

Population and habitat characteristics of two sympatric species of *Ctenomys* (Rodentia: Octodontidae)

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Demography, spatial distribution, body size and habitat characteristics of two sympatric species of *Ctenomys* have been studied seasonally at Necochea (Buenos Aires Province, Argentina). Densities were 11.3 individuals/ha for *Ctenomys talarum* and 5.2 indiv./ha for *Ctenomys australis*. Breeding was seasonal for both species. Sex ratios were unbalanced in favour of females in *C. australis* while there were not significant differences between sexes in *C. talarum*. The spatial distribution for both populations was clumped and related to habitat characteristics. *C. talarum* was found in areas with higher plant biomass and harder soils, while *C. australis* was restricted to the areas with lower plant biomass and less compact soils. Spatial separation of these two species may be caused by different commitment to life underground resulting from differences in body size and energetics. Two possible explanations for the spatial distribution of *C. australis* and *C. talarum* are given.

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Introduction

Fossorial rodents of the genus *Ctenomys*, commonly termed tuco-tucos, are among the most geographically variable mammals, being the most important genus according to number of species of subterranean rodents (Reig *et al.* 1990).

The evolutionary process in a subterranean ecotop, which is characterized by its simplicity, stability and predecibility, leads to an adaptive convergence. The major evolutionary determinants of this convergence are specialization, competition and isolation acting between and within species (Nevo 1979, 1982).

As in other subterranean rodents, tuco-tucos show disjuncts areas of distribution. Only one case of sympatry has been recorded, and that is in Monte Hermoso (Buenos Aires Province) between *Ctenomys australis* and *Ctenomys talarum* (Contreras and Reig 1965). In the present study, we found that the distribution of these two species also overlaps further to the north at Necochea (Buenos Aires Province) where previously only *C. australis* was recorded.

In the zone where *C. australis* and *C. talarum* are sympatric we hypothesize the development of life history traits and habitat selection mechanism that would prevent strong competitive interactions.

In this study we provide completely unknown information on demography, habitat characteristics, reproduction and body size in two sympatric species of *Ctenomys* with the aim of understanding how they coexist.

Study area

The study site is a 4 – 10 km wide coastal dune fringe which grades into the inland grassland, presently cultivated. The dune fringe is generally diagonal (Frenguelli 1928) and exhibits a vegetation cover of about 20%, composed mainly of *Poa* sp., *Panicum racemosum* and *Calystegia soldanella*. The sand dunes reach altitudes ranging from 30 to 50 m, above sea level, and extend 200 to 2000 m (Frenguelli 1928).

In the interdune areas, humid conditions prevailed allowing the development of a more dense vegetation cover (up to 80%). Dominant vegetation was: *Adesmia* sp., *Stipa tricotoma*, *Stipa neesiana* and *Bromus unioloides*. In these interdune depressions, thin soil is overlaying calcrete layers, locally known as "tosca". The alternation of dunes and interdunes areas, each one with different topography and vegetation patterns, can be considered as typical patchy-like environment.

Methods

From November 1987 to October 1988, 69 *Ctenomys australis* (*C. a.*) and 59 *Ctenomys talarum* (*C. t.*) were captured during four seasonal trappings. The captures took place in four different areas. These areas were staked in a grid pattern with the stakes spaced 20 m apart, one coordinate was indicated on the stakes by numbers, the other by letters. Exact trap site could thus be recorded. Snap traps Oncida-Victor No. 0 and plastics traps were placed at the entrances of the burrows to catch all animals present in the areas.

When a tuco-tuco was captured, the trap position was carefully estimated to the nearest meter on both coordinates and written on a map. This schedule allowed us to determine density and spatial distribution of both species.

All animals were autopsied to obtain information on reproductive condition, sex ratio, number of embryos and relative age. Females were classified as immatures (uterus threadlike, close vagina and no follicular activity) and mature (open or plugged vagina and ripe follicles). Pregnancy or post-partum pregnancy was also noted. The latter was determined from the period of overlap of visible pregnancy and lactation or placental scars. Males were also classified as immatures (seminal vesicles attached to the defferent ducts and lack of spermatozoa in epididymus). All these criteria were based on those from Pearson *et al.* (1968) and Malizia and Busch (in press). Relative age of animals was determined on the basis of dry weights of eye lens (Lord 1959).

