## GRAMINIVORY BY *DIPODOMYS ORDII* AND *DIPODOMYS MERRIAMI* ON FOUR SPECIES OF PERENNIAL GRASSES

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ABSTRACT—Kangaroo rats have been described as primarily granivorous; however, they also consume green vegetation. We investigated selectivity of grasses by kangaroo rats (*Dipodomys ordii* and *D. merriami*) presented with 4 common perennial grass species from the Jornada basin in the Chihuahuan Desert. All grass species offered were utilized, and there were differences in utilization. Our results suggest that water content may underlie these differences, although other factors are not excluded. Merriam's kangaroo rats removed more tillers from each tussock of grass than Ord's kangaroo rat. Ord's kangaroo rat may select grasses with higher water content per tiller.

RESUMEN—Las ratas canguro se han descrito como una especie principalmente granívora; sin embargo, también consumen vegetación verde. Investigamos la selectividad de las ratas canguro (Dipodomys ordii y D. merriami) presentadas con 4 especies de pasto perenne comunes del llano La Jornada en el Desierto Chihuahuense. Todas las especies de pasto ofrecidas fueron utilizadas, y hubo diferencias en la utilización. Nuestros resultados sugieren que el contenido de agua puede explicar estas diferencias, aunque otros factores no se excluyen. Las ratas canguro de Merriam utilizaron más vástagos de cada rama de pastos que las ratas canguro de Ord. La rata canguro de Ord puede seleccionar pastos con un contenido más alto de en agua por vástago.

Ord's kangaroo rat (Dipodomys ordii) and Merriam's kangaroo rat (D. merriami) occur in the grasslands and shrublands of southern New Mexico. Ord's kangaroo rats are often associated with areas of loose sandy soil, including sand dunes (Schmidly et al., 1988). Merriam's kangaroo rat prefers open habitats, and avoids areas with rocky ground cover and heavy clay or densely packed soils (Bartholomew and Casewell, 1951; Huey, 1951; Reynolds, 1958; Wondolleck, 1978). Where Ord's kangaroo rats occur sympatrically with Merriam's kangaroo rats, Ord's kangaroo rats occupy sandy soils, and Merriam's kangaroo rats typically inhabit gravelly or hard soils (Davis, 1966). In the Jornada basin of the Chihuahuan Desert in the southwestern United States, Ord's kangaroo rat is abundant in the grasslands and Merriam's kangaroo rat is found in the shrublands. Ord's and Merriam's kangaroo rats occur sympatrically in mesquite (Prosopis glandulosa)

dunes and tobosa (*Pleuraphis [Hilaria] mutica*) grasslands (Whitford and Steinberger, 1989). The only other kangaroo rat in the area is the much larger mound-building banner-tailed kangaroo rat (*D. spectabilis*).

Although kangaroo rats have been described as primarily granivorous (Reynolds, 1958, 1960; Chew and Chew, 1970; Alcoze and Zimmerman, 1971; Bradley and Mauer, 1971; Flake, 1973; Soholt, 1973; Pulliam and Brand, 1975; Soholt, 1977; Harris, 1986), they also consume significant quantities of green vegetation and insects (Beatley, 1969; Bradley and Mauer, 1971; Reichman, 1975; Beatley, 1976; Kerley and Whitford, 1994; Kerley et al., 1997). Kerley et al. (1997) reported that Ord's kangaroo rats selectively use the youngest portions of the stems of black grama (*Bouteloua eriopoda*) and other grasses.

Kangaroo rats do not drink free water (Frank, 1988). However, individuals need more

water during periods of gestation, lactation, or courtship than at other times (Beatley, 1969; Bradley and Mauer, 1971; Van de Graaff and Balda, 1973; Reichman and Van de Graaff, 1975; Soholt, 1977). Young grass stem portions have higher water content and may be more nutritious than older portions (Beatley, 1969). Reproduction in Merriam's kangaroo rat appears to be stimulated in part by consumption of short-lived vegetation that has appeared after seasonal rainfall (Beatley, 1969; Van de Graff and Balda, 1973; Reichman and Van de Graff, 1975; Zongyong and Brown, 1987). Thus, eating the most nutritious and water-rich portions of the grass stems represents a potentially important survival mechanism in desert rodents.

