

## Size and structure of burrow systems of the fossorial rodent *Ctenomys mendocinus* in the piedmont of Mendoza province, Argentina

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### Abstract

The structure and size of burrow systems of *Ctenomys mendocinus* were analysed in the present study. These burrows showed a linear pattern, with a main axis from which branches and laterals forked off. Burrow systems of males were larger than those of females, with a longer main tunnel and greater number of branches. Lengthening of the main tunnel was achieved by adding new segments rather than by excavating longer segments. Both male and female burrows showed the same geometric configuration. There were no differences in the percentages estimated for main tunnel, branches and laterals. The angular variables (directional angle, branch angle and angle of ascent of laterals) did not show any differences between both sexes either. Burrows showed a constant heading along their path with mean directional angles close to 0°, even though in most systems left- and right-ward deviations from the main tunnel followed a random sequence. Branches originated at right angles to the main tunnel. *C. mendocinus* appears to minimize the energy cost of burrowing by increasing the angle of ascent of the lateral instead of its length as the main tunnel grows deeper. Home range, perimeter, and linearity were significantly higher in males.

### Introduction

Fossorial mammals, just as subterranean mammals, are largely confined to underground life, but they venture a few centimeters outside their burrows for foraging (CONTRERAS and McNAB 1990). Both groups of herbivorous mammals construct complex tunnel systems, which ensure them a relatively constant microclimate, protection from predators and access to food (NEVO 1979; REICHMAN and SMITH 1990).

The subterranean environment is largely constant, and selection has led to the development of highly convergent structural features in the burrow systems of diverse mammalian taxa (NEVO 1979; HICKMAN 1990). Knowledge of burrow structure and its adaptive features is a major aspect in understanding the unique evolution and adaptive biology in subterranean mammals (HICKMAN 1990).

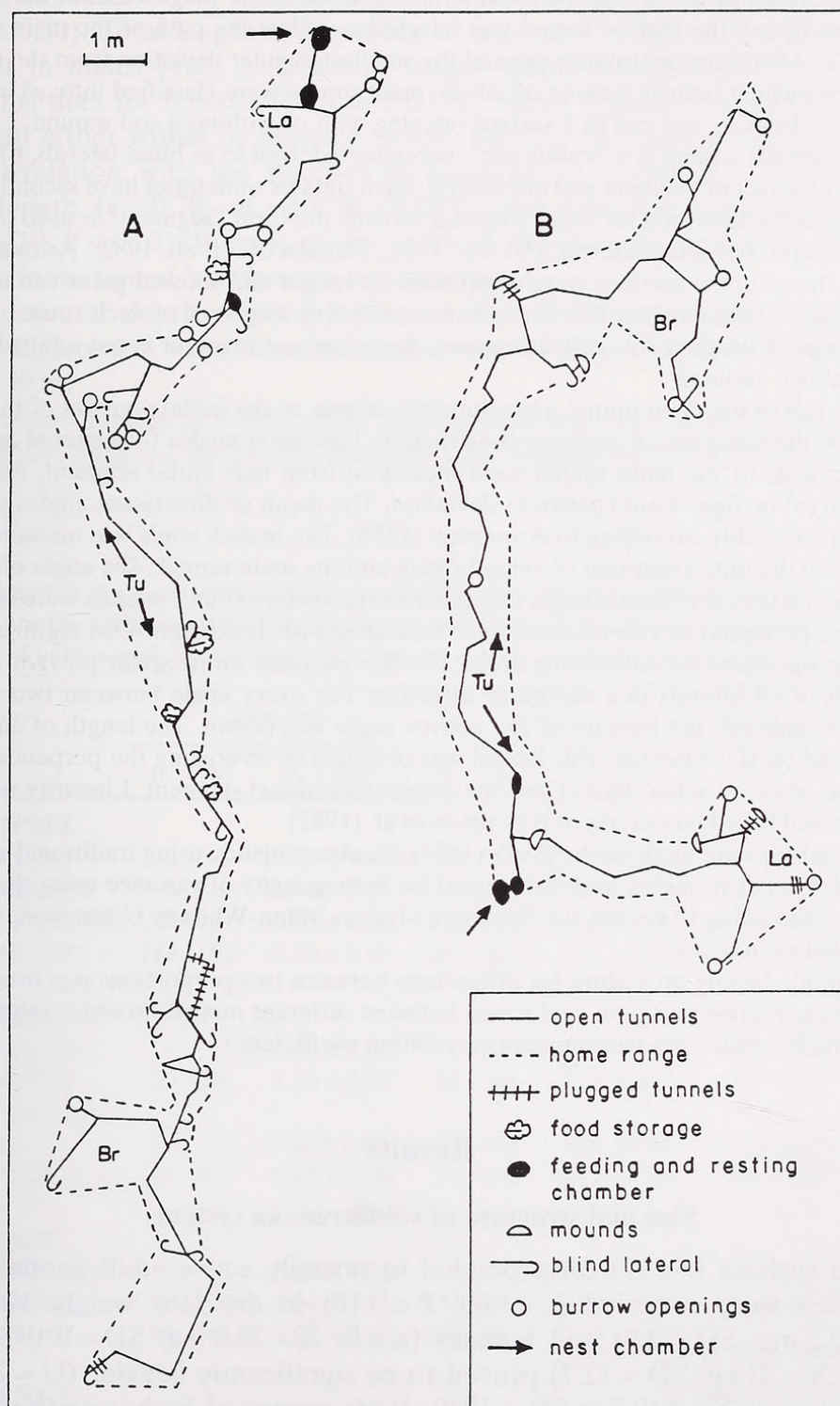
The architecture of burrow systems of the species of *Ctenomys* represents an almost unknown aspect of the ecology of this South American endemic fossorial rodent. Information available is either fragmentary or based on the study of only a few animals. Linear systems composed of a main axis and lateral tunnels have been reported for *C. opimus*, *C. peruanus* (PEARSON 1959) and *C. pearsoni* (ALTUNA 1983). A similar pattern was described for *C. mendocinus* in an environment of low productivity (PUIG et al. 1992). Linear systems associated with low resource availability have also been reported for *Thomomys bottae* (REICHMAN et al. 1982), *Tachyoryctes splendens* (JARVIS and SALE 1971) and *Spalax ehrenbergi* (HETH 1989).



