

# Ecological relevance of subterranean herbivorous rodents in semiarid coastal Chile

Importancia ecológica de roedores herbívoros subterráneos en el desierto costero de Chile

LUIS C. CONTRERAS<sup>1</sup>, JULIO R. GUTIERREZ<sup>1</sup>, VICTOR VALVERDE<sup>1</sup>  
and GEORGE W. COX<sup>2</sup>

<sup>1</sup> Departamento de Biología, Universidad de La Serena, Casilla 599, La Serena, Chile.

<sup>2</sup> Biology Department, San Diego State University, San Diego, CA 91182-0057, USA.

## ABSTRACT

We first call attention to the ecological relevance and characteristics of subterranean herbivorous rodent activities in different ecosystems. Second, we note that in arid coastal Chile the ecological impact of their activities is considerable, showing similarities, as well as important differences, to impacts in other areas of the world. The amount of excavated soil deposited on the surface is similar to that reported for pocket gophers in North America. These rodents also promote dominance of introduced mediterranean annual plants. In Chile, as in South Africa, however, they seem to greatly promote the growth of geophytes, which are their preferred food. Their activities promote large-scale soil homogeneity. We hypothesize that these aspects of their ecology in Chile reflect a close relationship between a fluctuating and unpredictable climate, a relatively constant availability of clumped geophytes, and the colonial social system of these rodents, all of which promote a slow but constant shifting of their foraging areas. Subterranean rodents certainly play an important role in determining the structure and dynamics of plants in the coastal arid ecosystem in Chile. However, very little is known about the mechanisms involved.

**Key words:** Chile, desert ecology, soil disturbance, *Spalacopus*, subterranean rodents, geophytes.

## RESUMEN

Primero destacamos la importancia ecológica de la actividad de roedores herbívoros subterráneos. Segundo, hacemos notar que la actividad de estos roedores tienen un impacto ecológico considerable en el ecosistema árido costero de Chile, presentando similitudes pero también importantes diferencias con sistemas investigados en otras partes del mundo. La cantidad de suelo depositado sobre la superficie del suelo es similar a la reportada para geómidos en Norteamérica. Estos roedores también promueven la dominancia de plantas anuales mediterráneas introducidas. Sin embargo, en Chile como en Sudáfrica, ellos también parecen promover en gran medida el crecimiento de geófitas que constituyen su alimento preferido. Sus actividades promueven la heterogeneidad del suelo en el corto plazo en escalas pequeñas, pero en el largo plazo ellos promueven la homogeneidad del suelo en una escala mayor. Proponemos que estas características ecológicas y diferencias con otros sistemas reflejan una estrecha relación entre un régimen climático fluctuante e impredecible, la disponibilidad relativamente constante de geófitas distribuidas en forma agrupada, y el sistema social en colonias de estos roedores, todo lo cual promueve un desplazamiento lento pero constante de los túneles de forrajeo. Ciertamente, los roedores herbívoros subterráneos juegan un rol importante en determinar la estructura y dinámica de plantas en el ecosistema árido costero de Chile; sin embargo, se conoce poco de los mecanismos involucrados.

**Palabras claves:** Chile, ecosistemas desérticos, perturbación del suelo, *Spalacopus*, roedores subterráneos, geófitas.

## INTRODUCTION

The importance of disturbance as a source of spatial and temporal variation in natural communities has become increasingly recognized as an important process in ecological theory. Recent hypotheses on the maintenance of species diversity have emphasized the role of natural disturbance, which both prevents intra and interspecific competitive displacement and provides sites for colonization by competitively inferior

species (Grubb 1977, Connell 1978, Huston 1979, Armesto & Contreras 1981, Sousa 1984, Pickett & White 1985). These ideas are in contrast to the old long-held view of communities as equilibrium systems, with high species diversity resulting from prevention of competitive displacement by resource subdivision (MacArthur 1972, Schoener 1974, Pianka 1976). In addition to being an important source of environmental heterogeneity, disturbance may act as a strong selective influence on the life history of organisms (Harper 1977, Denslow 1980).

Disturbance phenomena are often referred to abiotic causes affecting large areas, such as fire, and volcanic eruptions. At the same time, in ecological studies much attention has been paid to animals as consumers of primary production, even though they only consume a small fraction of the live biomass (Hairston *et al.* 1960), without noting their importance as agents affecting the structure, properties and processes of ecosystems (Whitford 1993). Nevertheless, the importance of disturbances occurring at smaller scales and produced by biotic agents has been increasingly recognized (Martinsen *et al.* 1990, Reichman & Smith 1991, Whitford 1993, Cox *et al.* in press).

Disturbance generated by animals, and particularly those created by subterranean mammals, are unique for several reasons: 1) they are caused by a biotic agent, whereas most forms of disturbance that have been studied are abiotic (*e.g.*, wind, fire, wave action), 2) they occur in small patches, in contrast to large-scale disturbance such as tree blow-downs, 3) they occur with a predictable and constant frequency compared to more unpredictable events like fires and storms (Martinsen *et al.* 1990), and 4) as a consequence of 2) and 3) they are of minor short-term impact, but accumulate and cause substantial long-term effects (Cox & Scheffer 1991, Reichman & Smith 1991).

In this article we first review information on the ecological role of subterranean herbivorous rodents. Second, we summarize the few available studies on their role in arid coastal Chile, noting similarities and differences to other ecosystems where subterranean mammals have been studied.

#### MAGNITUDE OF DISTURBANCE BY SUBTERRANEAN HERBIVOROUS MAMMALS

Soil disturbance and herbivory by subterranean rodents are now recognized as major influences on the structure and dynamics of many ecosystems, including deserts (Andersen & MacMahon 1981, 1985, Reichman *et al.* 1982, Gettinger 1984, Hobbs & Mooney 1985, 1991a, Cox & Gakahu 1986, Andersen 1987, Cox & Allen 1987a, Inouye *et al.* 1987, Kodie & Mooney 1987, Huntly & Inouye 1988, Reichman 1988, Reichman & Jarvis 1989,