Environmental variables (aboveground and belowground plant biomass, plant cover, percent of clay-loam fraction, soil moisture, depth and compaction) were measured from samples ($n = 54$) taken near burrows for the purpose of characterizing habitat preferences of both species. Aboveground and belowground plant biomass were estimated by dry weight of extracted vegetation samples of 30 cm diameter and 30 cm belowground depth. Plant cover was measured on 0.25 m² square using an ocular estimate method (Daubenmire 1959). Soil compaction was measured using a soil penetrometer and soil moisture was determined by differential weightings before and after drying the soil samples. Clay-loam fractions were separated using a sieve set.

An NTSYS Principal Component Analysis (PCA) program, through a correlation matrix to generate a reduced set of orthogonal vectors from original variables was performed. Results are given as $\bar{x} \pm SE$. Student's *t*-tests and χ^2 were used to analyze differences between means and frequencies, respectively.

Results

Density and spatial distribution

During the period of the study (November 1987 – October 1988) the average densities (without considering lactating individuals captured in the mother's burrow) were 11.32 ± 2.56 and 5.15 ± 0.76 individuals/ha for *Ctenomys talarum* and *Ctenomys australis*, respectively. *C. t.* had a peak density in autumn (June) whereas for *C. a.* highest numbers of individuals were recorded in spring (December) (Table 1).

Table 1. Seasonal densities (individuals/ha) of *Ctenomys talarum* and *Ctenomys australis*.

Species	Spring	Summer	Autumn	Winter
<i>C. talarum</i>	10.7	12.7	17.0	4.6
<i>C. australis</i>	7.4	4.5	4.0	4.6

Poisson distribution analysis indicated that both species had a clumped distribution ($p < 0.05$). Distance between individuals was smaller ($p < 0.01$) in *C. t.* than in *C. a.*; distance to nearest neighbour was $14.56 \text{ m} \pm 1.32$ ($n = 55$) and $20.79 \text{ m} \pm 1.49$ ($n = 40$), respectively. Interspecific distance to nearest neighbour was $17.12 \text{ m} \pm 1.28$ ($n = 43$).

Habitat characteristics

Spatial distribution of populations was related to habitat characteristics as expressed by different soils and vegetation preferences. The PCA analysis used for the characterization of habitats of both species showed the following results:

Plant cover, soil compaction and plant biomass (aboveground and belowground) load positively on PC 1, while soil depth loads negatively on this vector. The PC 1 explained 58.9% of the total variance. In Table 2, correlation coefficients for each of the first three PC vectors and the original measurements are given.

Table 2. Correlation coefficients for original environmental variables and the first three principal components (PC) axes.

Variable	PC 1	PC 2	PC 3
Aboveground plant biomass	0.664	-0.391	0.602
Belowground plant biomass	0.859	-0.225	0.144
Soil compaction	0.951	0.112	-0.164
Soil depth	-0.919	-0.013	0.279
Plant cover	0.956	-0.011	-0.164
Clay-loam fraction	0.528	0.724	0.105
Soil humidity	-0.042	0.907	0.233

Soil moisture and percent of clay-loam fraction load positively on PC 2, which explained 22.3% of total variance (81.2% cumulative). Only belowground biomass loaded on PC 3; this vector explained 8.3% of the variance (89.5% cumulative).

The significance of these differences in environmental variables to discrimination among the habitat of both species, is evident from the bivariate PC plots (Fig. 1). One group was formed by soil and vegetation samples taken near *C. t.* burrows, and it is characterized by the highest plant biomass, plant cover and shallowest and hardest soils. All these traits are related to interdune areas. A second group was formed by samples taken near *C. a.* burrows, having a lower plant biomass, lower plant cover and deeper and less compact soils, which characterized dune zones. Although it seems to exist a sharp delimitation of both habitats occupied by *C. t.* and *C. a.*, in zones where different soil and vegetation are intermingled this pattern is not clearly evident.

Table 3 shows mean values and statistical significances for environmental variables measured for both species.

