

## PORTAL ORIENTATION AND ARCHITECTURE OF BURROWS IN *TYMPANOCTOMYS BARRERAE* (RODENTIA, OCTODONTIDAE)

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The red viscacha rat, *Tympanoctomys barrerae*, is an octodontid rodent endemic to the Monte and Patagonian deserts of Argentina. It lives in burrows with numerous portals facing different directions. We studied climatic factors as possible determinants of burrow architecture and portal orientation, in 2 populations. Climatic factors examined were sunlight, direction of sun's rays, and wind frequency and intensity. Variables analyzed for burrow architecture were portal orientation, slope, and depth at the 1st turn. Mean number of portals per burrow was significantly different between populations. Burrows had few portals oriented toward predominantly cold and intense winds. More portals faced direct solar light in winter. Burrows are so constructed as to allow openings to receive direct sunlight in winter and indirect sunlight in summer.

Key words: burrows, deserts, ecology, Monte and Patagonia, Octodontidae

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*Tympanoctomys barrerae*, the red viscacha rat, is a rare octodontid rodent endemic to the provinces of Mendoza, La Pampa, and Neuquén, Argentina (Díaz et al. 2000; Justo et al. 1985). Representative species that are assignable to the family Octodontidae have been living in South America since the early Oligocene and show an extensive distribution on both sides of the Andes, 25–40°S (Contreras et al. 1987; Torres-Mura et al. 1989). *T. barrerae*, the only known tetraploid mammal (Gallardo et al. 1999), lives in arid environments of central western Argentina, in Monte and Patagonian phytogeographical provinces. This species is characterized by low population density and a restricted and patchy distribution (Díaz et al. 2000; Ojeda et al. 1996). It occurs in sand dunes along the vegetation belt that surrounds salt basins where halophytic

plants are dominant (Mares et al. 1997a, 1997b; Ojeda et al. 1996).

These rodents build their burrows in sand mounds (Mares et al. 1997a, 1997b; Ojeda et al. 1996) and have been reported to feed mainly on stems and leaves of chenopods, especially those of *Atriplex* species (Ojeda et al. 1996). Of species known to date, *T. barrerae* is the species most well adapted to halophytic habitats of South America (Ojeda et al. 1996). The special features of this species are a pair of stiff hair brushes placed on the sides of the mouth (Mares et al. 1997b), which are used to scrape away the external layer of *Atriplex* leaves (i.e., the plant part with the highest salt content—Giannoni et al. 2000); a highly specialized renal morphology and function (Díaz and Ojeda 1999); and a high convergence in tooth shape with other rodents that eat *Atriplex* such as *Dipodomys microps* and *Psamomys obesus* (Ojeda et al. 1999).

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The burrows, usually occupied by 1 adult (Mares et al. 1997a), have a complex structure, with at least 3 gallery levels, numerous portals (burrow openings), active and inactive tunnels, and food chambers (Mares et al. 1997a; Ojeda et al. 1996). Burrow systems are on average 13.6 m long, 8.7 m wide, and 1.3 m high (Ojeda et al. 1996). We hypothesized that construction of burrows and their resulting architecture could be the result of behavioral responses to climatic factors that tend to produce large fluctuations in temperature. Architecture of burrow systems could also be related to responses of these rodents to predation pressures associated with exits or entrances of their portals. Therefore, in this article, we describe near-surface features of burrows of *T. barrerae* and their relationship to extrinsic factors such as sun direction, sun altitude, wind intensity, and wind direction.

