The mammals of the Monte Desert revisited

R.A. Ojeda*, S. Tabeni

Biodiversity Research Group (GiB), National Council for Science and Technology of Argentina (CONICET), Institute for Aridland Research (IADIZA), CC 507, C.P. 5500 Mendoza, Argentina

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ABSTRACT

Great part of ecological thought in desert ecology is based on research findings in the northern hemisphere, and these have led to generalizations to other drylands. However, South American aridlands constitute an important scenario of aridland evolution in the Neotropical temperate biota. The degree of distinctiveness of the South American dryland biota is the result of the history of lineages and place (diverse topography, climates, vegetation) in the southern part of the continent since the Oligocene. The aim of our contribution is to provide an updated review of some aspects of the latest biogeographical, ecological, physiological, and behavioral research of the Monte Desert mammals and reassessment of their evolutionary ecology. The temperate Monte Desert extends from 24° to 43° south latitude and resembles parts of the North American warm deserts. The Monte is a heterogeneous mosaic of landscapes, from open sand dune habitats to *Larrea* shrublands and dense vegetation patches of *Prosopis* woodlands. The mammal assemblages show variations in richness, diversity and endemicity. The structure of mammal assemblages is closely related to vegetation structure over different spatial scales. The Monte mammal assemblages show a great diversity of niche types and ecological, physiological and behavioral attributes for desert existence, convergent, in greater or lesser degree, with ecological counterparts from other deserts of the world. We point out the need to be cautious when comparing heterogeneous arid ecosystems.

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1. Introduction

Desert mammals have played an important role in the development of ecological theory and in the understanding of adaptations to xeric environments (Brown, 1975; Mares, 1975, 1980; Noy-Meir, 1973, 1974; Pianka, 1975; Reichman, 1983; Rosenzweig, 1973; Schmidt-Nielsen, 1964). Years of ecological research on North American deserts—one of the world's best studied arid regions—have led to generalizations to other drylands, and consequently, much of ecological thought in desert ecology is based on research findings in the northern hemisphere (Mares, 1983; Reichman, 1991). Thus, the ecological, morphological and physiological attributes found for the North American desert rodents became paradigmatic features (i.e. bipedal locomotion, granivory, and so on) of adaptation to desert existence. In comparison with well-known deserts, some of the earlier research on southern hemisphere drylands were regarded as relatively impoverished in species diversity or in the repertoire of adaptive traits to desert

conditions (Mares, 1975, 1976; Murray and Dickman, 1994; Stafford Smith and Morton, 1990). Regardless of the role of North American deserts as model ecosystems, several studies have pointed out the need to be careful when accepting paradigms constructed largely from one continent and for more research in the various desert ecosystems, before broad generalizations can be made (Morton et al., 1994; Predavec, 2000; Reichman, 1991; Shenbrot et al., 1999).

The diverse mosaic of South American drylands was an important factor in the evolution of their biota (Hershkovitz, 1972; Mares, 1985; Mares and Ojeda, 1982; Reig, 1986). Among these aridlands, the Monte Desert was the focus in the pioneering research by the International Biological Program (IBP) (Mabry et al., 1977; Orians and Solbrig, 1977; Simpson, 1977) which was aimed at testing the hypothesis of convergent evolution in warm deserts ecosystems. As part of this Program, Mares's contributions (1975, 1976, 1977a, 1980) represent a milestone on the way to approaching a quantitative understanding in convergence of desert mammals, and in opening new avenues of research in ecophysiology and biogeography.

The aim of our contribution is to provide an updated review of some of the latest biogeographical, ecological, physiological, and behavioral research on the Monte Desert mammals and an overall reassessment of their evolutionary ecology.

* Corresponding author. Institute for Aridland Research (IADIZA), CC 507, C.P. 5500 Mendoza, Argentina. Tel.: +54 261 5244114; fax: +54 261 5244001.

E-mail addresses: rojeda@lab.cricyt.edu.ar (R.A. Ojeda), mariasol@lab.cricyt.edu.ar (S. Tabeni).

2. South American drylands and distinctiveness of their mammals

South America is covered by a high diversity of drylands: tropical, highland, coastal, and continental arid biomes (Morello, 1985). At a continental scale, drylands were characterized as having the highest mammal richness and endemisms (Mares, 1992). On a finer scale, the small mammal fauna varies widely (species richness and composition) among the major South American arid biomes (Ojeda et al., 2000). Andean drylands played a major role in the cladogenetic process of sigmodontine rodents (Reig, 1986), and this is reflected in their high species richness and in the number of endemics (e.g. rodents, Hershkovitz, 1972; Marquet, 1994a, b; Ojeda et al., 2000; Reig, 1986). The diversity of small mammals decreases in the lowland deserts on both sides of the Andes. This may be explained by low rainfall, scarce vegetation and climate unpredictability (i.e. precipitation; Ojeda et al., 2000, and references therein), and the great geographic barrier of the Andean chain, with peaks reaching 7000 m), especially in Chile, which has a depauperate mammal fauna compared to other South American countries (Mella et al., 2002). The Monte and Patagonia deserts show different species assemblages than do the Chilean Mediterranean scrublands on the western side of the Andes. Regardless of the marked differences in composition of their mammal assemblages, herbivores are the main trophic group (Ojeda et al., 2000). This consistency seems to be more the result of phylogenetic inertia (i.e. the lineage of herbivorous hystricognath rodents) than of similar ecological processes. However, some of the differences of our study (Ojeda et al., 2000) with the study reported by Kelt et al. (1996) on desert small mammals may rest on different species pool database (local trappable segment vs. complete biome lists) and dissimilar ratings of their trophic position.

