; linear regression: adjusted $r^2 = 0.64$; $P < 0.010$ —R. A. Ojeda, pers. obs.). This is a common pattern in arid regions, where primary productivity, and consequently, species diversity and abundances are controlled by precipitation (Brown 1975; Noy-Meir 1973; Polis 1991; Rosenzweig 1968).

Maximum and minimum densities of all small mammal species are 118 and 18 individuals/ha in the *Larrea* shrublands, and 78 and 7 individuals/ha in the *Prosopis* woodland (R. A. Ojeda, pers. obs.). Remarkable variability exists in small mammal abundances between years, especially during maximum density peaks (April–June), reflecting annual variation in precipitation, and consequently, productivity (Corbalán and Ojeda 2004; R. A. Ojeda, pers. obs.).

At the local scale of Ñacuñán the highest diversity is correlated with habitat heterogeneity and found in *Prosopis* woodland and *Larrea* shrubland (Corbalán and Ojeda 2004). No major differences exist in species composition among habitats; however, relative abundances show great variability across habitats, indicating differences in species' niche requirements (Corbalán and Ojeda 2004; Corbalán et al. 2006; Tabeni and Ojeda 2005; Fig. 5A). The silky mouse (*E. typus*) is the dominant species in sand dunes, whereas the common pericote (*G. griseoflavus*) dominates in the *Prosopis* woodland. No single species of small mammal is consistently dominant in the *Larrea* shrublands, although the vesper mouse (*C. musculus*) and grass mouse (*A. molinae*) reach their highest densities in this habitat (Corbalán and Ojeda 2004; Corbalán et al. 2006; Fig. 5B).

The associations between species and microhabitat variables are weaker than at the macrohabitat level (i.e., major habitat types). At the microhabitat level the grass mouse (*A. molinae*) is closely associated with densely vegetated patches with high cover of litter and trees, whereas *C. musculus* avoids bare soil and is associated with high cover of shrubs and herbs. The common pericote (*G. griseoflavus*) is associated with cover of litter, trees, and shrubs, whereas *E. typus* is associated with open sandy areas (Corbalán 2006; Corbalán and Debandi 2006; Corbalán and Ojeda 2004; Corbalán et al. 2006; Tabeni et al. 2007).

Among the medium-sized mammals the small southern cavy (*M. australis*) and the plains vizcacha (*L. maximus*)

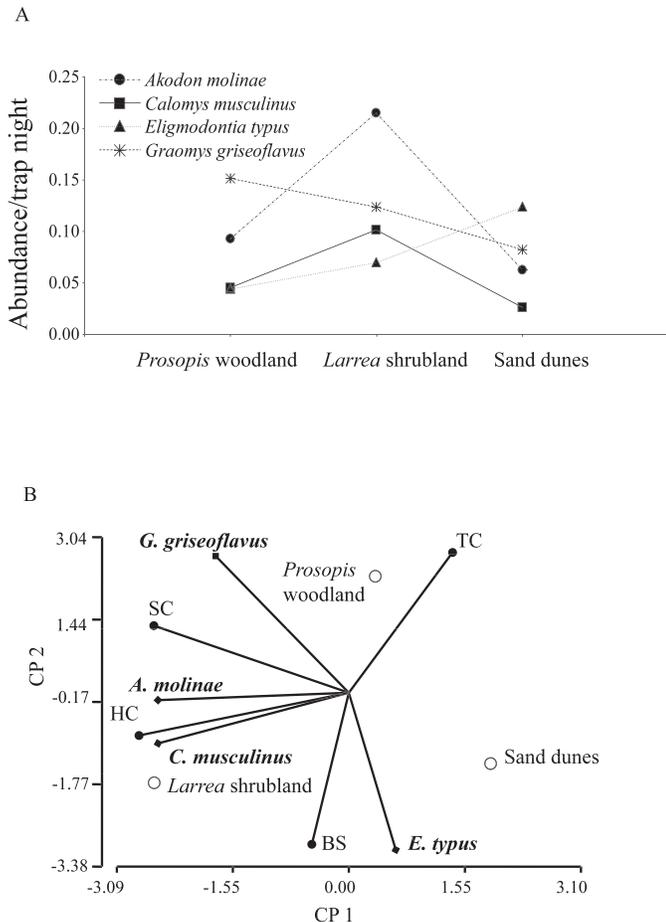


FIG. 5.—A) Small mammal abundance in major macrohabitats of the Monte Desert (1999–2001). B) Principal component analysis (PCA) of small mammal relationships and habitat types. BS, bare soil; HC, herb cover; TC, tree cover; SC, shrub cover.

