Saltbush Leaves: Excision of Hypersaline Tissue by a Kangaroo Rat

Abstract. Dipodomys microps *climbs into shrubs and harvests leaves of the halophyte* Atriplex confertifolia *throughout the year. The epidermal vesicles of these leaves are high in electrolyte concentration, but the specialized photosynthetic parenchyma which is arranged concentrically about the vascular bundles is low in electrolytes and high in starch. The lower incisors of* D. microps *are broad, flattened anteriorly, and chisel-shaped (unlike those of other kangaroo rats, which are rounded and awl-shaped) and are used to shave off the hypersaline, peripheral tissue of the leaves so that the inner tissue can be eaten. This atypical feeding behavior should minimize the reliance of* D. microps *on the unpredictable seed crops of desert annuals, and also favor its coexistence with other species of* Dipodomys, *which are primarily granivorous.*

The kangaroo rats of western North America (*Dipodomys*, Heteromyidae) are highly specialized, desert-dwelling seed eaters (*1*). They can survive on a diet of air-dried seeds without free water or succulent vegetation, mainly because they spend most of their time in the ground and can conserve body water by producing highly concentrated urine (*2*). Twenty-one species are recognized and sympatry is common. Two, three, or occasionally four species may be found at the same location (*3*). Recent discussion of competition among granivorous rodents (particularly heteromyids) suggests that qualities of soil and vegetation, and differential seed-husking abilities for different sized seeds by different sized rodents are possible correlates of differential resource allocation or microhabitat selection (*4*). I now report a striking dietary divergence and the behavioral and morphological specializations which have evolved with it in one species of *Dipodomys.*

Dipodomys microps (the Great Basin, or chisel-toothed kangaroo rat) and *D. merriami* (Merriam's kangaroo rat) occur together in a Great Basin scrub habitat in the Owens Valley of eastern California. *Dipodomys merriami* gleans seeds from the soil in typical kangaroo rat fashion, but *D. microps* climbs into shrubs and harvests leaves, which it stuffs into its hair-lined cheek pouches and carries back to its burrow to be eaten or cached. It harvests the leaves of saltbush (*Atriplex confertifolia*, Chenopodiaceae) throughout the year to the virtual exclusion of 11 other shrub species at the study site. It caches as much as 250 g of saltbush leaves in its burrow. The feeding of *D. microps* on *A. confertifolia* is intricately related to the unique anatomy and physiology of these leaves.

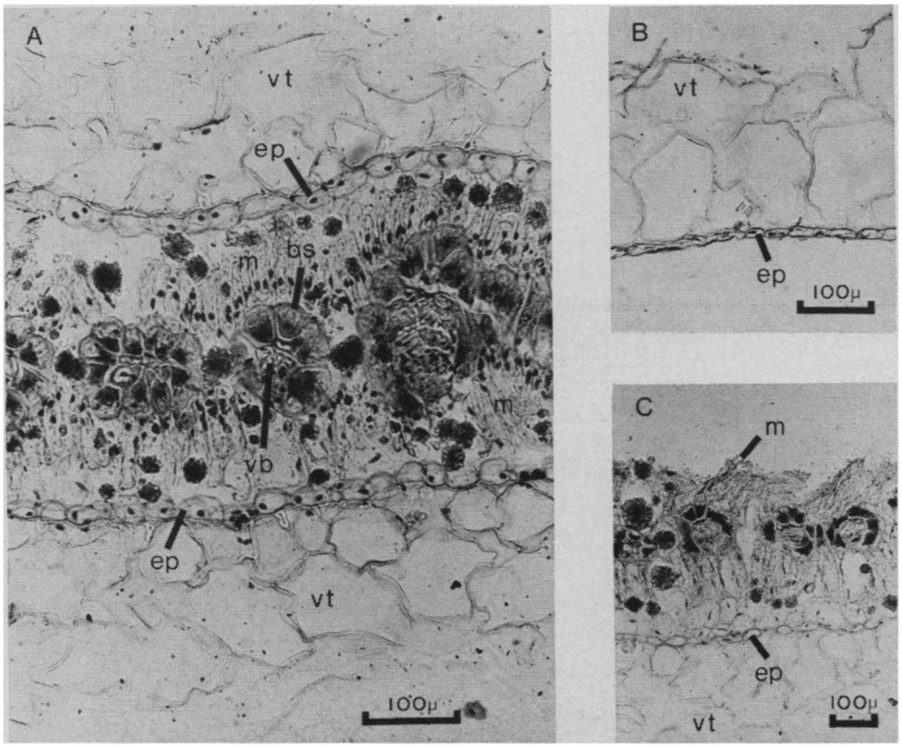
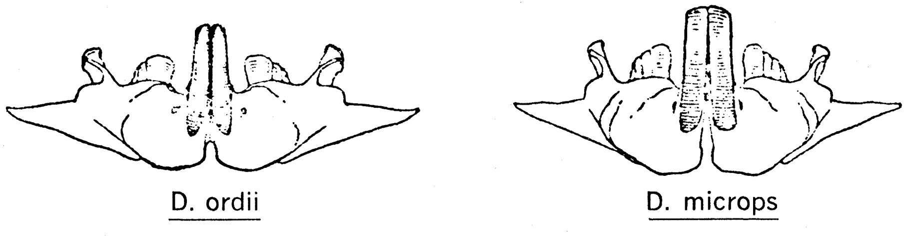


