

Effects of the subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile*

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Summary. The impact of the subterranean herbivorous rodent *Spalacopus cyanus* Molina on the herbaceous vegetation was studied by comparing biomass, species richness and species diversity at the end of the growing season in areas with and without burrows in coastal arid Chile. Total biomass was 60% higher in areas with burrows. This difference was mainly due to the large increase of *Mesembryanthemum cristallinum* L., a succulent prostrate annual herb. Unexpectedly, bulb biomass of geophytes, eaten by *Spalacopus*, did not differ between areas. However, in areas with burrows bulbs of geophytes were more numerous and smaller. It is possible that burrowing activities facilitate the occurrence of new small bulbs through seed germination. Species composition and diversity did not differ greatly between areas. Burrowing activities by *Spalacopus*, the life cycle of *Mesembryanthemum*, and climate seem to be the most important factors determining species abundance and diversity of herbs in this system.

Key words: Subterranean rodent – Geophytes – Plant-animal interaction – Plant species composition – Arid environment

Soil disturbance and herbivory by subterranean rodents are now recognized as major influences in many grassland and savanna areas throughout the world (Andersen 1987; Huntly and Inouye 1988; Reichman 1988; Reichman and Jarvis 1989). Members of all groups of subterranean rodents develop and continuously modify extensive tunnel systems, which result in the deposition of soil mounds on the surface (Hickman 1990). These

rodents are herbivores that locally may reach densities of 25–50 individuals per hectare (Nevo 1979). Their foraging activities have major effects on soil structure and nitrogen availability that, likewise, greatly affect vegetation succession and the abundance of food plants (Hobbs and Mooney 1985; Andersen and MacMahon 1985; Huntly and Inouye 1988; Thorne and Andersen 1990). Despite the worldwide ecological importance of these animals and their widespread occurrence in South America (Contreras et al. 1987; Reig et al. 1990), no study has analysed their impact within Neotropical ecosystems.

Spalacopus cyanus, locally known as the “cururo”, is an 80–120 g subterranean octodontid rodent endemic to Chile, where it occurs in the coastal regions from Caldera (27° S) to Quirihue (36° S) and in the Andes from Alicahue (32° S) to Los Cipreses (34° S), as well as in scattered localities of the Intermediate Depression (Contreras 1986; Contreras et al. 1987). *Spalacopus* occupies habitats ranging from alpine grasslands in the Andes to *Acacia* savannas in the Intermediate Depression, stabilized coastal dunelands and sandy grasslands, habitats that are typically characterized by low cover of woody plants (Contreras et al. 1987). Cururos feed extensively on shoots of grasses and forbs when available (Contreras pers. obs.), but mainly rely on bulbs of geophytes such as the “huilli”, *Leucocoryne ixiooides* (Hook.) Lindl. (Liliaceae) (Reig 1970). Although geophytes appear to be heavily grazed by *Spalacopus*, especially in arid regions, their numbers do not decline over time, and actually exhibit a noted overlapping distribution with cururos (Zoellner 1972; Contreras et al. 1987). The presence of fossorial herbivorous rodents in South America (Contreras et al. 1987; Reig et al. 1990), and presumably of geophytes too (Ehrendorfer 1976), seems to be quite old. Consequently, our objective is twofold: to understand the mechanisms involved in the maintenance of *Spalacopus* and geophyte interactions, and to quantify the effect of *Spalacopus* on the vegetation by comparing the diversity and biomass of herbs in areas with and without tunnels of this species.

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Methods

Study site

The study was conducted in Lagunillas (30° 06' S, 71° 21' W; 30 m elevation), 16 km south of Coquimbo, approximately 2 km east of the Pacific Ocean. The area is an old (late Miocene-early Pleistocene) marine terrace covered by sandy soils about 50 cm deep, lying on an impermeable layer of calcium carbonate formed by deposits of shells of mollusks (Paskoff 1970). The climate is arid mediterranean with a strong maritime influence. Climatological records from the Punta Tortuga Lighthouse (29° 55' S, 71° 22' W, 25 m) show a mean annual precipitation of 80.9 mm (C.V. = 68%, range 4.3–188 mm) for the last 18 years. Temperature and humidity are much less variable. Mean monthly temperature varies between 12° and 18° C (range 6–22° C). Mean relative humidity varies

between 80% and 85% (range 60–100%). The study area is sparsely vegetated by low-growing plants (heights \leq 1.5 m) whose shrub densities range from the dominant species *Encelia canescens* var. *tomentosa* (Walp.) Back (0.31 plants/m²), to densities less than 0.04 plants/m². The prostrate prickly pear cactus *Tephrocactus ovatus* (L. Pfeiffer) Back. reaches maximum densities of 0.17 plants/m². The site has been exposed to moderate grazing by goats and cattle over the past 30 years.

