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DIET OF THE MOHAVE GROUND SQUIRREL (*XEROSPERMOPHILUS MOHAVENSIS*) IN RELATION TO SEASON AND RAINFALL

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ABSTRACT.—The Mohave ground squirrel (*Xerospermophilus mohavensis*) is endemic to the western Mojave Desert of California. It is listed as threatened under the California Endangered Species Act, yet there is little published information on its habitat requirements. We studied the diet of Mohave ground squirrels at 4 sites in desert scrub habitat in Inyo County, California, primarily by microhistological analysis of 754 samples of fecal pellets collected from live-trapped animals. Over all sites and seasons, shrub foliage was the largest component of the diet (39.8% relative density) and mainly derived from several taxa of Chenopodiaceae: winterfat (*Krascheninnikovia lanata*), spiny hopsage (*Grayia spinosa*), and saltbushes (*Atriplex* spp.). Forb leaves were next in importance (34.1% relative density), especially from Fabaceae (*Astragalus* and *Lupinus*), Polemoniaceae (*Gilia* and *Linanthus*), and Asteraceae. Flowers, pollen, and seeds were also major components (20.3% relative density). Leaves composed nearly all of the diet in spring, whereas pollen, flowers, and seeds made up about a third of the diet in summer. Following dry winters when annual forbs were limited, Mohave ground squirrels depended primarily on foliage from perennial shrubs and forbs. Following wet winters when spring annuals were abundant and most plant species flowered and set seed prolifically, squirrels consumed a high proportion of leaves plus flowers, pollen, and seeds of annual forbs. Mohave ground squirrels reproduced only after winter rainfall >80 mm that resulted in a standing crop of herbaceous annuals ≥ 100 kg · ha^{-1}. Mohave ground squirrels consumed very little of the nonnative annual plant biomass present on our study sites (*Erodium, Salsola, Bromus,* and *Schismus* contributed <3% overall to the diet). Conservation implications include the following: (1) priority should be given to protecting habitats supporting preferred perennial forage plants, including winterfat and spiny hopsage; (2) habitats with an understory dominated by native annual forbs have higher value than those dominated by nonnative plants, especially annual grasses; and (3) if climate change results in lower and less regular winter precipitation, suitable habitat for Mohave ground squirrels may be reduced and fragmented in the drier portions of the geographic range.

RESUMEN.—La ardilla de Mojave (*Xerospermophilus mohavensis*) es endémica de la región occidental del desierto de Mojave, situado en California. Esta especie se encuentra en la lista de la Ley de California de las Especies como en peligro de extinción, sin embargo, existe poca información publicada acerca de sus requerimientos de hábitat. Estudiamos la dieta de las ardillas de Mojave en cuatro sitios de matorral desértico en el condado de Inyo, California, principalmente mediante el análisis microhistológico de 754 muestras fecales colectadas de animales vivos capturados en trampas. En todos los sitios y estaciones, el follaje arbustivo fue el componente más importante de la dieta de las ardillas, con una densidad relativa de 39.8%, derivado principalmente de varios taxa de Chenopodiaceae: *Krascheninnikovia lanata, Grayia spinosa* y *Atriplex* spp. Las hojas de hierbas siguieron en importancia con una densidad relativa de 34.1%, especialmente de Fabaceae (*Astragalus* y *Lupinus*), Polemoniaceae (*Gilia* y *Linanthus*) y Asteraceae. Las flores, el polen y las semillas fueron también componentes importantes, formando parte del 20.3% de la densidad relativa. Casi toda la dieta en primavera fue de hojas, mientras que el polen, las flores y las semillas constituían casi un tercio de la dieta en verano. Después de los inviernos secos, cuando las hierbas anuales eran limitadas, las ardillas de Mojave dependieron principalmente de follaje de arbustos y de hierbas perennes; después de los inviernos húmedos, cuando las plantas anuales de primavera eran abundantes y la mayoría de las especies de plantas florecieron y sembraron semillas prolíficamente, las ardillas consumieron una alta proporción de hojas, además de flores, polen y semillas de hierbas anuales. Las ardillas de Mojave se reprodujeron sólo después de lluvias invernales >80 mm que resultaron en un cosecha en pie de hierbas anuales ≥ 100 kg · ha^{-1}. Las ardillas de Mojave se alimentaron muy poco de plantas anuales no nativas que se encontraban en nuestros sitios de estudio (*Erodium, Salsola, Bromus* y *Schismus* contribuyeron con menos de 3% de la dieta total). Las implicaciones de conservación incluyen: (1) la prioridad debe ser la protección de los hábitats que tienen plantas perennes, incluyendo a *K. lanata* y *G. spinosa;* (2) los hábitats con un sotobosque dominado por hierbas anuales nativas tienen un valor más alto que los dominados por plantas no nativas, especialmente las hierbas anuales; y (3) si el cambio climático resulta en una menor y más irregular precipitación invernal, el hábitat adecuado podría reducirse y fragmentarse en las partes más secas de su rango geográfico.

The Mohave ground squirrel (*Xerospermophilus mohavensis* [formerly *Spermophilus mohavensis;* Helgen et al. 2009]) is found only in desert scrub habitats in the western Mojave Desert of California (Best 1995). It is listed as threatened under the California Endangered

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Species Act due to its limited and patchy distribution, relatively low abundance, and habitat loss from human land uses (Gustafson 1993). Mohave ground squirrels are active aboveground from February through July (Bartholomew and Hudson 1960). When conditions allow during this period, adults reproduce and then accumulate fat reserves in preparation for prolonged dormancy, approximately doubling in body mass from 70–80 g to ≥165 g (Best 1995). Mohave ground squirrels accomplish these physiological feats in an arid environment with highly variable annual precipitation. Effective conservation of the species requires an understanding of its habitat requirements and dietary patterns.