This study aims at elucidating the most relevant structural features of burrow systems of *C. mendocinus*, and their possible differences between sexes.

### Material and methods

Burrow systems of *C. mendocinus* were studied at Las Higueras (Mendoza, Argentina, 32°30' S and 68°55' W), located in the foothills of the Andes (1 125 m elevation). The zone presents low hillocks and depressions furrowed by wadis. Soils are made up of lithosols in a matrix of strongly compacted clay



**Fig. 1.** Schematic representations of excavated burrow systems of *Ctenomys mendocinus* from the piedmont of Mendoza (Argentina). Burrows of adult (A) male and (B) female. Tu = main tunnel, Br = branch, La = lateral.



and silt. Shrub communities of *Larrea divaricata* and *L. cuneifolia* prevail, alternating with dense riparian vegetation (ROIG 1976).

Complete burrow systems of 12 adults (6 males, 6 females) were excavated and mapped in September and October 1991. After occupants were captured, Oneida Victor kill-traps were kept for 24 hours in the burrow openings, in order to record the number of occupants per system. Sex, weight, reproductive condition and relative age were determined, based on criteria of Rosi et al. (1992).

Length, depth, diameter and directionality of tunnel sections and chambers were measured for every system. Burrow openings and surface mounds were mapped. Burrow structural features were described with the same terminology used for other subterranean mammals (VLECK 1981; REICHMAN et al. 1982; ANDERSEN 1988; HICKMAN 1990). The main tunnel was defined as the longest axis of the system (Fig. 1). When a fork was found, the longest tunnel was selected to follow the path of the main tunnel (REICHMAN et al. 1982). Most selected tunnels showed the smallest angular deviation from the main axis (ANDERSEN 1988). Branching tunnels forking off of the main tunnel were classified into: a) laterals: straight tunnels that never branch, and end in a surface opening with or without a soil mound. Laterals also included all those tunnels ending in a "cul-de-sac", hereafter referred to as blind laterals, b) branches: tunnels made up of at least one segment and one lateral. Such tunnels sometimes have secondary branches.

In burrow systems described for other fossorial rodents the term "segment" is used to define tunnel sections that extend between laterals (VLECK 1981; REICHMAN et al. 1982; ANDERSEN 1988). In *C. mendocinus*, these tunnel sections were comparatively longer and showed great variability, owing to the small number of laterals recorded. For this reason, every fragment of such tunnel sections determined by a change in heading was called segment, therefore our segment is not equivalent to the one defined by the above authors.

One of the ends of the main tunnel was arbitrarily chosen as the initial segment of the system, since we did not know the sequence of segment construction. Deviation angles (directional angles) between consecutive segments of the main tunnel were measured from that initial segment, considering their left-ward (negative) or right-ward (positive) deviation. The mean of directional angles permitted us to know system directionality, according to ANDERSEN (1988). The branch angle was measured as the smallest angle between the initial segment of every branch and the main tunnel. The angle of ascent (VLECK 1981) was estimated only for those laterals that reached the surface (blind laterals were excluded).

The area and perimeter in every system were measured with Tektronix 4958 digitizer using the INCYTH-CRA's programme for calculating areas. For this purpose, an irregular polygon was drawn, by joining the ends of all laterals in a clockwise direction. For every angle between two segments from which no lateral came off, the bisector of the convex angle was drawn. The length of an estimated lateral was projected on this bisector. This lateral was obtained by averaging the perpendicular distances between the end of every actual lateral and the originating tunnel segment. Linearity of a burrow system was determined based on criteria of REICHMAN et al. (1982).

Angular variables were analysed by ZAR's (1984) circular statistics, using traditional statistics for the remaining variables. All variables were first tested for homogeneity of variance using the variance ratio test (ZAR 1984). According to results, the Student's t-test or Mann-Whitney U test were used to analyse for differences between sexes.

An approximate testing procedure for differences between two proportions was used as applied by ZAR (1984). Linear regressions were performed between different metric variables estimating data adjustment by using Pearson's product-moment correlation coefficient  $r$ .

## Results

### Size and structure of subterranean systems

All excavated systems ( $n = 12$ ) corresponded to sexually active adult animals. No significant differences were recorded ( $t = 1.69$ ;  $P < 0.10$ ) in dry lens weight between males ( $n = 5$ ;  $\bar{X} = 32.2$  mg;  $SD = 2.9$ ) and females ( $n = 6$ ;  $\bar{X} = 29.0$  mg;  $SD = 3.19$ ). In contrast, males ( $n = 5$ ;  $\bar{X} = 219$  g;  $SD = 52.7$ ) proved to be significantly heavier ( $U = 27$ ;  $P = 0.025$ ) than females ( $n = 6$ ;  $\bar{X} = 140.5$  g;  $SD = 10.8$ ). Wide ranges of body weight were obtained within each sex (140 to 260 g for males, and 126 to 155 g for females).

Every burrow was inhabited by only one specimen, except for a female's burrow with five youngs in the nest.