Contreras & McNab 1990, Martinsen *et al.* 1990, Thorne & Andersen 1990, Contreras & Gutiérrez 1991, Heth 1991, Cox *et al.* in press). Members of all groups of subterranean rodents maintain and expand extensive gallery systems throughout all or much of the year, resulting in deposition of soil heaps on the surface (Hickman 1990, Reichman & Smith 1991). All are herbivores that locally reach densities up to 207 individuals per hectare or biomasses of 32.4 kg/ha (Nevo 1979, Reichman & Smith 1991), values that are usually greater than for surface dwelling mammals. Their burrowing activities exert major impacts on soil structure and nitrogen availability; affecting both plant succession and abundance of their food plants (Tilman 1983, Cox & Gakahu 1985, Hobbs & Mooney 1985, Andersen & MacMahon 1981, 1985, Reichman & Smith 1985, Cox & Zedler 1986, Andersen 1987, Inouye *et al.* 1987, Koide *et al.* 1987, Hobbs *et al.* 1988, Huntly & Inouye 1988, Reichman 1988, Cantor & Whitman 1989, Reichman & Jarvis 1989, Cox 1990, Thorne & Andersen 1990, Heth 1991, Hobbs & Mooney 1991a, Reichman & Smith 1991). Burrowing activity varies between different species and within species, mainly in relation to social and foraging systems (solitary vs. colonial species), food resources, soil moisture and temperature, hardness of the ground, and reproductive activity (Arieli 1979, Reichman *et al.* 1982, Hickman 1990, Heth 1991, Reichman & Smith 1991, Cox & Hunt 1992).

Subterranean rodents usually remove large amounts of soil. For the pocket gopher *Thomomys bottae* in southern California it may be as large as 26.6 ton/ha • year (Cox 1990). The most obvious impact of this mining on soil structure results from the deposition of excavated soil on the surface of the ground. Because mound formation is easily perceived, its rate is frequently used as an estimate of burrowing activities (Miller 1957, Hickman & Brown 1973, Arieli 1979, Bandoli 1981, Cantor & Whithan 1989, Cox & Hunt 1992). The mass of soil deposited on the surface values ranges from 0.8 to 34.5 ton/ha • year in natural conditions (Miller 1957, Downhower & Hall 1966 in Cox 1990, Richens 1966, Andersen & MacMahon 1981) and may reach 105 ton/ha • year in irrigated alfalfa fields (Miller 1957). A significant portion of the

excavated soil may not be deposited on the surface, but placed in abandoned tunnels below the surface of the ground. Soil may also be deposited in tunnels that have been formed in the snow pack, producing soil cores that remain on the surface of the ground after snow melt (Ingles 1952, Reichman & Smith 1991, Contreras pers. obser. for *Ctenomys maulinus*). Estimates of subsurface redeposition of soil range between 13 and 240% of the amount of soil deposited on the surface (Andersen 1987, Cox 1990, Thorne & Andersen 1990). Although subsurface redeposition is presumably significant because of the large amount of soil involved, its effect on the vegetation has not been evaluated. The total surface area disturbed by subterranean rodents may be considerable. For gophers this disturbance ranges from about 1% to 45% of the area per year, with an average value of 12.6% of the area/year for 12 cases (Tilman 1983, Hobbs & Mooney 1985, 1991a, Goldberg & Gross 1988). The only long-term (six years) study on the effect of burrowing activities on the vegetation found that 26% of the area per year was disturbed by gopher activities on serpentine grassland in California (Hobbs & Mooney 1991a). This study also found that about 50% of the disturbances occurred in previously disturbed places. Therefore, we calculate that the total surface of the ground is affected by at least one gopher disturbance in about 8 years.

Over the long term, mining and translocation of soil may modify topography, creating large-scale patterns of Mima mounds (Cox & Scheffer 1991). Mima mounds are earth mounds that range up to 2-3 m in height, 20-50 m in diameter, and 50-100 per ha in density, with mounded landscapes extending for kilometers. The mechanism of formation is the backward displacement of soil that occurs during outward tunneling from the center of animal activity, where this center is located in elevated sites with deeper or better drained soils (Cox 1984, Cox & Gakahu 1986, Cox & Scheffer 1991).

#### EFFECTS ON THE VEGETATION

Tunneling activity may reduce by 25 to 50% the biomass of plants directly over active burrows and the effect may still be detectable

3 years after the burrows have been abandoned (Reichman & Smith 1985). A similar impact has been noted over burrows of three sympatric species of bathyergids rodents from South Africa (Reichman & Jarvis 1989). Furthermore, the effects of burrows on the vegetation can be significant beyond the area of actual disturbance. For pocket gophers, effects may extend up to 1 m to each side of the tunnel in the form of waves of increased and suppressed plant biomass (Reichman & Benedict 1993).

The deposition of soil on the surface may physically cover and kill previously existing plants, creating open spaces for colonizer species that are competitively inferior in undisturbed sites (Tilman 1983, Hobbs & Mooney 1985, 1991a, Williams & Cameron 1990, Inouye *et al.* 1987, Kodie *et al.* 1987, Hobbs *et al.* 1988, Martinsen *et al.* 1990, Contreras & Gutiérrez 1991). Reichman & Smith (1991) speculate that plant species growing from rhizomes or underground storage organs have greater ability to overcome the effects of burial than other species, so that these types of storage structures might be selectively favored when burrowing mammals occur in significant densities. The physical clearing of space produced by the heaps soil produced by subterranean mammals may occur along with changes in the nutrient and moisture profiles, affecting seed germination and plant growth.

Over the long term, perhaps the most important feature of burrowing is soil formation and soil mixing. After soil is brought to the surface, it erodes and redistributes nutrients. In east-central Minnesota, gophers reduce average soil nitrogen near the surface and increase point-to-point heterogeneity of soil nitrogen by moving nitrogen-poor subsurface soil to the surface, affecting local species composition and old field succession (Inouye *et al.* 1987). In the same area, soil used by gophers to plug empty burrows contains less nitrogen than surrounding soil (Reichman 1988). The heaps and ridges generated by subterranean mammals also produce distinctive soil moisture profiles (Skoczen *et al.* 1976) which, in turn, probably affect plant success (Reichman & Smith 1991).

Mima mounds exert a large-scale influence on plant community structure because of their deep, loamy soils and favorable moisture

relations. In coastal southern California, these mounds, in the absence of frequent fire, are foci for the establishment of various suffrutescent and woody shrubs (Cox 1986). They also permit upland plants to extend their distribution into coastal salt marshes (Cox & Zedler 1986).

