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# Dietary preferences of two sympatric subterranean rodent populations in Argentina

## Preferencias dietarias de dos poblaciones simpátridas de roedores subterráneos en Argentina

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**ABSTRACT**

We determined the dietary habits of two sympatric and allotopic populations of *Ctenomys* (*C. australis* and *C. talarum*) that inhabit a natural dune grassland on the sea coast at Necochea, Buenos Aires Province, Argentina. Both species were found to be generalist herbivores as they consumed almost all plant species available in the grassland. Contrary to what we had expected, they fed principally on the aerial fraction of the vegetation, and preferred grasses over forbs. The greater proportion of the subterranean fraction in autumn and winter in *C. australis* diets compared to *C. talarum* might be related to differences in the vegetation around the burrows they inhabit. *Ctenomys australis* and *C. talarum* diets differed markedly only in September; however, these differences may not have been totally seasonal, there may also have been a spatial effect due to the soil structure of the sympatric area. *Ctenomys australis* and *C. talarum* distributions seem to be related to soil characteristics with individual animals feeding and selecting mainly among the vegetal species in their own home range. The results of this study show that these species of *Ctenomys* present a feeding strategy which is adaptative in subterranean rodents due to their high digging cost and to the low available energy to explore in their subterranean environment.
**Key words:** *Ctenomys australis*, *Ctenomys talarum*, Rodentia, Octodontidae, tuco-tuco.

**RESUMEN**

Se determinaron los hábitos dietarios de dos poblaciones simpátridas y alotópicas del género *Ctenomys* (*C. australis* y *C. talarum*) que habitan un pastizal natural en dunas de la costa de Necochea, Provincia de Buenos Aires, Argentina. Ambas especies resultaron ser herbívoros generalistas ya que consumieron gran parte de las especies vegetales presentes en el pastizal. Contrariamente a lo esperado, se alimentaron principalmente de la fracción aérea de la vegetación y prefirieron gramíneas sobre dicotiledóneas herbáceas. La mayor proporción de la fracción subterránea en las dietas de *C. australis* con respecto a las de *C. talarum* en otoño e invierno, pudo estar relacionada con diferencias en la vegetación cercana a sus cuevas. Las dietas de *C. australis* y *C. talarum* difirieron marcadamente en septiembre; sin embargo, estas diferencias no serían atribuídas totalmente a la estación ya que pudo haber existido un efecto espacial debido a la estructura del suelo del área de simpatría. La distribución de ambas especies parece relacionarse a las características del suelo, y los animales se alimentan principalmente de las especies vegetales en su área de acción. Los resultados de este trabajo muestran que las especies estudiadas de *Ctenomys* presentan una estrategia de alimentación adaptativa en roedores subterráneos debido a su alto costo de cavado y a la baja energía disponible para explorar en el ambiente subterráneo.
**Palabras clave:** *Ctenomys australis*, *Ctenomys talarum*, Rodentia, Octodontidae, tuco-tuco.

## INTRODUCTION

Rodents of the genus *Ctenomys* ("tuco-tucos") are subterranean herbivores that search for food principally by digging galleries (Contreras 1973). Nevo (1979) suggested that subterranean mammals are food generalists due to the high cost of digging burrows. In this respect, Vleck (1979), studying pocket gophers (Geomyids), which have similar habits to those of tuco-tucos, determined that digging a gallery requires from 360 to 3400 times more energy than walking the same distance over the surface. Furthermore, Heth *et al.* (1989) analyzing the feeding behavior of mole rats (Spalacidae), concluded that animals foraging underground, with large search expenditures and variable food resources, must collect all relevant food species found whereas burrowing. This, plus to a non-directed search pattern, will produce a generalist foraging behavior.

There are few studies on *Ctenomys* dietary habits (Torres-Mura et al. 1989, Del Valle 1990, Lohfeldt 1991), and the only one that

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considered species selectivity in the field (Lohfeldt 1991) is related to a unique population. On the contrary, the information referred to dietary habits of pocket gophers is greater. The diet of these rodents is broad due to the high foraging cost, but several authors found they consume certain plant species in a greater proportion than others (Russell & Baker 1955, Keith et al. 1959, Miller 1964, Vaughan & Hansen 1964, Laycock & Richardson 1975, Spencer et al. 1985). Furthermore, it has been stated that the pocket gopher *Geomys attwateri* eats a greater proportion of the subterranean fraction of vegetation respect to the aerial fraction (Williams & Cameron 1986).