Total length of tunnels in a system ranged from 15 to 31 m for females, and from 23 to 77 m for males. Significant differences were found ( $U = 34$ ;  $P = 0.005$ ) between male ( $n = 6$ ;  $\bar{X} = 50.5$  m;  $SD = 21.0$ ) and female burrows ( $n = 6$ ;  $\bar{X} = 22.4$  m;  $SD = 6.8$ ) concerning the average of the total length of tunnels. The diameter of feeding tunnels was largely constant, with mean values of 8.03 cm ( $n = 17$ ;  $SD = 1.72$ ) for females, and 8.5 cm ( $n = 33$ ;  $SD = 1.51$ ) for males. Slight enlargements were only observed in the branching points of the main tunnel.

**Main tunnel:** The main tunnel represented the greatest proportion of the total length of the system (males: 63.9%; females: 60.3%), there being no differences between sexes ( $Z = 0.68$ ;  $P < 0.50$ ). Total length and number of segments of the main tunnel were significantly greater in males (Tab. 1). Segment length varied within a wider range for males (0.20 to 3.20 m) than for females (0.20 to 1.60 m). Mean segment lengths were not significantly different either within or between sexes (Tab. 1). The main tunnel length showed a significant correlation with the number of segments ( $r = 0.92$ ;  $df = 10$ ;  $P < 0.001$ ), with their mean length ( $r = 0.78$ ;  $df = 10$ ;  $P < 0.005$ ), and with the occupant's body weight ( $r = 0.69$ ;  $df = 10$ ;  $P < 0.02$ ). In spite of the width of weight ranges within each sex, correlations with the main tunnel length were not significant.

The main tunnel depth showed little variation both within and between burrows; moreover, no differences were found related to sex (Tab. 1). Greatest depths recorded did not exceed 0.40 m.

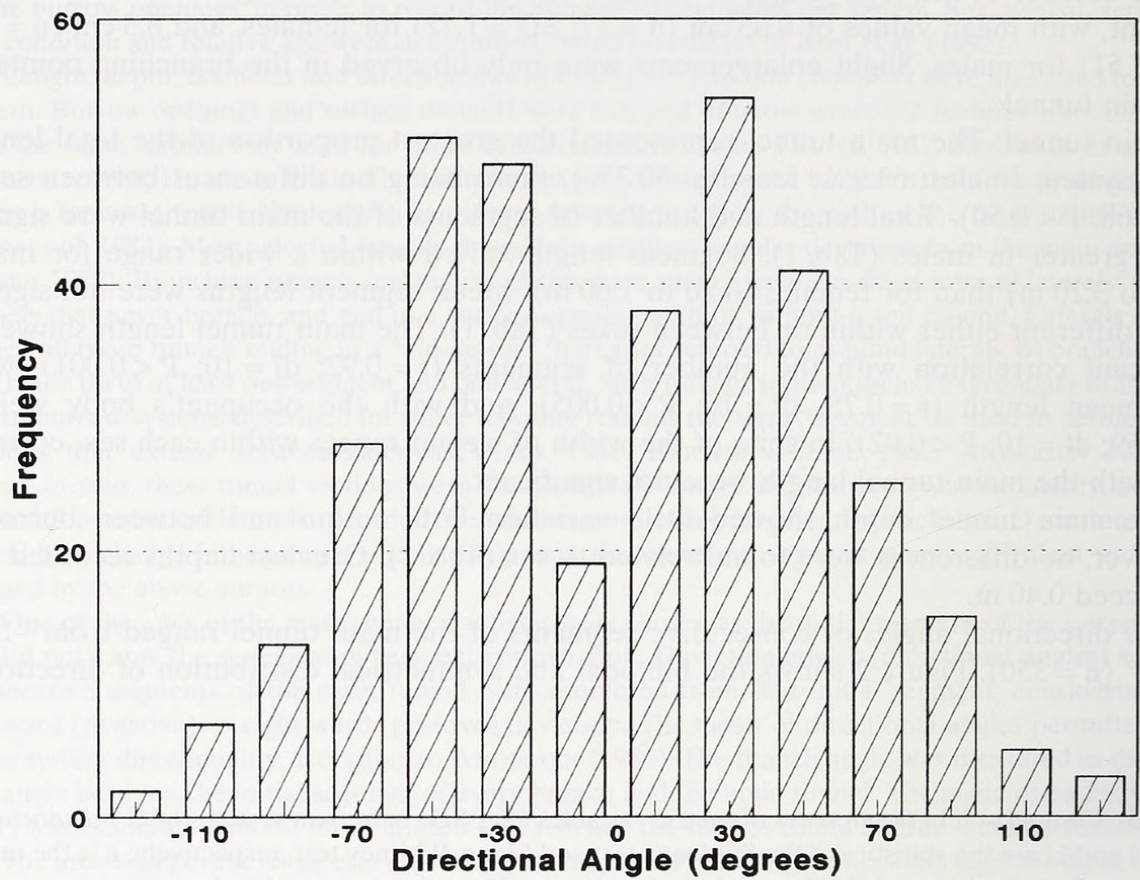
The directional angles of consecutive segments of the main tunnel ranged from  $-128^\circ$  to  $132^\circ$  ( $n = 350$ ). Figure 2 shows the bimodal and symmetrical distribution of directional

**Table 1.** Comparison between sexes of metric variables ( $\bar{X} \pm SD$ ) in burrow systems of *C. mendocinus*, where  $t$  and  $U$  are the statistics of the Student's test and Mann-Whitney test, respectively;  $n$  is the number of values and  $(k)$  the number of means used to estimate second-order means.