We hypothesized that these 2 partially sympatric species differ in their selectivity for grasses in ways that reflect differences between the habitats in which they usually occur. We further hypothesized that water content of the grasses was sufficient to explain any demonstrated selectivity. We tested these hypotheses with laboratory studies in which single captive kangaroo rats were presented overnight with potted grass plants of 4 species. Our results provide insight into grass selectivity and identify potential mechanisms for selectivity by both Ord's and Merriam's kangaroo rats.

METHODS AND MATERIALS—Kangaroo rats used in this study were collected from 3 sampling areas located ca. 56 km NE of Las Cruces, New Mexico, on the United States Department of Agriculture's Jornada Experimental Range and New Mexico State University's Chihuahuan Desert Rangelands Research Center.

The first sampling area was dominated by black grama (Bouteluoa eriopolda), although spider grass (Aristida ternipes) and mesa dropseed (Sporobolus flexuosus) occurred frequently. Ord's kangaroo rat was the most common heteromyid in this habitat. The second sampling area was situated on an upper bajada. The habitat was dominated by creosote bush (Larrea tridentata); grasses occured in very low numbers. This site was inhabited by Merriam's kangaroo rat. The third sampling area was located on a lower bajada slope where tobosa grass was abundant and both species of kangaroo rat occured sympatrically.

Kangaroo rats were trapped in Sherman live traps baited with a mixture of rolled milo and peanut butter. Trapping grids measured 50 m² with traps placed at 10-m intervals. Animals were trapped during and immediately after the summer rains (1 June

1997 to 30 September 1997 and 1 June 1998 to 16 August 1998) and included reproductively active males and females of both species. Twenty-one Ord's kangaroo rats (3 females, 18 males) and 17 Merriam's kangaroo rats (11 females, 6 males) were captured. Sex was determined as described by Bradley and Mauer (1971). Animals used during feeding trials were permanently tagged with passive integrated transponder (PIT) tags injected subcutaneously above the right thigh to prevent multiple uses of the same individuals. Captured animals were immediately transported to the laboratory for feeding trials. Animals captured during a trapping session were used in feeding trials the same or following night, and were released at the capture site within 2 days.

Four common perennial grasses, black grama, mesa dropseed, spider grass, and tobosa grass, were offered to the captive kangaroo rats in the feeding enclosures. These species were chosen because they are the dominant grass species in the areas in which kangaroo rats were trapped for the feeding trials. Grass tussocks were collected from the field at about the same time period as the trapping sessions. Tussocks were potted in 100 cm3 plastic pots and kept outdoors; supplemental water was provided to any plants that appeared to be water-stressed. Immediately before each plant was used in a feeding trial, the number of green tillers available on each plant was recorded; 20% of the tillers were clipped as reference tillers for biomass measurements. This fraction allowed a reliable measurement of biomass without drastically reducing the numbers of tillers remaining to be offered to the experimental animals. Reference tillers were immediately weighed and oven dried at 60°C for 24 h. Dry weights of reference tillers were then recorded. Water content was calculated as the difference between dry and wet weights. The number of tillers available to each kangaroo rat was the number of tillers remaining after clipping reference tillers. Dead and decadent tillers were not counted as available, nor were they removed from the plants offered to the experimental animals. Average total aboveground green biomass values for each plant species were 3.64 g for spider grass, 2.95 g for black grama, 4.78 g for tobosa, and 8.51 g for mesa dropseed.

Feeding trials were conducted in experimental exclosures (fiberglass boxes) that measured 122 × 61 × 61 cm (Kerley et al., 1997). Each box was filled to a depth of ca. 36 cm with soil. A barrier of 1 cm hardware cloth was placed over the soil and was covered with an additional 5 cm of soil. The hardware cloth barrier was breached by 4 holes measuring ca. 10 cm² allowing placement of 4 square pots containing 1 plant of each of the 4 grass species. An external burrow made of PVC pipe was attached to the outside of the chamber allowing the experimental animals protection from heat and cold. The soil sur-

Table 3—Mean biomass (g) of grass removed by kangaroo rat species. Standard errors of the means are given in parentheses. Means within a given species followed by the same lower-case letter are not significantly different (P > 0.05) according to a two-way analysis of variance.