By virtue of the large biomass that populations of subterranean mammals may reach (see above) their impact on vegetation by direct herbivory may be substantial (Andersen 1987). The only attempt to assess the magnitude of below-ground herbivory by subterranean mammals appears to be the field study by Andersen & McMahan (1981). These authors calculated that up to 30% of the annual primary production allocated to belowground plants parts may be consumed by these rodents. Direct herbivory by subterranean mammals may have major impacts on vegetation, such as preventing aspen trees from invading mountain meadows in northern Arizona (Cantor & Whitham 1989). Only 4 months after the removal of pocket gophers, aspen survival increased 3-fold, vegetative reproduction 2.5 times, and average tree growth rates 3 times compared to controls.

Estimates of the energetics of populations of pocket gophers in the western USA demonstrate that energy flow through this herbivore component often greatly exceeds that through other small and large herbivores (Anderson & MacMahon 1981, Gettinger 1984, see Contreras & McNab 1990). Therefore, in certain situations, subterranean rodents may act as keystone species, regulating the composition and productivity of plant communities.

IMPORTANCE OF THE SPACE AND TIME  
PERTURBATION REGIMES IN VARIABLE  
ENVIRONMENTS

The disturbance regime due to subterranean rodent activity is complex. During a six-year study in northern California, Hobbs & Mooney (1991a) found that disturbance levels varied considerably in both time and space. Over the study period annual rainfall varied 3-fold, strongly affecting the plant community. In particular, one species decreased and another increased in abundance with increasing rain-

fall. Abnormally high rainfall in 1982 and 1984 allowed the buildup of populations of a non-native species (*Bromus mollis*), which subsequently was virtually eliminated from the area by two consecutive years of severe drought. Invasion by this introduced species in 1983 was only on gopher heaps; in subsequent years recolonization of gopher heaps was predominantly by other species. Interannual variability in species abundance was most apparent on disturbed microsites. The same authors have previously portrayed *Bromus mollis* as the major colonizer of gopher heaps formed early in the season (Hobbs & Mooney 1985), but it is clear from the longer 6-year study that this observation holds only in years of high rainfall (Hobbs & Mooney 1991a). These results clearly point to the value of longer-term studies of community and ecosystem dynamics. This is especially true for mediterranean arid environments with high variability (Hobbs & Mooney 1991b).

Most of the information about the dynamics of arid ecosystems comes from works conducted in North American deserts, and the few studies yet conducted in South American deserts indicate at least that such generalizations are not fully applicable to historically, taxonomically and geographical distinct organisms of Neotropical arid ecosystems (Mares 1980).

SUBTERRANEAN MAMMALS IN  
SEMI-ARID CHILE

Three genera of subterranean herbivorous rodents are presently found in South America: *Ctenomys*, widespread in southern half of South America, *Spalacopus* found in central Chile (Contreras *et al.* 1987, Reig *et al.* 1990, Redford & Eisenberg 1992), and the recently discovered *Orthogeomys* (Geomyidae) from northwestern Colombia (Alberico 1990). Despite their relatively widespread distribution only a few studies have dealt, even indirectly, with their ecological importance in Neotropical ecosystems. Most data come from the few studies conducted on *Spalacopus*, which is the only subterranean herbivorous rodent found in the arid coastal desert of central Chile. Consequently, the following review is based on this monotypic genus.

*Spalacopus cyanus*, locally known as "cururo", is an 80-120 g subterranean octodontid rodent endemic to central Chile (Contreras *et al.* 1987, Contreras in press). It occupies a narrow range about 1,150 km long by 150 km wide on the western side of the Andes, and is found from sea level to an elevation of 3,000 m. *Spalacopus* occupies habitats ranging from mountain vegetation in the Andes to *Acacia* savannas in the Central Depression and coastal stabilized dunelands. Cururos exhibit a clear preference for open habitats. They are absent from habitats with shrub cover higher than 60% (Contreras *et al.* 1987), and are most frequently found in habitats dominated by grasses and forbs. When present in habitats with intermediate shrub cover, as the arid mediterranean coastal habitats found in Fray Jorge National Park (30° 38' S, 71° 40' W, 60% shrub cover), their tunnels are found in open spaces between shrubs (Fig. 1). The cause-effect nature of this relationship is unclear at the moment. It is possible that cururos simply prefer open spaces because of greater abundance of their food resources there. At the same time, however,

cururos may contribute substantially by their activities to the maintenance of open habitats, precluding the development of a climax matorral community by plant succession, much as gophers prevent the climax aspen forest from developing in mountain meadows in Arizona (Cantor & Whitham 1989).

Three considerations indicate that the plant-animal interaction between geophytes and *Spalacopus* is a strong one. 1) Although geophytes appear heavily grazed by *Spalacopus*, especially in arid areas where they seem to be the only food resource available to cururos during almost of the year, or even for several years of drought, their numbers do not seem to decline over time. 2) Geophytes and *Spalacopus* present highly overlapping distributions (Zoellner 1972, Contreras *et al.* 1987). 3) The presence of subterranean herbivorous rodents in South American (Reig *et al.* 1990), and presumably also of geophytes (Ehrendorfer 1976), seems to be quite old, allowing sufficient time for at least the independent development of characteristics favoring their coexistence in arid environments.