There are few published accounts of Mohave ground squirrel diet and feeding behavior. Recht (1977) observed 8 radio-collared individuals feeding on 11 plant taxa. Zembal and Gall (1980) reported incidental observations of Mohave ground squirrels feeding on the fruit and seeds of Joshua trees (*Yucca brevifolia*). No dietary data have been published based on the analysis of stomach contents or fecal material.

This study was carried out as part of a long-term ecological investigation of Mohave ground squirrel demography, movements, and habitat use (Leitner and Leitner 1998). The objective of this element of the study was to determine whether food requirements could help to characterize the essential habitat of this cryptic species, thus facilitating its conservation and management. The need for an understanding of habitat requirements is especially acute because the species occupies a region that is a high priority for renewable energy development.

METHODS

Study Area

The study area was situated in and near the Coso Range, about 20 km east of the Sierra Nevada in the northwestern Mojave Desert, Inyo County, California (36°04′ N, 117°48′ W). We established four 25-ha sites that ranged in elevation from 1000 m to 1500 m and were located on fine- to coarse-textured alluvial soils derived from igneous parent material. During the 9-year study from 1988 to 1996, annual precipitation averaged 140 mm at the Haiwee Power Plant, about 15 km to the northwest. Winter rainfall predominated, with 82% of mean annual precipitation (115 mm) received between 1 October and 31 March. Winter precipitation differed drastically between years, ranging from 14 mm (1989/1990) to 234 mm (1992/1993).

All 4 sites supported chenopod scrub represented by several vegetation alliances as defined in Sawyer et al. (2009). Site 1, located in Rose Valley just west of the Coso Range at 1015 m elevation, supported *Atriplex polycarpa* (allscale) and *Atriplex confertifolia* (shadscale) alliances. Both shrub cover (9%) and species richness were low, although annual herbaceous production was high. Joshua trees (*Yucca brevifolia*) were not present on the site and were rare nearby. Site 2, in the Coso Basin at 1085 m elevation, supported primarily *Atriplex confertifolia* and *Ephedra nevadensis* (Nevada jointfir) alliances. This site was dominated by low-stature shrubs including rayless goldenhead (*Acamptopappus sphaerocephalus*), Nevada jointfir, shadscale, cheesebush (*Ambrosia [=Hymenoclea] salsola*), and winterfat (*Krascheninnikovia lanata*). A few Joshua trees (*Yucca brevifolia*) were adjacent to site 2. Shrub cover (27%) and species richness were high and annual herbaceous production low. Joshua trees were not present on the site and were rare nearby. Site 3, situated in a small valley in the Coso Range at 1470 m elevation, supported *Atriplex confertifolia, Atriplex canescens* (fourwing saltbush), and *Grayia spinosa* (spiny hopsage) alliances. This site was codominated by spiny hopsage, shadscale, fourwing saltbush, and Cooper's boxthorn (*Lycium cooperi*). Joshua trees were present over much of site 3, with an average density of 17 per hectare. Shrub cover (16%) and species richness were high, and annual herbaceous production was also high. Site 4, located in a valley at 1500 m elevation in the Coso Range, supported *Grayia spinosa* and *Ephedra nevadensis* alliances. Shrub cover (20%) and species richness were similar to site 3, but annual herbaceous production was generally lower. Joshua trees were present at an average density of 15 per hectare.

Sample Collection and Analysis

We collected fecal samples from animals captured during regular trapping sessions. Each site was 500 × 500 m and contained an array of 441 traps spaced 25 m apart in a 21 × 21 configuration (Leitner and Leitner 1998).

Pymatuning (10 × 11 × 39 cm) and Sherman (8 × 9 × 23 cm) live traps were used. Trapping was carried out in spring (early March to mid-April) in 1990 and 1992–1996, and in early summer (late May to mid-June) during all 9 years. When an animal was captured, we collected fecal pellets according to instructions from the Composition Analysis Laboratory at Fort Collins, Colorado (T. Foppe, personal communication, 1988). Three individual pellets were shaken from the trap, placed in a labeled paper envelope, and allowed to air-dry, which occurred quickly in this arid environment. We then emptied the trap of all remaining fecal material. As many individuals as possible were represented in the samples analyzed, but when few Mohave ground squirrels were captured, we sometimes analyzed samples from the same individual captured on different days within the same trapping session. Our trapping and handling methods conformed to guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

The fecal samples were cataloged and within 2 months were sent to the Composition Analysis Laboratory. Methods for microhistological analysis followed Hansen et al. (1973). An individual microscope slide was prepared for each sample by grinding the pellets over a 1-mm screen and placing the cleared particles on a slide. Twenty fields were read from each sample slide using a phase-contrast microscope at 100× magnification. Plant items on the slides were identified by matching their epidermal patterns with those of plant tissues in a reference slide collection containing the plant species observed on the sites. All plant parts were identified to the lowest taxon possible. The percent frequency was computed for all items present in the sample by comparing the number of fields in which an item occurred to the total number of fields examined. Density for each species detected was determined by referring to a conversion table developed by the Composition Analysis Laboratory, and percent relative density was calculated by taking the percent of an individual density divided by total density. Percent relative density for each item is considered to be a reasonable estimate of its dry-weight contribution to the diet.

Bait consisted of a commercial livestock feed containing corn, oats, barley, and molasses. Prebaiting sometimes resulted in bait residues in the fecal samples. We discarded sample results when bait composed ≥50% mean relative density. For samples containing <50% bait, we calculated the percent mean relative density of the nonbait food items only.

