Z. Säugetierkunde **65** (2000) 172–182

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil

By Ana I. Malizia, M. J. Kittlein, and Cristina Busch

Laboratorio de Ecofisiología, Departamento de Biología, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

Receipt of Ms. 31. 07. 1998
Acceptance of Ms. 14. 09. 1999

Abstract

The influence of the subterranean herbivorous rodent *Ctenomys talarum* (tuco-tuco) on vegetation and soil was evaluated in a coastal grassland. Plant species composition, dry plant biomass, soil pH, moisture, and nutrient content (N, P, Na, K, Mg, and Ca) were compared between areas with and without the influence of tuco-tucos. *C. talarum* apparently does not affect either plant species diversity or plant species richness, but modifies plant species composition at sites contiguous to burrows, where forbs occur more frequently than at sites without burrows. Abundance of most common grass and forb species, soil nutrient content, pH, and moisture were modified by *C. talarum*. Nitrogen, phosphorous, sodium, potassium, and magnesium had higher concentrations in areas with *C. talarum*, whereas calcium showed the converse. Soil pH and percent moisture were lower in areas with burrows of *C. talarum*.

Key words: *Ctenomys talarum*, coastal grasslands, herbivores, soil disturbance

Introduction

Subterranean rodents of the genus *Ctenomys* (tuco-tucos) occur broadly in South America. They are distributed throughout Argentina, southern Brazil, and areas of Bolivia, Chile, Paraguay, Perú, and Uruguay (Woods 1984). All species are strictly herbivorous that excavate and inhabit extensive burrow systems and deposit the tailings as mounds on the soil surface or in abandoned tunnels.

Ctenomys talarum is a long-lived herbivore that inhabits a secure, permanently sealed burrow system. Although most of its activities are restricted to its tunnel system, it makes brief surface excursions for collecting plant material. Diet analysis showed that individuals consume almost all plant species available in the field. However, they strongly prefer some species. Contrary to the prevalent consumption of roots reported for other fossorial rodents, *Ctenomys* species eat mainly above-ground plant parts (Comparatore et al. 1995).

This species has a social system with individual territoriality; both sexes and all ages (except preweaned young that occupy their mother's burrow system) are sedentary and maintain exclusive territories (Busch et al. 1989). Individuals maintain and expand extensive tunnel systems, resulting in the deposition of soil mounds on the surface.

Subterranean rodents may have important effects on vegetation and soil due principally to both burrowing and feeding activities, which may strongly modify the structure

0044-3468/00/65/03–172 $12.00/0

and dynamics of many ecosystems (ANDERSEN and MACMAHON 1981; CONTRERAS and GUTIÉRREZ 1991; HUNTLY and INOUYE 1988; REICHMAN et al. 1982). Burrowing activities exert a major impact on soil structure and nutrient availability, affecting both succession and abundance of plants (ANDERSEN 1987; INOUYE et al. 1987; TILMAN 1983).

Mounds of fossorial rodents may cover 5–15% of the soil surface (TURNER et al. 1983), burying existing vegetation. However, mounds also can serve as important germination sites (PLATT 1975; SCHAAL and LEVERICH 1982), creating open spaces for colonizer species that are competitively inferior in undisturbed sites. Repeated soil disturbance may be necessary for the maintenance of some plant communities (WHITE 1979). Although plant community complexity may be similar on and off animal-generated soil disturbanees, the species composition of the community may not be (PLATT 1975). Over the long term, mining and translocation of soil can modify topography, creating large-scale patterns of Mima mounds, one of the most remarkable effects of animal activity on landscape formation (COX and SCHEFFER 1991; MIELKE 1977).

Effects of subterranean rodents on vegetation are difficult to assess experimentally, presumably because manipulating the presence of these animals is logistically much more difficult than performing manipulative experiments with above-ground species. Where manipulative experimentation is not achievable, one way to overcome this shortcoming is to conduct mensurative experiments (sensu HURLBERT 1984) having an appropriate sampling design.

The present study aims to quantify the impact of tuco-tucos on vegetation by comparing plant diversity and biomass in areas with and without burrows of *Ctenomys talarum*. In addition, the present study reports about the influence of tuco-tucos on soil nutrient characteristics, as well as on the extent of burrowing-related disturbances as compared to undisturbed areas.

Material and methods

Field work was conducted at Mar Chiquita (37°41′S, 57°23′W), 40 km north of Mar del Plata, Buenos Aires Province, Argentina. The area is a natural coastal grassland described by CABRERA (1941). Sampling was performed at the end of the growing season (December 1994), when plant productivity is greatest, thus enhancing the chance of detecting the effects of tuco-tucos on soil and vegetation characteristics.

To evaluate the impact of *Ctenomys talarum* on vegetation and soil, ten 10- by 10- m plots were established in areas where fresh mounds of tuco-tuco were found. In addition, ten equally sized control plots were established in areas where *C. talarum* activity was not observed. No obvious differences in vegetation and topography were apparent between these areas, other than the presence or absence of burrows of *Ctenomys*.

