

Use of resources by the subterranean rodent *Ctenomys mendocinus* (Rodentia, Ctenomyidae), in the lowland Monte desert, Argentina

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ARTICLE INFO

Article history:

Received 29 July 2008

Received in revised form

28 September 2009

Accepted 9 October 2009

Available online 20 November 2009

Keywords:

Diet

Fossorial

Habitat use

Herbivory

Heterogeneity

Soil properties

ABSTRACT

The feedback between organisms and their environment is of great relevance to the understanding of ecosystem functioning. Particularly, subterranean mammals living on desert systems play an important role in ecosystem processes modifying their environment and influencing the life strategies of plants and animals. The mendocino tuco-tuco *Ctenomys mendocinus*, is a fossorial rodent inhabiting a wide range of soil and climate conditions in the central arid lands of Argentina. The purpose of our study was to quantify the degree of environmental segregation: soil properties and vegetation in four habitat types, their impact on woody vegetation, and diet. The highest activity was recorded in sand dunes and was associated with high habitat heterogeneity and soft soils. Degree of herbivory varied among habitats, with *Lycium* (Solanaceae) being the most gnawed shrub. Tuco-tucos behave like folivorous grazers, feeding on leaves of grasses, mostly *Panicum* (Poaceae). This is the first study integrating multiple approaches of tucos' auto-ecology in a heterogeneous desert matrix, suggesting a differential use of its environment, possibly according to food supply and soil hardness. Despite life underground impose general constrains for most subterranean species, our results suggest that both above and under ground habitat features play important roles in the occurrence of fossorial rodents.

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1. Introduction

Subterranean habitats are considered to be more stable and simple than aboveground habitats. They are characterized by predictable temperature, relative humidity, darkness and ventilation fluxes, as well as by low productivity (Nevo, 1979). These environmental features, which characterize subterranean niches, have led to similar evolutionary pressures that result in convergent morphological, physiological and behavioral adaptations to underground life all around the world (Nevo, 1979; Reichman and Seabloom, 2002). Mammals that take advantage of these habitat features are found on all continents except for Antarctica. Particularly, subterranean rodents (e.g. *Geomys*, *Thomomys*, *Ctenomys*) are mostly found in open, arid or semiarid habitats where underground life is favored (Busch et al., 2000; Lacey et al., 2000).

Subterranean rodents play an important role in ecosystem dynamics. Some of them, such as pocket gophers (e.g. *Geomys*, *Thomomys*) and voles (e.g. *Myospalax*), have been considered to be ecosystem engineers (Reichman and Seabloom, 2002; Kerley et al.,

2004) because of their ability to directly or indirectly modify resource availability for other species (Jones et al., 1994). Their large burrow systems affect the texture, water-holding capacity and nutrient dynamics of soils, and consequently the composition and abundance of vegetation (Reichman and Seabloom, 2002; Kerley et al., 2004).

Just as these species modify their environment, so could some habitat features, such as soil and vegetation, influence their life strategies. Most subterranean rodents live in deep, soft and well-drained soils (Cameron et al., 1988; Heth, 1989) which could reduce thermal stress and the costs of burrowing (Walsberg, 2000; Whitford, 2002; Luna and Antinuchi, 2006). Moreover, vegetation not only supplies food but also affects patterns of ventilation and heat flow within burrow systems (Busch et al., 2000). This relationship between organisms and environment is of great relevance to the understanding of ecosystem functioning (Whitford, 2002).

The mendocino tuco-tuco, *Ctenomys mendocinus* (Rodentia, Ctenomyidae), is a middle-sized herbivorous rodent restricted to the arid lands of central Argentina (Rosi et al., 2002, 2005, and references therein). Previous research about tuco's ecology refers this species to be a potential keystone ecosystem engineer for its modifications of plant communities and soil in homogeneous habitat types (Lara et al., 2007; Borrue, unpublished data). The natural history of the mendocino tuco-tuco has been reported on

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a fragmented way, with the major focus of analyses being their feeding strategies (Madoery, 1993; Camín and Madoery, 1994; Puig et al., 1999; Rosi et al., 2003, 2009). Studies on the habitat use of *C. mendocinus* have only been anecdotic and partially reported (Puig et al., 1992; Rosi et al., 2002). Probably because of the importance of its subterranean niche, most research was focused on the structure of its burrowing systems (Puig et al., 1992; Rosi et al., 1996, 2000).