Evaluation of Diet Methodology

The protected status of the Mohave ground squirrel precluded using stomach content analysis to compare with microhistological analysis. However, in a diet study of the Piute ground squirrel (*Urocitellus mollis*), Van Horne et al. (1998) found a high degree of similarity (86%–92% similarity index) in triplicates of fecal samples and in stomach content–feces comparisons. They concluded that fecal analysis using a microhistological technique was a reasonably reliable method to determine food habits for that species. Similar studies have found a close correspondence between diet estimates from stomach contents and fecal samples in Columbian ground squirrels (*Urocitellus columbianus*) and black-tailed prairie dogs (*Cynomys ludovicianus*) (Wydeven and Dahlgren 1982, Harestad 1986).

Comparisons of Sample Groups

To determine whether fecal samples from juveniles and adults or from males and females should be grouped in characterizing the diet, we calculated similarity indices following the method of Anthony and Smith (1977):

$$SI = \sum_{i=1}^{n} Y_i .$$

In this equation, the similarity index (SI) is calculated as the sum of the lower of 2 mean relative density values (Y_i) for each shared food item, with n as the total number of items. We compared similarity indices for groups of animals of different age and sex captured within the same trapping session. We also calculated similarity indices for randomly separated groups of same-age as well as same-sex individuals from the same trapping session to evaluate the inherent variation within a particular group.

Vegetation Sampling

Beginning in 1989, we sampled herbaceous species composition and aboveground standing crop of annual herbs in late May to early June when most herbaceous vegetation was at

TABLE 1. Overall Mohave ground squirrel diet, by major category, at 4 study sites combined in the Coso Range, Inyo County, California, during 1988–1996.

Diet category	% Relative density	% Frequency among samples (n = 754)
Shrub leaves and stems	39.8	78.8
Perennial forb leaves	13.0	37.7
Annual forb leaves	21.1	66.0
Flowers, pollen, seeds	20.3	53.2
Grass leaves	2.5	25.2
Arthropods	2.6	33.7
Other (roots, fungi, bone)	0.7	6.9
TOTAL	100.0	

or nearing its full growth. At alternating trap stations on alternating lines of traps, we randomly selected pairs of 0.09-m^2 plots representing between- and under-shrub microsites, yielding 100 plot pairs per site. Within each plot, all herbaceous species were recorded. Annuals were clipped at ground level and plant material was collected in a paper container, air-dried at 40 °C to a constant weight, and then weighed. Clipping was not performed on perennial grasses or herbs at any time. To represent overall standing crop, the mean of between- and under-shrub plots was calculated for each year and site and expressed as kg · ha^{-1}.

In 1994 we sampled shrub species composition, cover, and frequency by a line intercept method. Ten alternating lines of traps were selected on each site. On each line, alternating 25-m sampling units were established, for a total of 100 units for each site. The species and length of intercept were recorded to the nearest 10 cm for each individual shrub intercepted, thus providing frequency and cover values by species. Percent cover for each shrub species was calculated by dividing the total length of its intercept by the total distance sampled at each site.

Visual Observations of Foraging

Mohave ground squirrels were rarely seen during trapping sessions because of their wary behavior and cryptic coloration. However, we observed foraging activity during radiotelemetry studies at site 3 in 1995–1997, when a number of radio-collared individuals became habituated to human presence. When we observed them feeding, we noted the identity of the animal, the date and time, and the food item being consumed.

TABLE 2. Overall percent mean relative density and frequency of 8 principal plant taxa in the Mohave ground squirrel diet at 4 sites combined in the Coso Range, Inyo County, California, calculated from all samples (n = 754) over 9 years.

Food item	% Mean relative density	% Frequency
Krascheninnikovia lanata leaves	18.2	44.0
Astragalus lentiginosus leaves	12.6	35.2
Grayia spinosa leaves	11.9	28.0
Atriplex spp. leaves	7.4	47.1
Gilia sp./*Linanthus* sp. leaves and seeds	7.4	34.3
Lupinus odoratus leaves, pods, and seeds	5.4	19.4
Asteraceae leaves, flowers, and seeds	4.5	20.7
Eriogonum spp. leaves	3.4	11.1
TOTAL	70.8	

RESULTS

Overview of Diet Composition

We analyzed a total of 754 fecal samples from 1988 to 1996. Microhistological analysis identified 77 distinct food items representing approximately 50 plant taxa in 24 families and including other material such as fungus, bones, and arthropod fragments (Appendix 1).

The Mohave ground squirrel diet was strongly dominated by foliage, which made up 76.4% relative density (Table 1). Leaves and stems of shrubs were the most important components in the diet, accounting for almost 40% relative density and appearing in over three-fourths of all samples analyzed. Forb leaves composed 34.1% of the total diet and were recorded in 88% of all samples; annual forbs contributed 21.1% relative density and perennial forbs 13.0%. Plant reproductive structures—including flowers, pollen, and seeds—totaled 20.3% of the diet (frequency 53.2%). Because much of the flower and pollen material could not be identified to family and much of the flower and seed identified as Asteraceae could not be identified to genus, the relative contribution of flowers and seeds from shrubs versus forbs could not be determined.

Despite the large number of food items recorded, only 8 plant taxa contributed almost 71% of the Mohave ground squirrel diet across all sites, years, and seasons (Table 2). Leaves

TABLE 3. Comparison of similarity indices for groups of Mohave ground squirrels based on age and gender within a site and sampling period.

