



## Feeding behaviour of *Tympanoctomys barrerae*, a rodent specialized in consuming *Atriplex* leaves

Stella M. Giannoni, Carlos E. Borghi & Ricardo A. Ojeda

GIB, Unidad de Zoología y Ecología Animal (IADIZA, CONICET),  
C. C. 507, Mendoza, Argentina

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*Tympanoctomys barrerae* is a monotypic octodontid. This species is endemic to the desert area of central-western Argentina where it is restricted to salt basins and sand dunes. *T. barrerae* shaves off the epidermis of *Atriplex* leaves before consuming them. This reduces electrolyte intake. Like two other unrelated salt-flat dwelling rodents, *Dipodomys microps* and *Psammomys obesus*, *T. barrerae* uses the lower incisors to scrape the hypersaline tissue away from *Atriplex* leaves, only it spends less time in the shaving process. This difference could be accounted for by a peculiar anatomical structure: two bundles of stiff hairs on either side of the mouth that may be functionally similar to a second set of lower incisors.

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### Introduction

Octodontids are one of the oldest families of South American rodents, and have evolved into a highly specialized desert species. *Tympanoctomys barrerae* is a monotypic octodontid (Galliari *et al.*, 1996) endemic to the desert area of central-western Argentina. This species exhibits a low population density and a patchy distribution restricted to salt basins and sand dunes (Ojeda *et al.*, 1996). *T. barrerae* has become highly specialized in consuming the leaves of halophytic plants, and has evolved several morphoecological adaptations to a desert life style (Mares *et al.*, 1997; Ojeda *et al.*, 1999).

The salt flats and sandy habitats where *T. barrerae* occurs are characterized by a high proportion of bare soil and sparse low vegetation dominated by chenopod species (Ojeda *et al.*, 1996). Thus, in *T. barrerae* habitats, salt-bush *Atriplex* spp. are the most abundant and year-long available plant species (Ojeda *et al.*, 1996). In other saline habitats, such as the Great Basin Desert of North America (Kenagy, 1972), the Sahara Desert of North Africa, and the Negev desert (Degen, 1988), this salt-bush appears as the most abundant plant species. Kenagy (1972) considers this chenopod to be the only food resource available year-round in the above habitats. Such availability could account for the specialized foraging characteristics for this resource found in at least three rodent species of different families: *Dipodomys microps* (Heteromyidae; Kenagy, 1972), *Psammomys obesus* (Gerbillidae; Daly & Daly, 1973; Degen, 1988), and recently in *Tympanoctomys barrerae* (Octodontidae; Ojeda *et al.*, 1996).

All three species seem to have a similar behavioural adaptation for reducing electrolyte intake when feeding on *Atriplex* spp. leaves. The two former species remove most of the electrolytes by scraping *Atriplex* spp. leaves with their teeth before consuming them. *T. barrerae* would use not only the lower incisors but the bundles of stiff hairs as well. The latter anatomical structures are located on either side of the mouth and have been reported as unique to *T. barrerae* (Mares *et al.*, 1997).

The aims of the present study were to describe the feeding behaviour of *T. barrerae* and to compare this behaviour with those of other saltflat-dwelling rodents showing similar habits. In addition, we tried to determine the function of two small bundles of stiff hairs located on either side of the buccal cavity of this rodent (Mares *et al.*, 1997).

### Materials and methods

The animals (6 adult females, 2 adult males, and 2 young) were captured during 1996 and 1997 with Sherman traps at a salt flat 30 km south of El Nihuil in the province of Mendoza, Argentina (35°02' S, 68°40' W). They were caged individually, except for two females that were kept with their litter, in 30 × 25 × 30 cm terraria. Animals were maintained on a 14:10 L:D schedule with light off at 10 00 h and on at 24 00 h, and fed on an *ad lib* mixture of carrots, rolled oats, apples, and *Atriplex* leaves (Chenopodiaceae).

Previous observations revealed that *T. barrerae* shaves off leaves before consuming them (Mares *et al.*, 1997). To analyse this procedure two behavioural aspects were observed: the way in which this rodent manipulates leaves of *Atriplex* species, and the time spent handling each leaf. All observations were made in the daytime using a glass terrarium. The method used was focal-animal sampling (Altmann, 1972).

