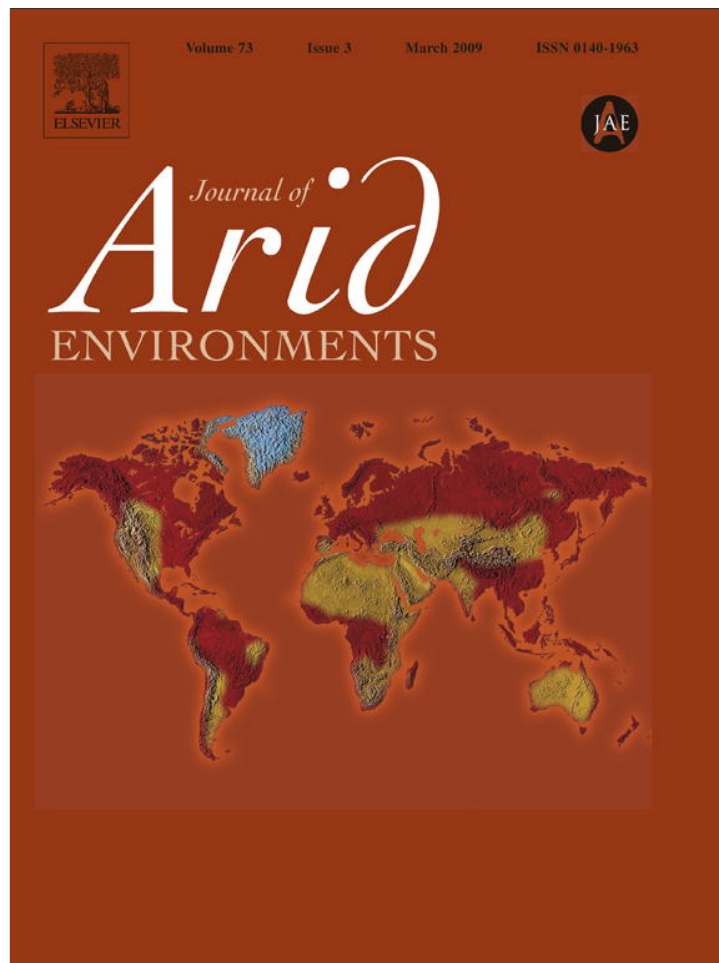


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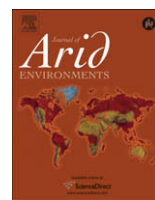
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Diet of a fossorial rodent (Octodontidae), above-ground food availability, and changes related to cattle grazing in the Central Monte (Argentina)

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ABSTRACT

Overgrazing by livestock has caused desertification in the Monte, where ctenomyids and livestock share grasses as main food items. The diet of *Ctenomys eremophilus*, above-ground food availability and changes related to cattle grazing are analyzed in the arid plain of Mendoza, Argentina. The most available categories were grasses, followed by low shrubs and tall shrubs. Tuco-tucos showed dietary generalism, ate mainly above-ground plant parts, preferred grasses and avoided shrubs at both grazed and ungrazed sites. Plant cover, grass diversity and availability decreased under livestock grazing, which was reflected in the diet by a lower percentage of grasses, a shift toward low shrubs and higher number of frequently used resources. Tuco-tucos in the grazed paddock compensated for lower consumption of vegetative plant parts by increasing the use of *Prosopis flexuosa* pods stored inside burrows. Moreover, greater dietary variation among individuals suggests foraging restricted to the items closest to burrow holes. These feeding tactics would allow them to reduce above-ground foraging as a response to high raptor predation risk due to increased bare soil. The plant recovery detected during the rest period, favoured by moderate stocking rate and rotational grazing system, would allow coexistence of tuco-tucos and cattle.

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1. Introduction

Livestock grazing is one of the major causes of degradation in arid and semiarid environments, producing high ecological costs in ecosystem composition, structure and function (Fleischner, 1994). Among the most usual effects of intense grazing detected in drylands are reduction of the herbaceous stratum, particularly of species with good forage quality, predominance of grazing-resistant species, dispersal of exotic species and increase in bare soil (Fleischner, 1994; Bertiller and Bisigato, 1998). All of these effects have been detected, particularly on infertile soils (Olf and Ritchie, 1998). Cattle ranching generates shifts in habitat structure that affect native fauna differently, whereby some species are favoured over others (Tabeni and Ojeda, 2003, and references therein).

The eco-region of plains and plateaus of the Monte in Argentina has been subjected to intensive livestock breeding which, together with inappropriate fire management and woody species removal, has resulted in desertification. Consequently, changes occurred in soil richness, landscape structure, and in composition and abundance of wild animal and plant species (Roig, 1991; Bertonatti and Corcuera, 2000). Cattle breeding began in the arid plain of Mendoza after 1910, and during the 1930s the high stocking rate probably led

to rangeland degradation (Guevara et al., 2002). Cattle grazing resulted mainly in reduced richness, cover, diversity, biomass of grasses and forage species height (Guevara et al., 1997). Disturbance by livestock in the central portion of Monte has brought about reductions in abundance and species richness of granivorous bird populations as well as in diversity and richness of small mammal assemblages, whereas densities of some medium-sized mammals increased (Gonnet, 1998). An increase in small mammal diversity associated with a greater plant heterogeneity produced by cattle grazing occurred in the same environment. Changes were also detected in the distribution of the abundance of some small mammal species among patches, related to the morphological and ecological attributes of each species (Ojeda and Tabeni, 2009, and references therein).