locate their colonies in association with plants that offer good protective cover (*Condalia microphylla*, *Prosopis flexuosa*, and *Larrea cuneifolia*—Kufner and Chambouleyron 1993; Tognelli et al. 1995). The red vizcacha rat (*T. barrerae*) inhabits sandy habitats and salt flats dominated by halophytic plants (e.g., *Heterostachys*, *Atriplex*, and *Suaeda*—Ojeda et al. 1996), whereas the fossorial Mendocino tuco-tuco (*C. mendocinus*) is associated with soft soils of sandy habitats (Albanese et al. 2010). In contrast, the cursorial Patagonian hare (*D. patagonum*) is associated with bare, hard soils and low shrub cover (Campos et al. 2001b).

The 2 main trophic specializations of the Monte mammals are herbivory and omnivory (Campos et al. 2001a). The most herbivorous small mammal is the common pericote (*G. griseoflavus*), whereas omnivory is exemplified by *C. musculus*, *E. typus*, *A. molinae*, and *T. pallidior*. Omnivory appears to be predominant in desert ecosystem food webs (Polis 1991) and is particularly advantageous when food resources are scarce or unpredictable, or both (Campos et al. 2001a; Glanz 1982; Meserve 1981; Reichman 1975; Stafford Smith and Morton 1990). Conversely, herbivory in the Monte Desert is characteristic of the medium-sized caviomorph rodents, such as cavies

(*M. australis* and *G. musteloides*), the Mendocino tuco-tuco (*C. mendocinus*), the Patagonian hare (*D. patagonum*), the plains vizcacha (*L. maximus*), and the exotic European hare (*L. europaeus*—Albanese et al. 2010; Campos et al. 2001a).

Despite different seed removal rates between North and South American desert taxa (e.g., ants, rodents, and birds—Brown and Ojeda 1987; Kelt et al. 2004; Mares and Rosenzweig 1978; Saba and Toyos 2003; Sassi et al. 2004), granivory seems to be important in the Monte Desert (Blendinger and Ojeda 2001; Folgarait and Sala 2002; Giannoni et al. 2001; Lopez de Casenave et al. 1998; Marone et al. 2000). The higher rate of seed removal by North American small mammals, when compared with other deserts, likely is coupled to the occurrence of a lineage such as the heteromyids, with morphological adaptations (e.g., cheek pouches) for granivory, rather than differential seed production between desert ecosystems (Marone et al. 2000). However, better techniques have been important in improving dietary analysis and detecting a higher percentage of seed consumption in recent studies of Monte Desert cricetid rodents (Giannoni et al. 2005).

In summary, assemblages of Monte Desert mammal are organized through habitat and food segregation. The available data (i.e., food and habitat use, foraging, and physiology) suggest that mammal assemblages are structured by specific niche requirements of different functional groups, although they vary in composition among localities (R. A. Ojeda, pers. obs.).

RESPONSES TO DISTURBANCES AND CONSERVATION

Superimposed on landscape heterogeneity and vegetation patchiness are effects of disturbances on the distribution and abundance of desert animals (Wiens 1985). The natural environmental heterogeneity that characterizes the Monte Desert, together with structural variations caused by human disturbance (e.g., logging, grazing, and fire), generates a mosaic of habitats that influences the structure and composition of mammal assemblages (Tabeni and Ojeda 2003).

Following more than 40 years of cattle exclusion at Ñacuñán, the area is dominated now by patches of shrublands and woodlands, with small open areas. In contrast, the extensive livestock grazing in the surrounding matrix produces a more heterogeneous landscape (Tabeni et al. 2007; Tabeni and Ojeda 2005).