#### MATERIALS AND METHODS

Studies were conducted in 2 localities in Mendoza province (Argentina), La Batra and Cueva del Tigre, where sand dunes are predominant. At both sites, vegetation is xerophytic and low, with a high cover of *Atriplex*. The climate is arid temperate with average annual precipitation of 334 mm. Mean maximum and minimum temperatures are 27.9°C (January) and -2.5°C (July), respectively. La Batra is located SW of Lago Llanquanelo (35°46'S, 69°22'W), at an elevation of 1,425 m. Soils are modern sedimentary, not consolidated, corresponding to sandy and friable formations deposited by fluvial and eolian action (Instituto Nacional de Tecnología Agropecuaria 1990). At this site, *T. barrerae* is found mainly on the banks of seasonal alluvial rivers. At Cueva del Tigre, located 50 km E of Provincial Route 40 and S of old Provincial Route 186 (35°47'S, 69°18'W), soils are modern sedimentary, not consolidated, and correspond to sandy and friable formations with volcanic slag and meteorized basaltic outcrops (Instituto Nacional de Tecnología Agropecuaria 1990). In this area, dunes are lower and smaller than those at La Batra. Shrubs (*Atriplex*) and burrows are placed in gullies that serve as alluvial watercourses that flow from north to south. In both study areas, plant cover ranged from 40% to 50%, with *Atri-*

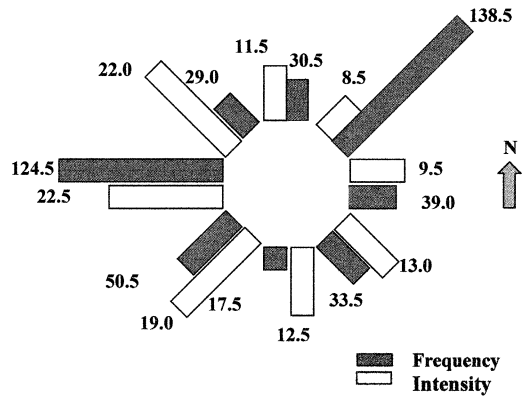


FIG. 1.—Wind frequency and intensity from different directions at Malargüe-Aero station, about 40 km from the study site. Values are shown as mean frequency (%) and mean intensity (%). Data from Estadísticas Cimatológicas 1981–1990 (1992).

*plex* being dominant. *Prosopis alpataco* and *Larrea nitida* as well as other herbaceous species were also present. Burrows of *Ctenomys* also were found.

Sampling was conducted at the same burrows for 2 weeks every 6 months from January 1999 to March 2000. Only active portals (determined by the presence of fresh tracks, feces, and diagonally cut saltbush stems around the portal) were considered for describing burrow architecture. We measured the following variables: orientation of portals to magnetic north (degrees), angle of slope of portals (degrees), and depth of portals, measured from ground level to 1st turn (cm).

Mean wind frequency and intensity were taken from Malargüe-Aero station (35°29'S, 69°35'W—Servicio Meteorológico Nacional 1992; Fig. 1), about 40 km from study sites. Angular data (orientation and slope) were analyzed by circular statistics (Batschelet 1981; Zar 1984). Watson–Williams test for 2 samples was used to compare means of angular variables for both populations.

To test randomness of burrow entrance orientation, a Rayleigh test was used (Batschelet 1981). Subsequently, data on entrance orientation for both populations were assigned to 8 quadrants: north, northeast, east, southeast, south, southwest, west, and northwest. Frequency distribution of portal orientation for both populations was compared using a chi-square test.

Each portal was categorized, according to its orientation, as sunlit all day (northeast, north, and northwest), sunlit half a day (east and west), and never sunlit (southeast, south, and southwest). Considering portal slope in relation to sun altitude in winter and summer, sunlit portals were categorized as directly sunlit (receiving sunlight directly) and indirectly sunlit. To test whether distribution of portals was associated with sunlight, expected and actual field distribution were compared using a chi-square test. Means for portal slope and orientation were obtained for both sites and compared using *t*-tests. Orientation–slope and orientation–depth relationships were analyzed using analysis of variance (ANOVA). Relationship between orientation and wind intensity and frequency was tested with Spearman correlations ( $P < 0.05$ ). All values are reported as mean  $\pm$  *SD*.

RESULTS

A total of 29 burrows of *T. barrerae* at La Batra and 30 burrows at Cueva del Tigre were sampled, and 135 and 116 portals, respectively, were recorded. Burrows varied in their number of portals. Nevertheless, mean number of portals per burrow at La Batra was significantly higher than at Cueva del Tigre ( $4.6 \pm 1.63$  and  $3.9 \pm 0.97$ , respectively; *t*-test,  $t = 2.26$ , *d.f.* = 57,  $P = 0.027$ ). We found other vertebrate species (*Eligmodontia* [Muridae] and *Bothrops amodytoides* [Viperidae]) and invertebrates (spiders and scorpions) sharing burrows of *T. barrerae*.