Competition for food and exposure to predators have been suggested as possible mechanisms to explain changes in abundance, diversity, species richness and body mass of small mammals caused by grazing ungulates (Keasing, 1998; Steen et al., 2005). High dietary overlaps occurred between domestic and wild herbivores in arid environments with low habitat heterogeneity or with plant diversity reduced by fire, overgrazing and woody plant removal (Kufner et al., 1992; Puig et al., 2007). Some studies reveal that diet composition of wild mammals shifted toward grasses or dicots depending on the type of livestock present in the environment (Mellado and Olvera, 2008), or on the range conditions resulting from the grazing history and management system

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involved (Rosati and Bucher, 1995). Small rodents depend on an extensive plant cover to escape from predators, and expansion of bare soil under intensive livestock grazing increases their predation risk. In contrast, bare soil would favour large rodents whose anti-predator behaviour is based on unobstructed visibility (Tabeni and Ojeda, 2003, and references therein).

The fossorial rodents of the genus *Ctenomys* (tuco-tucos) are herbivores endemic to South America, widely distributed in Argentina where about 43 species occur (Galliari et al., 1996). Populations of tuco-tucos present a discontinuous pattern of distribution across plains and plateaus of the Monte in Mendoza, and share most habitats with livestock. Grasses are an important dietary component for both cattle (Guevara et al., 1997) and tuco-tucos inhabiting either arid (Rosi et al., 2003) or wet environments (Comparatore et al., 1995; Del Valle et al., 2001). Dietary generalism characterizes the foraging behaviour of ctenomyids and other subterranean rodents (Busch et al., 2000), and has been ascribed to the high burrowing costs of food search as a way to optimize the energy intake predicted by the optimal foraging theory (Krebs, 1978). Also ascribed to the high burrowing costs, subterranean rodents with only belowground activity usually forage on food items according to the probability of encountering them (opportunistic behaviour according to Jaksic, 1989) and subterranean vegetation prevails in their diets. Conversely, ctenomyids with a predominantly above-ground foraging behaviour usually show a selective diet (i.e., proportions of items in the diet differ from those in the field; Jaksic, 1989) with considerable proportions of above-ground plant parts (Busch et al., 2000; Rosi et al., 2003).

The diet of the tuco-tuco (*Ctenomys eremophilus*) and plant availability in grazed and ungrazed sites of the arid plain of Mendoza were analyzed over three seasons in order to detect effects of cattle grazing on above-ground food availability, dietary attributes and food selectivity by this rodent. We expected that the *Ctenomys* diet on the grazed site would differ from that on the ungrazed site by: (a) lower grass percentage and greater dietary diversity, as a response to reduced food availability due to cattle grazing, (b) higher percentage of subterranean items due to a reduced search for food above-ground, as a response to the extensive bare soil that would increase raptor predation risk, and (c) greater dietary variation among individuals and lower food selectivity due to both reduced food availability and higher raptor predation risk.

2. Material and methods

2.1. Study area and species

This study was conducted at the “El Divisadero” Cattle and Range Experimental Station (19,334 ha), located in the north central plain of Mendoza (33°45'S and 67°41'W, Argentina). “El Divisadero” is a suitable area to develop studies on livestock and wildlife interactions. Since 1990, experiments have been carried out comparing different grazing systems and stocking rates, with the goal of optimizing livestock production and minimizing environmental impact (Guevara et al., 2002).

This area is located within the eco-region of plains and plateaus of the Monte region (Bertonatti and Corcuera, 2000). The climate is temperate-warm with annual precipitation averaging 323 mm, primarily concentrated in spring–summer (Guevara et al., 2002). Soils are deep, with a sandy composition and some silt in interdune depressions (Masotta and Berra, 1994). The vegetation is a xerophytic open shrubland of *Prosopis flexuosa* and *Larrea divaricata*, associated with *Condalia microphylla* and *Lycium chilense*, among other shrubs. The two forms of *P. flexuosa* (tree and tall shrub) occur in the study area, with the shrubby form being dominant. Warm-season perennial grasses, such as *Panicum urvilleanum*, *Setaria leucopila* and *Aristida* spp., dominate the herbaceous layer (Méndez et al., 1993).

The tuco-tucos present in the study area do not differ cytogenetically from topotypes of *C. eremophilus* Contreras & Roig (M. Gallardo, personal communication), a species whose designation was based on specimens from the Ñacuñán Biosphere Reserve, located 30 km southwest of the study area. This species is now considered *nomen nudum* because its formal description was not completed (Galliari et al., 1996).

2.2. Field and laboratory designs

Two paddocks of the “El Divisadero” Experimental Station were selected for this study: a control paddock (25 ha) free of cattle for four years (Guevara et al., 2002), and a grazed paddock (1150 ha) belonging to a rotational grazing system on 5000 ha stocked at a moderate rate (21 ha per AU) since 1990 (Guevara et al., 1997). Both the control and grazed paddocks are located within a same unit according to the physiographic classification (sandy plain) by Masotta and Berra (1994) and to the physiognomic classification (shrubland of *L. divaricata*) by Méndez et al. (1993). These paddocks constitute, on a local scale, a homogeneous environment with natural conditions representative of those of the Mendoza arid plain devoted to livestock production (Guevara et al., 1987).