TABLE 1

Vegetation groups, according to ordination and classification techniques, of a dune natural grassland where *Ctenomys australis* and *C. talarum* coexist (Necochea, Buenos Aires Province, Argentina, 1987-88), after Comparatore et al., (1992).

Grupos de vegetación, según técnicas de ordenamiento y clasificación, de un pastizal natural en dunas de Necochea (Buenos Aires, argentina, 1987-1988), en donde coexisten poblaciones de *Ctenomys australis* y *C. talarum*, según Comparatore et al., (1992).

| Group | Attributes | Species | Family |
|---|---|---|---|
| G1 | Forbs, Annuals, | *Senecio madagascariensis* | Asteraceae |
| | Cool season species, | *Gamochaeta spicata* | Asteraceae |
| | Pivotal roots, | *Lepidium bonariense* | Brassicaceae |
| | Without reserve organs, | *Stellaria media* | Caryophyllaceae |
| | Present in modified | *Geranium dissectum* | Geraniaceae |
| | fields | *Melilotus indicus* | Papilionaceae |
| | | *Medicago minima* | Papilionaceae |
| | | *Medicago lupulina* | Papilionaceae |
| G2 | Forbs, Perennials, | *Mesembryanthemum* sp | Aizoaceae |
| | Warm season species, | *Achyrocline satureioides* | Asteracea |
| | Pivotal roots | *Ambrosia tenuifolia* | Asteracea |
| | | *Solidago chilensis* | Asteracea |
| | | *Convolvulus hermanniae* | Convolvulaceae |
| | | *Oenothera mollisima* | Onagraceae |
| | | *Adesmia incana* | Papilionaceae |
| | | *Margyricarpus pinnatus* | Rosaceae |
| G3 | Forbs and Grasses, | *Hydrocotyle bonariensis* | Apiaceae |
| | Perennials, | *Calystegia soldanella* | Convolvulaceae |
| | With reserve organs, | *Panicum racemosum* | Poaceae |
| | Warm season species, | *Paspalum vaginatum* | Poaceae |
| | Creeping habit | *Solanum commersonii* | Solanaceae |
| G4 | Grasses, Perennials, | *Agrostis* sp. | Poaceae |
| | Glabrous | *Poa bonariensis* | Poaceae |
| | | *Sporobolus indicus* | Poaceae |
| G5 | Grasses, Fibrous roots, | *Bothriochloa laguroides* | Poaceae |
| | Without reserve organs, | *Stipa neesiana* | Poaceae |
| | Erect habit | *Stipa trichotoma* | Poaceae |
| | | *Bromus* sp. | Poaceae |
| | | *Lolium multiflorum* | Poaceae |
| | | *Poa annua* | Poaceae |
| | | *Hordeum leporinum* | Poaceae |
| | | *Catapodium rigidum* | Poaceae |
| | | *Lophochloa phleoides* | Poaceae |

In this study, we determined the dietary habits of two sympatric populations of *Ctenomys* (*C. australis* Rusconi, 1934 and *C. talarum* Thomas, 1898) that inhabit a natural grassland in dunes of Necochea, Buenos Aires Province, Argentina. Inside their overlap zones, the distribution of these species is linked to a micropattern of soil and vegetation. *C. australis* inhabits areas with sparse vegetation, sandy and deep soils, while *C. talarum* inhabits areas with dense vegetation, compact and shallow soils (Comparatore et al. 1992). Corporal size differences between these populations has been documented by Busch (1989), who determined *C. australis* weighs three times *C. talarum*. We tested that both species of *Ctenomys* are generalist herbivores and eat a greater proportion of the subterranean fraction of plants, especially in winter when aerial availability decreases. Moreover, we expected to find differences in *C. australis* and *C. talarum* feeding habits related to differences in their habitat use. We also expected to find a greater proportion of the subterranean fraction in *C. australis* stomachs with respect to *C. talarum*, due to its greater body size and energetic requirements (Busch 1989), and its relation with areas of sparse vegetation (Comparatore et al. 1992) where predation risks are higher.

## MATERIALS AND METHODS

This study was carried out from November 1987 to September 1988, in a natural dune grassland described by Vervoorst (1967) and Cabrera & Zardini (1978), in the coastal region of Necochea, Buenos Aires Province, Argentina. This zone is inhabited by sympatric populations of *C. australis* and *C. talarum*. To characterize the vegetation, we used the information from a simultaneous study carried out by Comparatore et al. (1992). In that study, plant species were grouped by ordination and classification techniques, according to bionomic attributes that we considered relevant to the spatial heterogeneity of the vegetation and plant-animal interactions. The attributes considered were: perennation, presence of reserve organs, phenology, pilosity, growth characteristics, presence in altered fields, and taxonomic class (Table 1).