Variable	Females			Males			Value of the statistic	Significance level
	n	(k)	$\bar{X} \pm SD$	n	(k)	$\bar{X} \pm SD$		
<b>MAIN TUNNEL</b>								
Total length (m)	6		$13.53 \pm 4.42$	6		$32.31 \pm 14.05$	U = 33.00	p = 0.01
Number of segments	6		$26.50 \pm 9.01$	5		$41.60 \pm 11.91$	t = 2.39	p < 0.025
Mean segment length (m)	159	(6)	$0.52 \pm 0.26$	208	(5)	$0.68 \pm 0.46$	t = 0.78	p < 0.25
Mean depth (m)	112	(6)	$0.30 \pm 0.09$	227	(6)	$0.27 \pm 0.06$	t = 0.63	p < 0.25
<b>BRANCHES</b>								
Number of branches	6		$2.50 \pm 1.22$	6		$4.00 \pm 1.51$	t = 1.86	p < 0.05
Mean length (m)	15	(6)	$1.54 \pm 1.07$	24	(6)	$2.25 \pm 0.63$	t = 1.40	p < 0.10
Mean number of seg- ments	15	(6)	$2.96 \pm 1.46$	24	(6)	$3.06 \pm 0.63$	U = 18.50	p > 0.10
Mean segment length (m)	15	(6)	$0.47 \pm 0.26$	24	(6)	$0.72 \pm 0.61$	t = 0.92	p < 0.25
<b>LATERALS</b>								
Mean number of laterals	6		$15.83 \pm 4.22$	6		$22.83 \pm 10.26$	t = 1.55	p < 0.10
Mean length (m)	95	(6)	$0.34 \pm 0.16$	137	(6)	$0.40 \pm 0.24$	t = 0.49	p > 0.25
Mean depth (m)	86	(6)	$0.26 \pm 0.08$	136	(6)	$0.26 \pm 0.06$		
<b>HOME RANGE</b>								
Area (m <sup>2</sup> )	6		$11.91 \pm 6.08$	6		$43.13 \pm 31.13$	U = 33.00	p = 0.01
Perimeter (m)	6		$31.67 \pm 11.00$	6		$74.43 \pm 33.33$	U = 34.00	p = 0.005
Linearity	6		$2.60 \pm 0.36$	6		$3.27 \pm 0.57$	t = 2.41	p < 0.05



angles  $>$  and  $<0^{\circ}$  in all twelve systems. Mean values for each system varied between  $-11^{\circ}$  and  $8^{\circ}$  ( $n = 12$ ) (Tab. 2), showing no significant differences either within or between sexes (Tab. 3). Moreover, when considering separately the positive and negative directional an-



**Fig. 2.** Frequency distribution of directional angles ( $n = 350$ ) in main tunnels of burrow systems of *C. mendocinus*.

**Table 2.** Mean values (degree) and angular deviations (S) of the directional angle for main tunnel and branches.

Animal		Mean directional angles of main tunnel (+ and -)			Directional angles of main tunnel (*)						Mean directional angles of branch segment (**)		
Num.	Sex	n			Positive			Negative			n		
			$\bar{X}$	S	n	$\bar{X}$	S	n	$\bar{X}$	S		$\bar{X}$	S
214	♀	15	8	40	8	39	30	5	-36	20			
215	♀	14	-3	43	7	40	23	7	-42	10			
228	♀	34	-1	49	16	47	23	16	-50	24	7	9	65
269	♀	26	-11	50	11	44	25	14	-53	25	4	16	27
270	♀	31	1	40	16	33	23	14	-37	24	11	18	43
272	♀	32	4	43	14	47	25	14	-36	23	4	14	72
216	♂	22	-5	52	11	45	25	11	-54	23	4	-80	56
218	♂	57	-1	52	29	45	26	26	-56	30	7	-19	46
224	♂	27	-3	48	14	39	34	11	-52	17	12	-1	43
225	♂	39	6	56	20	58	30	17	-53	25	16	0	45
227	♂	48	1	43	18	48	22	17	-49	24	4	-5	44
229	♂	36	-1	46	17	42	30	17	-41	22			

(\*) According to left-ward (negative) and right-ward (positive) deviations from the main tunnel.  
(\*\*) Estimated only for systems with branches composed of more than two segments.



gles in every system, differences in number and in mean values were found to be minor (Tab. 2). By use of the one-sample test for the mean angles (ZAR 1984) it was verified for every burrow that the mean directional angle did not deviate significantly from  $0^\circ$ . No significant deviation was recorded when analysing the mean values obtained for each sex (Tab. 3) at the 99% confidence level (length of mean vector  $r = 0.62$  in males and  $0.70$  in females).

**Table 3.** Comparisons within each sex (using Chi-square contingency test) and between sexes (using Watson's  $U^2$  test) of angular variables ( $\bar{X}$  = mean,  $S$  = angular deviations) of burrow systems of *C. mendocinus*, where  $n$  is the number of values, ( $k$ ) the number of means used to estimate second-order means and  $P$  level of significance.

Sex	Directional angle of main tunnel	Branch angle	Angle of ascent of lateral
<b>Females</b>			
$n(k)$	152(6)	13	31(6)
$\bar{X} \pm S$	$0.1 \pm 44.7$	$88.1 \pm 18.1$	$40.4 \pm 18.3$
Chi-square (df)	45.6(35)	23.4(18)	44.3(35)
	$p < 0.25$	$p < 0.25$	$p < 0.25$
<b>Males</b>			
$n(k)$	229(6)	21	39(5)
$\bar{X} \pm S$	$0.4 \pm 49.8$	$85.8 \pm 19.9$	$31.1 \pm 35.4$
Chi-square (df)	46.4(45)	30.0(20)	25.6(24)
	$p < 0.50$	$p < 0.10$	$p < 0.50$
<b>Comparison between sexes</b>			
$U^2(df)$	0.095(6, 6)	0.068(13, 21)	0.103(6, 5)
	$p < 0.20$	$p < 0.50$	$p < 0.50$

To test whether the sequence of construction of right-ward and left-ward segments was random, the two-tailed runs test (ZAR 1984) was used. In only three of the twelve systems considered was the null hypothesis for randomness rejected, which indicates that in most systems segment deviations towards either side of the main tunnel did not alternate.