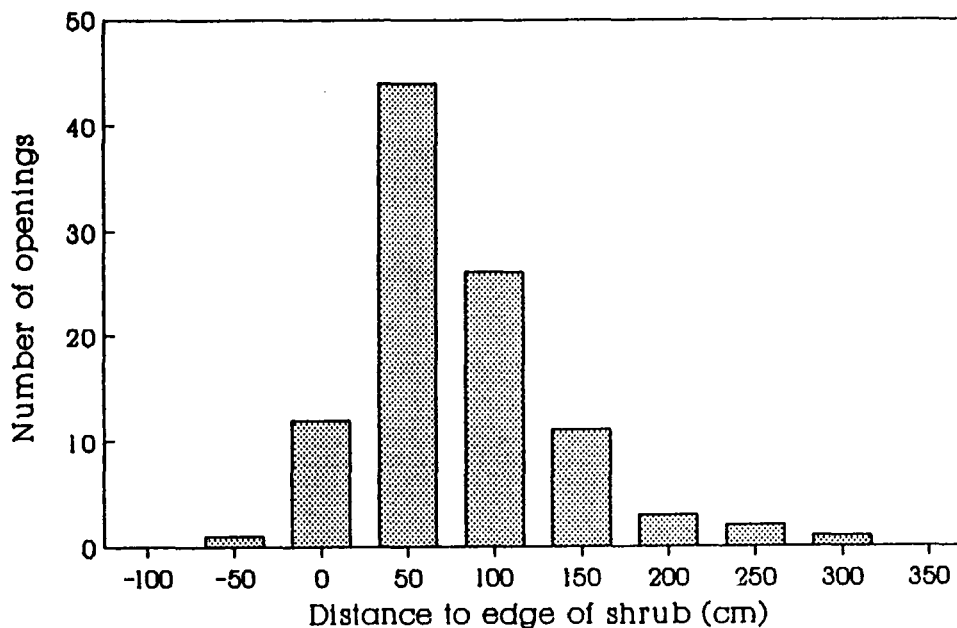


Fig. 1: Frequency distribution of the shortest distance from openings of tunnels of *Spalacopus cyanus* to the border of the nearest shrub. Negative values correspond to openings located under shrubs. Sample size equals a total of 100 tunnels from 5 different colonies taken in Fray Jorge National Park in October 1991.

Distribución de frecuencia de la distancia más corta entre bocas de túneles de *Spalacopus cyanus* y el borde de arbusto más cercano. Valores negativos corresponden a bocas bajo arbustos. Datos de 100 aberturas de 5 colonias en el Parque Nacional Fray Jorge en octubre de 1991.

Cururos have been reported to feed extensively on bulbs of geophytes such as the "huilli", *Leucocoryne ixiooides* (Alliaceae), *Rhodophiala* (Amaryllidaceae), and *Conanthera* sp. (Thecophylaeaceae) (Reig 1970, Torres-Mura 1990). They also feed on shoots of grasses and forbs when available (L.C. Contreras pers. obs.) Microhistological studies of stomach contents and feces of 10 *Spalacopus* from an arid coastal habitat, during the summer season (February 1991) when all herbaceous vegetation had dried up, indicated that bulbs of geophytes make the major part (55%), and in some individuals almost the only component, of the diet of cururos. Other items consumed were roots of woody plants (32%) and unidentified plant material (13%). Tunneling and harvesting of geophyte appears to be the primary mode of foraging throughout the year, as suggested by the constant rate of cumulative volume of soil deposited on surface heaps (see later).

Cururos are highly social, living in groups of about 6-15 individuals (Reig 1970, Torres-Mura 1990). Cururo colonies vary greatly in

density. In some locations, colonies and their areas of disturbance are hundreds of meters apart; in other areas closely packed colonies create continuous disturbance for many kilometers. Torres-Mura (1990) found a regular distribution of colonies both in the Andes and in coastal dunes of central Chile, with average distances of 32 and 37 m respectively, among them.

Surface soil deposition by cururos is substantial and comparable to that of most North American pocket gophers. Unpublished data on soil mining by a cururo colony over 21 months in Fray Jorge indicate that the monthly rate of mound production is variable, with an average of  $64 \pm 23$  (SD) heaps/month (range 29 to 110) (Fig. 2). Mound production was lowest during the rainy winter months of 1991 and coincided with the formation of an herbaceous stratum. It may be hypothesized that during that time consumption of above ground herbs, within a distance reachable from openings of burrows, made tunneling for geophytes less demanding. However, the volume of soil deposited on the surface was

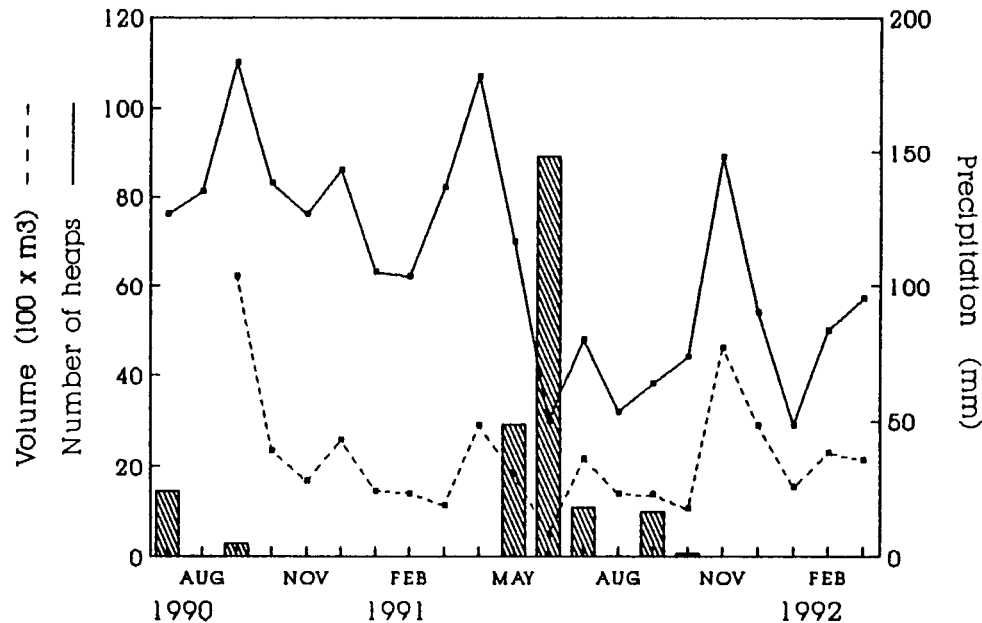


Fig. 2: Precipitation, number of heaps, and volume of soil deposited on the surface by one colony of *Spalacopus cyanus* in Fray Jorge National Park, Chile. The soil volume has been multiplied by 100 in order to use the same scale as for number of heaps.

Precipitación, número de montículos y volumen de tierra depositada en la superficie formados por una colonia de *Spalacopus cyanus* en el Parque Nacional Fray Jorge, Chile. El volumen de suelo ha sido multiplicado por 100 para usar la misma escala que para el número de montículos.

less variable and was unrelated to precipitation (Fig. 2). In central Chile Torres-Mura (1990) found a clear, direct relationship between the formation of heaps, precipitation, and herb growth. The cumulative volume of soil deposited on the surface of the ground by the colony studied was equal to 2.5 m<sup>3</sup>/year, and the total soil mass equal to 3.22 ton/year, at a bulk density of 1.31 g/cm<sup>3</sup> for mined soil. The surface area directly covered by heaps was 92.4 m<sup>2</sup>/year. At a density of three colonies per hectare (Reig 1970, Torres-Mura 1990), this would equal about 10 ton/ha. We do not know the magnitude, if any, of subsurface soil redeposition by cururos.