Fig. 1. Leaf tissue of the spiny saltbush, *Atriplex confertifolia*; cross sections 25 μm thick. (A) Intact leaf; *vt* = vesicular trichomes, *ep* = epidermis, *m* = mesophyll, *vb* = vascular bundles, *bs* = bundle sheath parenchyma. (B) Surface tissue removed from the leaf and discarded by a *Dipodomys microps* rat. (C) The remains of a leaf taken away from a *D. microps* rat after it had removed the epidermis and vesicular trichomes from only one side. The animal would ordinarily continue on to remove the epidermis and vesicular trichomes from the other side of the leaf and then eat the center. The effects of shear are apparent on the upper edge of the upper mesophyll.

It is well known that the electrolyte content of certain chenopods, *Atriplex* in particular, is high, and that sodium content is often greater than potassium, which is the reverse of the situation in most plants. Salt content in leaves of *Atriplex* may reach nearly 40 percent (ash in total dry weight) (*5*). Particularly large amounts of electrolytes are known to move into the vesicular cells at the leaf surface (*6*). The structure and function of the hypersaline surface tissue of *Atriplex* leaves appear to be related to water homeostasis under conditions of high light intensity and great aridity (*7*). Enzyme assays (*8*) indicate that *A. confertifolia* is among the species of *Atriplex* which employ the recently discovered C_4-dicarboxylic acid pathway of photosynthetic fixation of CO_2, instead of the more common Calvin cycle (*9*). The high photosynthetic rates associated with C_4 species are considered to be adaptive to conditions of high temperature, high light intensity, and aridity. Leaves of C_4 plants are atypical anatomically (Fig. 1A). A specialized layer of parenchyma cells (the bundle sheath parenchyma) which is concentrically arranged around the vascular tissue is the principal location of both chloroplasts and starch. Mesophyll cells lie between the bundle sheath parenchyma and the hypodermis and contain fewer and smaller chloroplasts and very little starch. In typical plants the chloroplasts are principally located in the mesophyll. The mesophyll of some C_4 species of *Atriplex* is concentrically arranged about the bundle sheath parenchyma, but in others it is arranged in more or less linear fashion beneath the hypodermis (*10*). *Atriplex confertifolia* has a continuous unicellular layer of mesophyll on both the upper and lower surfaces of the leaf.

The broad, flat-fronted, chisel-shaped structure of the lower incisors of *D.*

microps is unique among kangaroo rats and is commonly used as a character for identification (Fig. 2). However, these incisors have not previously been accorded any function. They were not mentioned in the original description of the species (*11*). In the spring when saltbush leaves are fresh and succulent (water content as high as 80 percent) *D. microps* may consume the leaves in toto. But in summer, winter, and fall, when the leaves dry out (water content as low as 50 percent), the animal uses a different procedure. It holds a leaf (diameter 7 to 10 mm) in the forefeet and draws it over the lower incisors about ten times, thus shaving off the outer layers of the downward side of the leaf. The leaf is turned over, the opposite side is shaved, and finally the inner tissue—bundle sheath parenchyma, vascular tissue, and mesophyll—is eaten. The discarded shavings generally consist of the vesicular trichome layer and the epidermis (Fig. 1, B and C), but at times may include some of the deeper tissue. It seems that the neat, linear arrangement of the columnar mesophyll cells should facilitate this neat separation by the shaving action of *D. microps*. Discarded leaf debris accumulates in the burrow tunnels throughout the year and beneath the nest in winter. *Dipodomys microps* does not eat the discarded shavings; a group of seven animals provided with this material was starving after 36 hours.


D. ordii

D. microps

Fig. 2. The lower incisors of two species of kangaroo rats of similar body size. The relatively narrow, rounded, and awl-shaped lower incisors of *D. ordii* are typical of the genus *Dipodomys* as a whole. The broad, anteriorly flattened, chisel-shaped lower incisors of *D. microps* are unique in the genus and represent a specialization.