Vegetation sampling

To evaluate the effect of *Spalacopus* on the herbaceous vegetation, we compared the diversity and biomass of plants found in three contiguous areas with and without cururo tunnels. No obvious differences were apparent among these areas other than the presence

Table 1. Comparisons of dry biomass of herbaceous vegetation in absolute values (g/m²), percentage of total biomass (%), species richness (*S*) and species diversity (*H'*) in areas with and without

burrows of the subterranean *Spalacopus cyanus* in a coastal semiarid zone of north-central Chile. *F*-values for one-way ANOVA are given. Significant differences are marked with asterisks

Plant species	With burrows			Without burrows			<i>F</i> -values ^b ** = <i>P</i> < 0.01 *** = <i>P</i> < 0.001
	\bar{x}	SE	% ^a	\bar{x}	SE	%	
Monocotyledons							
<i>Lamarckia aurea</i>	0.99	0.63		0.11	0.07		1.94
<i>Leucocoryne</i> sp.	5.79	0.65	5.1	4.42	1.53	6.2	0.68
<i>Schismus arabicus</i>	29.58	3.81	26.0	22.76	2.71	32.0	2.16 ^b
Dicotyledons							
<i>Adesmia</i> sp.	0.12	0.04		0.64	0.17		8.25**
<i>Calandrinia grandiflora</i>	1.74	0.76	1.5	0.51	0.23		2.40
<i>Calandrinia ramosissima</i>	0.0	0.00		0.07	0.07		1.26
<i>Camissonia dentata</i>	0.08	0.05		0.03	0.02		0.89
<i>Chenopodium album</i>	0.003	0.003		0.14	0.14		1.00
<i>Chaetanthera linearis</i>	0.04	0.04		0.00	0.00		1.00
<i>Crassula closiana</i>	0.04	0.04		0.002	0.001		1.10
<i>Cryptantha</i> sp.	2.24	0.57	2.0	0.55	0.25		7.30**
Crucifera 1	0.21	0.13		0.06	0.06		1.09
<i>Cuscuta micrantha</i>	0.001	0.001		0.00	0.00		2.03
<i>Eryngium coquimbantum</i>	6.11	1.07	5.4	4.92	0.92	6.9	0.70 ^b
<i>Erodium</i> sp.	10.71	2.04	9.4	16.99	2.76	23.9	3.35 0.07
<i>Helenium aromaticum</i>	0.007	0.004		0.06	0.03		2.51
<i>Lastarriaea chilensis</i>	0.00	0.00		0.02	0.01		2.46
<i>Linaria texana</i>	0.003	0.002		0.01	0.01		1.03
<i>Malva nicaensis</i>	0.00	0.00		0.20	0.19		1.09 ^b
<i>Medicago sativa</i>	2.23	0.55	2.0	1.33	0.63	1.9	1.17
<i>Mesembryanthemum crystallinum</i>	43.55	5.70	38.2	9.86	3.35	13.9	26.01***
<i>Microseris pygmaea</i>	0.04	0.03		0.00	0.00		2.03
<i>Moschardia pinnatifida</i>	0.02	0.02		0.16	0.14		0.96
<i>Nolana paradoxa</i>	7.30	1.67	6.4	4.48	1.17	6.3	1.91
<i>Oenothera</i> sp.	0.00	0.00		0.007	0.005		2.13
<i>Oxalis</i> sp.	0.01	0.01		0.01	0.01		0.04
<i>Paronychia chilensis</i>	0.01	0.01		0.10	0.10		0.79
<i>Pectocarya linearis</i>	0.41	0.19		1.30	0.48		3.00
<i>Plantago tumida</i>	0.29	0.14		0.40	0.20		0.21
<i>Schizanthus litoralis</i>	0.06	0.05		0.60	0.37		2.18 ^b
<i>Silene gallica</i>	0.057	0.30		0.02	0.02		3.28
<i>Stachys truncata</i>	0.00	0.00		0.09	0.08		1.35
<i>Taraxacum officinale</i>	0.00	0.00		0.03	0.03		1.00
Unknown	0.00	0.00		0.003	0.003		1.00
Totals	111.14	6.85		69.68	5.38		22.66**
Species richness (<i>S</i>)		27			31		
Species diversity (<i>H'</i>)		1.78			1.97		

