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Assessing mammal responses to perturbations in temperate aridlands of Argentina

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Abstract

Loss of species richness and reduced abundance have been the main responses to perturbations of small- and medium-sized mammals in arid and semi-arid areas. Nonetheless, some mammal species whose habitat requirements are met in disturbed patches may benefit from structural changes in the environment brought about by perturbations.

In desert areas of Argentina different mammal responses are attributable to both a lower complexity of disturbed patches and a decrease in sheltered places. Therefore, species associated with high plant cover either decrease in number or become locally extinct at sites affected by fire or grazing, whereas species using open areas are favored by these events.

The negative effects historically assigned to different disturbances may be mitigated by adopting a hierarchical approach that considers patch diversity in different successional stages as well as the multiple opportunities of patch occupation by mammal species.

Keywords: Perturbation; Response; Grazing; Fire; Small- and medium-sized mammals

1. Introduction

Almost all ecosystems on earth are subject to periodic disturbances by natural and anthropic causes. When these disturbances are extreme, alterations in ecosystem structure and function lead to a degradation commonly signalled by biodiversity

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loss, reduced primary and secondary productivity, and low resilience (Rapport and Whitford, 1999). In arid and semi-arid areas, degradation is closely connected to the concept of desertification (Whitford, 1993, 1997). This process, resulting from land mismanagement combined with aridity conditions, has contributed to the change in the physiognomy of deserts. Some of the most common disturbances in dryland biomes are erosion, fire, animal activities in disturbing the soil, logging and grazing (Wiens, 1985, pp. 169–193). Grazing by domestic herbivores, one of the human activities that has generated major changes in these regions, exerts high ecological costs in ecosystem composition, function and structure (Fleischner, 1994), which in some cases are beyond recovery in ecological time-scales (Perevolotozky and Seligman, 1998). The dynamics of natural and anthropic disturbances generates a complex pattern of patchiness and availability of resources, that results in a diversity of vertebrate responses (Wiens, 1985).

Desertification in the southern cone of South America has been especially pronounced during the last 150 years (Roig, 1991, pp. 239–279). Although some natural factors, such as climate, have accentuated this process, deforestation and overgrazing have been the major causes of this degrading process.

The purpose of this paper is to assess the responses of small- and medium-sized mammals to disturbances by grazing and other anthropic activities (i.e. fire, logging and agriculture) in the temperate aridlands of Argentina (Fig. 1).

We analysed most of the available literature so as to synthesize the main effects of grazing on the structure and processes of arid ecosystems. Then, we considered the diverse responses of small- and medium-sized mammals to this disturbance in different drylands of the world.

For the temperate aridlands of Argentina, we examined the existing literature on the effects of grazing on small- and medium-sized mammals of the semi-arid Chaco and Monte desert. Finally, we studied the incidence of other disturbance factors (fire, logging, conversion to agriculture) that affect mammal fauna in the above regions.

2. Impact of grazing on the structure and processes of arid ecosystems

The effects of grazing on the composition of plant communities in arid and semi-arid ecosystems have been widely documented (Soriano and Paruelo, 1990; Milton et al., 1994; Bisigato and Bertiller, 1997; Van de Koppel et al., 1997; Frank et al., 1998; Aguiar and Sala, 1999). Among these effects are the establishment of exotic species and increasing dominance by toxic and thorny woody species (Fleischner, 1994; Milton et al., 1994).

Changes in species composition generate spatial and temporal alterations in the nutrient cycle (Rapport and Whitford, 1999). In the arid grasslands of North America the nutrient cycle is affected both spatially and temporally. Temporal changes result from the creation of pulses of organic matter related to rainfall and production of ephemeral plants. Spatial changes in grasslands which have become shrublands imply the formation of fertility islands under shrub canopies where the organic matter is recycled (Rapport and Whitford, 1999). Otherwise, nutrients are