Sampling activities were carried out during the rest period of the grazed paddock, in autumn–winter (June 2004), spring (October 2004) and summer (March 2005). These activities began when cattle were removed, after the four-month grazing period set by the rotational system. A sampling area of approximately 2 ha was selected in each paddock, where vegetation and animals were sampled. A total of 68 tuco-tucos were captured during the three sampling seasons using rotating-jaw traps (Oneida Victor N° 0), which were checked every 2 h to minimize the time the animal was held in the trap. Most tuco-tucos were kill-trapped, and the few animals trapped alive were immediately euthanized *in situ* using inhalant anaesthetics. Both trapping techniques and animal handling followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee, 1998).

Stomach contents were analyzed individually using the micro-histological method developed by Baumgartner and Martin (1939). Two microscope slides were made for each animal and fifty fields per slide were systematically examined through a 400× microscope. Reference slides, a graphic catalogue and microphotographs were performed for different parts of all plant species present in both sampling areas, and were used for extensive training (Holechek and Gross, 1982a) and for examination of stomach content slides. Vegetative, reproductive and subterranean fractions of plants were quantified for each stomach content sample. Plant identifications were to species level when possible, and otherwise to genus level (for vegetative fragments) or to family level (for reproductive and subterranean plant fragments).

Plant cover and specific composition of the vegetation were estimated during the three sampling dates using the point-quadrat method (Daget and Poissonet, 1971) along ten 30-m transects established per area and sampling event, with 100 points per transect. Transects were regularly spaced 20 m apart. Plant species, whose complete names appear in Table 3, were grouped into five categories: grasses, forbs, low shrubs, tall shrubs and cacti. All forbs were annual, whereas grasses and shrubs were perennial. *Prosopis* was included in the category of tall shrubs, given that the shrubby form was the most abundant, whereas the tree form occurred as isolated individuals.

2.3. Data and statistical analyses

Relative frequencies of plants consumed by tuco-tucos were calculated for the vegetative fraction, and were considered equivalent to relative percent dry weight of plant species present in

stomach contents (Holechek and Gross, 1982b). Dietary variations among individuals were estimated by a multivariate coefficient of variation (Van Valen, 1978).

Relative plant cover was used as an estimator of above-ground food availability, considering only those species present on at least one occasion in the vegetative and reproductive fractions of the diet. Taking into account that grass spikes found in the diet were only identified to family level, all grass species registered in the field were included in estimating food availability.

Diversity in food availability and diet was estimated with the Shannon–Wiener function (H' , Colwell and Futuyma, 1971). In addition to dietary diversity, the number of frequently used resources, defined by Krebs (1989) as those species eaten with relative frequencies higher than the reciprocal of the total number of eaten species, was used as a simple measure of niche breadth. The minimal cut-off obtained (3%) was calculated considering all species eaten on some sampling site or season.

The test of spatial independence among sampling sites (Diblasi and Bowman, 2001) was applied to residuals of the linear model for plant cover, diversity, percentages of the main food category and species. The model considered the spatial location of each sample, and vegetation variables were previously transformed by arcsine of square root, except plant cover, which was transformed by Box & Cox. The null hypothesis of spatial independence among sampling transects was not rejected by this test ($p=0.78$ for plant cover, $p=0.77$ for plant diversity, $p=0.46$ for percentage of grasses, $p=0.22$ for percentage of *Panicum*).

Relative frequencies of categories and plant species in both diet and food availability were expressed as percentages. Differences in diet and availability among seasons and paddocks (grazed and ungrazed) were detected by using the non-parametric Kruskal–Wallis H test and the Tukey test (Zar, 1984) for multiple comparisons among seasons. Comparisons among percentages of species occurrence in the diet and in environmental availability included only frequently used species.

Patterns of food selection for vegetative parts of plants were detected from significant differences between observed and expected dietary percentages by using the χ^2 test (Zar, 1984). The expected value for each dietary item was equivalent to its percentage of above-ground food availability, assuming a non-selective use of food. Bailey's confidence intervals (Cherry, 1996) identified the selective use of frequently consumed plant species. Plant use was classified as preferred, indifferent or avoided depending on whether availability was respectively located below, within or above the confidence interval of dietary frequency.

3. Results

3.1. Diet of the tuco-tuco

The diet of *C. eremophilus* was mainly composed of vegetative plant parts, with low percentages of subterranean and reproductive parts (Table 1). The subterranean fraction of the diet was entirely made up of subterranean grass stems, whereas the reproductive fraction was composed of *Prosopis* fruits in autumn–winter and of grass spikes in spring and summer. Dietary percentages of subterranean plant parts did not differ between paddocks in any of the sampling seasons. The percentage of reproductive parts in the grazed paddock was higher ($H=10.56$, $p=0.001$), and that of vegetative parts lower ($H=5.82$, $p=0.016$), than in the control paddock in autumn–winter. Seasonal comparisons detected a higher percentage of subterranean fractions in autumn–winter than in spring and summer in the control paddock ($H=9.42$, $p=0.009$), and than in summer in the grazed paddock ($H=9.24$, $p=0.001$). Only at this site was the reproductive fraction higher in autumn–winter ($H=10.81$, $p=0.004$) than in spring, and the

vegetative fraction lower in autumn–winter ($H=12.83$, $p=0.002$) than in spring and summer.