The central Monte is a heterogeneous mosaic of landscapes, from open sand dune habitats to *Larrea* shrublands and dense vegetation patches of *Prosopis* woodlands, and salt flats (Morello, 1958; Ojeda and Tabeni, 2009). At a microgeographic scale, these landscape attributes make the Monte desert a good laboratory for carrying out research on the differential use of resources (e.g. habitat patches, soil and vegetation). In addition, tuco-tucos are the only exclusively fossorial species of the central Monte desert (Ojeda and Tabeni, 2009). They are easily detected due to the conspicuousness of their signs, which makes this species a good study model. The purpose of our study was to analyze the relationship between a fossorial rodent and its environment through a comparison of resource uses among habitat types in the heterogeneous matrix of the central Monte desert. Our particular objectives were to compare, for the first time, the use of soil and habitat resources by *C. mendocinus* and the degree of herbivory (i.e. damage) on woody vegetation among different habitat types, and to characterize and quantify its diet.

2. Materials and methods

2.1. Study area

The study was conducted in the wet season between September 2005 and October 2006 at the MaB Reserve of Ñacuñán (34°02'S, 67°58'W, Province of Mendoza, Argentina). The study area belongs to the Monte desert Biome (Morello, 1958). The climate is semiarid and markedly seasonal with cold dry winters and hot wet summers. Mean annual rainfall is 326 mm. (Ojeda et al., 1998).

The area presents three main habitat types: *Prosopis* woodland, *Larrea* shrubland and sand dunes. The *Prosopis* woodland is characterized by the presence of three vegetation layers: a tree layer dominated by *Prosopis flexuosa* and *Geoffroea decorticans*, a shrub layer dominated by *Larrea divaricata*, *Larrea cuneifolia* and *Condalia microphylla*, and a grass layer dominated by *Pappophorum caespitosum* and *Digitaria californica*. The *Larrea* shrubland shows the occurrence of two well differentiated layers: a shrub layer made up of *L. cuneifolia*, and a grass layer dominated by *Trichloris crinita* and *Stipa ichu*. The sand dune area is composed of two plant layers: shrubs and grasses. Dominant shrubs are *L. divaricata*, *Ximenea americana* and *Junellia seriphioides*, and the herb layer contains *Panicum urvilleanum* and *Portulaca grandiflora* among other plant species (Roig, 1971; Rossi, 2004).

2.2. Sampling methodology and statistical analysis

Four habitat types were considered: *Larrea* shrubland, *Prosopis* woodland, sand dunes and dirt roads (man-made roads), based on their vegetation and soil features. Six sampling sites were selected for each habitat type, spaced at least 500 m apart. For vegetation we used the modified point quadrat method (Passera et al., 1983), with 100 sample stations along a 30 m long transect. One vegetation sampling transect was placed at each site. Seven habitat variables were quantified: cover of trees, shrubs, sub-shrubs (<1 m high), herbs, grasses, bare soil and litter. Differences in vegetation structure between habitats were characterized and analyzed using PCA and Kruskal–Wallis tests. Heterogeneity (horizontal structure) and complexity (vertical structure) were quantified for each habitat type with the Shannon–Weaver diversity

index ($H' = -\sum p_i \log p_i$) (Magurran, 2004), and their differences were analyzed using a modified *t* test (Zar, 1999).