The discarded leaf shavings are very high in electrolytes. A *D. microps* rat was given a weighed amount of leaves. As soon as the rat had trimmed them as described above, the shavings were collected and weighed. Contents of the tissue of the inner leaf were determined by difference from whole leaves picked from the same twig as the leaves given to the rat. For winter leaves (54.9 percent water by wet weight) the concentration of sodium relative to water in the discarded tissue (32.2 percent water) was 4261 meq/liter. But within the same leaves the concentration of sodium in the inner layer which was eaten (67.4 percent water) was only 135 meq/liter. Average concentration of sodium in spring leaves (78.5 percent water), which may be consumed in toto by *D. microps*, was 252 meq/liter, whereas average concentration in the winter leaves, which are not generally consumed in toto, was 995 meq/liter. The sodium concentration of the inner tissue was only 3 percent that of the shavings, and therefore the leaf materials which are actually consumed impose a smaller osmotic load on the animals than would the discarded parts. Even though *D. microps* minimizes salt intake by discarding the hypersaline surface tissues of leaves, its salt consumption is nonetheless greater than in many other rodents for which the prime problem of electrolyte balance is one of sodium retention, rather than excretion.

A feeding experiment showed that *D. microps* gained weight on an exclusive diet of *A. confertifolia* leaves (50 to 60 percent water) provided daily for 16 days. During this experiment the animals produced large quantities of leaf shavings and urinated copiously in the cage. Under the same experimental conditions *D. merriami* would not eat the leaves and died within 2 days. Under laboratory conditions *D. merriami* thrived on a diet of bird seed without the availability of water or succulent vegetation, whereas *D. microps* did not survive (*12*). The mean total osmotic concentration of urine on the seed diet was 2827 milliosmol/liter for *D. microps* and 4675 milliosmol/liter for *D. merriami*; the value for *D. microps* is the lowest reported for the genus (*13*). When a ration of 50 sunflower seeds was provided daily in addition to freely available leaves, some individuals in a group of seven *D. microps* ate all of the seeds, but others ate no seeds at all.

It is well known that all kangaroo rat species include some green material in their diets, especially during the spring reproductive period when ephemeral grasses or forbs are available. Even *D. merriami*, considered to be one of the most strongly desert-adapted kangaroo rats, may have a diet of nearly 40 percent green plant material in spring, although its diet is nearly 100 percent seeds for much of the rest of the year (*1*). However, *D. microps* appears to be unique among kangaroo rats in its specialized extensive, year-round foraging for leaves.

The year-round availability of saltbush leaves in appropriate *D. microps* habitat amounts to the continuous availability of a single food resource in both space and time. Specialization on this resource should minimize the dependence of *D. microps* on the unpredictable seed crops of desert annuals, on which the typical, seed-specializing species of *Dipodomys* must rely. In habitats occupied by *D. microps* and other species of *Dipodomys*, it is to be expected that the coexistence of *D. microps* should be favored because this kangaroo rat heavily utilizes a resource essentially unused by its congeners. This reduction in competition for seeds could perhaps lead to a greater abundance and diversity of kangaroo rat species than one would expect from estimates of carrying capacity for a given habitat based solely on seed utilization. In fact, the only published occurrences of four species of *Dipodomys* in the same habitat are for associations which include *D. microps* (*3*).

Mayr (*14*) has recently emphasized that new behavior patterns may establish new selective pressures. Phenotypes of *D. microps* with increasingly broadened and more chisel-shaped lower incisors would have been favored selectively because of their greater efficiency at separating useful leaf material from whole leaves. The selective pressures for the evolution of the specialized behavior and morphology of *D. microps* for eating leaves of halophytes would have been brought to bear strongly in habitats where (i) there was competitive pressure from granivorous rodents for available seeds and (ii) the year-round source of available leaves was limited to halophytic shrubs.

It is well known that rodent faunas of differing taxonomic affinities have evolved in parallel in the major world deserts. Among the most conspicuous characteristics of these rodents are (i) seed diet and (ii) high urine-concentrating capacity (*2*, *15*). The gerbilline rodent *Psammomys obesus* of the Sahara Desert feeds almost exclusively on the succulent parts of plants of the family Chenopodiaceae, including some

Atriplex, whereas other gerbils are more typically seed eaters (*16*). *Psammomys obesus* differs from *D. microps* in that it apparently consumes leaves in toto and that it produces a much more concentrated urine, about 5000 milliosmol/liter (*17*). Thus, the diets of *D. microps* and *P. obesus* are similar, but the adaptive means of meeting the physiological challenge of high salinity were different, being primarily behavioral in *D. microps* and more physiological in *P. obesus*. It is, nonetheless, notable that in similar ecological settings, natural selection has produced a similar adaptive pattern of divergence—leaf eating—in two species which are members of separate, but parallel, systems of typically granivorous rodents.