Vegetation samples were extracted late in each season from one of four 2 ha grids randomly selected inside the overlap zones of both species. Soil blocks of 30 cm diameter and 30 cm depth were extracted every 20 m from each grid. Later the aerial and subterranean biomass were estimated and expressed as percentages after drying the material. In addition, the percentage represented by each group in the aerial fraction was computed.

Every animal present in the grids was captured, identified, and its location in the grid was registered. Data concerning population structures are published elsewhere (Malizia et al. 1991). In the overlap zone studied in spring, distributions of *C. australis* and *C. talarum* were clearly delimited. In contrast, in the summer, autumn and winter zones, the spatial distributions of the species were more intercalated.

Botanical composition of the diets was estimated using microhistological techniques. Stomach contents were processed individually according to Williams (1969), and the botanical composition of the diet

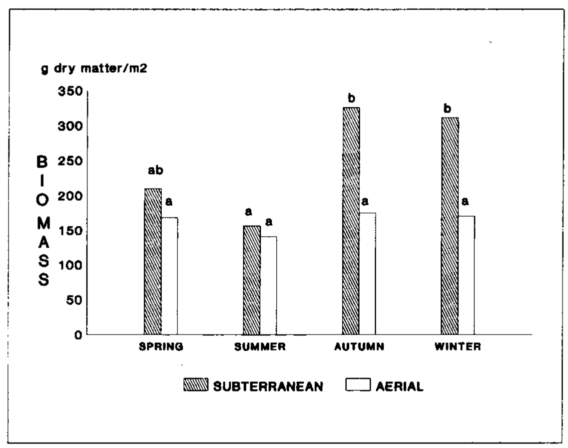


*Fig.* 1. Aerial and subterranean plant biomass in a natural grassland where *Ctenomys australis* and *C. talarum* coexist (Necochea, Argentina, 1987-88). For each fraction, seasonal means with tha same letter do not differ significantly ($p>0.05$).

Biomasa aérea y subterránea de la vegetación de un pastizal natural en el que coexisten *Ctenomys australis* y *C. talarum* coexist (Necochea, Argentina, 1987-88).Para cada fracción, las medias estacionales con la misma letra no difieren significativamente ($p>0.05$).

was quantified according to Sparks & Malechek (1968). Diet components quantified by microanalysis were: total subterranean fraction, total reproductive fraction and aerial vegetative fraction of each species. Later, the aerial fractions of each species were grouped (groups G1 to G5, see Table 1) according to Comparatore et al. (1992). There are studies that show that the species of the subterranean fraction can be quantified by microanalysis (Williams & Cameron 1986). However, we could not differentiate species in the subterranean or in the reproductive fractions; thus we combined all species in each of these fractions. For statistical analysis data normality and homogeneity were determined by Shapiro-Wilk and Levenne tests, respectively (SAS 1988). When these criteria were not satisfied, data were transformed by arcsin $\sqrt{x}$. The seasonal percentages of the components in *Ctenomys* diets were compared using Tukey Test ($\alpha$=0.05).

Data on the botanical composition of the diet were analyzed complementing ordination (Principal Component Analysis, PCA; Harris 1975) and classification (Cluster Analysis, CA; Orlóci 1978) techniques with the statistical package SYSTAT (1985). Analyses of annual and seasonal data were performed. The CA method applied was the nearest neighbor with simple linkage, and 1-Pearson correlation coefficient was used for sample distances. Among samples, mean similarity to delimit sample groups was established at ≥ 80%.

Botanical compositions of the diet and the grassland were contrasted to establish animal's preference for total aerial and subterranean fractions. In addition, aerial group preferences were computed. Preference for the reproductive fraction could not be established because its percentage was not determined in the grassland.

The following index (Krueger 1972) was used to determine relative species preferences (PI) by *Ctenomys*:

$$PI= \frac{\%Di \times fdi}{\%Gi \times fgi}$$

where %Di and fdi are the seasonal mean percentage and the frequency of component i in the diets, and %Gi and fgi are the seasonal mean percentage and the frequency of the component i in the grassland. PI values were determined for each *Ctenomys* population and for both populations pooled.

The Chi-square test with 95% of confidence was used to determine if the seasonal PI for each component was significantly different from one. A component was considered as preferred when PI>1, not preferred when PI<1, or indifferent when PI=1. The species considered in the analysis were those with seasonal mean percentage by frequency in the diets and/or in the grassland were over 2%.