To find out how *T. barrerae* handles chenopod leaves before consuming them, five adults (3 females and 2 males) were individually housed in glass terraria. In this first trial, each animal was provided with stems of *Atriplex patagonica* whose leaves had previously been painted with colours used in confectionery (red and green). Discarded leaf debris was collected 3 h later. We selected *A. patagonica* for this experiment because it was readily available in the capture area (Ojeda *et al.*, 1996). Four sets of painted leaves were offered to every animal: upward side red (adaxial face), downward side red (abaxial face), upward side green, and downward side green. The different colours and opposite sides were used in an attempt to find out whether they affected preference. In addition, stem manipulation including manner and efficiency (time (s) spent manipulating each leaf) was recorded on videotape, 30 min per animal and per trial, i.e. a total 600 min of observations (5 animals × 30 min × 4 sets of painted leaves).

Mares *et al.* (1997) found that *T. barrerae* has two small bundles of stiff hairs located on either side of the buccal cavity. In order to discuss the function of these bundles, a second trial was performed whereby we recorded time (s) spent manipulating each leaf. We used animals with stiff hairs intact (5 adults and 2 litters), and another two adults whose hairs had been previously cut. Observations of 30 min each were made in a sandless terrarium, where the animals were offered *Atriplex lampa* stems. Total observation time was 270 min, i.e. nine animals × 30 min each.

In the third trial, five individuals were tested for food preference. They were housed for 3 days in individual cages with sandless floors. A known quantity of *A. lampa* and *A. patagonica* branches was offered to find which species was preferred. After 24 h the amount consumed of each plant species was determined by difference in mass. In order to evaluate the amount of water lost by *A. lampa* and *A. patagonica* branches during the trials, branches of similar size of both salt-bush species were placed in a cage similar to those used in trials. Water loss was determined by difference in weight.

**Table 1.** Retrieved number of whole discarded parts of *Atriplex patagonica* leaves manipulated by *Tympanoctomys barrerae*. Only the painted side of the leaf is indicated. Goodness of fit test was used to compare differences in leaf handling

Painted side	Discarded parts		<i>p</i>	$\chi^2$ (df. = 1)
	Painted	Unpainted		
Adaxial green	6	57	0.0001	39.68
Abaxial green	85	17	0.0001	44.01
Adaxial red	2	16	0.002	9.38
Abaxial red	63	17	0.0001	25.31

## Results

*Tympanoctomys barrerae* cuts off one to three short sections from *Atriplex* stems, and carries them in the side of its mouth to a corner of the terrarium. The leaf and thicker portions of *Atriplex* stems are shaved before being eaten, while the apical ends of stems are consumed whole.

When shaving *Atriplex* leaves, *T. barrerae* seizes the branch with one of its front limbs and places it parallel to its body. Then, it cuts off the leaves one by one, holding them with a foreleg. While repeatedly moving the head up and down, it shaves off the outer hypersaline leaf tissue with the lower incisors, expelling it *ca.* 5 cm away in the shape of small wound ribbons. Subsequently, the animal ingests the green inner tissue of leaves, and drops near him the remaining outer tissue whole.

Results of the manipulation experiment with painted leaves show that *T. barrerae* more frequently discards the abaxial than the adaxial epidermis (goodness of fit test, abaxial = 221, adaxial = 42;  $\chi^2 = 121.83$ , df. = 1,  $p < 0.0001$ ). It handles *Atriplex* leaves in the following manner: first it shaves off the outer tissue of the leaf upward side (adaxial face), discarding it in tiny pieces, then it ingests the inner leaf tissue, dropping the downward side (abaxial face) whole (Table 1). *T. barrerae* showed no significant preference for either of the colours used to paint the leaves (adaxial painted,  $\chi^2 = 0.062$ , df. = 1,  $p < 0.8035$ ; abaxial painted,  $\chi^2 = 0.355$ , df. = 1,  $p < 0.5513$ ).