Mean slope was not significantly different between sampling sites (*t*-test,  $n = 240$ ,  $t = 0.683$ ,  $P > 0.05$ ) La Batra ( $19.72^\circ \pm 0.74$ ) and Cueva del Tigre ( $20.23 \pm 0.71^\circ$ ). Mean depth was not significantly different between sampling sites (*t*-test,  $n = 237$ ,  $t = 0.689$ ,  $P > 0.05$ ) La Batra ( $28.38 \pm 0.94$  cm) and Cueva del Tigre ( $28.94 \pm 1.05$  cm). There were no significant differences in slopes and depths among different quadrants (ANOVA,  $P > 0.05$  for both slopes and depths). Portal orientation was not randomly distributed in either study area (Rayleigh test, La Batra:  $z = 5.01$ ,  $n = 120$ ,  $P < 0.01$ , and Cueva del Tigre:  $z = 9.96$ ,  $n$

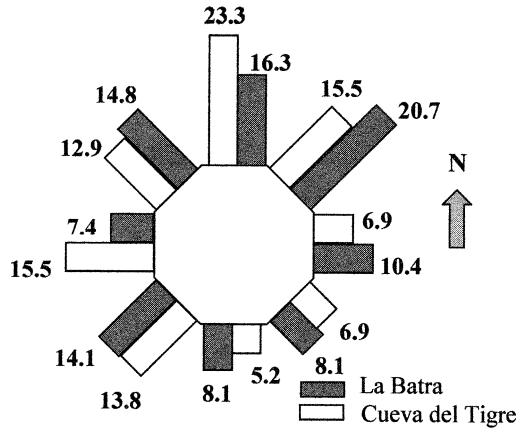


FIG. 2.—Distribution of directions for *Tympanoctomys barrerae* burrow openings per quadrant at La Batra and Cueva del Tigre, Argentina.

= 100,  $P < 0.01$ ; Fig. 2). The angular mean (orientation) in La Batra ( $14.75 \pm 72.80^\circ$ ; north) was significantly different (Watson-Williams test,  $n = 251$ ,  $f = 2,107.2$ ,  $P < 0.05$ ) from that in Cueva del Tigre ( $325.66 \pm 68.13^\circ$ ; northeast). At La Batra, the fewest number of portals was in south, southeast, east, and west quadrants, whereas at Cueva del Tigre, the fewest number of portals was in the south, southeast, and east quadrants. Greatest number of portals was recorded in the north, northeast, southwest, and northwest quadrants in both study areas (Fig. 2). There were no significant differences in portal distribution between populations ( $\chi^2 = 8.13$ ,  $n = 8$ , *d.f.* = 7,  $P = 0.32$ ). No significant correlations were found between number of openings per quadrant and wind intensity and frequency (Spearman correlation,  $n = 8$ ,  $P > 0.05$ ).

There was a significant difference between number of portals that were always in sunlight (130) and never sunlit (71;  $\chi^2 = 16.74$ , *d.f.* = 1,  $P < 0.0001$ ; Fig. 3). Because sun position changed during the year with a burrow mean slope of nearly  $20^\circ$ , rays of the sun reached inside burrows in winter (sun altitude at noon is  $31^\circ 45'$ ) but not in summer (sun altitude at noon is  $77^\circ 98'$ ; Fig. 4). Therefore, in summer, in-