3. The Monte Desert mammals revisited

The Monte Desert is a relatively young biome whose origin is connected with the uplift of Sierras Pampeanas during the Pleistocene (1–1.5 million years) (Bailey et al., 1977; Vuilleumier, 1971). The semiarid Chaco was suggested as the Monte ancestral biome. To a significant degree, the Monte is a subset of floristic elements originally derived from the Chaco (Morello, 1958). Evidence for this assertion was based on the fact that the Chaco is richer than the Monte in floristic elements from the Miocene–Pliocene (e.g. *Acacia*, *Jatropha*, *Prosopis*, etc.), and the area where xeric conditions first appeared in South America, at the end of the Pliocene (Vuilleumier, 1971).

The Monte extends over approximately 2000 km from 24° to 43° south latitude and resembles parts of the North American Sonoran and Chihuahuan deserts. The Monte has a diverse mosaic of habitats and plant associations. Xerophytic hillsides with bromeliads and cacti ("cardones" as *Trichocereus*), forests and woodlands of "algarrobos" (*Prosopis*) mixed with grasses, shrublands dominated by evergreen zygophyllaceous shrubs *(Larrea, Bulnesia)*, and saltbush (*Atriplex*), salt basins ("salares"), surrounded by rings of halophytic vegetation, sand dunes, bared muddy depressions "barreales", and bad-lands, make up most of the heterogeneous landscapes of the Monte (Morello, 1958).

The Monte is divided into two ecoregions, the northern Monte of mountains and close basins ("valles y bolsones"), between 24° and 32° SL, and the southern Monte of plains and plateau ("llanuras y mesetas"), between 32° and 37° (Burkart et al., 1999). There is a north-south gradient from a complex topographic relief with a basin and range topography to a more open and scrubland steppe in the south, whereas the precipitation ranges from seasonal summer rains, between 83 and 293 mm in the north, to an absence of a well-defined rainy season, between 89 and 187 mm in the

south (Mares et al., 1985). Maximun average temperatures in the Monte range between 27.0 °C in the north (Tinogasta, Catamarca Province) to 20.4 °C (Trelew, Chubut Province), while minimum temperatures range between 7.5 and 7.3 °C at the same localities (Cabrera, 1976). In the central portion of the Monte, at the Man and Biosphere Reserve of Ñacuñan, Mendoza Province, average annual precipitation is about 326 mm, with a marked seasonality of humid summers and dry winters (Ojeda et al., 1998).

The first syntheses of the Monte Desert animal and plant assemblages were compiled at various spatial scales by different scientists in a series of appendixes in the IBP volume on convergent evolution in warm deserts (Orians and Solbrig, 1977). In most cases these lists were based on records from few localities of the north and central Monte, as well as earlier published information. The description of new mammal taxa in recent years (Braun and Mares, 1995, 2002; Braun et al., 2000; Lanzone et al., 2007; Mares et al., 2000), has reverted previous generalizations of a depauperate mammal fauna (Mares, 1975). The Monte Desert over its total geographical range now accounts for approximately 73 mammal species (Table 1) and possesses a relatively high endemicity in comparison with other arid and semiarid biomes (Ojeda et al., 2002). The distinctiveness of the Monte ecoregions is also reflected in the different composition of their mammal faunas, particularly hystricognath and sigmodontine rodents, which comprise more than 50% of the total mammal species.

3.1. Mammal assemblages and evolutionary strategies

Deserts can be characterized by being strikingly heterogeneous in space and time, with low annual precipitation, high evapotranspiration, low productivity, and great variation in temperature, precipitation and productivity (Polis, 1991, and references therein). Abiotic conditions, species interaction and regional processes are important factors in the understanding of desert ecosystems and on how their communities are structured (Polis et al., 2005, and references therein).

In Fig. 1, we illustrate a simplified flowchart of climatic, vegetational features, consequences and evolutionary strategies of mammal assemblages to cope with desert environments (modified from Mares, 1976). The small (<100 g) and medium-sized (>100 g) desert mammal communities are characterized through a diversity of niche types, combining food, habitat utilization and mode of life, and coupled with morphological, behavioral and physiological traits summarized in Table 2.