In each control plot, 5 vegetation samples were taken by assigning random X-Y coordinates, hereafter referred to as CONTROL samples. In plots where activity of tuco-tucos was observed, we first identified all fresh mounds within a plot, and the burrow system associated to each mound was probed with a thin rod to locate branches over which samples could be taken. When a sample was taken, the underlying burrow was obvious so it was possible to verify that the sample actually was taken over a burrow. A total of 12 active burrow systems was identified. Three vegetation samples, ≅ 50 cm apart, were then taken directly above each burrow system (BURROW samples). Plant abundance and species composition in these samples were considered to illustrate the direct impact exerted by tuco-tucos on vegetation. Three additional samples (INTER-BURROW samples) were taken ≅ 1 m adjacent to each BURROW sample.

In addition, 5 vegetation samples (as determined by randomly chosen X-Y coordinates) also were taken in each tuco-tuco plot (RANDOM samples). At the time they were taken, RANDOM and INTER-BURROW samples clearly were not over old burrow systems. Comparisons between RANDOM and INTER-BURROW samples were intended to assess if tuco-tuco forage in the most productive areas.

Vegetation was sampled with vertical cores, 20 cm in diameter and 30 cm deep, which is the depth at which tuco-tucos are active. Samples included above- and below-ground vegetation and they were sieved to exclude most sand around plant roots, placed in plastic bags, labeled and transported to the lab. Plant fragments from each sample were identified to the species level, then separated into above- and below-ground fractions. Above-ground standing plant fractions were further classified into live and dead material. Unidentified roots and litter were also sepeated. All portions of a sample were bagged individually and oven-dried for 48 h at 60 °C, and then weighed to the nearest centigram.

Numbers and measurements (length, width, and height) of fresh mounds (1–2 days old) were recorded, and the surface area covered by the mounds in each plot was calculated as the area of an ellipse with the major axis equal to mound length and the minor axis equal to mound width. Volumes of mounds were calculated assuming that they had the shape of elliptical cones. These records would allow estimation of the average daily rate of excavation per ha, as well as the impact of tuco-tucos on vegetation by plant burial.

In areas where activities of tuco-tucos were observed, soil samples of approximately 200 ml were taken directly over each mound, whereas five randomly selected samples were taken in plots without tuco-tucos. Moisture, pH, N, Ca, Mg, Na, K, and P contents of the soil were determined. Nitrogen was determined by Kjeldahl, extractable P was determined colorimetrically, and Ca, Mg, Na, and K were determined by atomic absorption spectrophotometry.

Differences in mean dry biomass (g/sample) and Shannon-Wiener diversity index among groups of vegetation samples were statistically assessed by Kruskal-Wallis tests and Tukey-type multiple comparisons. Nutrient content of soil samples from plots with and without tuco-tucos was compared by Mann-Whitney U tests (ZAR 1984).

Similarity in plant species composition between sample categories with and without tuco-tucos (RANDOM, INTER-BURROW, BURROW, and CONTROL, respectively) was measured with Margalef's similarity index ($M_{ij} = \frac{a(a+b+c+d)}{(a+b)(a+c)}$; DIGBY and KEMPTON 1987), where a is the number of species common to both sample categories, b is the number of species present in sample category i but not present in sample category j, c is the number of species present in sample category j but not present in sample category i, and d is the number of species not present either in sample category i or in sample category j. This index measures similarity taking into account both joint occurrences and absences of species and lies between 0 and s/a, where s is the total number of species present in both sample categories.

The significance of observed similarity between sample categories was assessed by generating distributions of the similarity index in a computer, assigning randomly plant species to each sample with a probability equal to that species' frequency of occurrence in all samples. The presence or absence of each plant species in randomly generated samples was recorded for each sample category and Margalef's similarity index between sample categories was computed 5 000 times. Three distributions of the similarity index were thus generated: one for the similarity index between sample categories both with 50 samples (CONTROL vs. RANDOM), one for sample categories with 50 and 36 samples each (CONTROL vs. INTER-BURROW and BURROW, and RANDOM vs. INTER-BURROW and BURROW), and the other for sample categories both with 36 samples (INTER-BURROW vs. BURROW). If the observed values of similarity between sample categories were lower than the 5 percentile of the corresponding distribution these sample categories were considered significantly dissimilar at $\alpha = 0.05$. These procedures were programmed in Visual Basic for Excel® 5.0 (Microsoft Corp., Redmond, WA).

Results

A total of 20 plant species (5 grasses; 15 forbs) was recorded in all samples taken during this study. Grasses constituted 85% and forbs 15% in dry weight of all sampled vegetation. The grasses *Panicum racemosum*, *Poa lanuginosa*, *Androtrichum trigynum* and the forbs *Baccharis genistifolia*, *Hydrocotyle bonariensis*, *Margyricarpus pinnatus* and *Solidago chilensis* were the most abundant plant species (Tab. 1).