For characterizing soil hardness we used a modified penetrometer (Herrick et al., 2005) consisting of a 1 m scaled stick and a 500 g weight. At each site we made 25 measurements (10 m apart) along a 250 m transect, recording the number of strokes necessary to penetrate into three soil depth levels: 5 cm, 10 cm and 15 cm. A Kruskal–Wallis test was applied to determine differences in soil hardness between habitat types at different depths. The association of occurrence of *C. mendocinus* with soil hardness at different depths was analyzed through nonparametric regression using the R statistical software version 2.5.1 (Gentleman and Ihaka, 1997).

In order to quantify habitat use, at each site we sampled a 250 m long and 10 m wide transect (2500 m² per transect) and recorded the number, type and location of active burrows. These transects were the same used for measuring soil hardness. Burrows were considered active when the soil mounds around the holes and their plugs were not compacted. Burrows were classified as feeding burrows (circular burrow hole close to a plant) and mounds (soil accumulation in the shape of a horseshoe) (Pearson et al., 1968; Giannoni et al., 1996). We tested for differences in number of active burrows among habitats using a Kruskal–Wallis test. To assess the potential associations between environment variables and activity of *C. mendocinus* we carried out a regression analysis using heterogeneity, complexity and soil hardness at all three depth levels as independent variables.

Tuco-tucos prune and cut off diagonally the entire stems of woody plants with their incisors (Borrueal et al., 1998), as jackrabbits do in the Chihuahuan desert (Steinberger and Whitford, 1983). Because gnawing is not evident on herbs and grasses, herbivory was only quantified on woody plants. We settled a 2 × 2 m quadrat on each active burrow along the same band transects stated for habitat use. On each quadrat we recorded total number of individuals per plant species and categorized them as gnawed or not gnawed. Impact on the shrub community, based on plant availability in each habitat type, was compared using a Chi-square test with contingency tables. Plant availability was calculated as the sum of gnawed and not gnawed plants present on each quadrat. We determined the Preference index (PI) (Krueger, 1972) and its Standard Error (SE) (Hobbs, 1982) to assess whether tucos select plant species when gnawing. Resources are selected if the $PI \pm 2 SE$ confidence interval falls entirely above 1; not selected when this confidence interval falls entirely below 1; and used proportionately to their availability when the confidence interval includes 1.

Diet composition was analyzed on samples collected from 12 active burrows during the wet season. Each sample was composed of 4–5 feces. We used the microhistological technique to analyze fecal contents (Dacar and Giannoni, 2001). A microhistological slide was prepared for each sample and 50 microscopic fields were systematically examined for each slide using 40× magnification. Relative frequency of occurrence of the different food items in fecal samples was estimated by dividing the number of fields containing one item by the total number of fields (Holechek and Gross, 1982). Plant items were identified using plant reference material from the study site. We performed a Kruskal–Wallis test to detect differences between life forms (i.e. trees, shrubs and grasses) and plant parts (i.e. stems, leaves and root). All Kruskal–Wallis test and PCA analyses were performed with InfoStat software version 2008.

3. Results

3.1. Habitat characterization

Results of the PCA for habitat characterization and description showed that the two first axes explain 85% of the total variability.

PC1 is characterized by a combination of the variables: bare soil, litter, tree, sub-shrub and grass cover, comprising 63% of the variability. PC2 is characterized by shrub and herb cover (21.8%). Dirt roads were related to bare soil, *Larrea* shrubland was associated with shrubs, sand dunes with herbs and grasses, and *Prosopis* woodland with trees, sub-shrubs and litter (Fig. 1). Table 1 shows the percent coverage of different vegetation life forms in the four habitat types. *Prosopis* woodland and creosote bush are the most complex habitats, whereas sand dunes and *Prosopis* woodland are the most heterogeneous (Table 1). Plant species richness was highest in sand dunes (21) followed by *Prosopis* woodland (18), *Larrea* shrubland (15) and dirt roads (14).

Results of soil hardness at different depths are depicted in Fig. 2. Soil hardness was significantly lower in sand dunes than in the other 3 habitat types at all three depths ($H = 148.95$; $p < 0.0001$); whereas all four habitats had different soil hardness only at 15 cm depth ($H = 257.65$; $p < 0.0001$).