3.2. Habitat heterogeneity

Habitat heterogeneity is an important variable in the organization of desert communities (Rosenzweig, 1981; Rosenzweig and Winakur, 1969). The selection of habitats that provide food resources, cover against predators and protection from extreme temperatures are important in desert ecosystems. The spatial–temporal heterogeneity affects foraging and locomotion of animals. Therefore, habitat structure is a composite of co-evolutionary responses by organisms to biotic and abiotic factors (Shenbrot et al., 1999, and references therein). Although competition and predation have been mentioned as important factors in structuring desert rodent assemblages (e.g. Reichman, 1991, and references therein; Meserve et al., 1996), there is still a major gap in the understanding of their role in Monte mammal assemblages.

Local assemblages of small and medium-sized mammals comprise between 7 and 10 coexisting species, with a diversity of niche types, body sizes and spatial and temporal variations of their abundances (Table 3) (Corbalán and Ojeda, 2004; Gonnet, 1998; Gonnet and Ojeda, 1998; Tabeni, 2006; Tabeni and Ojeda, 2005). Their structure is closely associated with vegetation structure over

Table 1
Mammals of the temperate Monte Desert and ecoregions (modified after Barquez et al., 2006; Ojeda et al., 2002; Pardiñas et al., 2003).

	Northern Monte of Mountains and Basins	Southern Monte of Plains and Plateau
Didelphimorphia	*Didelphis albiventris*	*Didelphis albiventris*
	Thylamys pallidior	**Lestodelphys halli**
		Thylamys pallidior
Cingulata	*Chaetophractus vellerosus*	*Chaetophractus vellerosus*
		Chaetophractus villosus
		Chlamyphorus truncatus
		Tolypeutes matacus
		Zaedyus pichiy
Chiroptera	*Desmodus rotundus*	*Desmodus rotundus*
	Eptesicus furinalis	*Eptesicus furinalis*
	Histiotus montanus	**Eumops patagonicus**
	Lasiurus blosseivillii	*Histiotus montanus*
	Lasiurus cinereus	*Lasiurus cinereus*
	Molossus molossus	**Lasiurus varius**
	Myotis dinellii	*Myotis dinellii*
	Nyctinomops macrotis	*Tadarida brasiliensis*
	Sturnira lilium	
	Tadarida brasiliensis	
Carnivora	*Conepatus chinga*	*Conepatus chinga*
	Galictis cuja	**Conepatus humboldtii**
	Herpailurus yaguarondi	*Galictis cuja*
	Lynchailurus pajeros	*Herpailurus yaguarondi*
	Lyncodon patagonicus	*Lynchailurus pajeros*
	Oncifelis geoffroyi	*Lyncodon patagonicus*
	Pseudalopex culpaeus	**Lontra provocax**
	Pseudalopex griseus	*Oncifelis geoffroyi*
	Pseudalopex gymnocercus	*Pseudalopex culpaeus*
	Puma concolor	*Pseudalopex griseus*
		Pseudalopex gymnocercus
		Puma concolor
Rodentia	**Abrocoma schistacea**	**Abrocoma uspallata**
	Akodon albiventer	**Akodon azarae**
	Akodon simulator	**Akodon molinae**
	Akodon spegazzinii	**Akodon neocenus**
	Andalgalomys olrogi	**Akodon oenos**
	Andalgalomys roigi	*Andalgalomys roigi*
	Calomys musculinus	*Calomys musculinus*
	Ctenomys coludo	**Ctenomys azarae**
	Ctenomys famosus	**Ctenomys haigi**
	Ctenomys knighti	**Ctenomys johannis**
	Dolichotis patagonum	**Ctenomys mendocinus**
	Eligmodontia marica	**Ctenomys pontifex**
	Eligmodontia moreni	**Ctenomys validus**
	Eligmodontia typus	*Dolichotis patagonum*
	Galea musteloides	*Eligmodontia moreni*
	Graomys griseoflavus	*Eligmodontia typus*
	Lagidium viscacia	*Euneomys chinchilloides*
	Lagostomus maximus	*Galea musteloides*
	Microcavia australis	*Graomys griseoflavus*
	Myocastor coypus	*Lagidium viscacia*
	Octodontomys gliroides	*Lagostomus maximus*
	Octomys mimax	*Microcavia australis*
	Oligoryzomys longicaudatus	*Myocastor coypus*
	Phyllotis xanthopygus	**Oligoryzomys flavescens**
	Pipanacoctomys aureus	*Oligoryzomys longicaudatus*
	Salinoctomys loschalchalerosorum	**Reithrodon auritus**
	Salinomys delicatus	*Salinomys delicatus*
	Tympanoctomys barrerae	*Tympanoctomys barrerae*

different spatial scales. As in other biomes, the highest diversity of small mammals is positively correlated with habitat heterogeneity such as "algarrobo" woodlands (*Prosopis*) and *Larrea* shrublands (Corbalán and Ojeda, 2004; Tabeni and Ojeda, 2003). The mammal assemblages show different habitat utilization in association with particular morphoecological traits. In the central Monte, the dark colored grass mouse, *Akodon molinae*, prefers densely vegetated