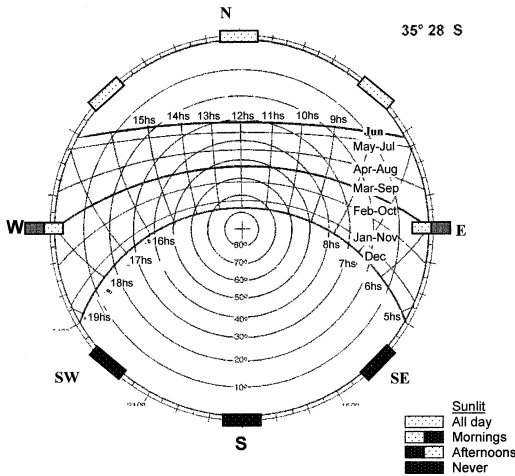


FIG. 3.—Orientation of openings of *Tympanoctomys barrerae* burrows and rays of sun at Malargüe-Aero station, Argentina.

directly sunlit portals were found in greater numbers than expected (chi-square test,  $P < 0.01$ ), and in winter, portals receiving direct sunlight inside were more numerous than expected (chi-square test,  $P < 0.01$ ; Fig. 5). For both seasons, numbers of never-sunlit portals were lower than expected (Fig. 5).

DISCUSSION

Deserts are characterized by high temperatures and low irregular precipitation, resulting in extensive drought and scarcity of vegetation. Animals living in such environments must keep body temperature at a level compatible with life (Ghobrial and Nour 1975). Desert rodents escape excessive heat imposed by high solar radiation, and high air and soil temperature by remaining below ground in their burrows during the heat of the day (Ghobrial and Nour 1975). Some studies of rodent species have related burrow architecture to nonenvironmental factors such as predation risk and the optimization of feeding in areas of low resources (Bozinovic and Simonetti 1992; Cameron et al. 1988). Other studies suggest a relationship between burrow architecture and abiotic factors such as air and soil tem-

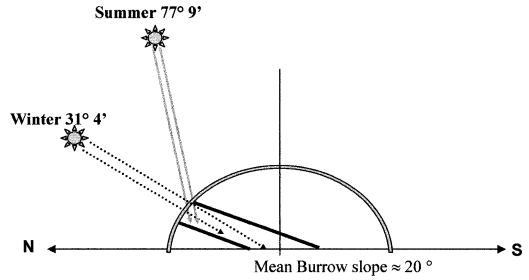


FIG. 4.—Diagram of sun altitude in winter and summer in Argentina and its relationship to sunlight shining into burrows of *Tympanoctomys barrerae*. Note that burrow entrances receive direct sunlight in winter but not in summer.

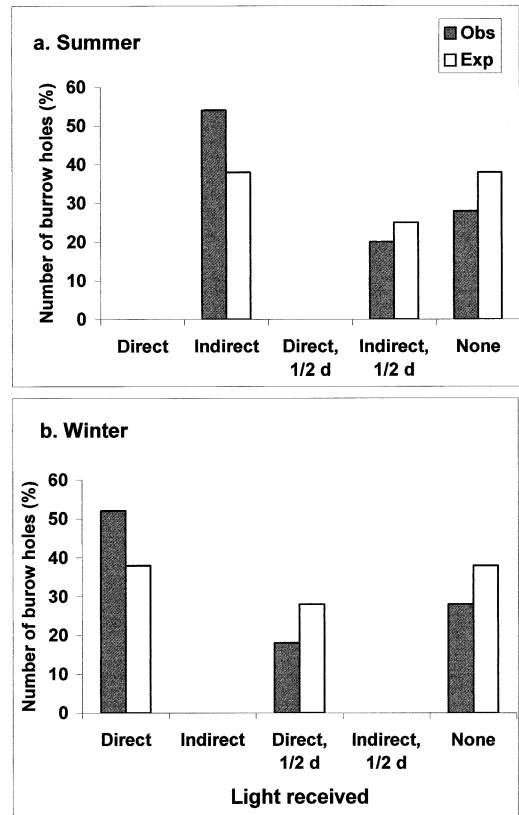


FIG. 5.—Number of burrow portals (observed and expected) and sunlight received in a) summer and b) winter. Differences between observed and expected values are statistically significant in summer and in winter (chi-square test,  $P < 0.001$ ). Note: when observed and expected values were zero (indicated by 0), they were excluded from the chi-square test.

perature, surface-wind velocity, relative humidity, and precipitation (Baumgardner 1991; Best 1982, 1988; Kay and Whitford 1978). In our study, orientation of portals was found not to be randomly distributed and seems to be related to environmental factors such as sunlight (Figs. 3–5) and, probably, prevalent direction of cold winds. Similar observations were made for *Dipodomys spectabilis* and *D. compactus* (Baumgardner 1991; Best 1988; Kay and Whitford 1978).