There were no significant differences in plant species diversity (Kruskal-Wallis statistic = 0.848, P = 0.83) and plant species richness (Kruskal-Wallis statistic = 1.700, P = 0.64)

Table 1. Occurence (% frequency) and abundance (g/sample) of plant species in areas with and without influence of tuco-tucos. tr indicates abundances less than 0.01 g/sample.

	Without Tuco-tucos		With Tuco-tucos	
	g/sample	% Freq.	g/sample	% Freq.
Grasses				
Androtrichum trigynum	1.96	28.00	4.42	50.82
Distichlis scoparia	–	–	tr	1.64
Oenothera mollissima	0.01	6.00	0.01	4.10
Panicum racemosum	10.23	100.00	5.21	83.61
Poa lanuginosa	1.26	92.00	4.89	92.62
Forbs				
Achyrocline satureioides	0.04	4.00	–	–
Adesmia incana	0.05	4.00	tr	0.82
Ambrosia tenuifolia	0.04	10.00	0.03	8.20
Baccharis genistifolia	–	–	0.71	12.30
Conyza blakei	–	–	0.15	3.28
Daucus pusillus	–	–	0.01	1.64
Gamochaeta sp	tr	8.00	tr	1.64
Hydrocotyle bonariensis	0.16	24.00	0.66	44.26
Margyricarpus pinnatus	2.64	42.00	0.26	13.93
Medicago lupulina	0.15	14.00	0.08	12.30
Medicago minima	tr	2.00	tr	2,46
Melilotus officinalis	0.01	4.00	0.09	7.38
Polygala cyparissias	0.01	2.00	–	–
Solidago chilensis	0.11	22.00	0.25	31.97
Tessaria absinthioides	–	–	tr	0.82

Table 2. Comparisons of species richness (S), species diversity (H′), and dry biomass of herbaceous vegetation in absolute values (g/sample), in areas with and without burrows of *Ctenomys talarum*. H′ values for one-way nonparametric ANOVAs (Kruskal-Wallis test). *P < 0.05. **P < 0.01. Shared lowercase letters among sites with and without tuco-tucos within vegetation components indicate statistically indistinguishable values at P = 0.05 for nonparametric Tukey-type muliple comparisons.

	Without Tuco-tucos	With Tuco-tucos				
	CONTROL	RANDOM	INTER-BURROW	BURROW	Kruskal-Wallis statistic	
Number of samples	50	50	36	36		
Species diversity (H′)	1.22	1.50	1.60	1.53	0.84	NS
Species richness (S)	15	15	15	14	1.70	NS
Total Biomass	26.60 ± 16.04 a	33.69 ± 16.09 bc	35.84 ± 21.2 ab	35.20 ± 19.6 ab	8.62	*
Live	18.97 ± 12.97	16.53 ± 8.93	20.34 ± 12.61	17.94 ± 10.64	1.85	NS
Dead	7.64 ± 7.38 a	17.16 ± 10.48 b	15.50 ± 11.97 b	17.26 ± 11.79 b	29.98	**
Above ground	7.19 ± 5.84	5.58 ± 4.84	8.87 ± 7.29	7.37 ± 6.82	7.00	NS
Live	4.00 ± 4.57 ab	2.73 ± 2.82 a	5.32 ± 4.82 bc	3.41 ± 2.69 ab	10.75	*
Dead	3.19 ± 3.30	2.85 ± 3.64	3.55 ± 4.51	3.96 ± 5.97	3.38	NS
Underground	14.97 ± 9.79	13.8 ± 7.4	15.02 ± 10.58	14.53 ± 9.73	0.27	NS
Litter	4.44 ± 6.22 a	14.31 ± 11.09 b	11.89 ± 12.82 b	13.25 ± 12.44 b	24.48	**
Unidentified roots	5.49 ± 6.18	4.43 ± 3.26	4.5 ± 7.37	5.25 ± 6.29	3.04	NS