Comparison	Number of comparisons	Samples compared	Mean similarity index	Range
Juvenile female vs. juvenile male	10	102 vs. 97	67.7	55.4–89.4
Adult female vs. adult male	9	97 vs. 71	73.0	53.1–87.5
Adult vs. juvenile	6	54 vs. 109	79.0	69.7–92.0
Same age and sex, randomly divided	7	39 vs. 38	73.0	52.0–88.6

TABLE 4. Annual herbaceous standing crop for each study site, with precipitation during the preceding winter (1 October–31 March) and data on Mohave ground squirrel reproduction.

	Annual herbaceous standing crop (kg · ha^{-1})								
Site number	1988	1989	1990	1991	1992	1993	1994	1995	1996
1	N/A	65	<0.1	334	517	635	11	753	43
2	N/A	11	<0.1	301	334	344	22	226	11
3	N/A	11	<0.1	441	603	603	65	474	22
4	N/A	22	<0.1	194	248	248	22	248	11
Precipitation (mm)	90.9	62.5	13.7	88.4	199.9	213.9	54.1	233.7	77.2
Reproduction	Yes	No	No	Yes	Yes	Yes	No	Yes	No

from 3 species of chenopod shrubs (winterfat, spiny hopsage, and saltbush) made up >37% of the diet. Leaves, flowers, and seeds from 5 herbaceous taxa contributed 33% of the diet. These were the perennial freckled milkvetch (*Astragalus lentiginosus,* Fabaceae) and the annual Mojave lupine (*Lupinus odoratus,* Fabaceae); annual species of the closely related genera *Gilia* or *Linanthus* (Polemoniaceae); composites or members of the sunflower family (Asteraceae); and buckwheat (*Eriogonum* spp., Polygonaceae). These 8 food items appeared with frequencies ranging from 11.1% to 47.1%.

Comparisons of Sample Groups

Table 3 presents the results of similarity index comparisons between groups of Mohave ground squirrels based upon age and sex. Means and ranges were very similar in comparisons of adults with juveniles and males with females. Seven comparisons were also made of randomly divided groups of same-age and same-sex animals within a given trapping session. This analysis yielded a mean similarity index of 73%, with a range of 52.0%–88.6%. Because these results showed no substantial difference between males and females or juveniles and adults within a given trapping session, all such samples were combined for further comparison between sites and seasons.

Influence of Winter Rainfall on Food Resources and Reproduction

Winter precipitation played a critical role in the productivity of annual herbaceous plants on our study sites. During 1988–1996, winter precipitation varied from 14 mm to 214 mm, and herbaceous standing crop ranged over nearly 3 orders of magnitude, from <0.1 kg · ha^{-1} to 753 kg · ha^{-1} (Table 4). Mohave ground squirrel reproduction was closely dependent upon annual herbaceous productivity. Reproduction occurred only following winters with precipitation >80 mm, when herbaceous standing crop was >100 kg · ha^{-1}. In the 4 years with winter precipitation <80 mm, standing crop was well below 100 kg · ha^{-1} in both between- and undershrub plots and there was reproductive failure in Mohave ground squrrels. Study years were henceforth divided into "dry" (winter rainfall <80 mm) and "wet" (winter rainfall ≥80 mm) years.

Influence of Season and Rainfall on Mohave Ground Squirrel Diet

Mohave ground squirrel diet differed between spring and summer sampling periods. Diet also varied in response to changes in the availability of annual herbaceous forage that were in turn correlated with rainfall amounts over the preceding winter. We analyzed dietary

TABLE 5. Plant taxa, by season and rainfall year, contributing ≥5% mean relative density in the diet of the Mohave ground squirrel in the Coso Range, Inyo County, California. Wet years (1988, 1991, 1992, 1993, and 1995) were defined as ≥80 mm rainfall during the preceding winter (1 October–31 March), while dry years (1989, 1990, 1994, and 1996) were defined as <80 mm rainfall for the same period.

	Spring			Summer		
Food items	All years (n = 9)	Wet years (n = 5)	Dry years (n = 4)	All years (n = 9)	Wet years (n = 5)	Dry years (n = 4)
Sample size	338	140	198	416	329	87
Leaves						
Shrubs						
Atriplex spp.	12.8	8.3	15.9	3.1	2.5	5.5
Grayia spinosa	25.4	6.3	39.0	0.9	0.1	4.0
Krascheninnikovia lanata	10.4	9.0	11.3	24.6	29.6	5.8
Total, shrub leaves	48.6	23.6	66.2	28.6	32.2	15.3
Forbs						
Astragalus lentiginosus	17.1	23.7	12.3	9.0	8.0	12.7
Gilia and *Linanthus*	6.9	9.5	5.1	9.7	4.6	28.7
Lupinus odoratus	4.2	8.2	1.3	0.7	0.9	0.1
Eriogonum spp.	4.4	8.7	1.4	0.6	0.5	1.1
Eremalche exilis	0.0	0.1	0.0	4.5	5.7	0.0
Total, forb leaves	35.0	50.2	20.9	24.6	19.7	42.6
Grass						
Bromus spp.	0.6	0.3	0.9	2.5	1.0	8.0
TOTAL, LEAVES	84.2	74.1	87.2	55.7	52.9	65.9
Flowers and seeds						
Shrubs						
Larrea tridentata seeds	0.1	0.1	0.1	3.3	3.5	2.4
Lycium spp. seeds	0.5	0.0	0.8	2.0	0.6	6.9
Opuntia fruits and seeds	0.0	0.0	0.0	4.4	5.6	0.0
Total, shrub seeds	0.6	0.1	0.9	9.7	9.7	9.3
Forbs						
Composite flowers and seeds	0.0	0.0	0.0	6.7	8.5	0.0
Legume seeds	0.2	0.4	0.1	5.6	7.1	0.0
Total, forb flowers and seeds	0.2	0.4	0.1	12.3	15.6	0.0
Other flowers and pollens	4.6	5.1	0.2	2.7	2.8	0.8
TOTAL, FLOWERS AND SEEDS	5.4	5.6	1.2	24.7	28.1	10.1
GRAND TOTAL	89.6	79.7	88.4	80.4	81.0	76.0

data separately for dry and wet years. Just 15 food items made up ≥5% mean relative density in at least one season in either dry or wet years (Table 5).