3.2. Habitat use

Density of active burrows was different among habitat types ($H = 16.33$; $p < 0.001$). The highest density was found in sand dunes (11.2 burrows/ha), followed by *Prosopis* woodland (7.69 burrows/ha), dirt roads (7.42 burrows/ha), and *Larrea* shrubland (2.85 burrows/ha). These differences were found in feeding burrows ($H = 12.12$; $p < 0.001$) as well as in mounds ($H = 8.19$; $p < 0.05$). The number of active burrows was positively associated with habitat heterogeneity ($R^2 = 0.46$; $p < 0.001$), whereas a negative association was found with soil hardness at the three depth levels ($p < 0.005$). We found no association with habitat complexity ($R^2 = 0.06$; $p = 0.251$).

3.3. Degree of herbivory

Thirty two percent of the woody plants ($n = 288$) surveyed in all four habitats were gnawed by the tuco-tuco. We found significant differences in degree of herbivory among habitats ($\chi^2 = 7.86$, $p < 0.05$). According to availability of woody vegetation, dirt roads were the most damaged habitat (57% of shrub were gnawed), followed by *Larrea* shrubland (41% gnawed), *Prosopis* woodland (32% gnawed), and sand dunes (23% gnawed). Regression between number of active burrows and gnawed shrub density was not significant ($R^2 = 0.15$; $p = 0.066$). Gnawed species were different

Table 1

Mean and standard deviation of vegetation variables (percent cover) and diversity index of heterogeneity and complexity for each habitat type.

	Sand dunes	<i>Larrea</i> shrubland	<i>Prosopis</i> woodland	Dirt roads
Bare soil	14.51 ± 3.91	13.33 ± 3.95	9.51 ± 3.32	77.78 ± 18.84
Litter	24.40 ± 6.81	21.45 ± 3.86	20.31 ± 3.52	10.37 ± 12.61
Grasses	20.66 ± 10.04	8.67 ± 4.42	11.27 ± 5.57	3.44 ± 3.55
Herbs	4.48 ± 2.63	0.15 ± 0.25	0.65 ± 0.93	6.50 ± 8.66
Shrubs	27.74 ± 13.02	56.55 ± 3.23	38.18 ± 7.51	1.31 ± 2.05
Trees	8.21 ± 5.18	0.59 ± 1.13	20.47 ± 7.88	0.00
Complexity	0.80	0.92	0.93	0.27
Heterogeneity	0.72	0.50	0.66	0.25

depending on habitat type, with *L. divaricata* being the most damaged in Mesquite forest and dirt roads (59% and 83% respectively), *Lycium* sp. in sand dunes (36%), and *Acantholippia seriphioides* (39%) in the *Larrea* shrubland.

Of the nine species recorded at the study site (*A. seriphioides*, *Fabiana peckii*, *L. divaricata*, *Lycium* sp., *P. flexuosa*, *J. seriphioides*, *L. cuneifolia*, *G. decorticans* and *Atriplex lampa*) only *A. lampa* was not gnawed. Moreover, 83% of available woody species are represented by *Lycium* sp. (44%), *A. seriphioides* (21%) and *L. divaricata* (18%). Even though 45% of *L. divaricata* available was gnawed by tucos, as well as 35% of *Lycium* sp., and 18% of *A. seriphioides*, none of them were selected (PI confidence intervals: 0.826–2.008; 0.925–1.243; 0.075–1.053, respectively).

3.4. Diet

The diet was composed of plants (93.53%) and arthropods (6.73%). A total of 18 plant species were recorded (Table 2). The most consumed species were *Panicum urvilleanum* (25.29%), *P. flexuosa* (14.64%) and *Setaria* sp. (12.55%). Leaves were the most representative item among plant parts (89.51%) ($\chi^2 = 399.67$; $p < 0.0001$) (Fig. 3), and grasses were the dominant life form (79%).