Taking into account all three sampling events, the vegetative parts in the diet comprised 28 plant items in the control and 31 in the grazed paddock, of which respectively 9 and 14 were items of frequent use. Neither paddock showed seasonal changes in the number of frequently used resources (Table 1). This number was higher in the grazed than in the control paddock only in autumn–winter ($H=6.73$, $p=0.010$). Diversity of plant species eaten by tuco-tucos, and particularly grass diversity, showed no significant differences between paddocks or among seasons. Grasses were the main dietary category, followed by low shrubs, and complemented by minor percentages of tall shrubs and forbs (Fig. 1). The grasses *Panicum* and *Setaria* and the low shrub *Junellia* were the major dietary items, and they contributed altogether about 73 and 67% of the diet in the control and grazed paddocks, respectively. Only in some cases were all other grasses and low shrubs frequently used (Table 2). The tall shrub *Prosopis* was consumed in both paddocks throughout the year, and frequently used only in the grazed paddock during summer and autumn–winter. The forbs *Clarkia* and *Conyza* only were frequently used in the grazed paddock in spring.

The grazed paddock differed from the control paddock only in autumn–winter due to a lower dietary percentage of grasses ($H=6.49$, $p=0.011$), particularly *Panicum* ($H=12.48$, $p=0.004$), and a higher percentage of low shrubs ($H=4.83$, $p=0.028$), particularly *Junellia* ($H=5.44$, $p=0.020$) (Fig. 1, Table 2). Dietary percentages of tall shrubs and forbs showed no significant differences between paddocks in any of the sampling seasons.

Seasonal differences in dietary percentages of plant categories and species were detected in both paddocks. A summer increase was found in the dietary percentages of grasses in both the grazed ($H=8.34$, $p=0.016$) and control paddocks ($H=7.83$, $p=0.020$), whereas the percentage of the grass *Panicum* increased only in the grazed paddock ($H=11.51$, $p=0.003$). The percentage of low shrubs in the grazed paddock decreased in summer ($H=9.78$, $p=0.008$), whereas that of forbs in the control paddock increased during spring ($H=11.15$, $p=0.004$).

Dietary variation among individuals was higher in the grazed than in the control paddock in autumn–winter and spring, but similar between paddocks in summer (Table 1).

3.2. Above-ground food availability

The vegetation in the study area, comprising 61 species, showed a mean cover of 78.3% (Table 1). The grazed paddock differed from the control paddock by a lower plant cover in autumn–winter ($H=14.33$, $p<0.001$), spring ($H=12.26$, $p<0.001$) and summer ($H=5.20$, $p=0.023$). A seasonal decline in plant cover was detected only in the grazed paddock in autumn–winter ($H=20.92$, $p<0.001$).

Most grasses, tall and low shrubs present in the environment were included in the vegetative fraction of the diet in the control paddock (22 out of 31 species) as well as in the grazed paddock (24 of 30 species). Few forbs (6 of 22 and 7 of 21 species, respectively) and none of the three cacti were eaten by tuco-tucos. In addition, reproductive parts of the other two grasses (*Stipa* spp. and *Cottea pappophoroides*) could have been eaten by tuco-tucos. Species diversity in the food availability showed no significant differences between paddocks. Seasonal comparisons detected a decrease in this variable during autumn–winter in both the grazed ($H=11.42$, $p=0.003$) and control paddocks ($H=6.19$, $p=0.045$). Grass diversity was lower in the grazed than in the control paddock during autumn–winter ($H=7.00$, $p=0.008$) and spring ($H=7.10$, $p=0.008$), and higher in summer ($H=3.86$, $p=0.050$). Seasonal differences were detected only in the grazed paddock, with grass diversity being higher in summer than in the other seasons ($H=20.58$, $p<0.001$).

Table 1
Mean seasonal values for general variables analyzed in the tuco-tuco diet and in aerial food availability in grazed and control paddocks. Standard deviations are given in parentheses.

	Grazed paddock			Control paddock		
	Autumn–winter	Spring	Summer	Autumn–winter	Spring	Summer
Diet	<i>n</i> = 11	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 14	<i>n</i> = 11	<i>n</i> = 12
Diversity of species (<i>H'</i>)	0.52 (0.15)	0.50 (0.21)	0.38 (0.22)	0.40 (0.15)	0.48 (0.22)	0.34 (0.19)
Diversity of grasses (<i>H'</i>)	0.29 (0.15)	0.27 (0.18)	0.28 (0.20)	0.28 (0.10)	0.35 (0.20)	0.29 (0.17)
Subterranean fraction (%)	12.20 (5.92)	7.72 (6.68)	3.87 (3.03)	13.05 (6.76)	6.55 (7.78)	5.23 (3.97)
Reproductive fraction (%)	11.58 (11.12)	1.12 (3.20)	3.05 (2.88)	0.76 (1.98)	10.17 (17.90)	3.75 (5.11)
Vegetative fraction (%)	76.22 (12.45)	91.16 (6.87)	93.08 (4.84)	86.19 (6.91)	83.28 (15.79)	91.01 (6.01)
Number of items frequently used	5.82 (1.33)	4.90 (2.08)	4.00 (1.83)	4.21 (1.31)	4.64 (1.57)	3.25 (1.29)
Dietary variation among individuals (%)	34.28	32.98	23.53	13.83	21.72	21.59
Aerial food availability	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10	<i>n</i> = 10
Relative plant cover (%)	60.50 (6.22)	74.86 (6.27)	78.30 (5.01)	84.50 (5.06)	84.29 (4.07)	86.10 (6.06)
Diversity of species (<i>H'</i>)	0.87 (0.06)	0.91 (0.11)	0.99 (0.06)	0.85 (0.12)	0.93 (0.09)	0.96 (0.09)
Diversity of grasses (<i>H'</i>)	0.27 (0.05)	0.27 (0.06)	0.47 (0.06)	0.34 (0.06)	0.34 (0.06)	0.40 (0.08)