TABLE 2.

Mean seasonal biomass in percentage (x±SD) and frecuency of appearance (f) of the subterranean (Sub) and aerial fractions of a natural grassland where *Ctenomys australis* and *C. talarum* coexist (Necochea, Argentina, 1987-88). Mean seasonal biomass of species groups (see Table 1) are expressed as percentages of the total aerial biomass.

Biomasa media estacional en porcentaje (x±SD) y frecuencia de aparición (f) de las fracciones subterránea (Sub) y área de un pastizal natural en donde coexisten *Ctenomys australis y C. talarum* (Necochea, Argentina, 1987-88). La biomasa media estacional de los grupos de especies (ver Tabla 1) se expresaa como porcentaje de la biomasa aérea total.

| | | Sub | Aerial | G1 | G2 | G3 | G4 | G5 |
|---|---|---|---|---|---|---|---|---|
| SPRING | x±SD | 54.3±13.3 | 45.7±13.3 | 13.2±18.9 | 34.4±37.1 | 39.8±41.0 | 7.2±12.5 | 5.5± 9.7 |
| n=24 | f | 1.00 | 1.00 | 0.63 | 0.54 | 0.83 | 0.67 | 0.5 |
| SUMMER | x±SD | 49.4±16.2 | 46.4±15.8 | 0.3± 0.7 | 6.5±13.9 | 72.7±26.3 | 11.7±11.8 | 4.1±14.4 |
| n=24 | f | 0.96 | 0.96 | 0.13 | 0.29 | 0.96 | 0.83 | 0.08 |
| AUTUMN | x±SD | 65.7± 7.5 | 34.4± 7.5 | 26.7±28.1 | 9.3±22.8 | 41.4±34.1 | 8.6± 9.7 | 12.5±22.2 |
| n=31 | f | 1.00 | 1.00 | 0.68 | 0.42 | 0.97 | 0.90 | 0.36 |
| WINTER | x±SD | 56.8±26.2 | 32.8±20.7 | 8.4±20.0 | 12.3±23.5 | 46.4±41.6 | 19.5±25.9 | 1.4± 8.6 |
| n=48 | f | 0.90 | 0.90 | 0.27 | 0.29 | 0.81 | 0.67 | 0.06 |

## RESULTS

### *Plant Biomass*

Subterranean biomass in the autumn and winter was twice that of the summer. However, no significant differences were found among seasonal aerial plant biomass (Fig. 1). The mean seasonal biomass percentages used to calculate the preference indices are shown in Table 2.

### *Botanical composition of diet*

Throughout the year, the diet of *C. australis* and *C. talarum* populations contained 11 and 17 species, respectively. Unexpectedly, both populations consumed a greater proportion of the aerial fraction than the subterranean one, whose annual average for all animals was 3%. The mean percentage of the subterranean fraction in the diets of all animals was lower than 5.5% in every season; however, *C. australis* consumed around 10% of this fraction in autumn and winter (Table 3a). In general, the average aerial vegetative fraction of the diet was greater than the reproductive fraction in all seasons except autumn (Table 3). Considering only the aerial vegetative fraction, G2, G3 and G4 represented 95% of the annual average in the diet of all the animals. Throughout the year, the diet of *C. australis* was composed principally of G3 (spring and summer) and G4 (autumn and winter). *Ctenomys talarum* diets showed a botanical composition similar to the former during autumn and winter.

TABLE 3

Botanical composition in percentage (x ± SD) and frequency of appearance (f) of subterranean (Sub), aerial vegetative (Veg) and reproductive (Rep) fractions in diets of sympatric populations of *Ctenomys australis* and *C. talarum* (Necochea, Argentina, 1987-88). Tukey test to differentiate among seasonal means by fractions (small letters), and among fractions in each season (capital letters); α= 0.05.

Composición botánica en porcentaje (x ± SD) y frecuencia de aparición (f) de las fracciones subterránea (Sub), aérea vegetativa (Veg) y reproductiva (Rep) en dietas de poblaciones simpátridas de *Ctenomys australis* y *C. talarum* (Necochea, Argentina, 1987-88). Se utilizó el test de Tukey para diferenciar entre medias estacionales de cada fracción (letras minúsculas), y entre fracciones en cada estación (letras mayúsculas); α= 0.05.