In spring, Mohave ground squirrel diets were strongly dominated by foliage from a few species of shrubs and forbs. Leaf material from just 3 chenopod shrub taxa (winterfat, spiny hopsage, and saltbush) plus a perennial forb (freckled milkvetch) made up 65.7% of mean relative density. Leaf material from 3 annual forb taxa (*Gilia/Linanthus, Lupinus odoratus, Eriogonum* spp.) contributed another 15.5%. However, their proportions differed in dry and wet years. In spring of dry years, Mohave ground squirrels relied primarily on foliage from the 3 chenopod shrubs, which composed >66% of the diet; spiny hopsage alone made up 39% mean relative density, while the contribution from freckled milkvetch and the other 3 forbs was much reduced. In the springs of wet years, shrub leaves made up only 23.6% of the diet, while leaf material from the 4 forb taxa contributed 50.1%; freckled milkvetch foliage alone accounted for almost one-quarter of the total.

In summer, foliage still made up over one-half of the diet, with winterfat leaves the largest single component at 24.6% relative density. Leaf material from freckled milkvetch and *Gilia/Linanthus* contributed 18.7%. Flowers and seeds were also important in summer, composing almost one-quarter of the diet. Most of the seeds were either Asteraceae or Fabaceae. Again, the proportion differed in dry and wet years. In the summers of dry years, over one-half of the diet was derived from herbaceous leaf material, mostly from freckled

TABLE 6. Food items observed being consumed by radio-collared Mohave ground squirrels at site 3 during 1995–1997. Spring observations spanned the period 22 February–27 April, while summer observations were made during the period 3 May–2 July.

	Observations		Mohave ground squirrels observed	
Food item	Spring	Summer	Spring	Summer
Shrubs				
Grayia spinosa flowers, leaves	4	2	3	2
Lycium andersonii leaves, stems	1	2	1	2
Lycium cooperi leaves	7	3	4	3
Tetradymia spinosa	1		1	
Yucca brevifolia fruits, seeds		18		13
Forbs				
Amsinckia tessellata leaves, flowers, fruits	5	3	3	2
Chaenactis sp. leaves, flowers	2		1	
Cryptantha pterocarya fruits	1		1	
Leptosyne (= *Coreopsis*) *bigelovii*	1	2	1	2
Lessingia glandulifera flowers		2		2
Lupinus odoratus leaves	1		1	
Malacothrix glabrata flowers	2		1	
Phacelia sp. leaves	1		1	
Stephanomeria sp.		1		1
Grasses				
Bromus sp. leaves	2		1	
Stipa sp. leaves	1		1	
TOTAL OBSERVATIONS	29	33	20	28

milkvetch and *Gilia/Linanthus*. Shrub material was also important, especially foliage from chenopod shrubs and seeds from creosote bush (*Larrea tridentata*) and boxthorn (*Lycium* spp.). In wet summers, herbaceous leaves made up only 20.7% of Mohave ground squirrel diet. Winterfat leaves were the most important single food item at 29.6% relative density, while flowers and seeds from both shrubs and forbs composed another 28.1% of the diet.

Visual Observations of Foraging

At site 3 we observed radio-collared Mohave ground squirrels feeding on plant material from 16 different taxa (Table 6). In spring, squirrels were most frequently seen foraging on spiny hopsage, Cooper's boxthorn, and desert fiddleneck (*Amsinckia tessellata*). In summer, squirrels were most often observed in Joshua trees. We also saw squirrels feeding on annual composites, such as coreopsis (*Leptosyne* [= *Coreopsis*]), desert dandelion (*Malacothrix*), lessingia (*Lessingia*), and wirelettuce (*Stephanomeria*); in addition, some Mohave ground squirrels were observed with deep yellow staining around their mouths, matching the pollen and flower color of coreopsis, one of the most common spring annuals.

DISCUSSION

Role of Perennial Foliage

Mohave ground squirrels at our study sites primarily consumed foliage, which made up three-quarters of the total diet. Just over 50% of the diet consisted of leaves from 4 perennial taxa: the herb freckled milkvetch and the shrubs winterfat, spiny hopsage, and saltbush. These perennial food sources were particularly important when annual forbs were limited, especially in early spring and during dry years. However, each appears to play a distinctive role in the diet of the Mohave ground squirrel.

Freckled milkvetch breaks dormancy and produces new foliage each year, even under the most extreme drought conditions, making it a more reliable food source than most annual forbs. *Astragalus* and the closely related *Oxytropis* have also been reported as major components of the diet in Richardson's ground squirrel (*Urocitellus richardsonii*) in Colorado (Hansen and Ueckert 1970) and in Arctic ground squirrel (*Urocitellus parryii*) in Yukon (McLean 1985), despite the fact that *Astragalus* and *Oxytropis* species (collectively known as locoweed) are toxic to livestock on rangelands of the western United States (James and Nielson 1988). The behavioral or physiological adaptations that allow Mohave ground squirrels to consume milkvetch foliage without suffering adverse effects are unknown.