areas and undisturbed patches with high plant cover (Corbalán and Ojeda, 2004; Tabeni et al., 2007), whereas the silky mouse (*Eligmodontia*) dominates in sand dunes and open shrublands, as its light coloration, elongated hind limbs, and single cushions on the soles, enable good substrate matching and saltatorial locomotion (Ojeda, 1989; Taraborelli et al., 2003). Densely covered habitats (e.g. shrublands and woodlands) are preferred by scansorial forms with good climbing abilities such as the desert common opossum, *Thylamys pallidior*, the common pericote, *Graomys griseoflavus*, and the colonial desert cavy, *Microcavia australis*. Coexisting with them are the cursorial grass mice, *Akodon* spp., the vesper mouse, *Calomys musculinus*, and the yellow-toothed cavy, *Galea musteloides* (Corbalán and Ojeda, 2004; Navarro, 1991; Ojeda et al., 1998; Tabeni, 2006). Desert rodent species living in sympatry in the Andean foothills segregate among microhabitat structures (Gonnet and Ojeda, 1998). The pericote, *G. griseoflavus*, prefers closed shrubby areas, whereas the vesper mouse, *C. musculinus*, utilizes microsites of high grass cover.

Locomotory strategies used by small mammals are a combination of both morphology and behavior. The mode of escape varies from quadrupedal gait in the grass mouse, *A. molinae*, that restricts its activities to areas beneath vegetation, to saltation with erratic escape behavior (zigzagging) and distracting effect of their tails in *E. typus* and *G. griseoflavus* (Taraborelli et al., 2003). At the extreme range of body sizes is the Patagonian hare, *Dolichotis patagonum* (>10,000 g), with cursorial locomotion, clavicle reduction, and well developed sensory organs to detect and avoid predators (Campos et al., 2001a; Kufner and Chambouleyron, 1991; Taber, 1987).

Selecting plant structures that provide good cover microhabitats could be a behavioral strategy to elude predators as well as to cope with extreme temperature fluctuations. A good example is the desert cavy or cuis, *M. australis*, which builds its colonies beneath vegetation with particular structures such as thorny, weeping branches (e.g. *Condalia* and *Prosopis*, among others; Tognelli et al., 1995). Previously, Mares et al. (1977b) had referred to the "algarrobo" (*Prosopis*), as one of these keystone species in organizing the Monte desert animal communities.

Changes in habitat structure produced by natural or anthropic events (e.g. fire, grazing, logging) bring changes in community structure (Gonnet, 1998; Maldonado Curti, 1990; Tabeni and Ojeda, 2005; see Villagra et al., this volume, and references therein). The diversity of small mammals increases in grazed patches with high spatial variability in the vegetation (Tabeni and Ojeda, 2005). However, in extremely simplified habitats (e.g. burned areas), desert vertebrates with particular morphoecological traits have the capacity to monopolize these risky and open patches, while other members of the assemblage disappear very rapidly (Marone, 1990; Ojeda, 1989).

3.3. Trophic ecology

The diversity of precipitation along the Monte determines a differential set of resources and promotes diverse niche types in trophic ecology and foraging behavior. The two main trophic strategies used by the small and medium-sized mammals of the central Monte Desert are herbivory and omnivory (Campos, 1997; Campos et al., 2001b). Herbivory is well represented by the medium-sized hystricognath rodent assemblage (e.g. chinchilla rats, *Abrocoma*, cavies, *M. australis*, *G. musteloides*, Patagonian hare, *D. patagonum*, plains viscacha, *Lagostomus maximus*, octodontids, *Octomys mimax*, *Tympanoctomys barrerae*, *Pipanacoctomys aureus*, and the pocket gopher-like tuco tucos, *Ctenomys* sp.) (Borruel et al., 1998; Campos, 1997; Campos and Ojeda, 1997; Madoery, 1993; Ojeda et al., 1996; Rosati and Bucher, 1995; Tognelli et al., 1999) (see Table 3). Among the herbivorous small mammals is the scansorial common pericote (*G. griseoflavus*). Omnivory (and trends towards
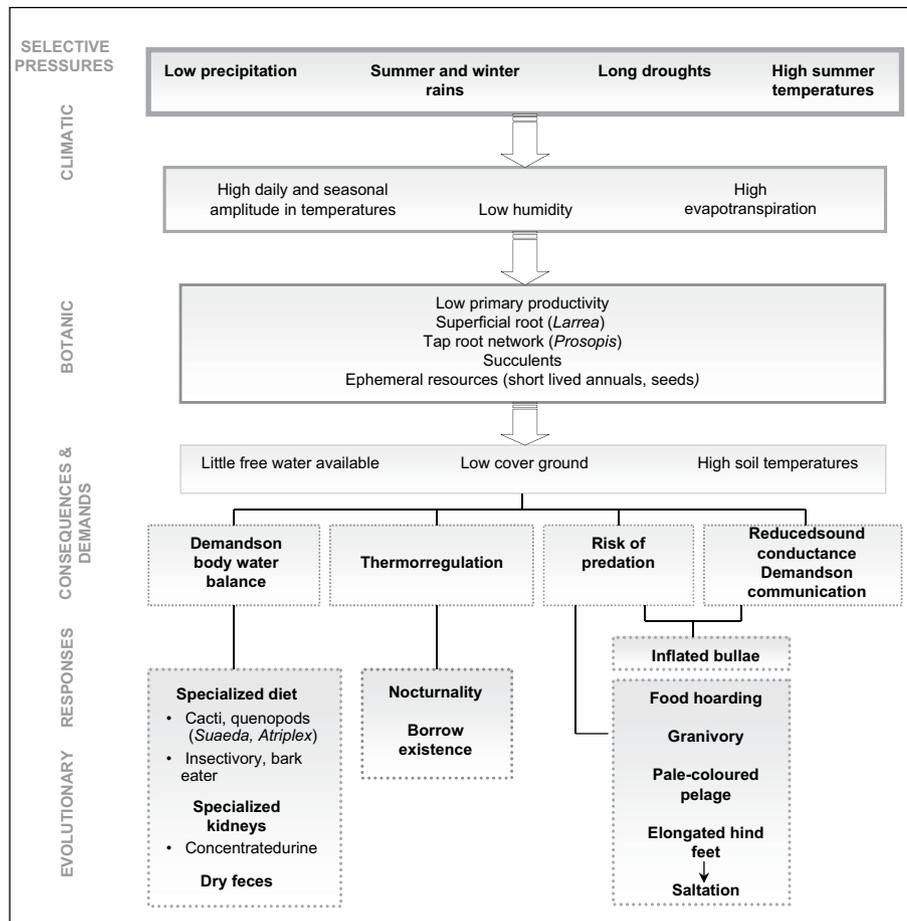
Fig. 1. Flow chart of desert climate, vegetation, consequences and evolutionary strategies (based on Mares, 1976).