a) *C. australis*

| | | Sub | Veg | Rep |
|---|---|---|---|---|
| Annual (n= 30) | % | 5.5 ± 6.1 | 58.7 ± 17.6 | 35.8 ± 16.4 |
| Spring (n= 12) | % | 1.2 ± 1.5 a,A | 67.6 ± 16.7 b,C | 31.2 ± 17.1 a,B |
| | f | 0.83 | 1.00 | 1.00 |
| Summer (n= 3) | % | 2.7 ± 1.7 ab,A | 62.5 ±7.9 b,C | 34.8 ±9.5 a,B |
| | f | 1.00 | 1.00 | 1.00 |
| Autumn (n= 3) | % | 12.9 ± 8.2 bc,A | 37.8 ±4.8 a,B | 49.3 ± 12.7 a,B |
| | f | 1.00 | 1.00 | 1.00 |
| Winter (n= 12) | % | 8.6 ± 5.9 bc,A | 54.2 ± 17.2 ab,C | 37.2 ± 17.1 a,B |
| | f | 1.00 | 1.00 | 1.00 |

b) *C. talarum*

| | | Sub | Veg | Rep |
|---|---|---|---|---|
| Annual (n= 49) | % | 1.5 ± 2.0 | 60.9 ± 16.8 | 37.6 ± 16.8 |
| Spring (n= 9) | % | 0.8 ± 1.9 a,A | 77.8 ± 11.3 a,C | 21.4 ± 10.8 a,B |
| | f | 0.44 | 1.00 | 1.00 |
| Summer (n= 13) | % | 2.1 ± 2.4 a,A | 56.3 ± 15.8 b,C | 41.6 ± 15.5 b,B |
| | f | 0.85 | 1.00 | 1.00 |
| Autumn (n= 14) | % | 0.9 ± 2.0 a,A | 52.5 ± 12.0 b,B | 46.6 ± 12.2 b,B |
| | f | 0.71 | 1.00 | 1.00 |
| Winter (n= 13) | % | 1.9 ± 1.7 a,A | 62.8 ± 17.6 ab,C | 35.3 ± 18.4 ab,B |
| | f | 0.92 | 1.00 | 1.00 |

However, they consumed principally G2 and G4 species in spring and summer, respectively (Table 4).

In the grassland, *Panicum racemosum* represented around 80% of G3 (warm season forbs and grasses with reserve organs) and *Poa bonariensis* 90% of G4 (perennial grasses). So, G3 and G4 in diets were almost exclusively represented by these species.

Individual spring diets were grouped by animal species when complementing ordination (PCA) and classification (CA) techniques (Fig. 2). Axis 1 opposed G2 (weight = 0.926) to G3 (weight = 0.842) and explained 28% of the total variance. *Ctenomys australis* and *C. talarum* diets contained 11 and 64% of G2, and 68 and 10% of G3, respectively (Table 4). In summer, autumn and winter, samples were not grouped by animal species.

Principal component and cluster annual analyses showed that the diets of *C. australis* and *C. talarum* in spring, besides differing between them, differed from summer, autumn and winter diets, which were very similar among them.

*Feeding preferences*

Contrary to what we expected, the aerial fraction was preferred while the subterranean fraction was not preferred by individuals of both populations in all seasons (Table 5). When preferences for the different groups were considered (Table

TABLE 4

Botanical composition in percentage (x±SD) and frequency of appearance (f) of the aerial vegetative fraction by groups of species (see Table 1) in diets of sympatric populations of *Ctenomys australis* and *C. talarum* (Necochea, Argentina, 1987-88). Tukey test to differentiate among species group seasonal means (small letters), and among species groups in each season (capital letters); α=0.05.

Composición botánica en porcentaje (x ± SD) y frecuencia de aparición (f) de la fracción aérea vegetativa por grupos de especies (ver Tabla 1) en dietas de poblaciones simpátridas de *Ctenomys australis* y *C. talarum* (Necochea, Argentina, 1987-88). Se utilizó el test de Tukey para diferenciar entre medias estacionales por grupos de especies (letras minúsculas), y entre grupos de especies en cada estación (letras mayúsculas); α= 0.05.

a) *C. australis*.