After heaps are made they progressively decrease in size by loss of their initially high water content, and by subsequent wind and rain erosion. The amount of soil collected in pitfall traps located at the surface level is about 3 times higher in areas with than without burrows (J.R. Gutiérrez, unpublished data).

The tunnel system excavated by *Spalacopus* provides refugia for other rodents. In Andean

environments it has been shown that small cricetid rodents are more abundant in areas with burrows (Simonetti *et al.* 1985).

Geophytes are plants that grow and store reserves underground during periods of short and unpredictable favorable conditions and remain dormant most of the time, which may extend for years of drought (Boeken 1989). Consequently, although they may be generally abundant in arid environments of Chile (Armesto *et al.* 1993), there must be a lapse of time for them to recover after they have been harvested locally by *Spalacopus*. This might explain the relatively continuous expansion of their foraging tunnels to contiguous areas and the concomitant slow but progressive abandonment of already exploited areas. Figure 3 shows the displacement of a colony of cururos in Fray Jorge from July 1990 to October 1991. This pattern of soil translocation and movement of the colonies implies local perturbation and increased heterogeneity over the short term, but extensive perturbation of the system with a mosaic of mounds with

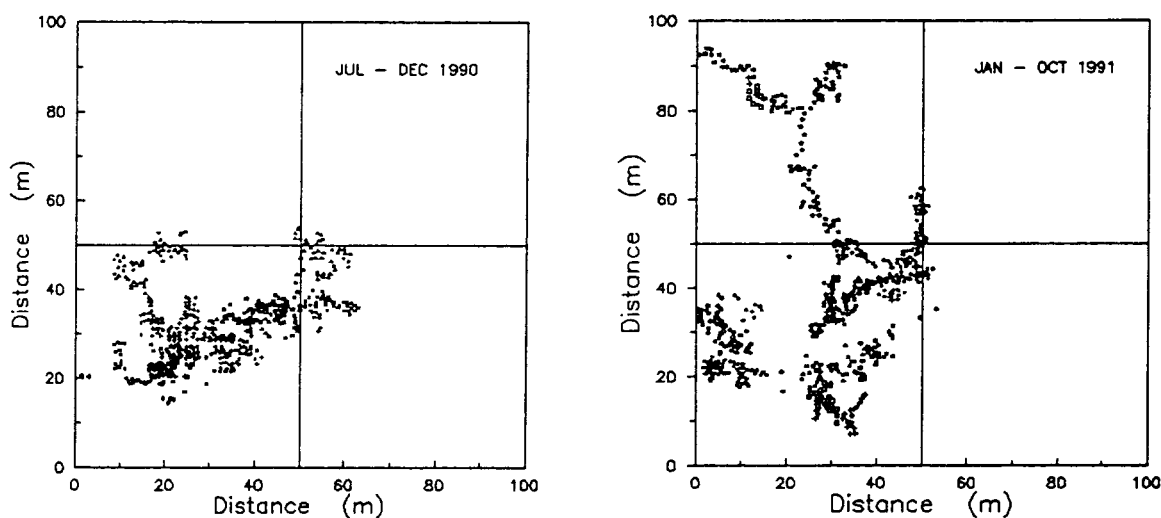


Fig. 3: Spatial distribution of soil surface deposition by one colony of *Spalacopus cyanus* in Fray Jorge National Park from a) July to December 1990, and b) from January to October 1991. Horizontal and vertical lines are for reference. Symbols are for different months, but the scale does not allow sufficient resolution. Broadly, at the beginning, mounds were located at the lower left corner, then they moved towards the center, to the bottom, to the center, and finally to the upper left corner. The colony moved outside the area by December 1992.

Distribución espacial de montículos de suelo formados por una colonia de *Spalacopus cyanus* en el Parque Nacional Fray Jorge desde a) julio a diciembre 1990, y b) desde enero a octubre 1991. Las líneas horizontales y verticales son de referencia. Los símbolos son distintos para cada mes, pero la escala no permite suficiente resolución. En forma general, al comienzo, los montículos estaban localizados en la esquina inferior izquierda, después se movieron hacia el centro, hacia abajo, hacia el centro y, finalmente, hacia la esquina superior izquierda. La colonia salió fuera del área en diciembre de 1992.

different age on a longer time scale. Despite the fact that the area actually used by cururos at any one time is relatively small, in many areas it is difficult to find a place without signs of cururo disturbance in the past. The different pattern of soil mining and deposition of cururos, as compared to that of pocket gophers, might explain why Mima mounds do not form in Chile despite the existence of similar soils and other abiotic conditions (Cox *et al.* in press).

In the arid coastal mediterranean area of north-central Chile burrowing activity by cururos appears to promote recruitment by at least some of their primary food species (Contreras & Gutiérrez 1991). Harvesting depleted the abundance of large corms of *Leucocoryne*, but stimulated germination, and perhaps growth of young plants, thus leading to an increase in density of small corms. Torres-Mura (1990) reported that cururos feeding on *Conanthera* cut the lower part of the corm leaving a growing bud in the upper portion which may regenerate a new corm. The time interval between consecutive harvests in a given area may depend at least on the time required for renewal of geophytes (Torres-Mura 1990).

In arid north-central Chile, surface soil deposition by cururos promotes the growth of certain annuals, such as *Mesembryanthemum crystallinum*, a prostrate, introduced succulent herb that occurs on sites disturbed by human related activities. The abundance of this species in areas with burrows was four times greater than in areas free of burrows, leading to an increase of more than 60% in total dry biomass of herbaceous plants (Contreras & Gutiérrez 1991). In undisturbed areas, however, *Mesembryanthemum* is not found in the system, heaps are colonized by native pioneer species and differences between areas with and without burrows are less impressive (authors' unpublished data).

Chemical analysis of 10 soil samples from heaps made by cururos and of surface soil not covered by heaps in Fray Jorge showed no differences in pH, electrical conductivity, nitrogen, phosphorus, potassium or organic matter. Thus, the effects of cururo activities on the herbaceous vegetation may be mediated by physical rather than chemical factors. However, cururo activities may contribute to

some extent to changes in soil chemistry. Their tunnels may act as traps for organic matter which may passively fall there, or by the accumulation of aerial parts of herbs brought into the tunnel by cururos, at least during the growing season.