granivory and insectivory) is represented by the vesper mouse (*C. musculinus*), silky mouse (*E. typus)* and grass mouse (*A. molinae*), while the only insectivorous small mammal is the common marsupial (*T. pallidior*).

Granivory and the absence of specialized strictly granivorous rodents (e.g. heteromyids and gerbilline rodents) in the Monte have been thoroughly summarized by several authors (Brown and Ojeda, 1987; Mares and Rosenzweig, 1978; Marone et al., 2000). However, recent studies (Giannoni et al., 2005) found that seeds comprise between 20% and 60% of the diets of small desert rodents, with *G. griseoflavus* being the less granivorous, and *C. musculinus* an important seed eater during the dry season. Thus, regardless of the heterogeneity of arid landscapes, and the relative importance of granivore taxa, the process of granivory seems to be important in the biomes of Monte and Patagonia as well (Blendinger and Ojeda, 2001; Folgarait and Sala, 2002; Lopez de Casenave et al., 1998; Marone et al., 2000; Saba and Toyos, 2003; Sassi et al., 2004, 2006, and references).

3.4. Physiological adaptations

The diet constitutes an important source of water in desert environments. Both food selection with high water content and renal adaptations are mechanisms for water ingestion and conservation where its availability is limited (Diaz, 2001). Renal morphology and physiology in Monte Desert marsupials, hystricognath and sigmodontine rodents are associated with habitat, body weight and diet (Diaz, 2001; Diaz and Ojeda, 1999; Diaz et al., 2001). South American hystricognath (e.g. *Microcavia*, *Tympanoctomys)* and sigmodontine

desert rodents, (e.g. *Calomys*, *Eligmodontia*, *Salinomys*, *Graomys*, *Adalgalomys)* have developed similar or greater adaptations (e.g. renal anatomy, urine concentration; changes in digestive tract morphology) than the paradigmatic heteromyid and gerbillid rodents (Bozinovic and Gallardo, 2005; Bozinovic et al., 2007; Diaz, 2001; Diaz and Ojeda, 1999; Diaz et al., 2001; Sassi et al, 2007). Furthermore, the maximum urine concentration for *Thylamys* (9015 mOsm/kg) is the highest value recorded for a desert marsupial. As for *Eligmodontia*, *Calomys*, *Graomys*, *Salinomys* and *Tympanoctomys*, maximum urine concentrations above 7000 mOsm/kg are among the highest values reported for world desert small mammals (Diaz, 2001; Diaz et al., 2001). Moreover, the delicate mouse, *Salinomys delicatus*, possesses the most elongated renal papillae among the Monte desert murids (Diaz and Ojeda, 1999).

Overall, South American desert rodents (e.g. Atacama and Monte) have been shown to possess a great diversity of ecophysiological and morphological attributes for water conservation and food digestion (Bozinovic et al., 2007, and references; Diaz and Ojeda, 1999; Sassi et al., 2007) reversing earlier generalizations of lack of specialization of sigmodontine rodents for inhabiting xeric habitats (Mares, 1975), although concentrating abilities for electrolytes for *Eligmodontia* and water "independence" in *C. musculinus* were reported by Mares (1977a, b).