| | | G1 | G2 | G3 | G4 | G5 |
|---|---|---|---|---|---|---|
| Annual (n=30) | % | 0.1 ± 0.3 | 8.4 ± 13.8 | 38.4 ± 35.1 | 51.0 ± 35.9 | 2.1 ± 4.8 |
| Spring | % | 0.1 ± 0.5 | 10.7 ± 16.1 a,AB | 67.8 ± 25.3 a,C | 16.5 ± 12.8 a,B | 4.8 ± 6.9 a,A |
| (n=12) | f | 0.17 | 0.75 | 1.00 | 1.00 | 0.67 |
| Summer | % | 0.1 ± 0.2 | 1.3 ± 2.3 a,A | 66.3 ± 27.5 a,B | 32.0 ± 27.5 a,AB | 0.3 ± 0.5 a,A |
| (n=3) | f | 0.33 | 0.33 | 1.00 | 1.00 | 0.33 |
| Autumn | % | 0 | 1.6 ± 2.8 a,A | 14.5 ± 10.7 b,B | 82.8 ± 11.6 b,C | 1.1 ± 0.6 a,AB |
| (n=3) | f | 0 | 0.33 | 1.00 | 1.00 | 1.00 |
| Winter | % | 0 | 9.6 ± 14.3 a,B | 7.9 ± 11.3 b,B | 82.3 ± 18.4 b,C | 0.2 ± 0.4 a,A |
| (n=12) | f | 0 | 0.58 | 1.00 | 1.00 | 0.33 |

b) *C. talarum*.

| | | G1 | G2 | G3 | G4 | G5 |
|---|---|---|---|---|---|---|
| Annual (n=49) | % | 0.4 ± 1.6 | 19.5 ± 29.4 | 16.3 ± 23.4 | 59.0 ± 34.2 | 4.9 ± 9.6 |
| Spring | % | 1.8 ± 3.5 | 63.6 ± 33.3 a,B | 9.5 ± 13.2 a,A | 11.6 ± 14.3 a,A | 13.6 ± 14.6 a,A |
| (n=9) | f | 0.33 | 1.00 | 1.00 | 1.00 | 0.89 |
| Summer | % | 0.1 ± 0.1 | 6.6 ± 10.5 b,A | 23.3 ± 27.8 a,A | 63.4 ± 26.1 b,B | 6.7 ± 10.9 ab,A |
| (n=13) | f | 0.08 | 0.69 | 0.92 | 1.00 | 0.85 |
| Autumn | % | 0.1 ± 0.2 | 8.1 ± 11.1 b,AB | 19.1 ± 24.4 a,B | 72.1 ± 25.9 b,C | 0.6 ± 0.8 b,A |
| (n=14) | f | 0.14 | 0.71 | 1.00 | 1.00 | 0.64 |
| Winter | % | 0 | 14.2 ± 25.6 b,A | 10.9 ± 22.9 a,A | 73.4 ± 32.1 b,B | 1.6 ± 3.4 b,A |
| (n=13) | f | 0 | 0.62 | 0.92 | 1.00 | 0.54 |

6), it was evident G4 was always preferred. On the contrary, G1 (annual forbs) was never preferred. The rank of relative preferences varied through the year and with animal species, and no common selection pattern was observed with respect to G2, G3 and G5. In summer, G5 (grasses without reserve organs) had the highest PI value among groups in *C. talurum* population (Table 6b).

## DISCUSSION

The results confirm that *C. australis* and *C. talarum* are generalist herbivores as they consume almost all the plant species available in the grassland, as found for *Geomys attwateri* and *Spalax ehrenbergi* by Williams & Cameron (1986) and Heth et al. (1989), respectively. Furthermore, similar results were found for *C. talarum* in a cafeteria trial (Del Valle 1990) and in a field study (Lohfeldt 1991). However, contrary to what we expected, they fed principally on the aerial fraction of the vegetation. The subterranean proportion in the diet of *Ctenomys* was low compared with the one found in other subterranean rodents. Thus, Cox (in press) determined that *Thomomys talpoides* diets averaged 21% of root material, ranging from 0 to 100% of individual stomach contents. *Ctenomys* individuals showed a smaller variability, and roots never constituted more than 22% of the total material. In addition, Luce et al. (1980) established for *G. bursarius* a value of 30% of subterranean fraction, and Williams and Cameron (1986) for *G. attwateri*, 60%. The latter authors suggested the difference between these two results

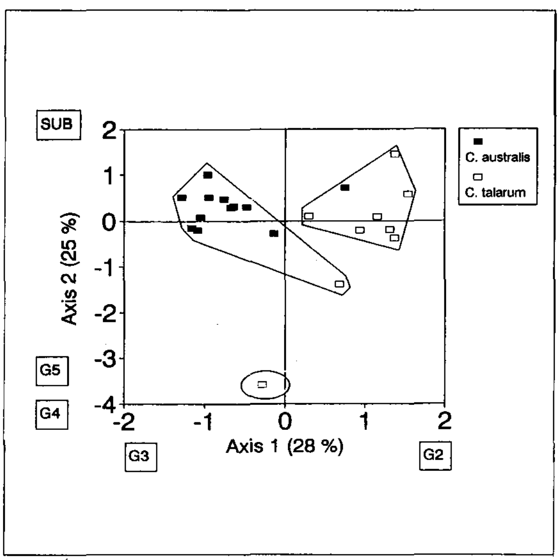


*Fig.*2.Scatter diagram of the spring diets of sympatric *Ctenomys australis* and *C. talarum* (Necochea, Argentina, 1987-88). Groups are based on cluster analysis. Values between brackets show the percentage of the variance explained by each axis. SUB = subterranean fraction; G1 to G5 see Table 1.