^a Values lower than 1.0% are not given.

^b Degrees of freedom in all cases were 1,58, except that when one value was missing it was 1,57

or absence of burrows of *Spalacopus*. We selected areas with 1-year-old mounds to allow colonization by plants. Shrub cover in the sampling areas was less than 10%. A series of three 10 × 10 m plots was established in each sampling area. All plots were within 100 m of each other. Within each plot, ten 1-m² quadrats were located randomly and all above- and below-ground plant material for each species was harvested inside each quadrat. Soil from each quadrat was sieved to 30 cm deep to collect *Leucocoryne* bulbs. The dry weight biomass of all species in each quadrat was determined by oven-drying the plants at 70° C for 48 h.

Species richness (S) and diversity (H') for areas with and without cururos were calculated from this biomass data. Vegetative parameters were recorded at the end of the growing season (October 1989), when primary or annual productivity is greatest, thus improving the chance of detecting cururo effects. Statistical differences were evaluated by one-way ANOVA.

Results

Total average biomass was 60% higher in areas with burrows than in those without (Table 1), primarily due to the large increase in the succulent, prostrate, annual herb *Mesembryanthemum crystallinum* (Vivrette and Muller 1977). Although the herbaceous species *Adesmia* sp. and *Cryptantha* sp. showed significant increase and decrease in total average biomass, respectively, between site types, both species were of minor abundance, less than 2% of total in both areas (Table 1). Four relatively common species, comprising each more than 5% of the total biomass in the study area (Table 1), *Leucocoryne* sp., *Eryngium coquimbantum* Phil. ex Urban, *Nolana paradoxa* Lindl., and *Schismus arabicus* Ness, had higher biomass in areas with burrows, although differences were not statistically significant. Only one common species, *Erodium* sp., had a larger biomass in areas without burrows, but the difference was marginally not statistically significant (Table 1).

The plant community site types, as characterized by species richness and diversity indices, showed interesting trends. Neither species richness nor species diversity values between site types showed statistically significant differences (Table 1). Unexpectedly, species diversity was not higher in areas with burrows. This in part due to similar proportional representation of the ten most common species in both sites types, thus making a similar and important contribution to the H' value. More specifically, *Mesembryanthemum* increased from the third most common species in areas without burrows to being the dominant species in the areas with burrows in biomass

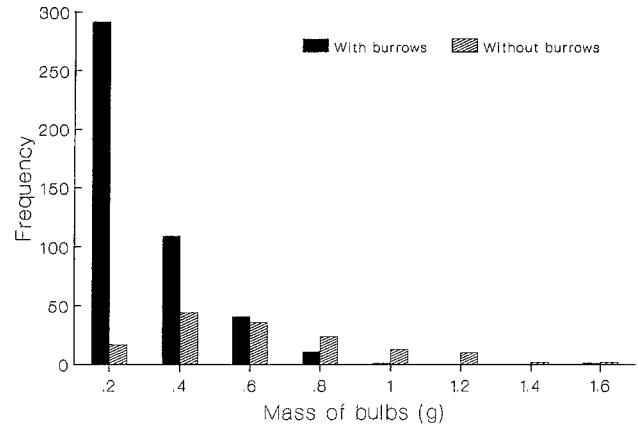


Fig. 1. Frequency distribution of bulb sizes of geophytes in areas with and without burrows of *Spalacopus cyanus* in coastal arid Chile, October 1989

terms (Table 1). This large increase of *Mesembryanthemum* does not occur at the expense of other plant species, which did not show significant differences between disturbed and undisturbed areas, except for *Adesmia* and *Cryptantha*.