Grasses and low shrubs were the most available food categories, complemented by tall shrubs and scarce forbs (Fig. 1). The grasses *Panicum* and *Setaria*, and the low shrubs *Junellia* and *Acantholippia* were the most available items while the other grasses showed low frequencies (Table 3). The grazed paddock differed from the control paddock in autumn–winter by a lower percentage of grasses ($H = 9.61, p = 0.002$), particularly *Panicum* ($H = 5.14, p = 0.023$) and *Setaria* ($H = 7.31, p = 0.007$). In summer, the grazed paddock differed from the control paddock by higher availability of grasses ($H = 6.22, p = 0.013$), particularly *Setaria* ($H = 12.09, p = 0.001$) and of the tall shrub *Prosopis* ($H = 3.92, p = 0.048$), and by lower percentages of the low shrub *Acantholippia* ($H = 8.25, p = 0.004$) and of the scarce forb *Conyza* ($H = 8.26, p = 0.004$) (Fig. 1, Table 3).

Low availability (<5%) was detected for most of the species which were never resources of frequent use (footnote of Table 2), except for the low shrub *Fabiana* and the tall shrub *Larrea* in the

control paddock (9 and 13%, respectively) as well as in the grazed paddock (13 and 10%, respectively).

Seasonal changes in availability included a decrease in forb availability during autumn–winter in both the grazed ($H = 18.69, p < 0.001$) and control paddocks ($H = 21.67, p < 0.001$). In the grazed paddock there was a summer increase in the percentage of grasses ($H = 14.72, p = 0.001$), particularly *Setaria* ($H = 22.28, p < 0.001$), and a summer decrease in low shrub availability ($H = 19.07, p < 0.001$), particularly *Acantholippia* ($H = 11.11, p < 0.004$). In the control paddock, a summer decline was detected for the low shrub *Junellia* ($H = 11.11, p = 0.004$).

3.3. Dietary selection of vegetative plant parts

A selective use of plant categories was detected in the control paddock during autumn–winter, spring and summer ($\chi^2 = 45.66$,

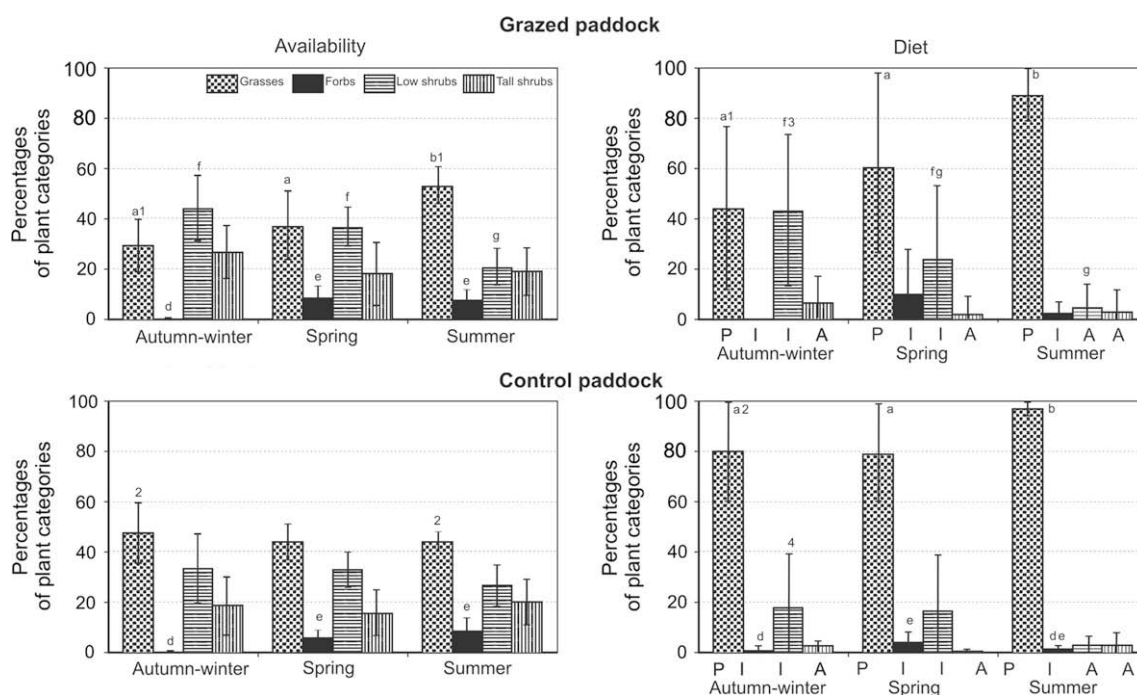


Fig. 1. Mean seasonal percentages of plant categories in the environment and in the tuco-tuco diet in grazed and control paddocks. Vertical lines represent standard deviations. Different letters in each panel indicate significant differences among seasons (a, b: grasses; d, e: forbs and f, g: low shrubs); different numbers indicate significant differences between paddocks in each season (1, 2: grasses and 3, 4: low shrubs). Seasonal preference (P), avoidance (A) and indifference (I) in the use of plant categories are given (P and A correspond to significant differences between percentages of use and availability).

Table 2

Mean percentages (SD in parentheses) of food items present in the vegetative fraction of tuco-tuco diet (only items $\geq 3\%$). Preference (P), avoidance (A) or indifference (I) in the use of species are given when dietary percentages were $\geq 3\%$. Acronyms (Acr) correspond to plant species names detailed in Table 3.