The process whereby adults with hair bundles in their mouths scrape away the epidermal vesicles of a leaf in preparation for eating takes 3 s ( $n = 50$ , S.D. = 1.1 s). On the other hand, individuals without bristles take 8.3 s ( $n = 29$ , S.D. = 2.1 s) to shave the *Atriplex* leaf. Thus, individuals of *T. barrerae* with and without bristles showed significant differences in the time spent in handling each leaf (*t*-test for dependent samples:  $t = -13.15$ , df. = 28,  $p = 0.0001$ ). Individuals do not start shaving the salt-bush leaves until they are 10 days of age. They cut and strip leaves in the same way as their mothers do, but preparation for eating a leaf takes them much longer (8.3 s;  $n = 15$ ; S.D. = 2.1 s; *t*-test for independent samples:  $t = 13.54$ , df. = 63,  $p = 0.0001$ ).

As regards food preference trials, *A. patagonica* was preferred over *A. lampa* (Kolmogorov-Smirnov test,  $-D$  max. = 0.83,  $p < 0.001$ ). The mean quantity ingested daily was  $47.0 \pm 2.9$  g for *A. lampa* and  $85.0 \pm 2.2$  g for *A. patagonica*. Body mass did not change significantly during the trials (*t*-test,  $p = 0.16$ ).

## Discussion

Desert mammals face a difficult task when obtaining water and food in arid habitats that are almost devoid of vegetation, such as salt flats. In these habitats, *D. microps* largely depends on *Atriplex*, since this salt bush is the only food resource available all year round.

According to Kenagy (1972), such availability minimizes this rodent's dependence on the unpredictable seed crops of desert annuals. However, feeding on *Atriplex* poses a problem for these animals. The electrolyte content is high in chenopods, particularly in *Atriplex* (Kenagy, 1972). The high salt concentration on the leaf surface appears to be associated with water homeostasis under conditions of high light intensity and great aridity (Kenagy, 1972).

Three species of salt-flat-dwelling rodents of different phylogenetic groups feed almost exclusively on *Atriplex*: *D. microps* (Kenagy, 1972), *P. obesus* (Daly & Daly, 1973; Degen, 1988), and *T. barrerae* (Ojeda *et al.*, 1996). All three species seem to have converged on feeding behaviour, since they all shave off the leaf before consuming it. Kenagy (1972) and Mares *et al.* (1997) suggest that specialization on this food resource could be accounted for by its predictability and abundance. In *T. barrerae* habitats, water can be obtained from *Atriplex* species as their leaves remain green and succulent all year round (Mares *et al.*, 1997). Also, these helophytes appear to be an ideal source of nutrients for *T. barrerae* given their year-round abundance and predictability (Ojeda *et al.*, 1996).

Kenagy (1972) found that the lower incisors of *D. microps* are unique in its genus, since they are broad, anteriorly flattened, and chisel-shaped, unlike those of other kangaroo rats that tend to be relatively narrow, rounded, and awl-shaped. This author suggests that the shape of the lower incisors serves to efficiently shave off the hypersaline peripheral tissue of *Atriplex* leaves. The lower incisors of *Tympanoctomys barrerae* are similar in shape to those of *D. microps* (Mares *et al.*, 1997). Furthermore, the lower incisors of *T. barrerae* are broader, more flattened and chisel-shaped than those of *D. microps* and other octodontids (Ojeda *et al.*, 1999). Thus, the lesser time spent by *T. barrerae* (3 s) in stripping each leaf, in comparison with *D. microps* (15–20 s; Kenagy, 1973), could be explained by the peculiar morphology of its lower incisors. Further, it could be accounted for by an anatomical structure unique to *T. barrerae*: two bundles of stiff hairs on either side of the mouth (Mares *et al.*, 1997). These hair bundles would function as additional incisors that would help the animal remove the hypersaline tissue of *Atriplex* leaves. The fact that animals possessing stiff bristles spend less time in shaving each leaf than those without them (2 s *vs.* 8 s) would indicate participation of the hair bundles in the scraping process, which seems to be otherwise similar for both types of animals. The results of this study are consistent with the suggestion made by Mares *et al.* (1997) that the specialized hair bundles of *T. barrerae* could be functionally similar to a second set of lower incisors.

In conclusion, *T. barrerae* shows high levels of morphological and behavioural convergence with at least two other unrelated salt-flat-dwelling rodents. In addition, it has developed a peculiar anatomical structure, the bristle bundles, which significantly reduce the time spent by this species removing the hypersaline surface tissue from *Atriplex* leaves.

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