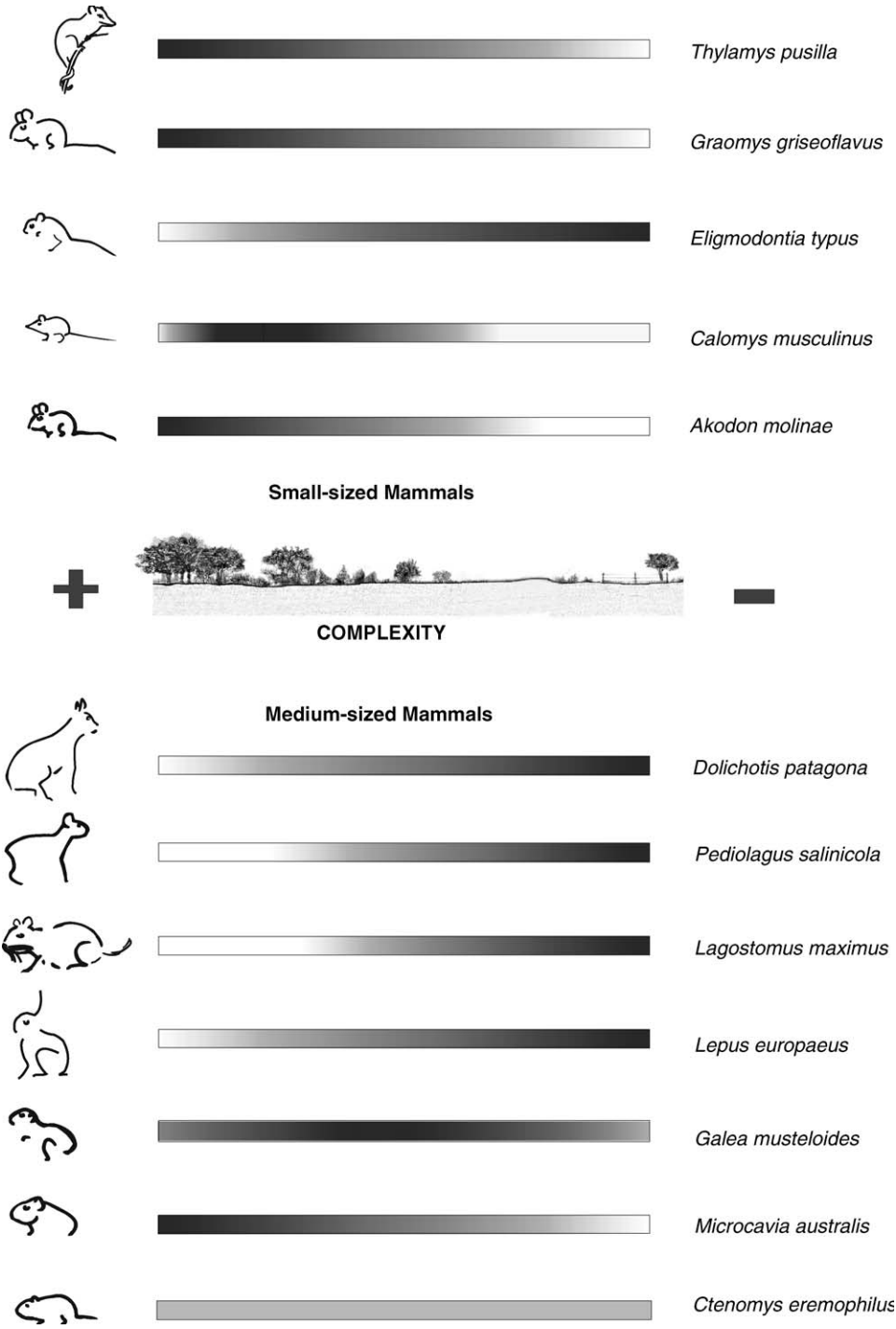

Fig. 1. Hypothetical assemblage of small- and medium-sized mammals in temperate aridlands of Argentina. Following a gradient of environmental structural complexity, different shades of gray indicate the degree of association of each species habitat, dark shades are related to higher preference, lighter shades to lower preference.

lost due to the absence of vegetation and to soil erosion (Rapport and Whitford, 1999). Physical alterations by livestock include changes in vegetational complexity and in soil surface, resulting in increased erosive processes, soil compactness and reduced water percolation rates. Altered soil stability and porosity contribute to changes in the spatial distribution of both nutrients and vegetation (Fleischner, 1994; Milton et al., 1994).