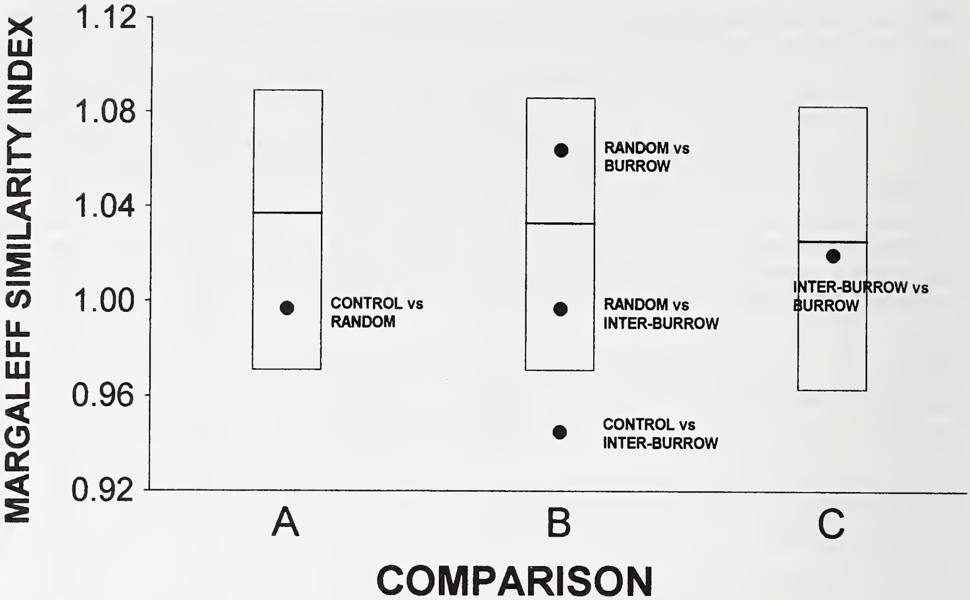

Fig. 1. Margalef's similarity index for plant species composition between sample categories with (BURROW, INTER-BURROW, RANDOM) and without burrows (CONTROL) of tuco-tucos. Top horizontal lines of boxes represent upper 2.5 percentiles of the index null distribution. The center and lower horizontal lines represent the median and the lower 2.5 percentile, respectively. A) Comparison of observed similarity indices between sample categories with 50 vegetation samples against the null distribution; B) between sample categories with 50 and 36 vegetation samples; and C) between sample categories both with 36 vegetation samples. Number of samples used to generate null distributions in each comparison was equal to that actually taken in the field.

between areas with and without tuco-tucos (Tab. 2). Although these indices suggest an overall similarity in plant community structure between areas, the composition of plant species differed substantially, principally owing to differences in the occurrence of forb species. *Baccharis genistifolia*, *Conyza blakei*, *Daucus pusillus*, *Tessaria absinthiodes* (forbs), and *Distichlis scoparia* (a grass) occurred only in samples from plots with tuco-tucos while *Achyrocline satureioides* and *Polygala cyparissias* (forbs) were recorded only in samples from sites without tuco-tucos. Differences in plant species composition were most marked between CONTROL samples and INTER-BURROW samples (Margalef's similarity index 0.945, $P = 0.012$); the remaining comparisons did not show significant differences (Fig. 1).

Several significant differences in plant biomass between areas with and without tuco-tucos were observed (Tab. 2). Comparisons among CONTROL, RANDOM, and INTER-BURROW samples indicated that tuco-tucos did not forage in areas with significantly more plant biomass. Litter was significantly higher in areas with tuco-tucos, resulting in increased total plant biomass and total dead material as compared to samples from areas without tuco-tucos. Above-ground live material was highest in INTER-BURROW samples, which differed significantly from RANDOM samples.

Abundances of total grasses and forbs did not differ between areas with and without tuco-tucos. Although individual species of each group differed significantly between areas (Kruskal-Wallis test, $P < 0.05$), some showed opposing directions in abundance, yielding no consistent pattern of change between areas.

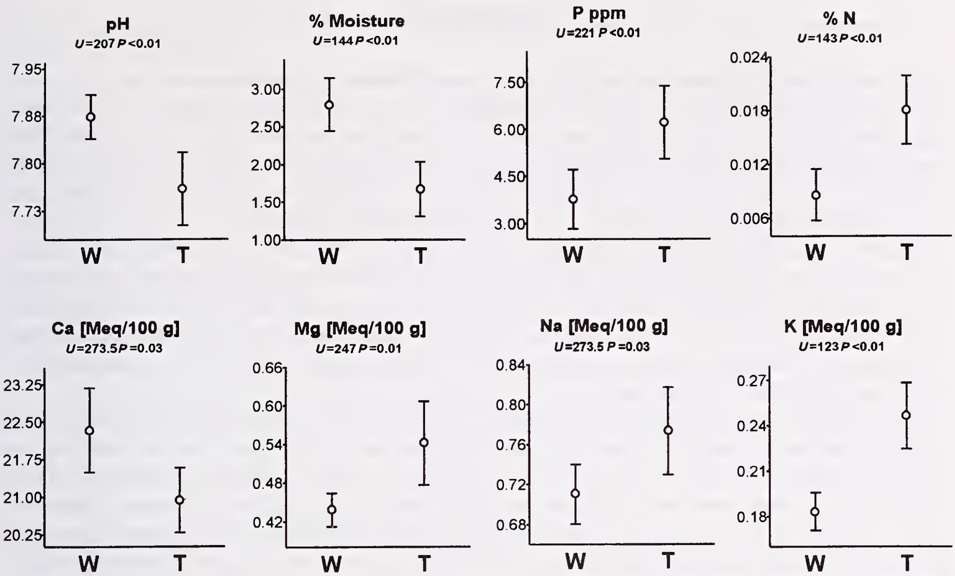

Fig. 2. Comparisons of mean (± 1.96 SE) pH, % moisture and soil nutrient concentrations in soil samples from sites with (T) and without (W) burrows of *Ctenomys talarum*.