In the Coso Range, the foliage of spiny hopsage and winterfat appear to be critical components of the Mohave ground squirrel diet. Spiny hopsage was by far the most important food item for Mohave ground squirrels in spring. Like freckled milkvetch, it breaks dormancy relatively early, and its spring growth is high in nutrition. The crude protein content of spiny hopsage leaves (18%) is reported to be higher than that of most other shrubs within its range (Krysl et al. 1984). Spiny hopsage is heavily utilized by livestock, wild ungulates, and black-tailed jackrabbits (*Lepus californicus*), especially from late winter through spring (Shaw 1992).

In contrast to the summer-deciduous spiny hopsage, winterfat is evergreen, thus providing a potential food source when annuals and deciduous shrubs are limited. Winterfat initiates leaf growth in late spring, and the new foliage may be a preferred food item, which could explain its high contribution to the summer diet of the Mohave ground squirrel.

Three saltbush species (shadscale, allscale, and fourwing saltbush) occurred on our study sites, but microhistological analysis could not distinguish the species. Saltbush was utilized more in spring than in summer by Mohave ground squirrels. Saltbush leaves averaged <8% in the overall diet, suggesting that it is less preferred than spiny hopsage and winterfat. This could be due to the high salt content in saltbush leaves.

Role of Annual Plants in Mohave Ground Squirrel Reproduction

The Mojave Desert is noted for its highly diverse annual flora (Jennings 2001). Winter precipitation plays a critical role in germination and growth of Mojave Desert annual plants (Beatley 1974). Our data showed that Mohave ground squirrel reproduction occurred only when winter rainfall was >80 mm and the resulting standing crop of herbaceous annuals was >100 kg · ha^{-1}. Thus, Mohave ground squirrel reproduction is closely associated with adequate winter rainfall and the resulting spring growth of annuals.

Little-utilized Food Resources

Although 77 distinct food items were detected in the 754 fecal samples reported here, only about 15 plant taxa contributed significantly to the Mohave ground squirrel diet (Appendix 1). Squirrels consumed little or no material from many shrub taxa that were common on our study sites, including white bursage (*Ambrosia dumosa*), cheesebush, goldenhead, and Cooper's goldenbush (*Ericameria cooperi*). Squirrels consumed little of the abundant native forb genera *Camissonia* (Onagraceae), *Cryptantha* (Boraginaceae), *Mentzelia* (Loasaceae), and *Phacelia* (Boraginaceae), which typically were among the most frequently occurring annual genera on the study sites. They consumed minimal amounts of grass, despite the fact that the nonnative genera *Bromus* and *Schismus* were always among the most frequently occurring annual genera and the native sixweeks fescue (*Festuca octoflora*) was abundant in some years. The native bunchgrasses in the genera *Stipa* and *Poa* were consumed little, if at all.

The nonnative forb redstem filaree (*Erodium cicutarium*) was present, especially at sites 1 and 2, but was consumed very little (and then primarily during dry years). We conclude that even when relatively common, this annual species is not a preferred food of the Mohave ground squirrel. The highly invasive Saharan mustard (*Brassica tournefortii*) was not present in our study area so its potential role in the Mohave ground squirrel diet is unknown.

Visual Observations of Items Consumed

Our visual observations of feeding Mohave ground squirrels were consistent with the results of microhistological analysis with 2 noteworthy exceptions. First, we never saw Mohave ground squirrels feeding on winterfat. Because winterfat is densely branched, it may have been difficult to observe squirrels feeding in or around winterfat shrubs.

The second discrepancy concerned Joshua tree fruits and seeds. While more than half of our May and June observations consisted of Mohave ground squirrels foraging in Joshua trees, fruit and seed material from this species made up <1% of mean relative density in fecal samples analyzed. However, the large number of observations may be explained by the high visibility of animals actively foraging in Joshua trees. Zembal and Gall (1980) also made many observations of Mohave ground squirrels foraging on Joshua tree fruits, then making repeated trips to their burrows. This strongly suggested seed caching behavior.

Recht (1977) studied foraging activities at a site in the southern part of the range. In 2400 visual observations of 8 radio-collared individuals, Recht recorded Mohave ground squirrels feeding on 11 plant taxa, primarily the native species Cooper's boxthorn, coreopsis, and fiddleneck, as well as the nonnative Russian thistle (*Salsola tragus*). He concluded that Mohave ground squirrels appeared to select plant species with the highest water content. Our observations of feeding behavior were reasonably consistent with those of Recht. We saw Mohave ground squirrels consume 5 of the 11 plant taxa reported by Recht; the other 6 were confirmed by microhistological analysis. However, while boxthorn, coreopsis, and fiddleneck composed 39% of our visual observations, they constituted no more than 10% of overall mean relative density in fecal samples, suggesting that foraging behavior on some food items may be more readily detectable than on others and that microhistological analysis may present a more complete picture of the Mohave ground squirrel diet.

Diet of Mohave Ground Squirrels Elsewhere in Range

Most of the Mohave ground squirrel range lies to the south and southeast of the Coso Range at lower elevation and with lower average precipitation. Creosote bush scrub is the dominant vegetation over much of the range, areas with high proportions of spiny hopsage and winterfat are relatively uncommon, and productivity of annual forbs is generally less than in the Coso study sites. As a result, caution is appropriate in generalizing about the Mohave ground squirrel diet elsewhere in its range.