Recovery of the vegetation structure of Ñacuñán has favored an increase in abundance of small mammals requiring dense vegetation (Tabeni and Ojeda 2005; S. Tabeni and R. A. Ojeda, pers. obs.; Table 1). However, at the same time the reduced availability of open patches has reduced the occurrence of cursorial mammals (e.g., Patagonian hare [*D. patagonum*] and European hare [*L. europaeus*]) and the common cavy (*M. australis*) in the reserve, whereas in the neighboring grazed lands their abundances have increased.

Likewise, changes in vegetation structure produced by fire affect the diversity of small mammals in the Monte Desert (Ojeda 1989). Fire-induced changes in vegetation resulted in a decrease of small mammal richness, from 5 to 1 species, favoring an

TABLE 1.—Total number of small mammals captured during 2001 and 2002, feces/ha recorded for medium-sized mammals (except colonies/ha for *Microcavia australis*), and species richness for each habitat type, in protected and grazed areas in the central Monte Desert.

	Protected area			Grazed area		
	<i>Prosopis</i> woodland	<i>Larrea</i> shrubland	Sand dunes	<i>Prosopis</i> woodland	<i>Larrea</i> shrubland	Sand dunes
Small mammals						
<i>Akodon molinae</i>	40	113	41	68	39	29
<i>Graomys griseoflavus</i>	62	69	56	53	46	41
<i>Calomys musculus</i>	21	47	21	17	42	18
<i>Eligmodontia typus</i>	7	7	21	9	18	31
Medium-sized mammals						
<i>Dolichotis patagonum</i>	0	0	0	202	18	0
<i>Microcavia australis</i>	25	0	0	128	25	13
<i>Galea musteloides</i>	75	142	3	59	21	8
<i>Lepus europaeus</i>	0	0	5	154	21	30
Number of species	7	6	7	9	9	8

increase in abundance of species having morphoecological features suitable for exploiting large open patches (e.g., *E. typus*).

The recognition of ecological heterogeneity in space and time requires conservation goals that focus on the interaction of each species with all components of the landscape (Noon et al. 1997; Rosenzweig 2003). Thus, the mosaic of grazed and ungrazed areas in the central Monte Desert appears to be an appropriate matrix to facilitate the occurrence of a diverse pool of mammals with different niche requirements.

CONCLUSIONS

South America contains a diverse set of drylands and mammal assemblages. This heterogeneity in species diversity and composition is repeated throughout different spatial scales (from continental to regional and local habitats), offering a rich background for diverse types of biogeographical and ecological research.

The main findings of our research and review of South American and Monte Desert mammal communities are that a high degree of between-habitat (beta) diversity exists across major drylands (continental scale) and ecoregions (regional scale); herbivory and omnivory are the dominant trophic strategies, associated with the caviomorph and cricetid rodent lineages; community structure and coexistence of the Monte Desert mammals can be explained by differential utilization of habitat and food resources; interannual comparisons of small mammal abundances show major fluctuations, with maximum population peaks occurring in autumn, after the spring–summer rainy season; highest small mammal diversity is associated with high habitat heterogeneity; and a matrix of grazed and ungrazed areas enhances the landscape heterogeneity, contributing to the persistence of a diverse pool of mammal species with different niche requirements.

Although our understanding of the Monte Desert has improved in recent decades (Ravetta 2009), major issues remain that call for studies to enhance basic knowledge of these small mammal communities. This need is particularly compelling given the heterogeneity of landscapes and

different selective pressures operating on mammal assemblages along its latitudinal extent (i.e., seasonality and water balance in the northern Monte compared to less seasonality and extreme low temperatures in the southern Monte, etc).

The establishment of a long-term research program with standardized protocols in worldwide deserts should be the aim of future ecological research in drylands. Our hope is that such long-term research will link biodiversity, ecosystem processes, human activities, and ecosystem services (Perevolotsky et al. 2004), thus uniting biodiversity conservation and management in aridlands.