Branches: in every system, one to six branches forked off from the main tunnel. The mean number of branches per system was significantly greater in males than in females (Tab. 1), whereas the mean number of branches per meter of main tunnel (males =  $0.13$ ;  $SD = 0.03$ ; females =  $0.20$ ;  $SD = 0.14$ ) did not differ significantly between sexes ( $U = 25$ ;  $P > 0.10$ ). Branch mean length, as well as length and mean number of branch segments, showed no variations related to sex (Tab. 1). The proportion of branching tunnels in the total system length did not differ significantly ( $Z = 0.32$ ;  $P > 0.5$ ) between male ( $\bar{X} = 17.5\%$ ) and female burrows ( $\bar{X} = 16.2\%$ ). Branch number, but not mean length, was significantly correlated with the main tunnel length ( $r = 0.79$ ;  $df = 11$ ;  $P < 0.002$ ).

The highest frequencies of branch angles ranged between  $80^\circ$  and  $100^\circ$  (Fig. 3). Means of these angles were similar for both sexes (Tab. 3) and did not depart significantly from  $90^\circ$  (length of mean vector  $r = 0.95$  in females and  $0.94$  in males, one-sample test for mean angles, at 99% confidence level, ZAR 1984).

Most branches composed of more than two segments showed a mean directional angle close to  $0^\circ$  (Tab. 2). Branch depth ( $\bar{X} = 0.26$  m;  $SD = 0.06$ ) did not differ significantly ( $t = 0.75$ ;  $df = 22$ ;  $P < 0.25$ ) from the main tunnel depth ( $\bar{X} = 0.28$  m;  $SD = 0.07$ ).



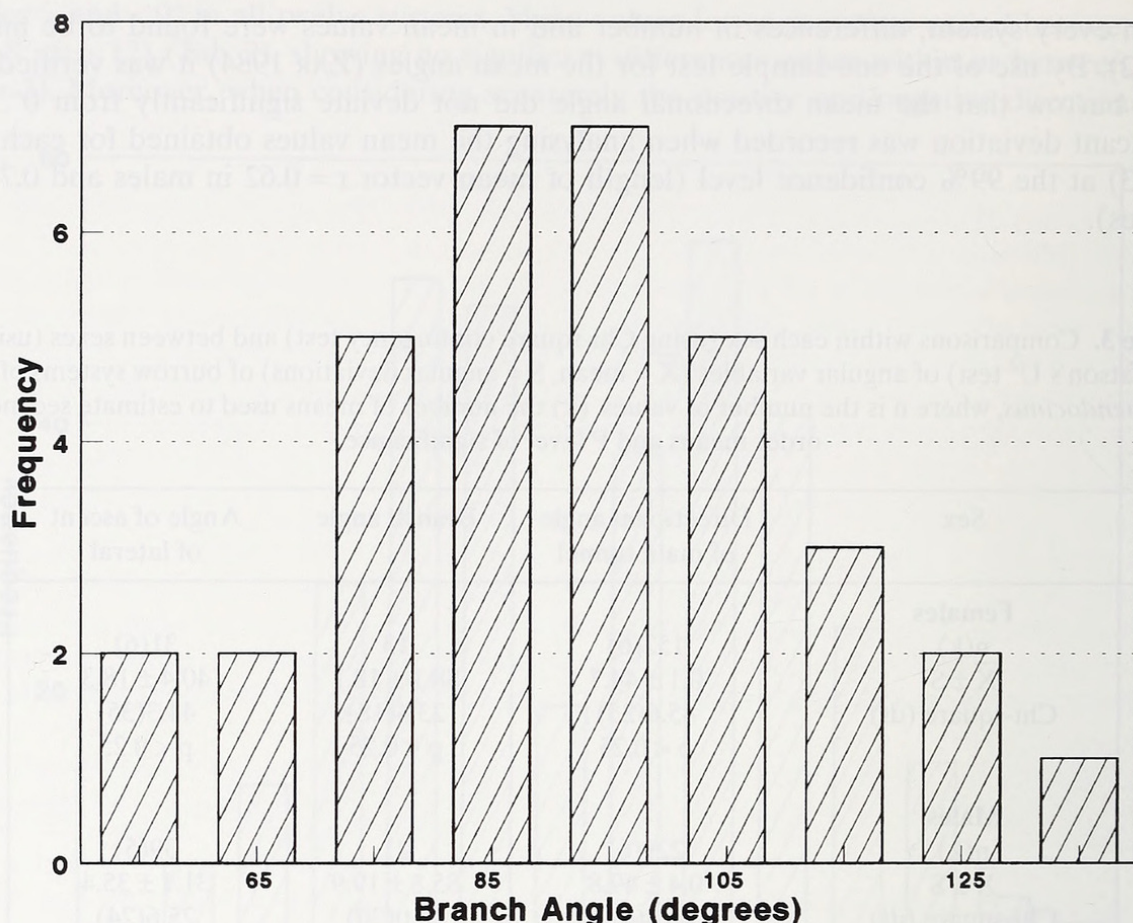


Fig. 3. Histogram of branch angles ( $n = 34$ ) measured in all excavated systems of *C. mendocinus*.