3. Mammal responses to grazing

Most studies on responses of mammals to disturbance by livestock have focused on changes in population (e.g. density) or community (e.g. richness, abundance) parameters in comparisons between grazed and ungrazed sites (Table 1). Overall, disturbed ecosystems may favor some species that can opportunistically use the

Table 1
Small and medium-sized mammal responses to cattle grazing in different world arid and semi-arid biomes.

Location	Organisms	Responses	Authority
Thar desert (India)	Small mammals	Increased density on grazed sites	Wada et al. (1995)
Plains and drainage lines, Karoo (South Africa)	Small mammals	Decrease in richness and abundance on grazed sites	Eccar et al. (2000)
Chilean matorral (Chile)	Small mammals Medium-sized mammals	Decrease small mammal abundance and increased medium-sized mammal abundance on grazed sites	Simonetti (1983)
Sagebrush rangeland and crested wheatgrass planting (North America	Small mammals	Decrease in richness and abundance on grazed sites	Johnson (1982)
East African savanna (Kenya)	Small mammals Medium- sized mammals	Lower diversity on grazed sites	Keesing (1998)
Great Basin (North America)	Small mammals Medium-sized mammals	Reduced abundance on grazed sites, increased abundance of one species (*Peromyscus maniculatus*)	Longland and Young (1995)
Desert grasslands (North America)	Small mammals	Increase in diversity, richness and abundance on desertified sites	Whitford (1993, 1997)
Salt desert (North America)	Small mammals	Higher density of species associated with open sites, lower density of species associated with high plant cover	Jones and Longland (1999)
Semi-desert grassland (North America)	Small mammals	Decrease abundance on grazed sites	Bock et al. (1984)
Sagebrush rangeland and crested wheatgrass planting (North America)	Small mammals	Decrease in richness and abundance on grazed sites	Reynolds and Trost (1980)

altered suite of environmental resources. Numerically dominant species in post-disturbance environments are oftentimes exceedingly rare in the undisturbed community (Parmenter et al., 1995). Thus, grazing by cattle because of its significant effect on vegetation composition, cover and architecture, can favor population increase of particular vertebrate and invertebrate species over others (Parmenter et al., 1995).

Reductions in the herbaceous layer and increased bare soil result in a simplification of habitat structure and in changes in food availability, to which small- and medium-sized mammmals respond differently. Plant cover provides refuge and safe places for reproduction and is therefore a major habitat feature in reducing predation risk. Although predation on vertebrates is poorly documented, increased predation risk in open patches has been reported (Wiens, 1985). In general, small mammal species (less than 100 g) with specific habitat requirements are directly affected by these structural changes, since their vulnerability and exposure to predators increase (Simonetti, 1983; Eccar et al., 2000). Soil compactness or layer alterations by erosive processes also may affect the availability of sheltered sites, which are essential to some small mammals for avoiding high temperatures (Wada et al., 1995; Walsberg, 2000).

Colonization of patches disturbed by exotics or increased abundance of resident species in the area represent a different kind of response to the same phenomenon of reduced habitat complexity. Those species with attributes enabling use of open patches (e.g. with strategies to escape predators based on visual detection, aposematic coloration, or larger body size) can benefit from the presence of grazed patches (Simonetti, 1983; Milton et al., 1994).

With respect to food availability, the quantity and quality of food resources have also been reported as factors determining the abundance of small mammals (Wada et al., 1995). Competition for food between small mammals and livestock in East Africa has been suggested as one of the mechanisms, among other factors (habitat disturbance and exposure to predators), that explains the increase in the abundance and body mass of small mammals in response to the exclusion of ungulates (Keesing, 1998). This has been mentioned as a signal of strong interaction among these taxa.