Interestingly, total plant biomass and bulb biomass of *Leucocoryne* were not significantly different between site types ($F_{1,58} = 0.68$, $P > 0.05$, and $F_{1,58} = 0.05$, $P > 0.05$, respectively, Table 2). However, the number of *Leucocoryne* bulbs was significantly higher ($F_{1,58} = 13.58$, $P < 0.01$, Table 2) in areas with burrows. At the same time they were smaller in those areas ($F_{1,600} = 284.73$, $P < 0.001$, Table 2, Fig. 1).

Discussion

Our results indicate that *Spalacopus* effects on the herbaceous vegetation are considerable. It has been documented that open areas or areas sparsely occupied by other plants, such as mounds produced by burrowing animals, provide favorable sites for *Mesembryanthemum* recruitment (Vivrette and Muller 1977). Once *Mesembryanthemum* has gained access to the system, the plants can proliferate into large colonies. *Mesembryanthemum* probably increases in areas with high soil turnover and decreases in undisturbed areas and old mounds.

Given that *Spalacopus* feeds on bulbs of geophytes, we expected both lower numbers and biomass of geophytes

Table 2. Biomass and density of bulbs of *Leucocoryne* in areas with and without burrows of *Spalacopus cyanus* in a coastal semiarid zone of north-central Chile

	With burrows			Without burrows			F-values ^b ** = $P < 0.01$ *** = $P < 0.001$	df
	\bar{x}	\pm SE	n	\bar{x}	\pm SE	n		
Biomass of bulbs (g/m ²)	2.83	0.38	30	2.60	0.94	30	0.05	1,58
Density of bulbs (No./m ²)	15.20	2.07 (CV = 74%)	30	5.46	1.64 (CV = 164%)	30	13.58**	1,58
Mass of each bulb (g)	0.196	0.008	455	0.530	0.026	147	284.73***	1,600

in areas with burrows. However, the opposite was the case. It seems that *Spalacopus* reduces the abundance of large bulbs, and facilitates the occurrence of small (new) bulbs. The reduction of large bulbs may result through direct herbivory, and the facilitation of new bulbs may occur through the development of favorable conditions for germination of seeds, or by reduction of competition with large bulbs. These conditions may be the result of a combination of different mechanisms. Burrowing may expose buried seeds to more favorable surficial conditions (i.e. highly aerated, moist soils), and/or burial of wind-blown seeds in areas with excavated subsoils of similar edaphic characteristics may be more conducive to seed germination than areas without burrows. In order to test the proposed facilitation of germination by the burrowing activities of *Spalacopus*, a year later (late September 1990) we sampled the number of *Leucocoryne* germinating in 45 30 × 30 cm quadrats randomly distributed in areas with and without burrows; and found a significant higher number of them in areas with burrows ($F_{1,89} = 5.22$, $P < 0.05$).

As demonstrated by the low coefficient of variation in Table 2, bulbs in disturbed areas were more abundant, smaller and less clumped than in undisturbed areas. Differential mortality of new bulbs could account for the spatial distribution observed in undisturbed areas.

Above-ground leaves and flower stalks among Chilean geophytes appear to be associated with large bulbs (Gutiérrez, pers. obs.), and high rainfall years (Vidiella and Armesto 1989). Since *Spalacopus* visually survey the ground surface from the mouth of their tunnels, visual cues may determine the direction of new tunnels, rather than the animals excavating at random. If this is true, the lag time between rodent disturbance cycles (i.e. the time between consecutive extensive burrowing activity in the same site) would allow smaller bulbs to grow larger and produce new seeds. This is possible given the fact that fresh mounds of a colony of *Spalacopus* were detected at practically the same point of an area abandoned the previous year, and that cururos persist in the same areas for long periods of time (Torres-Mura 1990).

It may be speculated that these geophyte-cururo relationships present interesting mechanisms that allow for their continued maintenance in time and space, analogous to those postulated for geophytes and mole-rats in South Africa (Lovegrove and Jarvis 1986). If this hypothetical relationship is widespread, it may account for the coexistence of large populations of geophytes together with the subterranean herbivorous *Spalacopus*.

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