4. Discussion and conclusions

The feedback between organisms and their environment is of great relevance to the understanding of ecosystem functioning. The strength of this association could be higher in arid lands where resource availability is a limiting factor (Whitford, 2002). For the tuco-tuco, *C. mendocinus*, we found that individuals mainly use habitats with high heterogeneity, soft soils, high plant species richness and the highest grass cover. Regarding herbivory on woody shrubs, the more impacted habitats were those with low heterogeneity, hard soils and low vegetation cover. Additionally, tucos feed mostly on leaves of grasses which are patchily distributed along the complex matrix of the Monte desert. These results suggest that *C. mendocinus* takes advantage of this edaphic and vegetation complexity by making a differential use of its environment, possibly according to food supply and soil hardness.

The tuco-tuco occurs over the whole lowland habitat matrix, although its highest activity was recorded in sand dune habitats with soft soils. Soil hardness has been considered a limiting factor for the distribution of some fossorial rodents (Nevo, 1979; Giannoni et al., 1996). Previous studies on the sand-dwelling tuco-tuco of the Atlantic coast (*Ctenomys talarum*) showed that the energetic cost of digging is lower in soft than in hard soils (Luna and Antinuchi, 2006). Sandy habitats not only provide food resources but also facilitate the occurrence of ventilation fluxes inside tuco-tuco burrows (Comparatore et al., 1991; Busch et al., 2000). Our findings of higher activity on sand dunes could imply higher density of tuco-tucos or larger and more complex

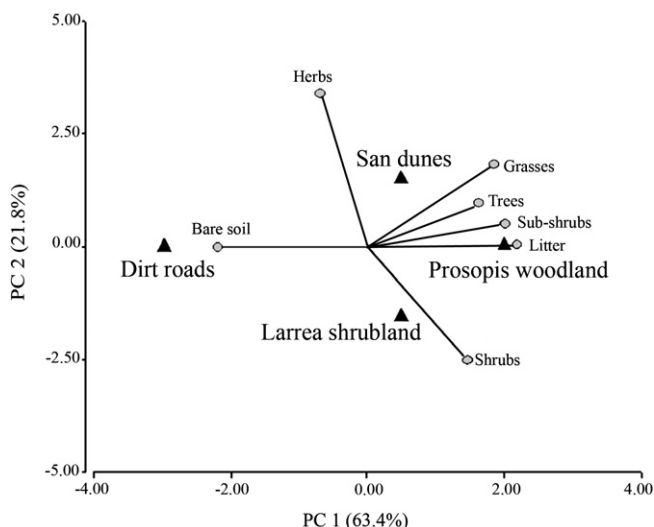


Fig. 1. : Result from the PCA biplot of habitat types and heterogeneity variables.