3.5. Plant–animal interactions

The relationship between animals and plant consumption (e.g. the physical disturbance caused by herbivory) influences plant community structure and diversity in the Monte Desert (Tognelli

Table 2
Major adaptive traits of Monte Desert small and medium-sized mammals at the physiological, ecological, morphological, and behavioral levels.

Attributes	Adaptive explanation	Species
High urine concentration and specialized kidneys (elongated renal papillae, high ratio medulla/cortex)	Prevent water loss, efficiency in regulation of water balance	*Thylamys, Calomys, Graomys, Eligmodontia, Salinomys, Andalgalomys,Tympanoctomys*
Low metabolic rate, torpor	Energy maintenance, prevention of water loss by evaporation	*Thylamys, Calomys*
Fat storage	Response to water deficit and scarce food	*Thylamys*
Dry feces	Reduce water loss	*Calomys, Graomys, Eligmodontia, Salinomys, Andalgalomys, Tympanoctomys*
Inflated tympanic bullae	Predator avoidance: specialized acoustic sense for low frequency; open and risky habitats	*Salinomys, Eligmodontia, Octomys, Tympanoctomys*
Long tail, countercoloration (pale colors)	Balance and predator avoidance	*Salinomys, Eligmodontia, Andalgalomys, Calomys, Graomys, Tympanoctomys*
Feet pads and long hind feet	Saltatorial (richochetal) locomotion in open sandy substrate	*Eligmodontia*
Diet of halophytic chenopods	Exploitation of stable food resources	*Tympanoctomys*
Diet of cacti	Allows incorporation of water	*Octomys, Eligmodontia*
Diet of insects	Allows incorporation of water	*Thylamys, Akodon*
Nocturnality	Avoidance of high temperatures	*Calomys, Graomys, Eligmodontia, Salinomys, Andalgalomys, Akodon, Tympanoctomys*
Fossoriality, burrows	Avoidance of high temperatures	*Ctenomys, Calomys, Graomys, Tympanoctomys, Eligmodontia, Salinomys, Andalgalomys, Akodon*
Foot drumming	Communication in open areas; alarm	*Microcavia australis*
Changes in digestive tract morphology	Increase poor food exploitation and processing	*Microcavia australis*

et al., 1999). A common foraging behavior in deserts which is associated with ephemeral and unpredictable food resources is food hoarding, and it has been reported for two of the dominant rodents, the silky mouse, *E. typus* and the common pericote, *G. griseoflavus* (Giannoni et al., 2001). Taraborelli et al. (2003) observed that the plant cover affects the foraging activity of rodents because both consumption and a higher number of caches occur below shrubs. Manipulation and ingestion of food (e.g. pods and seeds) are also likely to affect seed viability and germination (Campos et al., 2007). In the central Monte, "algarrobo" (*P. flexuosa*) pods suffer high pressure from ants and mammals (Claver, 2000; Milesi and Lopez de Casenave, 2004; Villagra et al., 2002). Most pods and seeds are removed within a few days after reaching the soil (Villagra et al., 2002). The Patagonian hare, *D. patagonum* and cattle are good dispersal agents of viable *Prosopis* seeds, whereas the exotic wild boar, *Sus scrofa*, acts as a predator (Campos and Ojeda, 1997). Moreover, the seeds contained in the fecal pellets of *Dolichotis* seem to be less vulnerable to predation, promoting greater longevity in the soil (Villagra et al., 2002). Pod removal by small rodents showed no signs of direct harmful effects as most seeds maintained their endocarp undamaged (Campos et al., 2007). Other animal–plant interactions such as gnawing and cuttings of vegetation (e.g. leaves, bark, branches) can cause severe damage. Bark consumption by the desert cavy, *M. australis*, is possibly associated with water and carbohydrate content during the dry season, when availability of green plants is low (Borruel et al., 1998; Tognelli et al., 1999).

The desert cavy, *M. australis* and the tuco-tuco, *Ctenomys*, may reduce the abundance of dominant grasses and forbs and affect their survival, condition and production of reproductive structures (Borruel et al., 1998; Campos et al., 2001b, 2006; Tognelli et al., 1999; Tort et al., 2004). The plains vizcacha, *L. maximus*, is considered an ecological equivalent to the black-tailed prairie dog, *Cynomys* sp, a herbivorous species in North American prairies (Branch, 1993). Vizcachas create large patches of bare soils in the desert landscape dominated by dense shrublands. In heavily grazed areas at the centers of their colonies, species richness of forbs are higher than species richness of grasses (Branch et al., 1999).

Aspects such as use of space, habitat and burrowing behavior of tuco-tuco (*Ctenomys*) have been investigated (Camin et al., 1995; Giannoni et al., 1996; Puig et al., 1992; Rosi et al., 2000) although its activity on soil dynamics (Reichman and Seabloom, 2002; Whitford and Kay, 1999) and effect on vegetation heterogeneity as a potential ecosystem engineer is scarcely known.