The two most frequent grasses in the study area, *Panicum racemosum* and *Poa lanuginosa*, clearly illustrates this situation. *Poa lanuginosa* was more abundant where tuco-tucos occurred, whereas *Panicum racemosum* was more abundant in areas without burrows of tuco-tucos.

The most abundant forb in the area, *Margyricarpus pinnatus*, was considerably less abundant where tuco-tucos occurred. Conversely, *Baccharis genistifolia* and *Hydrocotyle bonariensis*, showed increased biomass in areas with tuco-tucos.

In areas where activities of tuco-tucos were observed 23 fresh mounds were measured, giving an estimate of mound coverage of 43.5 m^2/ha of soil surface. If we assume that this is the initial influence of mounds, they could have reduced the above-ground plant biomass in the field only by as much as 0.43%. Taking into account that mean burrow length and mean tunnel diameter for *Ctenomys talarum* are 14 m and 0.08 m, respectively (Antinuchi and Busch 1992), the total area covered by underlying burrows is 737 m^2/ha (7.4% of total area). Volume of excavated soil per ha was 4.7 m^3/ha; estimated from mean burrow volume (0.07 m^3) and mean animal density (approx. 65 ind/ha; Busch et al. 1989). Thirty percent (1.4 m^3/ha) of excavated soil remained as mounds on the ground surface. Multiplying mound soil volume by soil density (2,750 kg/m^3) gives us 3,824 kg/ha of soil deposited in mounds in 15 days (the span of the sampling period), which represents an excavation rate of 91,785 kg/ha/yr.

Soil nutrient concentration differed between areas with and without tuco-tucos (Fig. 2). Phosphorous (P), Nitrogen (N), Magnesium (Mg), Sodium (Na), and Potassium (K) had significantly higher concentrations in areas with tuco-tucos than in areas without tuco-tucos, whereas Calcium (Ca) showed the converse. Both soil pH and moisture content were significantly lower where tuco-tucos occurred.

Discussion

Our results show that tuco-tucos exert substantial effects on vegetation and soil. In reference to the effects of tuco-tucos on vegetation, they reduce the abundance of the most prevalent species of grasses and forbs, thereby increasing the occurrence of typically less common species from both plant groups. The differential occurrence of forb species, mainly in inter-burrow areas (INTER-BURROW samples), suggests that a slightly distinct plant community is maintained by the activities of tuco-tucos.

Zenuto and Busch (1995) found that the impact of *Ctenomys australis* on a dune grassland was to increase the abundance of early colonizers such as *Panicum racemosum* and *Hydrocotyle bonariensis.* Effects of *C. talarum* documented here differ with regard to *P. racemosum*, possibly due to differences in the successional stage of plant communities at both study sites. The plant community studied here represents a later successional stage than that impacted by *C. australis.*

Studies of North American pocket gophers (Geomyidae) have consistently concluded that burrows and mounds of these animals generate a notable reduction in overlying vegetation, enhancing plant biomass directly adjacent to the distubance (Reichman et al. 1993). Our results show that changes in plant species composition are most marked in areas adjacent to the disturbance produced by mounds and burrows of *Ctenomys talarum*, yet plant biomass in these areas did not differ from that in areas directly over burrows or from that in areas without burrows.

Generally, forbs would suffer greater impact from a fossorial herbivore than grasses because of the differences in root configuration (Reichman and Smith 1985). However, most of the difference in plant species composition noted above was made by forb species, which occurred most frequently adjacent to disturbed areas. Vegetation adjacent to the burrow could be stimulated by altering local soil-water relations, or by being freed from competition by the depletion of vegetation directly over the burrows (Reichman and Smith 1985). Rather than increasing the growth of grass species, the disturbance generated by mounds and burrows of *C. talarum* apparently promoted a replacement by forbs. The loss of roots in burrows and the burying of vegetation by mounds produce small-scale gaps in the grassland. Hence, physical disruption of the soil by digging activities, breaks up stable aggregates of soil particles, thus increasing mineralization rates. Thus, the combined effects of reduced competition for resources and increased mineralization rates (along with water runoff from mounds, decomposition under mounds, and urine and fecal deposits within burrows) may be responsible for stimulating plant biomass and changing plant species composition directly adjacent to the disturbances. In addition, roots of grasses have an intricate configuration that, under certain soil conditions, may prevent settlement of forb propagules, therefore monopolizing the local grassland. If burrow construction causes the removal of roots of grasses, forb species would have a higher probability of settlement in areas with increased nutrient content adjacent to the burrows.

We found no evidence that *Ctenomys talarum* choose to forage in portions of the field that contain more plant material than unused areas, unlike what was generally found in pocket gophers (Reichman and Smith 1985).