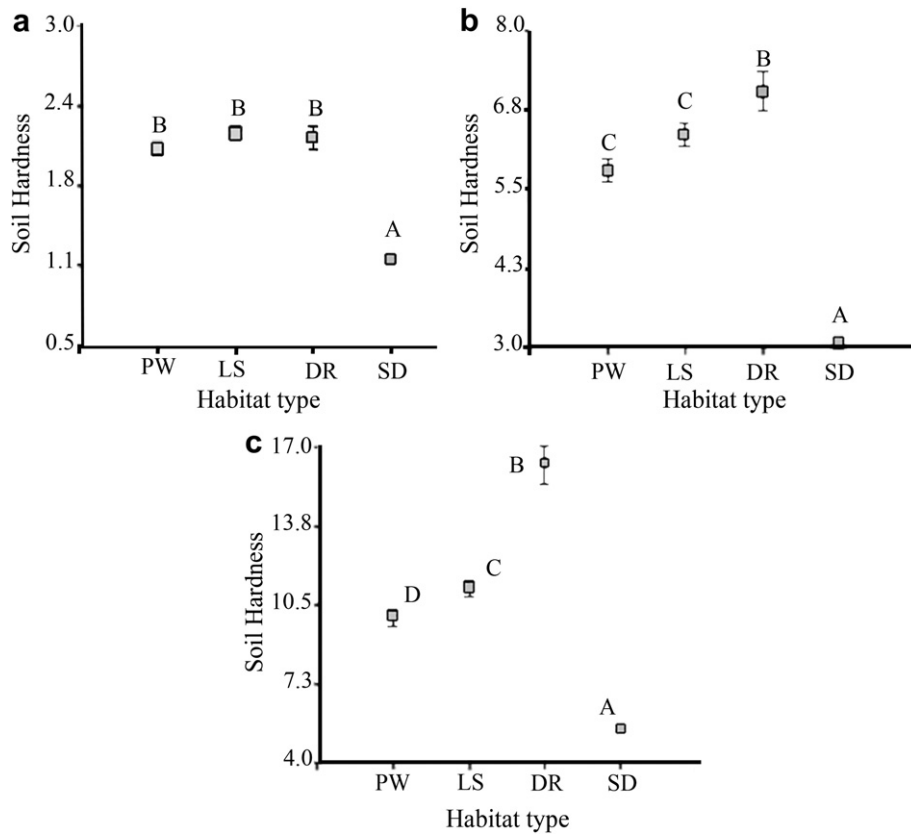


Fig. 2. Soil hardness for four habitat types at different depths: a) 5 cm, b) 10 cm, c) 15 cm. PW: *Prosopis* woodland; LS: *Larrea* shrubland; SD: sand dune; DR: dirt roads.

burrowing systems (caused by a higher digging activity), as in the case of pocket gophers (Romañach et al., 2005).

Subterranean rodents seem to be partitioned into three major dietary groups: the Bathyergidae and Spalacinae, which mainly feed on underground organs of plants (Sumner et al., 2007; Zhang,

2007), the Geomyidae with a generalist diet (Reichman, 2007), and the Ctenomyidae with their basic diet made up of aerial plant parts (Madoery, 1993). The mendocino tuco-tuco is a herbivorous rodent whose diet is mainly composed of leaves of grasses of the genus *Panicum*. This folivorous strategy seems to be well maintained among populations of this species (e.g. Andean foothill, Madoery, 1993, desert lowland, this study), and among other species of the genus (*C. talarum*, del Valle et al., 2001; *Ctenomys pearsoni*, Altuna et al., 1999; *Ctenomys australis*, Comparatore et al., 1995). The presence of a small proportion of arthropods in the diet of *C. mendocinus* could act as a protein supplement in times of food shortage and be related to the physiological mechanism for keeping a positive water balance (Diaz and Cortes, 2003).

The degree of herbivory on *Larrea* shrublands varies between 9 and 39 percent at different sites of the Monte desert (Borrueal et al., 1998; Campos et al., 2001; Tort et al., 2004). Nevertheless, our results show higher values for this habitat type (41%). We also found that the impact (e.g. damage) of tuco-tucos on vegetation varies according to habitat type. Dirt roads are the habitats with the highest degree of herbivory (57%), whereas sand dunes, despite having the highest tuco-tuco activity (number of active burrows), have the lowest level of herbivory (23%). This pattern could be reflecting a different availability of plant life forms. Where grasses are less abundant, the tuco-tuco also feeds on shrub forms. This could explain why dirt roads had the highest number of gnawed shrubs and a small number of active burrows.

Despite the intense gnawing on *L. divaricata* (45%), its presence on the diet is insignificant (0.19%). A possible explanation is that tuco-tucos do not feed on *Larrea* in the wet season, because grass supply is remarkably larger compared to the dry season (Roig, 1971). Some authors suggest that *Larrea* stems gnawed by tuco-tucos could be used to construct their nest chambers (Rosi et al.,

Table 2
Plant species present in the diet of *C. mendocinus*.