Comparison with Other Aridland Ground Squirrels

The Piute ground squirrel (*Urocitellus mollis*)—formerly Townsend's ground squirrel—inhabits the shrubsteppe of the Great Basin and Snake River Valley. Its diet has been studied in southwestern Idaho where habitats dominated by native shrubs and perennial bunchgrasses are being replaced by exotic annual grasses and forbs (Yensen and Quinney 1992). Major native food items include Sandberg bluegrass (*Poa sandbergii*), a native perennial bunchgrass, and shrub foliage from winterfat and big sagebrush (*Artemisia tridentata*) (Van Horne et al. 1998). Yensen and Quinney (1992) reported that Piute ground squirrels at their study sites also consumed significant amounts of exotic annuals, particularly cheatgrass (*Bromus tectorum*) and Russian thistle. However, Yensen et al. (1992) found that Piute ground squirrel burrow densities were negatively correlated with cheatgrass and other exotic annuals in the vegetation communities that they sampled. Van Horne et al. (1998) concluded that winterfat and, to a lesser extent, big sagebrush provided a relatively reliable food source under drought conditions, and that habitats dominated by annuals were unlikely to sustain viable populations of Piute ground squirrels. Thus, in comparing the Piute ground squirrel with the Mohave ground squirrel, both appear to utilize shrub foliage extensively. The former, however, is highly dependent on perennial bunchgrasses when available and will also consume large amounts of cheatgrass and other exotic annuals at sites dominated by these invasive species. Mohave ground squirrels are able to rely on native chenopod shrubs and annual forbs, thus avoiding the need to consume exotic grasses.

The round-tailed ground squirrel (*Xerospermophilus tereticaudus*) is closely related to the Mohave ground squirrel. It inhabits the eastern Mojave, Colorado, and Sonoran deserts (Ernest and Mares 1987), which differ from the western Mojave Desert in receiving significant summer rainfall and supporting a distinctive "summer annual" flora. In Arizona, green vegetation constitutes the majority of the round-tailed ground squirrel diet, along with insects and seeds, especially those of creosote bush and cactus (Drabek 1970). There has been no diet study of round-tailed ground squirrels in the California deserts, so it is not clear whether chenopod shrubs or native forbs are important there.

Future Research

Our findings raise a number of questions regarding the Mohave ground squirrel diet. First, the diet of the Mohave ground squirrel in the central, southern, and eastern portions of its range should be compared with the results presented here. Second, it would be of interest to investigate the mechanism underlying the association between reproduction and herbaceous annual plant production in the diet of the Mohave ground squirrel, in particular the relative importance of energy versus moisture content as limiting factors. Third, further analysis is needed to determine the relative importance of individual saltbush species in the Mohave ground squirrel diet. Fourth, further investigation could help to clarify how Mohave ground squirrels can consume milkvetch foliage, apparently without adverse effects. Finally, the potential importance of creosote bush should be investigated. Our study sites contained little creosote bush, but much of the geographic range of the Mohave ground squirrel is dominated by this species. Creosote bush usually produces large quantities of seeds in late May, when Mohave ground squirrels are preparing for dormancy.

Conservation Implications

Since the Mohave ground squirrel occurs only within a small area of the western Mojave Desert and is threatened by habitat loss and degradation, it is important to identify and conserve lands with the food resources needed to support persistent populations. This is particularly urgent because the species occupies a region of high priority for the siting of renewable energy facilities. This study showed that several perennial plant species, especially spiny hopsage and winterfat, play an important role in the Mohave ground squirrel diet, especially in the spring and in drought periods when annual plants are scarce. Habitats supporting some minimum density of these plant species are of high value for conservation. The importance of annual plant productivity for Mohave ground squirrel reproduction indicates that areas with abundant native forbs should also be a high conservation priority. Our data suggest that sites dominated by the invasive nonnative filaree, brome grasses, and Russian thistle are of less value to Mohave ground squirrels. This is consistent with the observation of Lohr et al. (2013) that sites with higher percentages of exotic annual plant cover tended to have low densities of southern Idaho ground squirrel (*Urocitellus endemicus*) burrows.

Anthropogenic climate change may adversely affect forage plants important to the persistence of Mohave ground squirrel populations. Climate models project that the deserts of the southwestern United States will experience a progressively warmer and more arid climate over the 21st century (Seager et al. 2007, Diffenbaugh et al. 2008). Winterfat and spiny hopsage are primarily Great Basin species adapted to lower temperatures for germination and growth than more typical Mojave Desert species such as creosote bush. There is evidence that spiny hopsage in particular is quite sensitive to drought. From 1975 to 2001 spiny hopsage decreased an average of 80.1% in 32 permanent study plots at the Nevada Test Site in southern Nevada (Webb et al. 2003). This drastic decline was attributed to the severe drought episode of 1989–1991. Future climate change with higher temperatures and more limited and erratic rainfall is likely to reduce the distribution and abundance of winterfat and spiny hopsage in the Mojave Desert. This could further restrict and fragment the geographic range of the Mohave ground squirrel.

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APPENDIX 1. All dietary items identified in Mohave ground squirrel fecal samples collected at 4 sites in the Coso Range, Inyo County, California, during 1988–1996. Mean relative density is given for all usable samples by season and by study site (n = number of samples). Columns show mean value among all usable samples analyzed for each season and site and therefore sum to 100.