RESUMEN

Gran parte del territorio de Sudamérica se compone de una extraordinaria diversidad de regiones áridas y semiáridas, caracterizadas por un alto número de mamíferos endémicos. En esta revisión caracterizamos la estructura de los ensambles de pequeños mamíferos de las tierras áridas de Sudamérica, con particular atención en el Desierto del Monte. Proveemos información sobre características poblacionales, estructura de comunidades, uso de alimentos y hábitats, y respuestas a perturbaciones. Entre los principales resultados a diferentes escalas se incluyen: la particularidad de los mamíferos y la tasa de cambio de riqueza entre las tierras áridas de Sudamérica y ecorregiones del Monte; fluctuaciones poblacionales sincrónicas, pero con gran variabilidad interanual; las estrategias tróficas dominantes son la herbivoría y omnivoría; la estructura comunitaria se asienta en el uso diferencial de recursos de alimentos y hábitats, y finalmente, en la importancia de la matriz de ambientes pastoreados y no pastoreados para el mantenimiento de la biodiversidad.

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Special Feature Editor was Barbara H. Blake.

APPENDIX I

Small and medium-sized mammals (marsupials and rodents) recorded for the ecoregions of the Monte Desert and ecotonal areas. Names in boldface type are species whose geographic ranges are restricted to each ecoregion (modified after Barquez et al. 2006).

	Northern Monte of mountains and basins	Southern Monte of plains and plateau
Didelphimorphia	<i>Didelphis albiventris</i> <i>Thylamys pallidior</i>	<i>Didelphis albiventris</i> <i>Lestodelphys halli</i> <i>Thylamys pallidior</i>
Rodentia	<i>Abrocoma shistacea</i> <i>Akodon albiventer</i> <i>Akodon simulator</i> <i>Akodon spegazzinii</i> <i>Andalgalomys olrogi</i> <i>Andalgalomys roigi</i> <i>Calomys musculus</i> <i>Ctenomys coludo</i> <i>Ctenomys famosus</i> <i>Ctenomys knighti</i> <i>Dolichotis patagonum</i> <i>Eligmodontia bolsonensis</i> <i>Eligmodontia moreni</i> <i>Eligmodontia typus</i> <i>Galea musteloides</i> <i>Graomys griseoflavus</i> <i>Lagidium viscacia</i> <i>Lagostomus maximus</i> <i>Microcavia australis</i> <i>Myocastor coypus</i> <i>Octodontomys gliroides</i> <i>Octomys mimax</i> <i>Oligoryzomys longicaudatus</i> <i>Phyllotis xanthopygus</i> <i>Pipanacoctomys aureus</i> <i>Salinoctomys loschalchalersorum</i> <i>Salinomys delicatus</i> <i>Tympanoctomys barrerae</i>	<i>Didelphis albiventris</i> <i>Lestodelphys halli</i> <i>Thylamys pallidior</i> <i>Abrocoma usspallata</i> <i>Akodon azarae</i> <i>Akodon molinae</i> <i>Akodon neocenus</i> <i>Akodon oenos</i> <i>Andalgalomys roigi</i> <i>Calomys musculus</i> <i>Ctenomys azarae</i> <i>Ctenomys haigi</i> <i>Ctenomys johannis</i> <i>Ctenomys mendocinus</i> <i>Ctenomys pontifex</i> <i>Ctenomys validus</i> <i>Dolichotis patagonum</i> <i>Eligmodontia moreni</i> <i>Eligmodontia morgani</i> <i>Eligmodontia typus</i> <i>Euneomys chinchilloides</i> <i>Galea musteloides</i> <i>Graomys griseoflavus</i> <i>Lagidium viscacia</i> <i>Lagostomus maximus</i> <i>Microcavia australis</i> <i>Myocastor coypus</i> <i>Oligoryzomys flavescens</i> <i>Oligoryzomys longicaudatus</i> <i>Phyllotis xanthopygus</i> <i>Reithrodon auritus</i> <i>Salinomys delicatus</i> <i>Tympanoctomys barrerae</i>