In reference to the effects of burrowing mammals on soils, the most obvious one is illustrated by the deposition of soil on the surface that results in mound formation that bury existing vegetation. The magnitude of this primary effect of subterranean rodents varies greatly; from 8% (Grant et al. 1980) to 28% (Reichman and Jarvis 1989) of surface area covered by mounds. Our estimate of 0.43% suggests that the effect of *C. talarum* is relatively low. However, the highest effect reported by Reichman and Jarvis (1989) for three species of Bathyergids contains miscalculations, that resulted from equating one ha. to 1,000 m^2 instead of 10,000 m^2. The correct estimate for this study is 2.8% of surface area covered by mounds (2.4% for *Bathyergus suillus*, 0.28% for *Geory-*

chus capensis, and 0.12% for *Cryptomys hottentotus*), which now comes closer to the estimate for *C. talarum*.

The rate of soil excavation for different species of subterranean rodents varies by as much as two orders of magnitude from 0.8 ton/ha/yr (Mielke 1977) to 105 ton/ha/yr (Cox 1990; Miller 1957). The excavation rate for *C. talarum* at Mar Chiquita (91.78 ton/ha/yr) ranks in the upper 28% of 12 reports (Buechener 1942; Cox 1990; Cox et al. 1995; Ellison 1946; Grant et al. 1980; Mielke 1977; Miller 1957; Richens 1966; Spencer et al. 1985). It seems to be very unlikely that the above rate of mound formation, estimated for such a short period, applies uniformly throughout the year. Nevertheless, in our calculation we did not consider backfilling of tunnels, which for some pocket gophers may involve 86% of excavated soil (Andersen 1988, 1990). Hence, the estimation of the excavation rate for *C. talarum* can be considered rather conservative.

Tuco-tucos provide an example of the importance of non-consumptive behaviour in altering ecosystem structure. Most obviously, the physical structure of the soil as well as the structure of the above-ground plant community are modified, but the nutrient status of the soil also may be affected, as reported by Grant et al. (1980) for pocket gophers. Formation of new mounds by tuco-tucos increased the levels of P, Na, K, and Mg. Nitrogen also increased significantly in areas with tuco-tucos. On the other hand, Ca, pH, and moisture content of soil were higher in undisturbed areas.

Soil moisture may be affected by tunnel construction by tuco-tucos, since burrowing changes soil characteristics, e.g. by creating spaces in the soil matrix, decreasing soil moisture content by aeration that promotes evaporation. However, in areas characterized by harder soils, holes in the surface makes it easier for the water to penetrate the ground during dry seasons, which counteracts losses by evaporation and run-off.

Like other burrowing mammals, tuco-tucos may alter the habitat near burrows either indirectly by moving, mixing, and bringing soil to the surface from lower horizons, or directly by feeding, by burying vegetation, or by deposition of feces and urine in the vicinity of burrow systems, thus creating patches of high nutrient availability. Furthermore, the relative increase of nutrients in tuco-tucos mounds may also occur because of the presence of a litter layer next to the mounds. This layer is important in holding nutrients near the surface, serving as a nutrient trap. Hence, movements of chemical subtances from deeper to upper soil layers may add to the nutrients already present in surface soil to yield a higher total nutrient content near tuco-tucos mounds. This additive effect of nutrients in combination with the distribution of litter may enhance the area on the perimeter of mounds as microsites for plant germination and growth. On the other hand, the presence of an acidic litter layer off the mounds may be responsible for the lower soil pH recorded in these areas.

Differences in Na concentration between areas with and without tuco-tucos may be explained by the influence of the marine breeze on the study area, which was located a few hundred meters from the sea-shore. Greater quantities of Na found in soils with tuco-tucos mounds may be thus related to their external morphology, since their dome-shaped surface would increase the deposition of Na through salt spray from the sea.

Several studies have examined the effects of burrowing organisms on nutrient availability and have reported increased levels of cations in the surface soil as a result of soil moving activities. Nevertheless, the specific cations affected have not always been the same. For pocket gophers, mound soil frequently differs from that of surrounding undisturbed soil in the levels of various soil nutrients, including N, P, K, Na, Ca, which may be significantly higher (Abaturov 1972; Andersen and MacMahon 1985; Grant and Mc Bryer 1981; Hole 1981; Koide et al. 1987; Laycock and Richardson 1975; Mielke 1977; Zinnel 1988) or lower (Huntly and Inouye 1988; Inouye et al. 1987; Koide et al. 1987; Mc Donough 1974; Spencer et al. 1985) in comparison with undisturbed soil. For other burrowing mammals, soil near burrows did not differ from mound soil (Contreras et al. 1993; Swihart 1991). The inconsistency of these results may be due primarily to regional differences in soil types.

Our evidence suggests that the influence of tuco-tucos is certainly not trivial, and that at high densities such as those found in Magdalena, Argentina, (Pearson et al. 1968) where density of tuco-tucos reaches 203 individuals/ha, these animals may have a profound impact on vegetation and soil.

Acknowledgements

This research was supported by grants from Universidad Nacional de Mar del Plata and from the International Foundation for Science, Sweden (C/1706-1 and C/1707-1). L. Ricci kindly supervised and helped with the identification and processing of plants. We appreciate the assistance of an anonymous reviewer who greatly improved this study and wrote the German abstract. We wish to express our gratitude to our colleagues at Laboratorio de Ecofisiología for their constant interest and encouragement.