4. Adaptive traits and convergence

Pioneering studies addressing form and function for several traits of the Monte Desert small mammals were those of Mares (1975, 1976), who utilized the statistical techniques developed for numerical taxonomy (e.g. multivariate analyses) to quantify convergent evolution of desert rodents. Later, similar analyses were expanded to other deserts (Mares 1980). Overall results showed morphoecological convergence among the Monte and Sonoran desert mammals. Several ecological equivalents were identified and clustered in distinct morphoecological groups (e.g. the fossorial tuco-tucos, *Ctenomys* spp. and gophers, *Thomomys* spp., desert ground squirrels *Spermophilus* spp. and desert caviids, *Microcavia* spp., small heteromyids *Reithrondontomys* spp., and phyllotine

Table 3
Macroniche diversity (habitat, diet, substrate and locomotion) in the Monte Desert small and medium-sized mammals.

	Species	Habitat	Diet	Substrate/locomotion
Small mammals (<100 g) marsupials and rodents	Didelphimorphia			
	Thylamys pallidior	*Larrea* shrubland, *Prosopis* woodland, dense vegetation	Omnivore/insectivore	Scansorial/quadrupedal
	Rodentia			
	Eligmodontia typus, *E. marica, E. moreni*	salt basin, sand-dunes, *Larrea* shrubland open areas, low shrub cover	Omnivore, tendency towards insectivory	Cursorial/saltator
	Graomys griseoflavus	*Larrea* shrubland, *Prosopis* woodland, high shrub cover	Herbivore–folivore	Scansorial/saltator
	Calomys musculinus	*Larrea* shrubland, high forb cover	Granivore–omnivore	Cursorial, quadrupedal
	Akodon molinae	*Larrea* shrubland, *Prosopis* woodland, high forb cover	Omnivore, tendency towards insectivory	Cursorial, quadrupedal
	Akodon oenos	halophytic vegetation	Omnivore, tendency towards insectivory?	Quadrupedal
	Salinomys delicatus	salt flats, sand-dunes	Omnivore?	Scansorial?
	Andalgalomys olrogi, A. roigi	*Larrea* shrubland, gulley woodlands, salt basins, sand dunes	Omnivore?	Quadrupedal
Medium-sized mammals (>100 g)	Rodentia			
	Microcavia australis	*Prosopis* woodland, forb and bare soil	Herbivore	Scansorial, semifossorial, quadrupedal
	Galea musteloides	grasslands, high forb cover and humid areas	Herbivore	Cursorial, quadrupedal
	Abrocoma uspallata	rocky hillsides, rock outcropings	Herbivore specialized on *Larrea*	Saxicollous, quadrupedal
	Dolichotis patagonum	*Larrea* shrubland, *Prosopis* woodland, open habitats, low forb and bare sandy soils	Herbivore	Cursorial, quadrupedal
	Lagostomus maximus	*Larrea* shrubland, *Prosopis* woodland, open habitats low forb and shrub cover	Herbivore	Semifossorial, quadrupedal
	Pediolagus salinicola	Monte-Chaco ecotone; open understory *Prosopis* woodland, thorn scrub bare soil	Herbivore	Cursorial, quadrupedal
	Ctenomys mendocinus	thorn scrub, *Larrea* shrubland, sand dunes, grassland	Herbivore	Fossorial, quadrupedal
	Tympanoctomys barrerae	salt basins, saltbush (*Atriplex*) shublands	Herbivore	Semifossorial, quadrupedal
	Pipanacoctomys aureus	salt basins, saltbush (*Heterostachys*) shrublands	Herbivore	Semifossorial
	Salinoctomys loschalchalerosorum	Monte-Chaco ecotone, salt basins	Herbivore	Semifossorial
	Octomys mimax	rocky outcropings	Herbivore	Cursorial

Sources: Campos et al. (2001a, b), Corbalán and Ojeda (2004), Diaz et al. (2000), Giannoni et al. (1996), Kufner and Chambouleyron (1991), Lanzone et al. (2007), Mares and Ojeda (1982), Ojeda (1989), Ojeda et al. (1999), Rosi et al. (2002), Taraborelli et al. (2003), and Tognelli et al. (1995, 1999).

mice, *Eligmodontia* spp., pack rats *Neotoma* spp., and leaf-eared mice, *Graomys* spp., among others) (Mares, 1975, 1976).

The evolution of similar traits as response to comparable environmental pressures has been regarded as strong evidence of the efficacy of selection (Simpson, 1953). However, a thorough review on small desert mammals of the world suggests that exact niche equivalence is seldom observed (Mares, 1993a, b). Despite the fact that desert animal assemblages possess similar suites of adaptive attributes, any pair of species living in disjunct deserts do not necessarily share the same array of traits.

Major adaptive attributes and evolutionary responses of desert small and medium-sized mammals are synthesized in Table 2. It is interesting to note that a remarkable diversity of features is shown by many taxa of the Monte Desert.