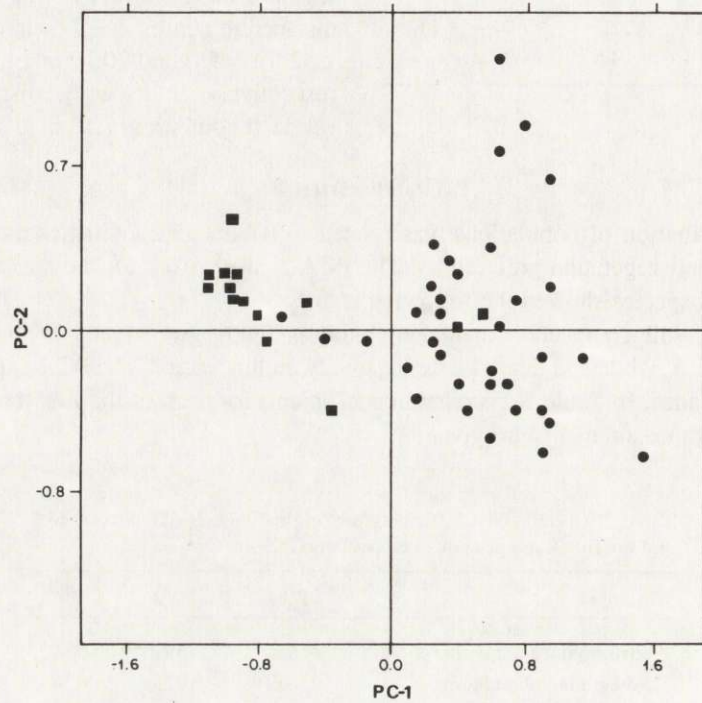


Fig. 1. Principal - component plot for soil and vegetation samples taken near burrows of *Ctenomys talarum* (circles) and *Ctenomys australis* (squares).

Table 3. Habitat variables measured for *Ctenomys talarum* and *Ctenomys australis*. Mean \pm S.E. are given.

Variable	<i>C. australis</i>	<i>C. talarum</i>	<i>p</i>
Plant cover (%)	29.7 \pm 5.6	85.5 \pm 2.6	0.001
Soil depth (cm)	91.7 \pm 4.9	34.8 \pm 2.4	0.001
Soil compaction (kg/cm ²)	6.9 \pm 1.6	25.3 \pm 0.9	0.001
Clay-loam fraction (%)	0.2 \pm 0.0	0.9 \pm 0.2	0.01
Soil humidity (%)	4.1 \pm 0.2	3.6 \pm 0.3	NS
Aboveground plant biomass (g)	4.8 \pm 0.9	11.2 \pm 1.1	0.001
Belowground plant biomass (g)	11.3 \pm 2.1	25.5 \pm 1.7	0.001

Reproductive characteristics

Although males of both species of tuco-tucos showed a year round reproductive competence, breeding was seasonal. Fig. 2 shows the percentage of females in each sample exhibiting evidence of reproductive activity. Since there are no pregnant females in June and taking into account a mean gestation period of 102 days, estimated by Weir (1974) for *C. t.*, and since at the end of winter (September) pregnant females were recorded with embryos in an advanced stage of development, we estimated that reproductive activity started in July. In March there are no *C. a.* pregnant females and only 12.5% of *C. t.* (1 in 8) were pregnant. Thus, the reproductive cycle reached the end of the summer.

Prevalence of pregnancy in *C. a.* peaked at the end of winter, when 100% ($n = 10$) of the females were pregnant. On the other hand, the highest activity for *C. t.* was recorded in spring, when 67% ($n = 6$) of the females were pregnant (Fig. 2). *C. a.* had a lower number of embryos/females than *C. t.* ($0.1 < p < 0.2$). Mean number was 3.18 ± 0.95 and 4.17 ± 1.94 embryos/females for *C. a.* and *C. t.*, respectively.

In spring 78% ($n = 9$) of the *C. a.* pregnant females were also lactating suggesting that this species has a post-partum pregnancy and two litters/year. On the other hand, there is no evidence of a post-partum pregnancy in *C. t.*, since no female was recorded pregnant and lactating at the same time.

Sex ratio

Adult sex ratio, expressed as male/female + male, was unbalanced in favour of females in *C. a.* (sex ratio = 0.32; $p < 0.05$; $n = 47$). In *C. t.*, the sex ratio did not depart significantly from expected 0.5 (0.51; $p > 0.5$; $n = 47$). In both species subadult sex ratios were not different from the expected 0.5 ($p > 0.25$).

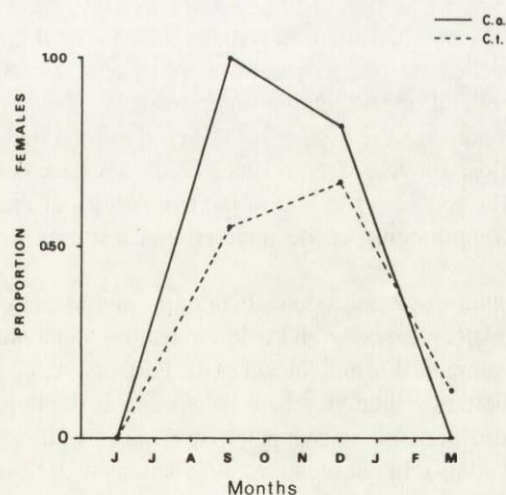


Fig. 2. Proportion of pregnant females of *Ctenomys talarum* and *Ctenomys australis*.