Family	Species	Percentage
Poaceae	<i>Bromus brevis</i>	0.95
	<i>Chloris castilloniana</i>	3.42
	<i>Digitaria Californica</i>	7.42
	<i>Panicum urvilleanum</i>	25.29
	<i>Pappophorum</i> sp.	4.56
	<i>Poa lanuginosa</i>	0.38
	<i>Setaria</i> sp.	12.55
	<i>Stipa ichu</i>	1.71
	<i>Undetermined grasses</i>	2.09
	Total grasses	58.37
	Asteraceae	<i>Hyalys argentea</i>
Malvaceae	<i>Sphaeralcea miniata</i>	5.89
	Total herbs	6.08
Verbenaceae	<i>Acantholippia seriphoides</i>	2.66
Verbenaceae	<i>Aloysia gratissima</i>	2.09
Capparaceae	<i>Capparis atamisquea</i>	4.94
Solanaceae	<i>Fabiana peckii</i>	0.19
Verbenaceae	<i>Junellia aspera</i>	1.14
Verbenaceae	<i>Junellia seriphoides</i>	1.52
Zygophyllaceae	<i>Larrea</i> sp.	0.19
Solanaceae	<i>Lycium</i> sp.	6.08
	Total shrubs	18.82
Fabaceae	<i>Prosopis flexuosa</i>	14.64
	Total trees	14.64
	Undetermined roots	2.09

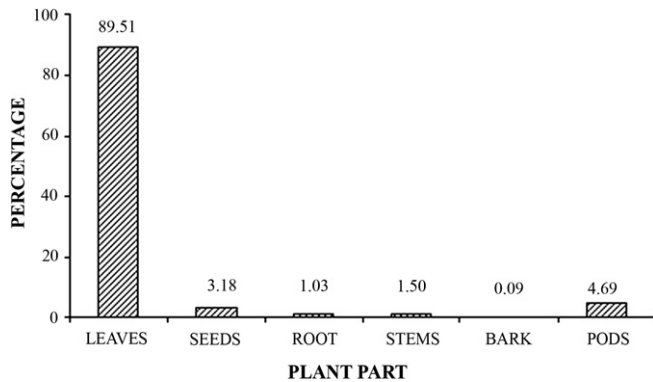


Fig. 3. Percentage of plant parts present in the diet of *C. mendocinus*.

2002; Cuello, pers. com.). Nevertheless, this hypothesis has not been corroborated so far. Another explanation is that *Larrea* could be used as a water supplement in the dry season, as seen in jack-rabbits of the Chihuahuan desert (Steinberger and Whitford, 1983). Furthermore, despite not having been tested, we suggest that tuco gnaw on shrubs to wear away their continuously growing teeth.

Life underground imposes general constrains for most subterranean rodent species (Nevo, 1979; Lacey et al., 2000), with below ground habitat traits being the focus of most researches. However, our results suggest that both above and belowground environments play important roles in the occurrence of fossorial rodents. Above ground use at macrohabitat scale could be driven by food supply, in this case by grass abundance (Busch et al., 2000; Romañach et al., 2005), and/or by availability of potential refuges against aerial predators favored by a higher habitat heterogeneity (Ebensperger and Hurtado, 2005; Taraborelli et al., 2008). Underground habitat use seems to be driven, by the relationship between digging cost and soil hardness (Vleck, 1981; Romañach et al., 2005; Luna and Antinuchi, 2006), shown in *C. mendocinus* by a higher activity on sandy soils. Ongoing research through capture–mark–recapture methods could provide a better understanding of factors regulating the abundance and occurrence of the mendocino tuco-tuco and its potential role as an ecosystem engineer in the lowland Monte desert.

Acknowledgements

We appreciate the helpful comments of Natalia Borrue, Verónica Chillo, Solana Tabeni and Pablo Cuello on earlier versions of the manuscript. We thank Solana Tabeni, Benjamin Bender, Claudia Campos, Stella Giannoni and Roland Brandl for their helpful suggestions on the methodological design. Nelly Horak assisted us with the English translation. Thanks to three anonymous reviewers for their valuable suggestions and critical reading of the manuscript. This research was partially supported by research grants (SECyT – PICT 11778; and CONICET – PIP 5944) to RAO.

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