Some of these results paved the way to later analyses of particular cases of convergence by including key traits for desert existence at ecophysiological (e.g. kidneys morphology, urine concentration), behavioral (foraging, burrows), and ecological (habitat, diet) levels (Ojeda et al., 1999).

One of the South American desert model species is the polyploid red vizcacha rat, *T. barrerae* (Diaz et al., 2000; Gallardo et al., 2007, and references therein). The red vizcacha rat seems to possess a metapopulation structure (A. Ojeda, pers. comm.), patchy distribution and occupies salt basins and sandy habitats in west central Argentina (Mares et al., 1997; Ojeda et al., 1989, 1996). Solitary individuals live in complex mounds and their main diet consists of halophytic vegetation of the genus *Suaeda, Heterostachys, Atriplex*, among others. The red rat also has a unique morphological feature-

bundles of stiff hairs located on either side of the buccal cavity, which remove the salty epidermis from the leaves of *Atriplex* spp., before the edible parts of the leaves are consumed (Giannoni et al., 2000; Mares et al., 1997). The integration of ecology, physiology and behavior (Ojeda et al., 1999) showed greater similarities between *T. barrerae*, and non-related rodents of North America (e.g. the chissel-like kangaroo rat, *Dipodomys microps*, Heteromyidae), Africa and Asia (the fat rat *Psamommys obesus*, and *Rhombomys opimus*, Muridae), than with their close relatives, *O. mimax* and *Octodontomys gliroides*. Similarities include convergence at physiological (kidney morphology, high urine concentration), ecological (halophytic diet composition, burrows, salt basins), and behavioral levels (shaving of leaves before ingestion like *D. microps* and *P. obesus*), among other traits (Mares et al.,1997; Ojeda et al., 1999).

5. Concluding remarks

There is no doubt that in the last few decades there has been a tremendous leap in our understanding of the natural history of South American aridland biodiversity (see this volume). Just an example, other than the Monte, is the long-term ecological program carried on in the semiarid North of Chile, where we have gained an in-depth comprehension of particular processes and dynamics in relation to "El Niño" event and its impact on vertebrate assemblages and rodent outbreaks among others (Jaksic et al., 1997; Lima et al., 1999; Marquet et al., 1998; Meserve et al., 2003, and references).

In retrospective, we have witnessed a gradual and thorough understanding and reassessment of the evolutionary ecology of the temperate Monte desert mammals since the IBP's ground-breaking research in the early 1970s. During the IBP program, the bulk of the research was oriented towards a global assessment of their plant and animal diversity, regional and local distributions, and the detection and quantification of convergence with other deserts, at species, community and ecosystem levels (Orians and Solbrig, 1977; Simpson, 1977).

Later research, some of which we summarized here, focused on the distinctiveness and heterogeneity of the Monte mammal assemblages at various scales. Overall, different pieces of evidence have shown that

- Mammal assemblages of the South American drylands are distinctive. Topography, climate, history of site and lineages may account for their distinctiveness, high degree of endemicity and diversity of niche types.
- The Monte Desert mammals have evolved a diverse set of ecological, morphological, ecophysiological and behavioral attributes for desert existence, and convergent with those found for other desert mammals.
- Sigmodontine desert rodents have evolved physiological attributes similar to those found in the heteromyid, gerbillid and murid desert rodents. Consequently, at least from the physiological data, we should discard Mares' (1975) proposal that the lack of physiological adaptation in the sigmodontine rodent lineage supported their recent colonization to South America through the Panamian Bridge.
- Small and medium-sized desert mammal communities coexist through segregation of habitat and food resources coupled with morphoecological and behavioral attributes.
- In the central Monte desert, small mammal assemblages, are similar in composition but their abundances are markedly different between patches of habitat.
- Herbivory and omnivory are the dominant feeding strategies in Monte Desert mammals.

Thus, at a broad scale, the diversity of location, topography, climate and biogeographic history of South American drylands may account for the distinctiveness of their assemblages (Ojeda et al., 2000 and references therein). Because of this environmental heterogeneity and biogeographic history, generalizations based on few dryland ecosystems might lead to contrasting interpretations, as earlier pointed out. Moreover, when this is coupled with macroecological analysis at different scales (e.g. regional vs. local) (Kelt et al., 1996, 2000; Ojeda et al., 2000) the identification of patterns (if any), is even more complicated.

We adhere to MacArthur's (1972) introductory remarks in "Geographical ecology" when he pointed out that doing science is the search for patterns, as well as to the stimulating macroecological approach in exploring and understanding patterns of distribution, abundance, trophic ecology, body sizes and biodiversity (Brown, 1995; Gaston and Blackburn, 2000 and references therein). However, we also raise a word of caution when comparing distinctive desert ecosystems (Ojeda et al., 2000) with their particular history of place and lineages (Brown et al., 1996). A challenge lies ahead to identify common denominators in order to detect patterns, or which aspects are truly generalizable when comparing heterogeneous arid ecosystems at different scales.

Acknowledgments

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