It is interesting to note that a more significant contribution to changes in soil chemistry, mainly by accumulation of feces, leading to soil heterogeneity is made by the degu, *Octodon degus*. This abundant, large, colonial, diurnal, rodent mainly restricts its activities to microhabitats under shrubs (Fulk 1976, Jaksic *et al.* 1979, Meserve 1981, Iriarte *et al.* 1989). It is possible that the activities of *Spalacopus* and *O. degus*, among other possible animals, have important opposing effects on the dynamics of the arid coastal mediterranean ecosystem of north-central Chile, leading to maintenance of a mosaic vegetation.

#### CONCLUSIONS AND REMARKS

This review of the few available data on the role of cururos in arid coastal ecosystems in Chile indicates some similarities as well as differences to what is known about the role of subterranean mammals in other ecosystems of the world. As for other ecosystems, *Spalacopus* promotes the dominance of annual plants through soil disturbance. These plants are primarily introduced mediterranean annuals, especially in heavy disturbed places. In North America disturbance by subterranean herbivorous rodents promotes short-term and long-term heterogeneity of soil conditions. In Chile *Spalacopus* also promotes short-term physical heterogeneity, but in the long-term the disturbed area is expanded by the slow and constant displacement of their foraging tunnels. In north-central Chile this trend seems to oppose that probably generated by other abundant and permanent resident rodents mainly restricted to microhabitats under shrubs.

Pocket gopher herbivory limits the local distribution of certain preferred plants to unsuitable foraging habitats (Cox & Allen 1987b, Cox 1989). In contrast, exploitation by cururos apparently promotes increased recruitment of some geophytes, much as reported



for certain bathyergid molerats and geophytes in South Africa (Lovegrove & Jarvis 1986), but we do not know its effect on climax shrubs of the Chilean matorral.

Probably most differences between cururos and pocket gophers derive from differences in a few basic conditions. Precipitation is relatively infrequent and unpredictable within and among years in arid coastal central Chile, with the common occurrence of several years of drought (Armesto *et al.* 1993). Geophytes capitalize on favorable conditions for growth and store reserves in underground organs, such as bulbs, corms, or tubers. In arid coastal Chile geophytes are abundant, apparently constituting a reliable resource during the dry seasons or even for several years of drought, when all other herbs have dissappeared from the surface. After geophytes have been foraged in a given place, they cannot grow and recover to pre-foraging levels until favorable conditions occur. In years of enough precipitation the recovery of geophytes may occur by growth of small organs (bulbils and cormlets) which may be shed or dispersed when a bulb or a corm is harvested, or by the germination of seeds. Germination of geophytes in Chile seems to be favored by the physical rather than by chemical conditions provided by the loose soil of heaps. Consequently, an adequate foraging strategy for subterranean herbivorous rodents in these habitats would be to expand their foraging area slowly, but continuously abandoning previously exploited areas where the high cost of burrowing (Vleck 1981) cannot be compensated by the benefits obtained.

Coloniality in subterranean mammals is infrequent and has been proposed to relate to unfavorable climatic and/or resource conditions in general (Nevo 1979), and to low density and random distribution of large geophytes for African molerats (Lovegrove & Wissel 1988, Lovegrove 1991). We do not know whether those factors can adequately explain the coloniality of *Spalacopus*. Certainly cururos are found in xeric environments. However, food resources (geophytes) seem to be abundant, relatively constant through time, of small size, and clumped in distribution (authors unpublished data).

The present information indicates that activities of *Spalacopus* seem to be an important determinant of the structure and

dynamics of the arid coastal ecosystems of north-central Chile. However, more research is needed in order to better understand the functioning of this system. We hope that the ideas presented here are provocative enough to attract the interest of investigators to this subject. This is especially important since the arid coastal ecosystem in Chile has been greatly degraded, mainly by clearing of shrubby vegetation to grow wheat, the cutting of wood for fuel and goat raising (Solbrig 1984, Shcofield & Bucher 1986). We hypothesize that the desertification process, mainly affecting shrub vegetation in the first stages, will promote the occurrence of geophytes and cururos. However, both may be adversely affected by intense and persistent per-turbations, such as those produced by intense goat raising.

Finally, it should be noted that the few available studies summarized here come from only one of the species of South American subterranean rodents and mainly from just one of the ecosystems where this species is found. The situation may be quite different for other species in different ecosystems in South America. For instance, there are many species of *Ctenomys* that have a larger body size than *Spalacopus*, are solitary and feed on more constantly available food resources above-ground.

#### ACKNOWLEDGMENTS

Most of the work of *Spalacopus* reported here has been conducted in the Parque Nacional Fray Jorge as part of the Program of Sponsored Research in the System of Protected Wildlife Areas launched by Corporación Nacional Forestal (CONAF) of Chile, IV Region. Waldo Canto and Juan Cerda kindly allowed us to work in the park and provided logistic support. We are grateful to Carlos Pino for assistance with the graphic programs. W. Whitford and P. Marquet as reviewers made critical comments on the manuscript. This research has been partially funded by grants FONDECYT-Chile 90/930 and 90/376, US-NSF BSR 90-20047 and INT 8919473 and Universidad de La Serena DIULS 120-2-32 and 120-2-35. This paper is based on a presentation at the International Workshop Desertification: A

landscape-ecosystem perspective held in La Serena, October 1991, and is a contribution of the Arid Zone Study Program of Universidad de La Serena.