Grass	D. ordii $n = 21$	D. merriami $n = 17$
Pleuraphis mutica	1.194 (0.260) a	2.484 (0.602) a
Bouteloua eriopoda	1.064 (0.232) b	1.569 (0.381) a
Aristida ternipes	0.926 (0.202) b	2.154 (0.523) a
Sporobolus flexuosus	1.742 (0.380) a	3.340 (0.810) b

cent tillers removed from each plant species. Percent tillers removed and water content per tiller of grass were positively correlated ( $T_c$  = 0.17 in a 1-sided test of  $H_o$ :  $T_c = 0$  vs.  $H_a$ :  $T_c >$ 0; P = 0.0183, z = 2.094, n = 38). Unfortunately, we did not have sufficient data to draw valid inferences about water content for individual grass species. Ranks of water content per tiller for each grass species varied from trial to trial. Mesa dropseed had the highest water content per tiller most frequently, but each grass species had the highest water content in at least 1 trial. Although neither kangaroo rat species strongly selected any particular grass species, kangaroo rats may have been selecting grasses on the basis of water content.

Number of tillers available and percent tillers removed were negatively correlated ( $T_c = -0.19$ , 1-sided hypothesis test as above; P = 0.0103, z = -2.314, n = 38), in spite of a positive correlation between tillers available and number of tillers removed ( $T_c = 0.42$ , 1-sided hypothesis test as above; P = 0.1736, z = 0.4513, n = 38). This correlation and our personal observations suggest that tillers positioned toward the center of larger tussocks of grass were used less often.

DISCUSSION—Merriam's kangaroo rat removed a greater proportion of available tillers and larger total amounts of grass biomass than did Ord's kangaroo rat. Merriam's kangaroo rat removed the greatest number of tillers from black grama grass, whereas Ord's kangaroo rat removed the greatest number of tillers from mesa dropseed. Percent tillers removed from all 4 grass species by both kangaroo rat species was positively related to water content

of the tillers. Mesa dropseed usually had the highest water content per tiller. Number of available tillers was negatively related to percent tillers removed.

We investigated no factors other than water content per tiller that might provide a mechanistic explanation for the observed selectivity of the kangaroo rats for these grass species. Kerley et al. (1997) found that nitrogen content of cut grass stems was significantly higher than that of standing senesced stems. Although they interpreted this in terms of litter production in desert grasslands, this observation also may provide additional insight into the basis for selectivity not directly available from our results.

Reichman and Price (1988) discussed diet preference in the context of habitat and food availability. We found that Ord's kangaroo rat, which is abundant in the grasslands of southern New Mexico, clipped less grass both in terms of biomass and percent tillers than did Merriam's kangaroo rat, which is most common where grasses are sparse. Thus one could conclude that *D. ordii* has a narrower diet than *D. merriami*. This finding seems in accord with predictions of the general diet breadth model (Charnov, 1976), which states that foragers in environments with a greater variety of food types will be more specialized than foragers in less productive environments.

Our observations in the laboratory and in the field suggest that kangaroo rats clip grass tillers near the base early in the growing season. We also found a positive relation between water content and percent tillers removed. The youngest, most nutritious and water-rich portions of the tiller are located at the base of the plant (Beatley, 1969). Thus we tentatively conclude that water content plays a major role in feeding selectivity for green vegetation in these 2 kangaroo rat species.

We found that as the number of available tillers increases, percent available tillers removed decreases, in spite of a positive correlation between available tillers and number of tillers removed. This is especially true of Ord's kangaroo rat, which consistently removed tillers from the outer margin of the grass tussock and did not remove any tillers from the center of the largest tussocks. Merriam's kangaroo rat removed more tillers from the centers of plants of all species during the late summer.

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