Diagrama de dispersión de las dietas de primavera de poblaciones simpátridas de *Ctenomys australis* y *C. talarum* (Necochea, Argentina, 1987-88). Los grupos están basados en el análisis de agrupamiento. Los valores entre paréntesis muestran el porcentaje de la varianza explicado por cada eje. SUB = fracción subterránea; G1 a G5 ver Tabla 1.

TABLE 5

Seasonal values of preference index (PI) for subterranean and aerial fractions of sympatric populations of *Ctenomys australis* and *C.talarum* (Necochea, Argentina, 1987-88). Chi-square test, (*) PI≠1, (p≤0.05).

Valores estacionales del índice de preferencia (PI) por las fracciones subterránea y aérea de poblaciones simpátridas de *Ctenomys australis* y *C.talarum* (Necochea, Argentina, 1987-88). Test Chi-cuadrado, (*) PI≠1, (p≤0.05).

a) *C. australis*

| | Subterranean | Aerial |
|---|---|---|
| Spring (n= 12) | 0.03 * | 2.16 * |
| Summer (n= 3) | 0.07 * | 2.18 * |
| Autumn (n= 3) | 0.37 * | 2.54 * |
| Winter (n= 12) | 0.30 * | 3.10 * |

b) *C. talarum*

| | Subterranean | Aerial |
|---|---|---|
| Spring (n= 9) | 0.01 * | 2.17 * |
| Summer (n= 13) | 0.06 * | 2.20 * |
| Autumn (n= 14) | 0.02 * | 2.88 * |
| Winter (n= 13) | 0.04 * | 3.33 * |

was due to the different behavior of animal species, *Geomys bursarius* spends more time out of its burrow than *G. attwateri*. Therefore, it would be expected *C. australis* and *C. talarum* spend still more time out. Our field observations seem to confirm this behavior.

In *Ctenomys* diets, the subterranean fraction was five times lower in spring than in winter. This difference can be related to the active growth of plants in the spring resulting in a greater ratio of live:dead biomass aboveground. In agreement, Luce et al. (1980) found *G. bursarius* stomach contents had more subterranean material than sheaths and leafs during autumn and winter. The contrary occurred in spring. Similar results were obtained by Williams & Cameron (1986) in a grassland dominated by perennial grasses and annual forbs. These authors found *G. attwateri* stomach contents had a greater proportion of subterranean material in autumn and winter than in spring and summer, since in the latter seasons there was more aerial biomass available. They suggested that *G. attwateri* is able to obtain its food by pulling down entire plants from belowground, because although it rarely occurs aboveground, 40% of its diet was aerial biomass. It could be expected tuco-tucos digging their burrows would eat a greater proportion of the subterranean fraction of plants than we determined. However, once tunnels are constructed, they would obtain their food principally from aboveground, as said before, and pulling down whole plants into the burrows.

The different consumption of the subterranean fraction by the animal species seems to be influenced by vegetation features and plant-animal relationships. The

TABLE 6

Seasonal values of preference index (PI) for the aerial fraction by groups of species (see Table 1) of sympatric populations of *Ctenomys australis* and *C. talarum* (Necochea, Argentina, 1987-88). Chi-square test, (*) PI≠1, (NS) PI=1, (p≤0.05). NC= non computed (% in diet and grassland < 2).