Zusammenfassung

Einfluß des unterirdischen herbivoren Nagers Ctenomys talarum auf Vegetation und Boden

Der Einfluß des unterirdisch lebenden und herbivoren Nagers *Ctenomys talarum* (Tuco-Tuco) auf die Vegetation und den Boden wurde auf einer Küstenwiese in Argentinien untersucht. Das Artenspektrum der Pflanzen, das Trockengewicht der Pflanzenbiomasse, Boden-pH, Feuchtigkeit und Nährstoffgehalt des Bodens (N, P, Na, K, Mg und Ca) wurden dazu zwischen Gebieten mit und ohne Besiedlung durch Tuco-Tucos verglichen. Offensichtlich beeinflußt die Besiedlung weder die Artendiversität noch den Artenreichtum der Pflanzengesellschaft. Dagegen ändert sich die Artenzusammensetzung, da in der Umgebung der Baue ein höherer Anteil krautiger Pflanzen festgestellt wurde als an Stellen ohne Baue. Ebenso wurden die Abundanzen der häufigsten Gräser und Kräuter, der Nährstoffgehalt, sowie Boden-pH und Feuchtigkeit durch die Aktivität von *C. talarum* beeinflußt. Die Stickstoff-, Phosphor-, Natrium-, Kalium- und Magnesiumgehalte lagen in Gebieten mit Tuco-Tuco-Besiedlung höher, während der Kalziumgehalt erniedrigt war. Boden-pH und relative Feuchtigkeit waren in Gebieten mit Bauen geringer.

Literature

Abaturov, B. D. (1972): The role of burrowing animals in the transport of mineral substances in the soil. Pedobiologia **12**, 261–266.

Andersen, D. C. (1987): Belowground herbivory in natural communities: a review emphasizing fossorial animals. Quart. Rev. Biol. **62**, 261–286.

Andersen, D. C. (1988): Tunnel-construction methods and foraging path of a fossorial herbivore, *Geomys bursarius.* J. Mammalogy **69**, 565–582.

Andersen, D. C. (1990): Search path of a fossorial herbivore, *Geomys bursarius.* J. Marnmalogy **71**, 177–187.

Andersen, D. C.; MacMahon, J. A. (1981): Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides.* Ecol. Monogr. **51**, 179–202.

– (1985): Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides.* Amer. Midl. Nat. **114**, 62–69.

Antinuchi, C. D.; Busch, C. (1992): Burrow structure in the subterranean rodent *Ctenomys talarum.* Z. Säugetierkunde **57**, 163–168.

Buechener, N. K. (1942): Interrelationships between the pocket gopher and land use. J. Mammalogy **3**, 346–348.

Busch, C.; Malizia, A. I.; Scaglia, O. A.; Reig, O. A. (1989): Spatial distribution and attributes of a population of *Ctenomys talarum* (Rodentia: Octodontidae). J. Mammalogy **70**, 204–208.

Cabrera, A. L. (1941): Las comunidades vegetales de las dunas costeras de la Provincia de Buenos Aires. Publicaciones Técnicas Dirección de Agricultura, Ganadería e Industria. Tomo 1, No 2.

Comparatore, V. M.; Cid, M. S.; Busch, C. (1995): Dietary preferences of two sympatric subterranean rodent populations in Argentina. Rev. Chil. Hist. Nat. **68**, 197–206.

Contreras, L. C.; Gutiérrez J. R. (1991): Effect of the subterranean herbivorous rodent Spalacopus cyanus on herbaceous vegetation in arid coastal Chile. Oecologia (Berlin) **87**, 106–109.

Contreras, L. C.; Gutiérrez, J. R.; Valverde, V.; Cox, G. W. (1993): Ecological relevance of subterranean herbivorous rodents in semiarid coastal Chile. Rev. Chil. Hist. Nat. **66**, 357–368.

Cox, G. W. (1990): Soil mining by pocket gophers along topographic gradients in a Mima moundfield. Ecology **71**, 837–843.

Cox, G. W.; Scheffer, V. B. (1991): Pocket gophers and Mima terrain in North America. Natural Areas Journal **11**, 193–198.

Cox, G. W.; Contreras, L. C.; Milewski, A. V. (1995) Role of fossorial animals in community structure and energetics of mediterranean ecosystems. In: Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Ed. by M. T. Kalin Arroyo, P. H. Zedler, and M. D. Fox. New York: Springer-Verlag. Pp. 383–398.

Digby, P. G. N.; Kempton, R. A. (1987): Multivariate Analysis of Ecological Communities. London: Chapman and Hall.

Ellison, L. (1946): The pocket gopher in relation to soil erosion in mountain ranges. Ecology **27**, 101–114.

Grant, W. E.; Mc Bryer, J. F. (1981): Effects of mound formation by pocket gophers (*Geomys bursarius*) on old-field ecosystems. Pedobiologia **22**, 21–28.