## LITERATURE CITED

- ALBERICO M (1990) A new species of pocket gopher (Rodentia: Geomyidae) from South America and its biogeography significance. In: Peters G & R Hutterer (eds) Vertebrate in the tropics: 103-104. Museum Alexander Koenig, Bonn.
- ANDERSEN DC (1987) Belowground herbivory in natural communities: a review emphasizing fossorial animals. *Quarterly Review of Biology* 62: 261-286.
- ANDERSEN DC & JA MacMAHON (1981) Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides*. *Ecological Monographs* 51: 179-202.
- ANDERSEN DC & JA MacMAHON (1985) The effect of catastrophic ecosystem disturbance: the residual mammals at Mount S. Helens. *Journal of Mammalogy* 66: 581-899.
- ARIELI R (1979) The atmospheric environment of the fossorial mole rat (*Spalax ehrenbergi*): Effects of season, soil texture, rain, temperature, and activity. *Comparative Biochemistry and Physiology* 63A: 596-575.
- ARMESTO JJ & LC CONTRERAS (1981) Saxicolous lichen communities; Non-equilibrium systems? *American Naturalist* 118: 597-604.
- ARMESTO JJ, PE VIDIELLA & JR GUTIERREZ (1993) Plant communities of the fog-free coastal desert of Chile: Plant strategies in a fluctuating environment. *Revista Chilena de Historia Natural* 66: 271-282.
- BANDOLI JH (1981) Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. *Journal of Mammalogy* 62: 293-303.
- BOEKEN B (1989) Life history of desert geophytes - the demographic consequences of reproductive biomass partitioning patterns. *Oecologia* 80: 278-283.
- CANTOR LF & TG WHITHAM (1989) Importance of belowground herbivory: Pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70: 962-970.
- CONNEL JH (1978) Diversity in tropical rain forest and coral reefs. *Science* 199: 1302-1310.
- CONTRERAS LC (In press) Biogeografía de mamíferos terrestres de Chile. In: Muñoz A, J Yáñez and J Rau (eds) *Manual de Mamíferos de Chile*.
- CONTRERAS LC & BK McNAB (1990) Thermoregulation and energetics of subterranean mammals. In: Nevo E & O Reig (eds) *Evolution of Subterranean Mammals at the Molecular and Individual Level*: 231-250. Wiley-Liss, New York.
- CONTRERAS LC & JR GUTIERREZ (1991) Effect of the subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile. *Oecologia* 87: 106-109.
- CONTRERAS LC, JC TORRES-MURA & JL YAÑEZ (1987) Biogeography of octodontid rodents: an eco-evolutionary hypothesis. *Feldiana Zoology (New Series)* 39: 401-411.
- COX GW (1984) The distribution and origin of Mima mound grasslands in San Diego County, California. *Ecology* 65: 1397-1405.
- COX GW (1986) Mima mounds as an indicator of the presettlement grassland-chaparral boundary in San Diego County, California. *American Midland Naturalist* 116: 64-77.
- COX GW (1989) Early summer diet and food preferences of northern pocket gophers in north central Oregon. *Northwest Science* 63: 77-82.
- COX GW (1990) Soil mining by pocket gophers along a topographic gradient in a Mima moundfield. *Ecology* 71: 837-843.
- COX GW & CG GAKAHU (1985) Mima mound microtopography and vegetation pattern in Kenyan savannas. *Journal of Tropical Ecology* 1: 23-36.
- COX GW & CG GAKAHU (1986) A latitudinal test of the fossorial rodent hypothesis of Mima mound origin in North America. *Zeitschrift für Geomorphologie* 30: 485-501.
- COX GW & DW ALLEN (1987a) Soil translocation by pocket gophers in a Mima moundfield. *Oecologia* 72: 207-210.
- COX GW & DW ALLEN (1987b) Sorted stone nets and circles of the Columbia Plateau: A hypothesis. *Northwest Science* 61: 179-185.
- COX GW & JB ZEDLER (1986) The influence of Mima mounds on the vegetation patterns in the Tijuana Estuary salt marsh, San Diego, California. *Bulletin of the Southern California Academy of Sciences* 85: 158-172.
- COX GW & J HUNT (1992) Seasonal activity patterns of valley pocket gophers: Importance of temperature, rainfall and food availability. *Journal of Mammalogy* 73: 123-134.
- COX GW & VB SCHEFFER (1991) Pocket gophers and Mima terrain in North America. *Natural Areas Journal* 11: 193-198.
- COX GW, LC CONTRERAS & AV MILEWSKI (In press) Role of fossorial animals in community structure and energetics of mediterranean ecosystems. In: Arroyo MTK, PH Zedler & MD Fox (eds) *Ecology of Convergent Ecosystems of Chile, California and Australia*: 000-000. Springer-Verlag, New York.
- DENSLow JS (1980) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.
- EHRENDORFER F (1976) Evolutionary significance of chromosomal differentiation patterns in gymnosperms and primitive angiosperms. In: Beck CB (ed) *Origin and Early Evolution of Angiosperms*: 220-240. Columbia Univ. Press, New York.
- FULK GW (1976) Notes on the activity, reproduction and social behaviour of *Octodon degus*. *Journal of Mammalogy* 57: 495-505.
- GETTINGER RD (1984) Energy and water metabolism of free-ranging pocket gophers, *Thomomys bottae*. *Ecology* 65: 740-751.
- GOLDBERG DE & KL GROSS (1988) Disturbance regimes of midsuccessional old fields. *Ecology* 69: 1677-1688.
- GRUBB PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107-145.
- HAIRSTON NG, FE SMITH, LB SLOBODKIN (1960) Community structure, population control, and competition. *American Naturalist* 94: 421-425.
- HARPER JL (1977) *Population Biology of Plants*. Academic Press, London.
- HETH G (1991) The environmental impact of subterranean mole rats (*Spalax ehrenbergi*) and their burrows. *Symposia Zoological Society London* 63: 265-280.
- HICKMAN G (1990) Adaptativeness of tunnel systems features in subterranean mammals. In: Nevo E & O Reig (eds), *Evolution of Subterranean Mammals at the Molecular and Individual Level*: 185-210. Wiley-Liss, New York.