According to previous studies, *T. barrerae* burrows reach a depth of approximately 1.25 m (Ojeda et al. 1996). Under extreme conditions, physiological limits of thermoregulation are exceeded by surface climatic conditions, and the only available thermal shelters are underground burrows. Near 1 study site (Malargüe-Aero station), absolute minimum and maximum temperatures recorded were  $-15^{\circ}\text{C}$  (winter) and  $35^{\circ}\text{C}$  (summer), respectively. Although we have no data on temperature inside *Tympanoctomys* burrows, the depth reached (having 3 gallery levels—Ojeda et al. 1996) suggests that *T. barrerae* would use different levels in the burrow according to season. Differential use of burrows was found for *Jaculus jaculus* (nocturnal jerboa), with burrows being deeper and extending more vertically in summer and winter than those built and maintained in autumn (Ghobrial and Nour 1975).

There are factors that likely change conditions of temperature stability inside burrows, such as wind and the sporadic draining of surface rain waters. At La Bata, superficial draining of rainwater occurs from west to east; as expected, we found a smaller percentage of burrow portals facing west, doubtless because they would not succeed at keeping rainwater from entering the burrow. The strongest prevailing winds are from west to east and are warm and dry (locally called zonda wind). Therefore, a reduction in the percentage of portals facing this direction was expected. The percentage of portals oriented west was only 7.4%,

suggesting that burrow openings were built to avoid being oriented toward the west. A low percentage of southeast-oriented portals was recorded (Fig. 2), and this can be attributed to the effect of Patagonian winds, which are nonseasonal winds characterized by low temperature.

At Cueva del Tigre, when both sporadic draining of surface rain water and winds were analyzed, orientation of portals was expected to have a distribution similar to that at La Bata. This is true for the portals facing south and southeast because they are the least frequent. The direction of cold winds coincides with that of surface drainage because both come from the southeast. Burrows at this site do not show a reduction in the number of west-oriented portals, which can be attributed to their being located in the low part of a small gully where its edges provide a protective barrier against west high-intensity, zonda-type winds.

We highlight that *T. barrerae* avoids building never-sunlit burrow portals, that directly sunlit portals were absent in summer, and that in winter, directly sunlit portals were more numerous than expected (Fig. 5). Moreover, in winter, 1 individual was observed sunning early in the morning (0830 h) outside an east-oriented portal (a directly sunlit portal). Results strongly imply an important role of sunlight in orientation and slope of burrow portals, and possibly in differential use of burrows and even individual portals within a burrow seasonally, likely influenced by different positions of the sun during the day and throughout the year. Environmental factors including wind, temperature, draining of surface rain water, and sunlight during summer and winter undoubtedly act as determinants in architecture of *T. barrerae* burrows.

#### RESUMEN

La rata viscachita colorada, *Tympanoctomys barrerae*, es un roedor octodóntido endémico de los desiertos del Monte y la Patagonia de Argentina. Habita en galerías con numerosas bocas de entrada orientadas

en diferentes direcciones. Estudiamos en dos poblaciones los factores climáticos como posibles determinantes de la arquitectura de las galerías y de la orientación de las bocas de entrada. Los factores climáticos estudiados fueron la luz solar, la dirección de los rayos solares, y la frecuencia e intensidad de los vientos. Las variables analizadas para la arquitectura de las galerías fueron orientación de la boca de entrada, pendiente, y profundidad hasta la primera curva del túnel. El número medio de bocas por sistema de galería difirió significativamente entre las poblaciones. Las galerías tuvieron escasas bocas orientadas hacia los vientos intensos y fríos. En invierno la mayoría de las bocas estaban orientadas hacia la luz solar. Las galerías están construidas de tal manera que permiten recibir luz directa en invierno e indirecta en verano.

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