	Site 1		Site 2		Site 3		Site 4	
Food item	Spring $n = 23$	Summer $n = 55$	Spring $n = 107$	Summer $n = 115$	Spring $n = 132$	Summer $n = 133$	Spring $n = 76$	Summer $n = 113$
Plant material								
Ambrosia dumosa leaves		0.15	1.08	0.02				
Astragalus lentiginosus leaves	64.49	15.62	0.87	0.39	19.59	5.02	21.09	19.05
Atriplex leaves	7.06	3.03	18.00	4.00	12.78	3.31	7.11	1.92
Baileya pleniradiata leaves		1.59	1.78	1.78	0.50		0.06	0.06
Boraginaceae leaves		0.38	0.09	0.16	0.05	0.18	0.12	
Bromus leaves	0.24	2.27	0.67	2.46	0.68	3.03	0.73	2.01
Camissonia campestris leaves	0.14	0.10		0.43	0.02	0.04		0.04
Chenopodiaceae leaves			0.23					
Chenopodiaceae seed				0.04				0.72
Centrostegia/Chorizanthe seed		0.09		1.84		1.38		
Chrysothamnus leaves				0.07		0.41	0.04	
Composite flower		0.89		1.40		0.59		1.54
Composite seed		4.96		4.56	0.05	10.38		1.44
Cryptantha leaves	0.97	0.23	0.09		0.01		0.81	0.08
Cryptantha seed		0.05		0.05		0.28		0.40
Descurainia pinnata leaves			0.74		0.15			
Dichelostemma pulchella leaves					0.05		0.11	0.56
Ephedra nevadensis stem	0.36		0.50	2.54	0.02	0.04	0.02	0.38
Eremalche exilis fruit		9.60		0.38				
Eremalche exilis leaves		32.21		0.57	0.03	0.07	0.11	0.16
Eriastrum leaves		0.03				0.19		0.04
Eriogonum leaves	5.26	0.14	10.58	1.44	2.94	0.61	8.07	0.38
Erodium cicutarium leaves	0.47	0.06	3.64	0.01	0.10	1.99		0.18
Erodium cicutarium seed		0.12				0.02		0.54
Festuca leaves			0.06	0.12	0.03		0.09	
Flower	3.09	2.19	4.68	1.84	0.40	1.50	1.45	0.28
Fungus		1.38		0.28		1.13		0.02
Gilia/Linanthus leaves		0.47	1.87	2.66	8.95	10.38	12.65	20.56
Gilia/Linanthus seed		0.43	0.22	0.21		1.45		3.88
Grayia spinosa leaves	0.55		14.21	1.02	31.26	1.18	38.61	0.85
Gutierrezia microcephala leaves			0.25					
Krascheninnikovia lanata leaves	2.48	2.33	21.32	42.04	6.43	24.47	4.17	17.81
Larrea tridentata leaves			2.03	1.10		0.08	0.35	
Larrea tridentata seed		0.10	0.13	6.31		0.35	0.23	5.16
Layia glandulosa leaves		0.08						0.12
Legume seed	0.11	3.38	0.42	1.17	0.08	13.96	0.17	1.29
Loeseliastrum matthewsii leaves		0.90		0.21		0.05		0.14
Loeseliastrum matthewsii seed		1.53		1.20		4.26		1.98
Lomatium mohavense leaves		0.26	0.10		0.12		0.14	
Lupinus odoratus leaves	10.30	0.96	1.70	0.32	7.39	1.09	0.21	0.58
Lycium leaves			0.23	0.03	0.15	0.03	0.39	0.32
Lycium seed			0.05	3.32	1.14	2.47	0.06	0.90
Mentzelia albicaulis leaves		0.13	0.27	0.09	0.05	0.04	0.19	0.17
Monardella exilis leaves		0.05	0.03		2.93			
Moss		0.38		0.03		0.06	0.37	
Opuntia basilaris seed		3.13		6.83		1.86		6.40
Opuntia basilaris stem		0.34	0.03	0.07	0.06	0.99	0.17	3.31
Pectocarya leaves	0.61		0.84	0.13			0.00	0.03
Phacelia/Nama leaves	0.11		0.18		0.64		0.11	
Poa secunda leaves		0.08		0.15	0.02			

APPENDIX 1. Continued.

	Site 1		Site 2		Site 3		Site 4	
Food item	Spring $n = 23$	Summer $n = 55$	Spring $n = 107$	Summer $n = 115$	Spring $n = 132$	Summer $n = 133$	Spring $n = 76$	Summer $n = 113$
Plant material								
Pollen			7.49		0.13	2.15		2.34
Root					0.98			0.02
Salvia leaves			2.96	0.14			0.18	0.03
Schismus leaves	0.32	0.93	0.07	2.76	0.04		0.17	0.01
Sphaeralcea ambigua leaves	1.80	0.66		0.02		0.95	0.04	0.09
Stipa leaves	0.14	0.05	0.24	0.87	0.10	0.10	0.28	0.11
Tetradymia leaves	0.28		0.07		0.05		0.04	
Unknown dicot leaves	0.00	0.11	0.13	0.05			0.06	0.72
Unknown seed		3.50	0.05	0.17	0.04	1.05	0.11	0.80
Yucca brevifolia seed			0.28		0.07	0.11		0.53
Other plant material[a]		0.05	0.17	0.12	0.07	0.15	0.06	0.12
Animal material								
Arthropod parts	1.23	4.72	1.74	4.57	1.89	2.59	1.44	1.94
Bone		0.34						
TOTAL	100.0	100.0	100.1	100.0	100.0	100.0	100.0	100.0

[a]Other plant material contributions were very small (<0.1 percent mean relative density) in all sites and sampling periods. They include the following: bark, Boraginaceae seed, composite leaves, *Delphinium parishii* leaves, fern, *Leptosyne* (= *Coreopsis*) *bigelovii* leaves, lily leaves, *Monardella exilis* seed, *Oenothera primiveris* leaves, *Plantago purshii* leaves, *Salsola tragus* leaves, *Stephanomeria* leaves, Unknown grass leaves, and *Yucca brevifolia* leaves.