Other studies comparing the diversity of small mammals along a desertification gradient in North American desert grasslands have suggested that the degradation of this ecosystem has not resulted in decreased species richness and relative abundance, despite changes in vegetation patterns (Whitford, 1997). Grassland species continue to inhabit degraded habitats. The coexistence of grassland and shrubland species has led to a competitive interaction between them, which eventually results in local extinctions of the grassland species. This happens primarily in periods of extreme climatic conditions and limited food availability.

4. Effects of grazing on mammals of the temperate aridlands of Argentina

The effects of cattle on habitat structure and food availability in the temperate Monte desert biome (Morello, 1958) have affected the assemblages of small- and

medium-sized mammals differently (Table 2). Maldonado Curti (1990) reports a lower abundance of small mammals at grazed sites. The differential responses to grazed and ungrazed conditions may be the result of a decrease in the quality of disturbed sites. That is, cattle are the major modifier of vegetation in the area. Different species could respond individually to the same type of disturbance. Other studies have reported higher densities of larger species such as the native Patagonian hare, *Dolichotis patagona* and the exotic European hare, *Lepus europaeus*, in grazed areas (Gonnet, 1998).

5. Responses of mammals to different range management systems

Most studies fail to describe the intensity of grazing due to the absence of a standardized terminology and a specific methodology. Thus, the use of relative terms such as "heavy", "moderate", "slight", or "overgrazed" is based on diverse criteria, such as the presence of livestock tracks, or the amount of grasses left at the end of the grazing season (Fleischner, 1994).

In arid and semi-arid habitats of Argentina, some studies have addressed the influence of various cattle management practices upon the native fauna. The semi-arid Chacoan biome was originally composed of patches of forest and grasslands, and maintained by natural factors (e.g. storms) or artificial means (e.g. periodic fires by indigenous people), preventing the establishment of woody species and stimulating rapid grassland germination and reproduction (Bucher, 1987).

When domestic herbivores (cows and goats) were introduced, the reduction of fuel (organic matter) caused by overgrazing produced a decrease in fire, and consequently, open areas were rapidly invaded by woody plants, thus turning them into homogeneous landscapes of dense thorn scrub forest (Bucher, 1987). Currently, most of the Chaco grasslands have been replaced by dense thorn scrub vegetation (Morello and Saravia, 1959). The impact of these transformations on the native fauna has brought a quick decline in large herbivores such as deer, *Ozotoceros bezoarticus*, and guanacos, *Lama guanicoe*, due to reduced suitable habitats, competition with domestic herbivores, and hunting pressure. On the other hand, densities of medium-sized rodent species, such as the vizcacha *Lagostomus maximus*, and the dwarf Patagonian cavy *Pediolagus salinicola*, have been increased by the presence of open patches (Bucher, 1987; Saravia Toledo, 1987). The low density or absence of Chacoan cavies found in rangelands of good and very good condition could be attributable to two factors: changes in food availability (variation in plant composition associated with grazing pressure), and preference for open spaces (poor range condition) where predation risk is lower (Rosati and Bucher, 1995). When comparing the effects of different grazing systems on the mammal fauna of the semi-arid thorn scrub Chaco, Saravia Toledo (1987) noticed that under traditional systems of continuos grazing there is a reduction in large mammals (canids, deer and cats), and an increase in the above-mentioned rodent species. The changes undergone by fauna following the recovery of rangeland productivity (e.g. rotation

Table 2
Habitat preferences of small- and medium-sized mammals (marsupials, rodents and lagomorphs) and responses (e.g. changes in density) to cattle grazing in the aridlands of the Chaco and Monte biomes of Argentina