Acr ^a	Grazed paddock			Control paddock								
	Autumn–winter		Spring	Summer	Autumn–winter	Spring	Summer					
Grasses												
Po	3.18 (2.89)	P	2.20 (4.66)	0.00 (0.00)	0.14 (0.36)	5.82 (9.18)	P	5.92 (14.82)	P			
Ar	0.00 (0.00)		4.60 (13.86)	I	1.70 (5.38)	0.00 (0.00)		1.45 (4.20)	0.75 (1.60)			
Ch	6.91 (14.12)	P	2.50 (6.10)		10.10 (20.62)	I	0.00 (0.00)	0.27 (0.90)	2.08 (7.22)			
Pa	11.00 (16.80)	A	26.50 (31.31)	A	55.30 (33.28)	P	56.86 (25.16)	P	44.09 (27.58)	I	57.17 (32.19)	P
Di	1.36 (3.29)		0.00 (0.00)		0.10 (0.32)		1.86 (3.11)		3.73 (8.95)	I	0.58 (1.38)	
Sp	0.00 (0.00)		0.10 (0.32)		3.30 (6.04)	I	0.00 (0.00)		2.36 (7.84)		5.33 (11.36)	P
Br	0.00 (0.00)		0.00 (0.00)		0.10 (0.32)		0.00 (0.00)		8.27 (14.61)	P	0.00 (0.00)	
Se	17.36 (22.77)	P	21.10 (19.32)	P	13.80 (16.20)	I	15.93 (10.70)	P	9.36 (13.25)	I	19.50 (23.07)	P
Forbs												
Cl	0.00 (0.00)		4.30 (13.60)	I	0.00 (0.00)		0.00 (0.00)		0.18 (0.60)		0.00 (0.00)	
Co	0.00 (0.00)		4.90 (10.29)	I	0.00 (0.00)		0.50 (1.87)		1.73 (3.23)		0.08 (0.29)	
Low shrubs												
Ju	32.00 (31.22)	P	18.80 (21.02)	I	4.80 (9.22)	I	7.86 (16.18)	I	9.36 (15.86)	I	0.17 (0.58)	
Hy	4.55 (11.25)	I	1.60 (3.13)		0.00 (0.00)		1.21 (4.54)		0.27 (0.90)		1.25 (4.33)	
Ep	2.91 (9.32)	I	0.00 (0.00)		0.00 (0.00)		0.00 (0.00)		0.00 (0.00)		0.00 (0.00)	
Ac	3.18 (10.23)	I	0.70 (1.49)		0.20 (0.63)		0.00 (0.00)		0.00 (0.00)		0.00 (0.00)	
Ly	0.00 (0.00)		2.90 (9.17)	I	0.00 (0.00)		0.71 (1.73)		5.73 (15.54)	I	0.33 (0.78)	
Ba	0.00 (0.00)		0.10 (0.32)		0.00 (0.00)		6.29 (17.03)	P	0.00 (0.00)		0.17 (0.58)	
Tall shrubs												
Pr	5.27 (10.41)	I	2.20 (6.96)		3.20 (8.77)	I	1.71 (2.30)		0.09 (0.30)		1.67 (5.77)	

^a Species eaten with $<3\%$ were: grasses *Aristida inversa*, *Trichloris crinita*, *Eragrostis pilosa*, *Bouteloua aristidoides*, *Pappophorum philippianum*; forbs *Lecanophora* spp., *Plantago patagonica*, *Chenopodium papulosum*, *Phacelia artemisioides*, *Tweedia brunonis*, *Cryptantha albidia*; low shrubs *Fabiana denudata*, *Senecio* spp.; tall shrubs *Condalia microphylla*, *Bougainvillea spinosa*, *Larrea divaricata*, *Bulnesia retama*, *Prosopidastrum globosum*.

53.99, and 104.17, respectively, $p < 0.001$ in all cases) as well as in the grazed paddock ($\chi^2 = 23.31$, 32.64 and 50.84, $p < 0.001$ in all cases). Grasses were the preferred plant category, and tall shrubs were avoided in all cases (Fig. 1). Low shrubs were mainly used with indifference in the grazed paddock and were avoided in the control paddock. The forb category was mostly used with indifference.

A selective use of plant species was also detected over the three seasons in the control paddock ($\chi^2 = 1052.81$, 1311.07 and 449.93, $p < 0.001$ in all cases) and in the grazed paddock ($\chi^2 = 707.04$, 180.04 and 83.42, $p < 0.001$ in all cases). Among the main food items, the grasses *Panicum* and *Setaria* were mostly preferred in the

control paddock, although in spring both grasses were used with indifference (Table 2). In the grazed paddock, *Panicum* was mostly avoided and *Setaria* mostly preferred. The low shrub *Junellia* was mostly used with indifference in both paddocks except in autumn–winter when it was preferred in the grazed paddock. Forb species of frequent use were consumed with indifference.

4. Discussion

C. eremophilus behaves as a generalist herbivore under both grazed and ungrazed conditions, since most plant categories and

Table 3

Mean percentages (SD in parentheses) of relative plant cover in the environment (aerial food availability). Only the items with dietary percentages $\geq 3\%$ were included. Species acronyms (Acr) are mentioned.