Laterals: 8 to 37 laterals per system were found. Their mean number was significantly lower than the mean number of segments composing the system, both in males ( $t = 3.8$ ;  $df = 10$ ;  $P < 0.001$ ) and in females ( $U = 32$ ;  $df = 6.6$ ;  $P < 0.025$ ). No significant differences between sexes were recorded in the mean number of laterals (Tab. 1) or in the proportion of laterals relative to total segments (females: 47%; males = 45%;  $Z = 0.45$ ;  $P > 0.50$ ). The length of main tunnel sections, comprised between two laterals reaching the surface, showed a wide range of variation ( $n = 71$ ;  $\bar{X} = 3.7$  m;  $SD = 3.9$ ). This high variability was also observed when blind laterals were included ( $n = 151$ ;  $\bar{X} = 1.8$  m;  $SD = 1.8$ ).

Lateral length varied considerably both within and between burrows (0.15 to 1.50 m), although few laterals exceeded 0.90 m in male (6.6%) and female (1%) systems.

Lateral depth at the originating point was not significantly correlated with lateral length. Nevertheless, depth and angle of ascent of laterals were correlated ( $r = 0.46$ ;  $df = 69$ ;  $P < 0.001$ ). These three variables showed no significant differences between sexes (Tabs. 1 and 3). Angles of ascent varied between  $21^\circ$  and  $58^\circ$  with their highest frequencies between  $15^\circ$  and  $45^\circ$ , and only 7% were higher than  $60^\circ$  (Fig. 4).

Total length of laterals in proportion to total length of system tunnels was similar for both sexes (males: 19%; females: 23%;  $Z = 1.10$ ;  $P < 0.50$ ). The proportion of laterals reaching the surface (54.7%,  $n = 127$ ) was similar to that of blind laterals (45.3%). The latter were usually as deep as the main tunnel; 11.4% of them ( $n = 105$ ) were plugged with shredded plant material mixed with loose soil.

About 25% of laterals (30.4% of their overall length) were totally or partially plugged with slightly compacted soil.

Chambers: eight systems showed oval chambers (1 to 3) that outsized the diameter of feeding tunnels. Considering their contents and location, they were classified into nest chambers, and feeding-resting chambers. No defecation chambers were found.



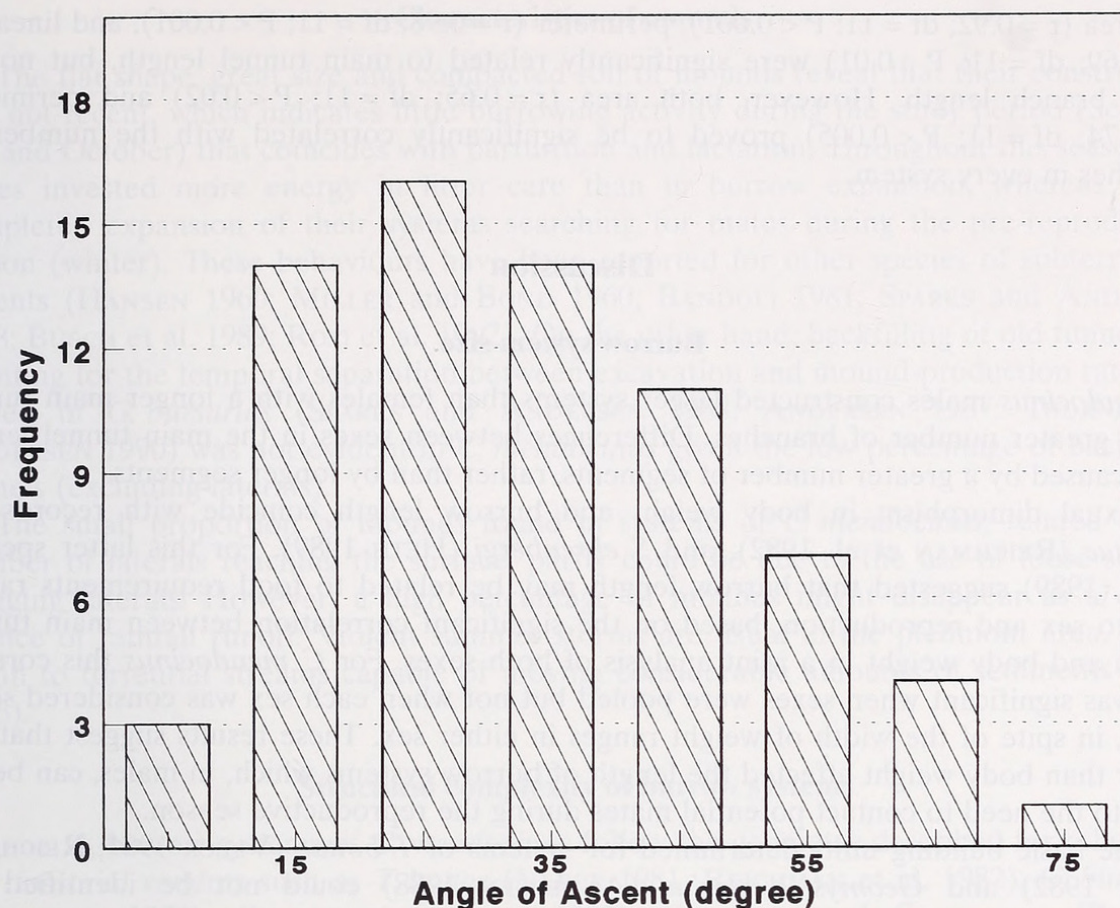


Fig. 4. Angles of ascent of laterals ( $n = 70$ ) measured in eleven burrow systems of *C. mendocinus*.