Organism	Habitat/microhabitat	Macroniche	Densities
Small mammals (less than 100 g)			
Didelphimorphia			
Thylamys pusillus	Creosote bush, mesquite forest; areas with dense thorny vegetation	Scansorial, insectivore-omnivore	↓ (2)
Rodentia			
Eligmodontia typus	Sand-dunes, open areas; low shrub cover	Terrestrial, granivore/ omnivore	↓ (1–2)
Graomys griseoflavus	Mesquite forest, creosote bush; high shrub cover	Scansorial, herbivore/ frugivore	↓ (1–2)
Calomys musculinus	Creosote bush; high forb cover	Terrestrial, granivore / omnivore	↓ (2)
Akodon molinae	Creosote bush, mesquite forest; high forb cover	Terrestrial, omnivore	0 (2)
Medium-sized mammals (more than 100 g)			
Rodentia			
Lagostomus maximus	Creosote bush, open mesquite forest, open habitats; low forb and shrub cover	Semi-fossorial, herbivore	↑ (4)
Dolichotis patagona	Creosote bush, open mesquite forest, open habitats; low forb and bare sandy soils	Cursorial, herbivore	↑ (3)
Microcavia australis	Open mesquite forest; forb and bare soil	Scansorial, semi-fossorial, herbivore	↑ (1)
Galea musteloides	Creosote bush and grass; high forb cover and humid areas	Terrestrial, herbivore	0 (1)
Pediolagus salinicola	Dry open forest, thorn scrub bare soil	Cursorial, herbivore	↑ (4–5)
Ctenomys eremophilus	Desert, scrub, thorn scrub	Fossorial, herbivore	↓ (pers. obs.)
Lagomorpha			
Lepus europaeus	Sand dunes, creosote bush, open habitats; areas with low plant cover	Cursorial, herbivore	↑ (pers.obs.)

Decrease in density ↓; increase, ↑, and 0: unchanged; habitat/microhabitat and macroniches follow Mares (1973), Mares and Ojeda (1982), Ojeda and Mares (1989), Puig et al. (1999), with minor modifications; sources: 1—Gonnet (1998), 2—Maldonado Curti (1990), 3—Kufner and Chambouleyron (1991), 4—Saravia Toledo (1987), 5—Rosati and Bucher (1995).

grazing) are the decrease or disappearance of medium-sized rodent species from open areas.

When livestock is excluded or its intensity reduced, effects can be varied. Perevolotozky and Seligman (1998) report that ecosystems under some of these

situations tend to become vegetationally dense and with low biological diversity. Other studies report a greater number of rodent species in areas where livestock has been excluded (Brooks, 1995). Thus, depending on the different practices and grazing intensity, this kind of perturbation can be regarded as beneficial for natural communities under certain conditions (Brooks, 1995).

6. Other disturbances

Other disturbances have affected the native fauna of arid and semi-arid environments in Argentina, including conversion to agriculture, logging and fire. The first process has consumed the largest area of native forests, over 70% of the 700,000 km^2 of woody vegetation since colonial times in the arid to semi-arid Espinal, Monte, western Chaco and Patagonia (Morello and Mateucci, 1999, pp. 463–498). The use of traditional land clearing (e.g. slash and burn techniques) dates back to the turn of the twentieth century (Morello and Mateucci, 1999).

The modification of large natural areas has been made with little knowledge of the functioning of natural ecosystems, resulting in deleterious consequences to biodiversity, and in loss of soil fertility, structure and water retention capacity (Morello and Mateucci, 1999). The conversion of forests into grasslands through fire is a process that has been used in the Chacoan and Patagonian arid regions for over 150 years. This practice, combined with extensive livestock raising, has generated a mosaic of vegetation modifying their species diversity and promoting the establishment of exotic species (Morello and Mateucci, 1999). On the other hand, cutting down of forests for wood used for fuel and as building material has been the major factor leading to the disappearance of forests, and to the desertification processes (Roig, 1991). Selective logging and uncontrolled deforestation of Argentinean forest areas began 200 years ago and has continued to the present (Cabido et al., 1999, pp. 421–442). A clear example of this was the disappearance of mesquite forests of *Prosopis flexuosa* in the Monte desert, and of *P. caldenia* and *Shinopsis* sp. forests in the Espinal and Chacoan regions (Roig, 1991). Changes in landscape structure are related to a reduction in the population of large vertebrates, such as the guanaco *L. guanicoe*, the ñandú *Rhea americana*, and various carnivores and edentates (Roig, 1991; Cabido et al., 1999).