Acr		Grazed paddock			Control paddock		
		Autumn–winter	Spring	Summer	Autumn–winter	Spring	Summer
Grasses							
<i>Poa lanuginosa</i>	Po	0.06 (0.18)	0.35 (1.32)	0.04 (0.13)	0.05 (0.15)	0.03 (0.12)	0.11 (0.35)
<i>Aristida mendocina</i>	Ar	2.08 (2.41)	0.39 (0.55)	1.88 (1.67)	2.21 (2.55)	2.34 (2.31)	0.57 (1.38)
<i>Chloris castillaniana</i>	Ch	1.18 (1.49)	0.61 (0.72)	3.60 (2.59)	0.90 (1.56)	0.38 (0.58)	2.00 (1.56)
<i>Panicum urvilleanum</i>	Pa	18.97 (10.10)	28.32 (12.00)	22.52 (3.00)	32.86 (13.89)	30.75 (8.21)	25.44 (8.09)
<i>Digitaria californica</i>	Di	0.56 (0.94)	0.03 (0.12)	2.09 (1.65)	0.52 (0.60)	2.18 (3.51)	3.38 (3.38)
<i>Sporobolus cryptandrus</i>	Sp	0.05 (0.17)	0.04 (0.17)	1.19 (1.35)	0.05 (0.16)	0.03 (0.11)	0.47 (0.52)
<i>Bromus brevis</i>	Br	0.06 (0.19)	0.03 (0.13)	0.03 (0.10)	0.05 (0.17)	0.99 (1.64)	0.06 (0.20)
<i>Setaria</i> spp.	Se	1.01 (1.43)	3.46 (3.55)	17.99 (4.69)	5.50 (4.30)	3.66 (2.27)	6.62 (4.33)
Forbs							
<i>Clarkia tenella</i>	Cl	0.00 (0.00)	1.24 (1.39)	0.00 (0.00)	0.00 (0.00)	0.66 (1.18)	0.00 (0.00)
<i>Coryza</i> spp.	Co	0.07 (0.21)	4.95 (3.33)	2.16 (1.92)	0.03 (0.11)	3.02 (2.05)	7.55 (5.41)
Low shrubs							
<i>Junellia seriphioides</i>	Ju	8.27 (6.15)	9.82 (8.37)	8.24 (4.73)	9.32 (7.44)	15.18 (6.33)	6.26 (3.46)
<i>Hyalis argentea</i>	Hy	2.22 (5.97)	1.83 (3.64)	0.60 (1.89)	3.59 (9.16)	0.32 (1.21)	0.84 (1.85)
<i>Ephedra</i> spp.	Ep	0.06 (0.18)	0.24 (0.68)	0.03 (0.11)	0.04 (0.13)	0.13 (0.47)	0.31 (0.97)
<i>Acantholippia seriphioides</i>	Ac	7.79 (9.40)	6.73 (5.28)	1.11 (1.44)	2.98 (2.67)	4.49 (2.56)	7.02 (5.73)
<i>Lycium chilense</i>	Ly	4.47 (2.67)	2.51 (1.33)	3.68 (1.99)	5.30 (3.92)	4.28 (2.58)	3.66 (2.07)
<i>Baccharis darwinii</i>	Ba	0.39 (1.23)	0.13 (0.33)	0.03 (0.10)	0.04 (0.12)	0.36 (0.70)	0.61 (1.72)
Tall shrubs							
<i>Prosopis flexuosa</i>	Pr	3.35 (4.44)	7.08 (5.25)	5.58 (4.83)	5.01 (5.92)	3.53 (3.67)	2.21 (2.16)

species were included in the diet. Preference for grasses, which were the main dietary component, and a high prevalence of above-ground plant material characterized the food habits of this rodent at both sites. The shared use of grasses by tuco-tucos and cattle, with grasses being the most important food for cattle (Guevara et al., 1997), reinforces the expectation that cattle grazing should force tuco-tucos to alter their diet. Consistently with our predictions, the tuco-tuco diet in the grazed paddock differed from that in the control paddock by a lower percentage of grasses, higher dietary diversity evidenced by the higher number of frequently used resources, less selective consumption of the low shrub category, and greater dietary variation among individuals. Despite the diet at the grazed site failed to show the expected higher proportion of subterranean items compared to the control site, other dietary changes were evidenced, such as a higher consumption of low shrubs and of reproductive parts of plants.

The observed dietary generalism, the prevalence and preferential use of grasses, and the preponderance of above-ground plant parts also characterized the diet of other *Ctenomys* species coping with food scarcity and severe climate conditions in the Andean Precordillera (Rosi et al., 2003), or living in humid climate in grasslands of the Pampean plain (Comparatore et al., 1995; Del Valle et al., 2001). The generalist strategy of *Ctenomys* is consistent with expectations for subterranean rodents, taking into account the high burrowing costs of searching for food (Busch et al., 2000), and the optimization of energy intake predicted by the optimal foraging theory (Krebs, 1978). The dominance of grasses in the diet of tuco-tucos inhabiting the abovementioned environments, where grasses are the dominant resource, could suggest an opportunistic response of *Ctenomys* to high grass availability. However, selectivity for this category allowed *C. eremophilus* to maintain a dietary prevalence of grasses, despite the fact that shrub layers were dominant in the xerophytic scrubland studied. Grasses are important for tuco-tucos as they would fulfil most of their energy, protein and fibre requirements (Del Valle et al., 2001), and would be easier to harvest and handle than are dicots (Randolph et al., 1991). The prevalence of above-ground items in the diet of *C. eremophilus*, and in other species of the genus, shows the tendency of tuco-tucos to feed mostly above-ground, a behaviour also evidenced by signs of foraging on the vegetation closest to the burrow holes (Del Valle et al., 2001; Rosi et al., 2003). The seasonal decline in above-ground vegetation, particularly the absence of sprouts and green leaves during autumn–winter, could account for the dietary increase of subterranean plant parts during this period, in both grazed and ungrazed paddocks. A similar foraging behaviour has been documented for other subterranean rodents, coinciding with a decrease in available above-ground biomass (Busch et al., 2000; Comparatore et al., 1995).