Grant W. E.; French, N. R.; Folse, L. J. Jr. (1980): Effect of pocket gopher mounds on plant production in a shortgrass prairie ecosystem. South. Nat. **2**, 215–224.

Hole, F. D. (1981): Effects of animals on soils. Geoderma **25**, 75–112.

Huntly, N.; Inouye, R. (1988): Pocket gophers in ecosystems: Patterns and Mechanisms. BioScience **38**, 786–793.

Hurlbert, S. H. (1984): Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. **54**, 187–211.

Inouye, R. S.; Huntly, N. J.; Tilman, D.; Tester, J. R. (1987): Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesotta. Oecologia (Berlin) **72**, 178–184.

Koide, R. T.; Huenneke, L. F.; Mooney, H. A. (1987): Gopher mound soil reduces growth and affect ion uptake of two annual grassland species. Oecologia (Berlin) **72**, 284–290.

Laycock, W. A.; Richardson, B. Z. (1975): The long term effects of pocket gopher control on vegetation and soils of a subalpine grassland. J. Range Manage. **28**, 458–462.

McDonough, W. T. (1974): Revegetation of gopher mounds on aspen range in Utah. Great Basin Nat. **34**, 267–274.

Mielke, H. W. (1977): Mound building by pocket gophers (*Geomyidae*): their impact on soils and vegetation in North America. J. Biogeogr. **4**, 171–180.

Miller, M. A. (1957): Burrows of the Sacramento Valley pocket gopher in flood irrigated alfalfa fields. Hilgardia **26**, 431–452.

Pearson, O. P.; Binztein, N.; Boiry, L.; Busch, C.; Di Pace, M.; Gallopín, G.; Penchaszadeh, P.; Piantanida, M. (1968): Estructura social, distribución espacial y composición por edades de una población de tuco tucos (*Ctenomys talarum*). Invest. Zool. Chil. **13**, 47–80.

Platt, W. J. (1975): The colonization and formation of equilibrium plant species associations on badger mounds in a tall-grass prairie. Ecol. Monogr. **45**, 285–305.

Reichman, O. J.; Smith, S. (1985): Impact of pocket gopher burrows on overlying vegetation. J. Mammalogy **66**, 720–725.

Reichman, O. J.; Jarvis, J. U. M. (1989): The influence of three sympatric species of fossorial mole rats (Bathyergidae) on vegetation. J. Mammalogy **70**, 763–771.

Reichman, O. J.; Witham, T. G.; Ruffner, G. (1982): Adaptive geometry of burrow spacing in two pocket gopher populations. Ecology **63**, 687–695.

Reichman, O. J.; Benedix, J. H.; Seastedt, T. R. (1993): Distinct animal-generated edge effects in a tall-grass prairie community. Ecology **74**, 1281–1285.

Richens, V. B. (1966): Notes on the digging activity of a northern pocket gopher. J. Mammalogy **47**, 531–533.

Schaal, B.; Leverich, W. (1982): Survivorship patterns in an annual plant community. Oecologia (Berlin) **54**, 149–151.

Spencer, S. R.; Cameron, G. N.; Eshelman, B. D.; Cooper, L. C.; Williams, L. R. (1985): Influence of pocket gopher mound on a Texas coastal prairie. Oecologia (Berlin) **66**, 111–115.

Swihart, R. K. (1991): Influence of *Marmota monax* on vegetation in hayfields. J. Mammalogy **72**, 791–795.

Tilman, D. (1983): Plant succession and gopher disturbance along an experimental gradient. Oecologia (Berlin) **60**, 285–292.

Turner, G. T.; Hansen, R. M.; Reid, V. H.; Tiejten, H. P.; Ward, A. L. (1983): Pocket gophers and Colorado Mountain Rangelands. Colorado State Univ. Agricult. Experim. Station Bull. 554 S.

White, P. S. (1979): Pattern, process and natural disturbance in vegetation. Bot. Rev. **45**, 229–299.

Woods, C. A. (1984): Histricognath rodents. In: Orders and Families of Recent Mammals of the World. Ed. by S. Anderson and J. K. Jones. New York: John Wiley. Pp. 389–446.

Zar, J. H. (1984): Biostatistical analysis, (2nd ed.). New Jersey: Prentice Hall.

Zenuto, R. R.; Busch, C. (1995): Influence of the subterranean rodent *Ctenomys australis* (Tuco-tuco) in a sand-dune grassland. Z. Säugetierkunde **60**, 277–285.

Zinnel, K. C. (1988): Telemetry studies of the ecology of plains pocket gophers (*Geomys bursarius*) in east-central Minnesota. Ph. D. thesis, University of Minnesota, Minneapolis.

Authors' address: Ana I. Malizia, Marcelo J. Kittlein, and Cristina Busch, Laboratorio de Ecofisiología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, C.C. 1245, Funes 3250, 7600 Mar del Plata, Argentina.