Sexual maturity and age structure

Sexually mature *C. a.* are heavier than 250 g and their eye lens weighted more than 38 mg. *C. t. talarum* is smaller and matured at an average body weight of 95 g and 17 mg eye lens weight. Both populations contain a high proportion of breeding adults; 80% (n = 59) of *C. t.* and 68% (n = 69) of *C. a.* captured were adults. The high proportion of breeding adults found in both populations is a fact commonly reported for other subterranean mammals (Nevo 1982) and for *C. t.* in particular (Busch *et al.* 1989).

Relationships between body length and weight

Body weight and body length are shown in Table 4. *C. a.* is 3 times heavier and 1.5 longer than *C. t.* Males of both species are heavier than females, but not longer.

Table 4. Intraspecific body size relationships for adults of *Ctenomys talarum* and *Ctenomys australis*. Mean values \pm S.E. and sample size (in parenthesis) are given.

Measurement	<i>C. australis</i>		<i>p</i>	<i>C. talarum</i>		<i>p</i>
	females (n = 32)	males (n = 12)		females (n = 22)	males (n = 24)	
Total length (mm)	280.1 \pm 2.4	297.3 \pm 9.2	< 0.05	197.9 \pm 2.4	207.4 \pm 2.2	< 0.01
Body length (mm)	187.4 \pm 2.1 ¹	195.4 \pm 9.2	NS	139.9 \pm 2.2	144.4 \pm 1.8	NS
Tail length (mm)	93.1 \pm 0.9 ¹	102.9 \pm 1.9	< 0.01	57.9 \pm 1.2	62.9 \pm 0.9	< 0.01
Body weight (g)	297.7 \pm 6.8 ²	425.3 \pm 19.8 ³	< 0.01	102.5 \pm 2.9	134.6 \pm 3.7	< 0.001

¹ n = 31, ² n = 21, ³ n = 12

Discussion

Although trapping indicates that there is contact between *C. a.* and *C. t.* distributions in the coastal dunes of Necochea, the two species of tuco-tucos are distributed in a spatial pattern, corresponding to different soil and vegetation microhabitats. Since energetics and body size of fossorial rodents are related to the high cost of obtaining food by burrowing (Vleck 1979) and to thermal stress in closed caves (McNab 1966, 1979) they have been ascribed to particular environmental factors. The spatial separation of the two species of tuco-tucos may be caused, therefore, by different commitment to life underground resulting from differences in body size.

As it is reported for other fossorial rodents (Contreras and McNab 1990), the bigger *C. a.*, with a better thermoregulatory capacity and a lower resting metabolic rate (Busch 1989), is restricted to the sandier, more friable and thicker soils. Furthermore, *C. t.* tolerates a wide range of soil types. In its northern distribution, where the species is in allopatry, it is found in both habitats, those occupied in the zone of sympatry by *C. t.* as well as by *C. a.* (Vassallo and Busch 1989, Busch *et al.* 1989). In consequence, interactions with *C. a.* would be a factor that affects *C. t.* distribution in Necochea, being the former the dominant species in the sand dunes.

Our results on average nearest neighbour distance (intra and interspecific) are related to burrow size (home range). Thus, we can infer that distances between interspecific burrows are

no different from intraspecific burrow distances. These data suggest about the potential for actual interaction between both species.

On the other hand, our results show the existence of a post partum pregnancy and a higher proportion of pregnant females in *C. a.* This high reproductive potential may be adaptive for an habitat specialist whose dispersers would have a reduced probability of finding suitable habitats.

Laboratory experiments showed that males from an allopatric population of *C. t.* are more aggressive than males from the sympatric one (Giannoni and Busch 1989). These results would explain the differences in adult sex ratio found between the allopatric population (0.38, males/females + males; Malizia and Busch, in press) and our data for the sympatric population (0.51, males/females + males).

The absence of *C. t.* in the sand dunes, may be the result of competitive exclusion. However, an alternative explanation could be the existence of an habitat selection mechanism, which would prevent strong competition. Thus, the competition could have been stronger in the past (Schroder and Rosenzweig 1975).

Further research to find out the causes of habitat differentiation are planned.

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