The chamber located at a greater depth than the remainder of the system with dry plant material covering its walls was regarded as the nest. Nests occupied an eccentric position in most systems, never being situated in the distal ends of main tunnels or branches. No significant differences were recorded ( $t = 0.64$ ;  $P > 0.25$ ) in nest size between males ( $n = 4$ ;  $\bar{X} = 0.32$  m;  $SD = 0.005$ ) and females ( $n = 4$ ;  $\bar{X} = 0.29$  m;  $SD = 0.003$ ). Depth of female nests ( $n = 4$ ;  $\bar{X} = 0.64$  m;  $SD = 0.04$ ) was significantly greater ( $t = 3.16$ ;  $P < 0.01$ ) than that of male nests ( $n = 4$ ;  $\bar{X} = 0.34$  m;  $SD = 0.001$ ).

Feeding-resting chambers were smaller than nests and were located in the main tunnel, at the same depth. They were usually empty, although fresh plant material was found in some of them. Storage of plant material was found into little blind laterals in most burrows.

Mounds: the mean number of mounds recorded per burrow was 6.2 ( $n = 10$ ;  $SD = 3.08$ ). Most of them were roughly circular, with a mean diameter of 0.52 cm ( $n = 21$ ;  $SD = 0.14$ ). Connection of these mounds with the burrow could not be found in 44% of them, in spite of their adjacent position to the main tunnel or blind laterals. Nearly all the mounds (95%) were old, given their flattened shape and high degree of soil compactness.

### Home range

Area, perimeter and linearity were significantly higher in male than in female burrows (Tab. 1). Home range size varied between 7 and 16 m<sup>2</sup> in females, and between 14 and 99 m<sup>2</sup> in males. In both sexes, the perimeter of home ranges ( $n = 12$ ;  $\bar{X} = 53.1$  m;  $SD = 32.5$ ) departed significantly ( $U = 135$ ;  $df = 12.12$ ;  $P < 0.005$ ) from the value expected for a circular system having the same area ( $n = 12$ ;  $\bar{X} = 17.0$  m;  $SD = 7.8$ ).



Area ( $r = 0.92$ ;  $df = 11$ ;  $P < 0.001$ ), perimeter ( $r = 0.98$ ;  $df = 11$ ;  $P < 0.001$ ), and linearity ( $r = 0.69$ ;  $df = 11$ ;  $P < 0.01$ ) were significantly related to main tunnel length, but not to mean branch length. However, both area ( $r = 0.65$ ;  $df = 11$ ;  $P < 0.02$ ) and perimeter ( $r = 0.74$ ;  $df = 11$ ;  $P < 0.005$ ) proved to be significantly correlated with the number of branches in every system.

## Discussion

### Burrow system size

*C. mendocinus* males constructed larger systems than females with a longer main tunnel and a greater number of branches. Differences between sexes in the main tunnel length were caused by a greater number of segments, rather than by longer segments.

Sexual dimorphism in body weight and burrow length coincide with records for *T. bottae* (REICHMAN et al. 1982), and *S. ehrenbergi* (HETH 1989). For this latter species, HETH (1989) suggested that burrow length may be related to food requirements rather than to sex and reproduction, based on the significant correlation between main tunnel length and body weight in a joint analysis of both sexes. For *C. mendocinus* this correlation was significant when sexes were pooled but not when each sex was considered separately, in spite of the width of weight ranges in either sex. These results suggest that sex rather than body weight affected the length of burrow systems which, in males, can be related to the need to contact potential mates during the reproductive season.

The basic building units determined for systems of *T. bottae* (VLECK 1981; REICHMAN et al. 1982) and *Geomys bursarius* (ANDERSEN 1988) could not be identified for *C. mendocinus* systems, owing to the scarce number of laterals. Increased compactness of the soil plugging the laterals could cause loss of laterals. There are several points of evidence that strengthen this assumption: a) great number of laterals plugged with slightly compacted soil, b) high percentage of soil mounds near the system but showing no evident connection with it, and c) presence of numerous blind laterals. The latter might have originated from increased compactness of partially plugged laterals, although a small percentage of them may reflect probings for food as suggested by HICKMAN (1983).

### Tunnel depth and slope of laterals

Feeding tunnels and chambers composing the burrow systems of *C. mendocinus* were deeper than expected, considering the high energy cost of burrowing that a fossorial animal must afford in cohesive soils (VLECK 1979, 1981). Although deeper systems demand higher energetic expense (VLECK 1981), they are more stable regarding temperature and humidity (LLANOS 1947; ROSENMAN 1959; ALTUNA 1985). This stability is a factor of great importance in arid regions, where free access to water sources is usually restricted (HICKMAN 1990).

Several authors have reported the importance of the level of subterranean parts of plants for determining the depth of feeding tunnels of subterranean rodents (MILLER 1957; PEARSON 1959; JARVIS and SALE 1971; HETH 1989; WILLIAMS and CAMERON 1990). This did not seem to be the most important factor accounting for system depth in *C. mendocinus*, since the record of foraging signs above ground (stems cut on the bias near burrow openings) indicates that feeding is not based exclusively on subterranean parts of plants.

*C. mendocinus* seems to minimize burrowing cost by increasing the angle of ascent of laterals rather than their length, as the main tunnel deepens. However, values over  $60^\circ$  are not very frequent, which would counteract the tendency of loose soil to fall back into the burrow, thus being helpful in plugging the laterals.