Valores estacionales del índice de preferencia (PI) por grupos de especies en la fracción aérea (ver Tabla 1) de poblaciones simpátridas de *Ctenomys australis* y *C.talarum* (Necochea, Argentina, 1987-88). Test Chi-cuadrado, (*) PI≠1, (NS) PI=I, (p≤0.05)NC=no calculado (% en la dieta y en el pastizal < 2).

| a) *C. australis* | G1 | G2 | G3 | G4 | G5 |
|---|---|---|---|---|---|
| Spring (n= 12) | 0.01 * | 1.61 NS | 1.58 * | 2.72 * | 2.95 * |
| Summer (n= 3) | NC | NC | 0.91 NS | 4.78 * | NC |
| Autumn (n= 3) | 0.00 * | 0.14 * | 0.23 * | 9.83 * | 0.24 * |
| Winter (n= 12) | 0.00 * | 1.48 NS | 0.18 * | 8.74 * | NC |

| b) *C. talarum* | G1 | G2 | G3 | G4 | G5 |
|---|---|---|---|---|---|
| Spring (n= 9) | 0.03 * | 1.04 NS | 0.97 NS | 4.32 * | 1.51 NS |
| Summer (n= 13) | NC | 2.46 * | 0.29 * | 5.87 * | 17.36 * |
| Autumn (n= 14) | 0.00 * | 2.19 NS | 0.56 * | 7.13 * | 0.05 * |
| Winter (n= 13) | 0.00 * | 0.77 NS | 0.62 NS | 2.39 * | NC |

greater proportion of the subterranean fraction in autumn and winter in *C. australis* diets with respect to *C. talarum* ones could be related to differences in the vegetation around the burrows they inhabit. Some of us stated (Comparatore et al. 1992) that the vegetation around *C. australis* burrows was sparser, which implies lower aerial biomass availability. In addition, we also stated that in autumn there was a positive correlation between *C. australis* density and availability of plant species with reserve organs. This suggests a micropattern in vegetation distribution and a different habitat use by the two populations.

Reproductive structures, which are rich in proteins, particularly when the grain is formed (McDonald et al. 1975), represented a high proportion of the diet. Recognized reproductive structures were glumes. These structures were found in all seasons and in every stomach content, varying their mean seasonal percentages from 20 to 50%. In addition, Cox (in press) found that *Thomomys talpoides* consumed up to 7% of reproductive structures. Supporting the idea that herbivore rodents are usually granivorous, Wang (1987) observed that two species of pocket gophers of the genus *Thomomys* carried to their burrows every wheat and sorghum grain that was supplied to them. Whether they ate the seeds or simply carried them to their burrows was not confirmed. Except in autumn, both species ate a higher proportion of the vegetative fraction than of the reproductive one. As the availability of reproductive structures was not estimated, whether tuco-tuco consume them in relation to their abundance or search actively for them remains to be determined.

Both species of *Ctenomys* preferred grasses over forbs throughout the year; the inverse was found for pocket gophers. There is evidence that geomyids prefer forbs over grasses (Kieth et al. 1959, Miller 1964, Laycock & Richardson 1975, Spencer et al. 1985, Cox in press). Myers & Vaughan (1964) found *G. attwateri* ate a greater proportion of perennial monocotyledons than forbs, but the former predominated in the grassland.

Group 4 vegetal species were preferred by all animals in all seasons. Nevertheless, the proportion of G4 in the pasture aerial biomass was never greater than 20%. The high preference for *Poa bonariensis* in the area could be related to the relative high nutritional value of the *Poa* species and to the fact that these species maintain high digestibility and percentage protein at the reproductive stage. Working in the Flooding Pampa, Buenos Aires Province, Argentina, Ernie (1992) established for whole plants of *Poa lanigera* 67 and 60% of digestibility and 10.6 and 10.2% of protein for vegetative and reproductive stages, respectively. On the other hand, the annual forbs group (G1) was, in general, not preferred, perhaps related to its low accessibility due to the plant's growth form.

In summer, autumn and winter, when animal distribution by species was intercalated, diets of *C. australis* and *C. talarum* were similar. On the contrary, in spring, when animal species separation was clearer, diets were different. Botanical composition of the spring diets of each population reflected the one found in the grassland. Group 2 mean percentage in the vegetation samples of the *C. australis* area was 17%, and in the *C. talarum* area it was 61%; on the contrary, G3 mean percentage in the *C. australis* area was 54%, and in *C. talarum* area it was 10%. Nevertheless, these differences may not have been totally seasonal; there may also have been a spatial effect due to soil structure distribution in the sympatric area. Thus, *C. australis* and *C. talarum* distributions appear to be related to soil characteristics (Comparatore et al., 1992) and each population principally feeds and selects among vegetal species in its own home range.

The results of Ward & Keith (1962) and Williams & Cameron (1986) support that the important diet components of pocket gophers are the most abundant and palatable species from their distribution area, being preferred species less frequently found, but consumed. The results of this study show that *Ctenomys* presents the same feeding strategy, which is adaptative in subterranean rodents due to their high digging costs and the low available energy to explore in their subterranean environment (Reichman et al. 1982).

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