Cattle grazing on the study site would be responsible for the reduction of plant cover and of grass availability and diversity occurred in the grazed paddock during autumn–winter. Vegetative dormancy in this season would not be enough to reduce plant availability, since there were no seasonal changes in the control paddock. The diet of tuco-tucos inhabiting the grazed paddock showed in autumn–winter the expected response to cattle grazing, with a lower percentage of grasses, particularly *Panicum*, which is intensively eaten either by cattle (Guevara et al., 1997) or by tuco-tucos. A higher intake of low shrubs, and particularly of *Junellia*, would compensate for a lower use of grasses. Shrubs, as green food available in autumn–winter, are important for tuco-tucos in areas where grass availability has been reduced by cattle grazing. The importance of leaves of the tall shrub *Prosopis* as a source of protein (Van den Bosch et al., 1997) accounts for its inclusion in the tuco-tuco diet across the year, and especially for its frequent use in the grazed paddock. The marginal use of *Larrea* despite its moderate availability is justified by its high resin content, which increases

water loss through faeces and energy loss through urine, and usually produces a decrease in body weight (Mangione et al., 2004). *Larrea* could be a complementary food in environments where green vegetation is scarce during the dry season, since it was included in the winter diet of *Ctenomys mendocinus* in a Piedmont environment (Puig et al., 1999), and presented cuts made by tuco-tucos in a creosote bush community (Borrueal et al., 1998).

The enlargement of the spectrum of frequently used resources also allowed tuco-tucos to make up for reduced autumn–winter food availability caused by cattle grazing. The inclusion of alternative items when availability of preferred plant species becomes lower agrees with our prediction, in the framework of the optimal foraging theory. A similar dietary shift was detected for a Piedmont population of *C. mendocinus* (Puig et al., 1999), whereas the extremely arid environment of Precordillera bound tuco-tucos to the opposite dietary shift (Rosi et al., 2003), consistently with the selective quality hypothesis (Weckerly and Kennedy, 1992).

Tuco-tucos maintained a selective use of food resources despite the changes in vegetation associated with cattle grazing, evidenced by their preference for grasses, particularly *Setaria*, and avoidance of high shrubs. The use with indifference of the low shrub category, always avoided in the ungrazed paddock, agrees with the prediction of a lower dietary selectivity in the grazed paddock. This feeding behaviour would allow tuco-tucos to compensate for the dietary reduction of grasses in autumn–winter, and to reduce raptor predation risk by increasing their non-selective consumption of the most available items. The shift from indifference to preference for *Junellia*, one of the main low shrubs, could help tuco-tucos reduce the dietary overlap with cattle, as this low shrub has been classified as unpalatable for livestock (Guevara et al., 1997).

The great dietary variation among individuals in the grazed paddock would respond to an increased risk of raptor predation due to the extensive bare soil rather than to lower food availability, in view of the minor seasonal changes in dietary variation in the control paddock. The high risk of raptor predation would force tuco-tucos to restrict their above-ground search for food to the scarce items closest to their burrow holes, particularly within shrub patches. In fact, when plant cover increased in summer, the dietary variation among individuals decreased until it was similar in both paddocks. The high risk of predation, expected in environments with extensive bare soil (Cassini and Galante, 1992; Tabeni and Ojeda, 2003, and references therein), usually causes reductions in the foraging effort of rodents (Verdolin, 2006). Raptor predation would be significant for tuco-tucos, since they are important dietary items for diverse birds of prey (Busch et al., 2000; Rosi et al., 2003).

Contrary to what we expected, the increase in raptor predation risk in the grazed paddock did not force tuco-tucos to forage on subterranean items in higher proportions than on the control site. The important proportion of *P. flexuosa* pods in the diet of tuco-tucos in the grazed paddock during autumn–winter allowed them to compensate for the lower consumption of vegetative plant parts, and to reduce above-ground foraging by eating fruits stored inside the burrows as a food reserve. Indeed, the presence of pods in the diet of tuco-tucos only in autumn–winter indicates a deferred use of these fruits, given that their dispersal occurs in summer, and their persistence on the soil surface is very brief (Villagra et al., 2002). These fruits represent an important dietary contribution as a good hydrocarbonated food item with relatively low fibre and discrete quantities of protein and fat (Wainstein and González, 1971).

Müller et al. (2007) mentioned that reduced stocking rates and long rest periods without grazing are important for the sustainability and recovery of systems under livestock management, particularly in arid environments. Chapman and Ribic (2002) also considered rotational grazing management and buffer strips as

useful tools to make livestock use compatible with wildlife conservation. According to a recent critical analysis of experiences comparing rotational and continuous systems (Briske et al., 2008), stocking rate was considered one of the most consistent management variables affecting livestock and plant production. Increases in stocking rate or in grazing period length in our study area would intensify changes found in food availability and in the diet of tuco-tucos, and even become a survival risk for these subterranean rodents. In fact, a dramatic decline in abundance of tuco-tucos occurred near the study area, at sites subjected to continuous heavy use by cattle (Cona et al., unpublished data). Increases in plant cover and grass availability during the rest period of the grazed paddock were evidence of vegetation recovery, allowed by a moderate stocking rate and the rotational grazing system, which would reduce the risk of tuco-tucos disappearing from the area. The diverse effects of livestock grazing on populations of wild animals, unusually included in analyses to improve the management of rangelands, appear as relevant issues for a sustainable development compatible with wildlife conservation in arid environments.

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