- HICKMAN GC & LN BROWN (1973) Pattern and rate of mound production in the southeastern pocket gopher (*Geomys pinetis*). *Journal of Mammalogy* 54: 971-975.
- HOBBS RJ & HA MOONEY (1985) Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia* 67: 342-351.
- HOBBS RJ & HA MOONEY (1991a) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* 72: 59-68.
- HOBBS RJ & HA MOONEY (1991b) Effect of episodic rain events on Mediterranean-climate ecosystems. In: Roy J, J Aronson & F di Castri (eds) *Timescales of biological response to water constraints*. Springer, New York.
- HOBBS RJ, SL GULMON, VJ HOBBS & HA MOONEY (1988) Effects of fertilizer addition and subsequent gopher disturbance on serpentine annual grassland community. *Oecologia* 75: 291-295.
- HUNTLY NH & RS INOUE (1988) Effects of gophers (*Geomys bursarius*) on ecosystems. *Bioscience* 38: 786-793.
- HUSTON M (1979) A general hypothesis of species diversity. *American Naturalist* 113: 81-101.
- INGLES LG (1952) The ecology of the mountain pocket gopher, *Thomomys monticola*. *Ecology* 33: 87-95.
- INOUE RS, NJ HUNTLY, D TILMAN & JR TESTER (1987) Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* 72: 178-184.
- IRIARTE JA, LC CONTRERAS & MF JAKSIC (1989) A long-term study of a small-mammal assemblage in the central Chilean matorral. *Journal of Mammalogy* 70: 79-87.
- JAKSIC FM, ER FUENTES & JL YAÑEZ (1979) Spatial distribution of the Old World rabbit (*Oryctolagus cuniculus*) in central Chile. *Journal of Mammalogy* 60: 207-209.
- KOIDE RT & HA MOONEY (1987) Spatial variation in inoculum potential of vesicular-arbuscular mycorrhizal fungi caused by formation of gopher mounds. *New Phytologist* 107: 173-182.
- KOIDE RT, LF HUENNEKE & HA MOONEY (1987) Gopher mound soil reduces growth and affects ion uptake of two annual grassland species. *Oecologia* 72: 284-290.
- LOVEGROVE BG (1991) The evolution of eusociality in mole-rats (Bathyergidae): a question of risk, numbers, and costs. *Behavioral Ecology and Sociobiology* 28: 37-45.
- LOVEGROVE BG & JUM JARVIS (1986) Coevolution between mole-rats (Bathyergidae) and a geophyte, *Micranthus* (Iridaceae). *Cimbebasia* 8: 79-85.
- LOVEGROVE BG & C WISSEL (1988) Sociality in mole-rats. *Metabolic scaling and the role of risk sensitivity*. *Oecologia* 74: 600-606.
- MacARTHUR RH (1972) *Geographical Ecology*. Harper and Row, New York.
- MARES MA (1980) Convergent evolution among desert rodents: A global perspective. *Bulletin of Carnegie Museum of Natural History* 16: 1-51.
- MARTINSEN GD, JH CUSHMAN & TG WHITHAM (1990) Impact of gopher disturbance on plant species diversity in a short-grass prairie community. *Oecologia* 83: 132-138.
- MILLER MA (1957) Burrows of the Sacramento Valley pocket gopher in flood-irrigated alfalfa field. *Hilgardia* 26: 431-452.
- MESERVE PL (1981) Resource partitioning in a Chilean semi-arid small mammal community. *Journal of Animal Ecology* 50: 745-757.
- NEVO E (1979) Adaptive convergence and divergence of subterranean mammals. *Annual Review of Ecology and Systematics* 10: 269-308.
- PICKETT STA & PS WHITE (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- PIANKA ER (1976) Competition and niche theory. In: RM May (ed) *Theoretical Ecology: Principles and applications*. Chapter 7: 114-141. Blackwell.
- REDFORD KH & JF EISENBERG (1992) *Mammals of the Neotropics: The Southern Cone*. University of Chicago Press, Chicago.
- REICHMAN OJ (1988) Comparison of the effects of crowding and pocket gopher disturbance on mortality, growth and seed production of *Berteroa incana*. *American Midland Naturalist* 120: 58-69.
- REICHMAN OJ, JH BENEDIX Jr. & TR SEASTEDT (1993) Distinct animal-generated edge effects in a tallgrass prairie community. *Ecology* 74: 1281-1285.
- REICHMAN OJ & JUM JARVIS (1989) The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. *Journal of Mammalogy* 70: 763-771.
- REICHMAN OJ & SC SMITH (1985) Impact of pocket gopher burrows on overlying vegetation. *Journal of Mammalogy* 66: 720-725.
- REICHMAN OJ & SC SMITH (1991) Burrows and burrowing behavior by mammals. In: Genoways HH (ed) *Current Mammalogy* 2: 197-244.
- REICHMAN OJ, T WHITHAM & G RUFFNER (1982) Adaptive geometry of burrow spacing in two pocket gopher populations. *Ecology* 63: 687-695.
- REIG OA (1970) Ecological notes on the fossorial octodon rodent *Spalacopus cyanus* (Molina). *Journal of Mammalogy* 51: 592-601.
- REIG OA, C BUSCH, MO ORTELLS & JR CONTRERAS (1990) An overview of evolution, systematics, population biology, cytogenetics, molecular biology and speciation in *Ctenomys*. In: Nevo E & O Reig (eds) *Evolution of Subterranean Mammals at the Molecular and Individual Level*: 71-96. Wiley-Liss, New York.
- RICHEMS VB (1966) Notes on the digging activity of a northern pocket gopher. *Journal of Mammalogy* 47: 531-533.
- SCHOENER TW (1974) Resource partitioning in ecological communities. *Science* 185: 27-39.
- SCHOFIELD CJ & EH BUCHER (1986) Industrial contribution to desertification in South America. *Trends in Ecology and Evolution* 1: 78-80.
- SIMONETTI JA, ER FUENTES & RD OTAIZA (1985) Habitat use by two rodent species in the high Andes of central Chile. *Mammalia* 49: 19-25.
- SKOCZEN S, H NAGAWIECKA, K BORON & A GLAKA (1976) The influence of mole tunnels on soil moisture on pastures. *Acta Theriologica* 21: 543-548.
- SOUSA WP (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.

- SOLBRIG OT (1984) The southern Andes and Sierras Pampeanas. *Mountain Research and Development* 4: 97-190.
- THORNE DH & DC ANDERSEN (1990) Long-term soil disturbance pattern by a pocket gopher, *Geomys bursarius*. *Journal of Mammalogy* 71: 84-89.
- TILMAN D (1983) Plant succession and gopher disturbance along an experimental gradient. *Oecologia* 60: 285-292.
- TORRES-MURA JC (1990) Uso del espacio por el roedor fosorial *Spalacopus cyanus*. Magister's Thesis, Facultad de Ciencias, Universidad de Chile.
- VLECK D (1981) Burrow structure and foraging cost in the fossorial rodent, *Thomomys bottae*. *Oecologia* 49: 391-396.
- WHITFORD WG (1993) Animal feedbacks in desertification: an overview. *Revista Chilena de Historia Natural* 66: 243-251.
- WILLIAMS LR & GN CAMERON (1990) Dynamics of burrows of Attwater's pocket gopher (*Geomys attwateri*). *Journal of Mammalogy* 71: 433-438.
- ZOELLNER O (1972) El género *Leucocoryne*. *Anales Museo Historia Natural de Valparaíso* 5: 9-81.