### Characteristics of mounds

The flat shape, great size and compacted soil of mounds reveal that their construction was not recent, which indicates little burrowing activity during the study period (September and October) that coincides with parturition and lactation. Throughout this season, females invested more energy in litter care than in burrow expansion, whereas males completed expansion of their systems searching for mates during the pre-reproductive season (winter). These behaviours have been reported for other species of subterranean rodents (HANSEN 1960; MILLER and BOND 1960; BANDOLI 1981; SPARKS and ANDERSEN 1988; BUSCH et al. 1989; ROSI et al. 1992). On the other hand, backfilling of old tunnels accounting for the temporal separation between excavation and mound-production rates observed in *G. bursarius* (SPARKS and ANDERSEN 1988; ANDERSEN 1987; THORNE and ANDERSEN 1990) was not evident in *C. mendocinus* given the low percentage of backfilled tunnels (excluding laterals).

The small proportion of mounds found in systems of *C. mendocinus*, related to the number of laterals reaching the surface, partly could be due to the use of loose soil for plugging laterals. However, a high percentage of mounds might disappear as a consequence of rainfall runoff. Violent summer storms are usual in the piedmont area, giving origin to torrential streams capable of moving considerable amounts of sediments (ROIG 1976).

### Structural complexity of burrow systems

In general, burrow systems of *C. mendocinus* follow the geometry described for other solitary fossorial rodents such as *T. bottae* (VLECK 1981; REICHMAN et al. 1982), *G. bursarius* (ANDERSEN 1988), *C. pearsoni* (ALTUNA 1983), *C. opimus* and *C. peruanus* (PEARSON 1959). In all these species burrows show a linear configuration, with a main axis composed of a sequence of straight short segments, and a variable number of branches and laterals forking off along such an axis.

Burrows of *C. mendocinus* show a similar geometric configuration in both sexes. Not only the proportions of main tunnel, branches and laterals per system were similar between sexes but also all angles considered.

Mean directional angles close to  $0^\circ$  and similarities in number and mean value of left and right deviations from the main tunnel proved a constant heading along the systems' path. REICHMAN et al. (1982) believe that the linear configuration of burrow systems in *T. bottae* enables males to intercept a greater number of female burrows. ANDERSEN (1988) concluded that the directed movement used by *G. bursarius* to locate resources would also be optimal for contacting females.

Branches are originated perpendicularly to the main tunnel and tend to keep the right angle along their path. ANDERSEN (1988) reported that both linearity and orthogonal branching of *G. bursarius* systems were consistent with the search path predicted for a "harvesting animal" (PYKE 1978) from the optimal-foraging theory. Nonetheless, ANDERSEN (1988) does not discard the influence of physical and physiological constraints on the burrowing process as being responsible for the geometric pattern.

### Home range

*C. mendocinus* is a solitary species, even during the reproductive season (PUIG et al. 1992). Moreover, absence of linking tunnels between burrow systems suggests a strongly territorial behaviour for this species.

In subterranean rodents, home range is considered to be coincident with territory, and is restricted to the burrow system (INGLES 1952; HOWARD and CHILDS 1959; MILLER 1964; NEVO 1979).



Studies reporting data on home range size in solitary fossorial rodents are few (see review in NEVO 1979; REICHMAN and SMITH 1990). In general, home range has been determined by calculating the area of the polygon formed by joining all capture sites (INGLES 1952; HOWARD and CHILDS 1959; BUSCH et al. 1989). For *T. bottae*, in excavated burrows, REICHMAN et al. (1982) regarded equidistant lines from adjacent burrows as the sides of the polygon. These methods tend to overestimate the area actually defended by the animal. The procedure of study used for *C. mendocinus* would yield a more accurate estimation of the size of its home range.

In this species home range size enhanced as the main tunnel lengthened and the number of branches increased. Area, perimeter and linearity of male burrows were significantly larger than those of female burrows. In *C. talarum*, ANTINUCCI and BUSCH (1992) did not detect differences between sexes in total tunnel length or degree of convolution, even though male burrow areas were larger than those of females. In *C. mendocinus*, the higher linearity of male home range, in addition to the longer main tunnel, also facilitates their contacting potential mates, as has been reported for other subterranean rodents (REICHMAN et al. 1982; BUSCH et al. 1989).

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### Zusammenfassung

#### *Maße und Struktur der unterirdischen Gänge von Nagetieren der Art Ctenomys mendocinus auf dem Piedmont in der Provinz Mendoza, Argentinien.*

Es wurden Struktur und Dimensionen unterirdischer Gangsysteme von *C. mendocinus* untersucht. Die Gänge zeigten eine Struktur linearen Typs mit einer Hauptachse, aus der Arme und Seitengänge abgeleitet werden. Männchen besetzen längere Systeme, mit längerem Haupttunnel und größerer Anzahl Abzweigungen. Die Verlängerung des Haupttunnels erfolgt durch Aneinanderreihen neuer, nicht so sehr durch Graben längerer Segmente. Das geometrische Gebilde ist für beide Geschlechter gleich, ohne bemerkenswerte proportionale Unterschiede der Anteile für Haupttunnel, Arme und Seitengänge innerhalb des Systems. Die sich auf die Winkel beziehenden Variablen (direktionaler Winkel, Winkel der Arme und aufsteigender Winkel) zeigten auch keine Unterschiede zwischen beiden Geschlechtern. Die Gänge haben vorwiegend direktionale Durchschnittswerte von ca. 0°, obwohl die meisten Systeme nach rechts und links des Haupttunnels Zufallsabweichungen zeigten. Die Arme liegen in rechtem Winkel zum Haupttunnel. Bei Tieferwerden des Haupttunnels scheint *C. mendocinus* Grabarbeiten auf das Minimum zu reduzieren, indem es den aufsteigenden Winkel von Seitengängen vergrößert und nicht die Länge erweitert. Homerange, Umfang und Linearität waren bei Männchen auffallend größer.

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