Unlike the semi-arid Chaco biome in Argentina, where periodic fire plays a major role in community composition, this is an unusual and infrequent phenomenon in the Monte desert. A study conducted in the central portion of the Monte desert showed that changes in vegetation induced by fire (Ojeda, 1989) include a decrease in small mammal species (from five to one species) on the one hand, and an increase in the relative abundance of species having ecomorphological features suitable for exploiting large open patches (e.g. the silky mouse *Eligmodontia typus*, the plains vizcacha *L. maximus*, and the Patagonian hare *D. patagona*) on the other hand.

7. Conclusions

The mechanisms whereby vertebrates respond to a particular disturbance regime depend on its characteristics (frequency, intensity) as much as on the attributes and habitat requirements of the species. A way of predicting the potential effects of grazing is having a good understanding of the natural history of desert rodents (Jones and Longland, 1999). A better understanding of the attributes of each species would enable prediction of the degree to which they might become endangered or enhanced by continuing modification of arid–semi-arid habitats. Thus, the Patagonian hare *D. patagona* is positively influenced by livestock grazing in the Monte desert, and prefers open sites with low plant cover (Campos et al., 2001). On the other hand, a small mammal such as the grass mouse *Akodon molinae*, which is associated with habitats having high plant cover (Corbalan and Ojeda unpubl.; Ojeda, 1989), has contrasting coloration against bare soil, and would be exposed to higher predation risk in grazed areas.

Two problems have led to an unclear and conflicting view of vertebrate responses to grazing in desert environments. The first is the scanty historical data regarding range management in study areas: information on herbivory in arid and semi-arid environments of Argentina is very limited and it has been seldom explored systematically (Bucher, 1987). The European colonization of western Chaco and Monte resulted in a dramatic alteration of the ecosystem because of the introduction of domestic herbivores and other related activities (fire, logging, hunting). In the Chaco, overgrazing favored the establishment of woody plants, the disappearance of grasslands, and the extinction of large herbivores, along with an increase in populations of medium-sized rodents. In the Monte and Patagonia, the effects of overgrazing on the natural vegetation have also been dramatic, although less spectacular in terms of landscape alteration. These effects include reduction in plant diversity, in shrub density, in the relationship of live to dead tissue in the dominant grasses, in the frequency of occurrence of large denuded patches, and increase in ephemeroids (Bucher, 1987).

The second problem is inadequate selection of scales. Most studies have analysed the response of biodiversity at local spatial scales, and only a few have used a hierarchical approach at multiple scales (Rosenstock, 1996). This has led to a generalized idea of the negative effects of grazing on native mammals, overlooking other beneficial aspects such as landscape modification by livestock activities and their possible implications in conservation (Severson, 1990). Habitat selection and variation in responses operate at different spatial scales (Kotler and Brown, 1988; Rosenstock, 1996). Recognition of patches in a mosaic by an organism depends on its level of resolution of spatial structure and the area over which it ranges during a given time (Wiens, 1996, pp. 93–107). The existence of patchiness in an environment offers organisms the option of responding to the patch structure in a nonrandom fashion (Wiens, 1985). For a particular kind of organism, patches may convey benefits (food, shelter) as well as costs (predation risk, more intense competition) (Wiens, 1996).

Landscape patterns are the consequence of numerous disturbances or perturbations creating patches. Each distinct patch type is likely to provide each species with different opportunities, making it possible for species to coexist without competitive exclusion (Longland and Young, 1995).

If biological diversity is considered to be a direct function of habitat diversity (Longland and Young, 1995), patches having slight or moderate grazing levels can maintain greater habitat diversity by reducing landscape homogeneity, contributing to the maintenance of regional diversity. From this perspective, ecologically responsible range management can be a powerful tool for conservation (Curtin, 1995).

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