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12. For the feeding experiment with leaves, $N = 7$ for each species and ambient temperature was 12° to 15°C. For the experiment with a seed diet, $N = 8$ for each species and ambient temperature was 15°C. Mean survival for *D. microps* on a seed diet was 16 days.
13. For *D. microps*, $N = 8$, S.E. = 233; for *D. merriami*, $N = 7$, S.E. = 140.
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18. I was supported by NSF predoctoral fellowships GZ1147 and GB27707 and in part by NSF grant GB18744 administered by G. A. Bartholomew. I thank G. A. Bartholomew, H. J. Thompson, and M. A. Nobs for their helpful comments on this study. I thank M. Natzler for assistance with histological preparations for the photographs, and D. M. Gross for advice on photomicrographic technique. Drawings in Fig. 2 are copied, with permission of the author and publisher, from E. R. Hall, *Mammals of Nevada* (Univ. of California Press, Berkeley, 1946), p. 417.

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Running Up and Down Hills: Some Consequences of Size

Abstract. *Small mammals are able to run at about the same maximum speed vertically as horizontally, but larger mammals cannot do this. During level running a mouse weighing 30 grams uses about eight times as much energy per unit of body weight as does a chimpanzee weighing 17.5 kilograms (42.6 joules per kilogram meter versus 5.17 joules per kilogram meter). The additional energy required to lift 1 kilogram of body weight 1 meter while running uphill was similar for the two species (about 15.5 joules per kilogram meter). Therefore the increment in energy expenditure for mice to run uphill compared to running horizontally is about one-eighth that for a chimpanzee. Both mice and chimpanzees were able to recover about 90 percent of the energy stored running uphill on the way down.*

Some small animals appear to accomplish extraordinary energetic feats when they run vertically. Squirrels run up tree trunks at about the same speed that they run on level ground. Intuitively this seems unreasonable, for man must increase his metabolism markedly to maintain his speed upon encountering even a slight incline. How do small animals accomplish this feat of vertical running? Are they able to increase their metabolism by a relatively greater amount than man, or does it take them relatively less energy to run uphill?

Kleiber's familiar equation states that resting metabolism is proportional to the body weight to the ¾ power in mammals (*1*), and thus each gram of tissue from a 30-g mouse consumes oxygen at about 13 times the rate per gram of tissue from a 1000-kg horse. The mechanical work involved in lifting 1 kg 1 vertical meter, however, is the same for both the mouse and the horse (9.80 joules or 2.34 cal; 1 joule = 4.19 cal). If the mechanical efficiency of muscles of different sized mammals is also the same (*2*), then the same amount of energy should be expended in lifting 1 kg 1 vertical meter by both the mouse and the horse. Thus the relative increase in metabolic rate for the vertical component of running uphill in the mouse should be about 1/13th that for the horse.

Table 1. The values of various parameters of oxygen consumption as determined from the data in Fig. 1. *S* is the slope, determined by the method of least squares, of the relationship between oxygen consumption and running velocity and is given in milliliters of O_2 per kilogram meter. The *y* intercept of the oxygen consumption line is given in liters of O_2 per kilogram hour, *n* is the number of trials, and *r* is the correlation coefficient. The predicted values are the slopes for level running calculated on the basis of body weight (*4*).

Type of running	*S*	*y* intercept	*n*	*r*
		Mice		
Uphill	2.28	2.66	26	0.94
Downhill	1.96	2.68	22	0.87
Level	2.07	2.57	22	0.90
Predicted	2.17			
		Chimpanzees		
Uphill	0.44	0.85	23	0.90
Downhill	0.13	0.79	25	0.94
Level	0.25	0.79	69	0.92
Predicted	0.17			

Can small animals indeed run up inclines with relatively small increases in metabolism above that for level running, and how does the energetic cost of running up and down hills depend on an animal's size? To answer these questions we used three white mice (*Mus musculus*; average weight, 30.2 g) and two chimpanzees (*Pan troglodytes*; average weight, 17.5 kg). We trained the animals to run on treadmills while we measured oxygen consumption and carbon dioxide production. The animals ran at various speeds, on the level, on a +15° incline, and on a −15° incline. Wind velocity was approximately matched to tread speed. Air temperature was 22°C and relative humidity was less than 30 percent. We used only steady-state values for oxygen consumption (*3*).

The oxygen consumption of mice running on the level increased nearly linearly with running speed (Fig. 1), and the slope of this line was approximately the same as that predicted by