

INFLUENCE OF HABITAT, SEX, AGE, AND DROUGHT ON THE DIET OF TOWNSEND'S GROUND SQUIRRELS

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We assayed diets of Townsend's ground squirrels (*Spermophilus townsendii*) in a semi-arid shrub steppe in Idaho by analyzing 1,432 fecal samples during 1991–1994. Dietary composition differed between adults and juveniles but not between males and females. Sandberg's bluegrass (*Poa secunda*), a perennial bunchgrass, was the most common item in diets. Diets varied among habitats that differed in plant cover. Diets also broadened progressively during the active season of this hibernating species (February–June) to include more shrub material, annuals, and other foods. A drought at the end of the active season in 1992 caused lower body mass and survival of individuals because there were fewer annual plants during the mid- and late-season periods and fewer seeds in the late-season than in non-drought years. Sandberg's bluegrass was consumed in higher proportions during the late-season of the drought year, but most of it was senescent with reduced levels of essential fatty acids and other nutrients. Among native shrubs, winterfat (*Ceratoides lanata*) was preferred over big sagebrush (*Artemisia tridentata*). Adults in habitats that lacked shrubs had a lower probability of being recaptured the year following the drought. We conclude that preferred native shrub species provided a relatively constant food source under drought conditions, compared with perennial grasses and annual plants. Perennial grasses were the most commonly eaten food, and habitats dominated by them provided a good food resource except under drought conditions. Low germination rates of annual plants under drought conditions and their short period of succulence make them a poor food source, and habitats dominated by them are unlikely to sustain viable populations of ground squirrels.

Key words: *Spermophilus townsendii*, diet, fecal analysis, food preference, hibernation, survival, drought, shrub steppe

Ecologists considering if food limits distribution and abundance of herbivores often find an apparent plentitude of food available. Food limitation of herbivores, however, may be a complex process that varies spatially among habitats within a region and temporally among and within years. Nutrients in food may change in ways that render food insufficient as a source of nutrition. Insights into food preferences can be gained from laboratory "cafeteria" studies, but preferences may be confounded by availabilities of alternate foods under field conditions. Experimental manipulation of the food base, usually through addition of food, can produce insights about the role of food limitation, although the timing of such

manipulations relative to background levels of the resource may greatly influence the results. Some studies have been designed to ascertain the relative importance of nutrients, calories, and water in the choice of foods by ground squirrels. Ritchie (1988) found Columbian ground squirrels (*Spermophilus columbianus*) to be largely energy maximizers. Females that did not forage optimally relative to an ideal proportion of monocots and dicots produced fewer successful offspring (Ritchie, 1990). Eshelman and Jenkins (1989) indicated that Belding's ground squirrels (*S. beldingi*) selected plants on the basis of both water and protein content, consistent with Pulliam's (1975) model of "partial preferences."

In a 4-year study we followed population dynamics of Townsend's ground squirrels (*Spermophilus townsendii*—Hoffmann et al. (1993) included this population in *S. mollis* on chromosomal grounds, but we maintained original nomenclature for consistency with Rickart's (1987) review and with other publications from this study) in the Snake River Birds of Prey National Conservation Area (Birds of Prey Area, hereafter). We expected that population change would be linked closely to the ground squirrels' food supply because they have a short active season of ca. 4 months, followed by ca. 8 months in which they remain underground and are largely torpid. During the active season, both adults and recently emerged juveniles generally double their body mass prior to immergence into torpor (Van Horne et al., 1997). The diet is mostly herbaceous vegetation, a food source that is low in caloric content relative to animal matter or seeds. Adults emerge from the inactive season in late January or early February, although female emergence may be delayed for 1–2 weeks when weather conditions are unsuitable. Young are born in early March and begin to emerge from their natal burrows in early April. There is a short period during which both adults and juveniles are active above ground. Adult males immerge as early as late April, but adult females generally do not immerge until after the first week of May. Juveniles immerge during early- to mid-June.

Several approaches are needed to understand factors influencing diet and the way in which food affects demography. We have investigated the role of fats in food, temporal and habitat-specific differences in body composition, and effects of experimental food supplementation (Van Horne et al., 1997). To gain further insight into the extent that food limits ground squirrels, we report the quantity and nutrient content of food from stomachs of ground squirrels. If food does indeed play a critical role in population dynamics of this species, individu-

als should show food preferences that may manifest themselves differently among sexes, age classes, and habitats. A major objective of our research was to analyze how diet and dietary preference vary with sex, age, and habitat.

An extreme drought occurred near the end of the second breeding season during our study, providing us with a natural experiment to investigate responses of vegetation and diets of ground squirrels to drought. An additional a posteriori objective of our study was therefore to describe any habitat-specific differences in diet between drought and non-drought conditions. Such variation in diet gave us additional insight into why populations declined during drought and post-drought periods and if the pattern of decline varied among habitats.

METHODS

Study area.—The Birds of Prey Area (43°N, 116°W; 900–950 m above mean sea level) is historically a shrub-steppe habitat, but it is increasingly dominated by exotic annual grasses and forbs, rendering it fire-prone when there is high net primary production followed by low precipitation. Because those annuals inhibit re-establishment of native shrub species, the area appears to be changing from shrub steppe to grassland (D. L. Yensen, in litt.). Sandberg's bluegrass (*Poa secunda*), a native perennial bunchgrass, is common in grasslands resulting from burns and in big sagebrush (*Artemisia tridentata*) habitats, but less common in shrub habitats dominated by winterfat (*Ceratoides lanata*).

Precipitation averages ca. 20 cm annually. Our study was structured in part to compare diets of ground squirrels in native shrub habitats with those in grassland habitats. Native shrub habitats included those dominated by winterfat—a low-stature shrub, big sagebrush—a taller shrub, and a mosaic of patches of winterfat and big sagebrush.

We studied ground squirrel populations on 20 study sites of ≤ 9 ha each from 1991 to 1994. Ten of our study sites were in grassland habitats where fire had occurred 7–10 years previously. Two of these had been reseeded artificially with several species, including winterfat. Although coverage of winterfat was sparse, diets were af-

ected sufficiently by reseeding that we chose to analyze diets on these reseeded sites separately from those in other grasslands. Six of our study sites were in big-sagebrush habitat, two were in winterfat habitat, and two others were in sagebrush-winterfat mosaic habitats. We live-trapped ground squirrels on each site throughout the active season and uniquely marked each captured animal with a passive integrated transponder (Schooley et al., 1993).

Climatic patterns.—We obtained data from a weather station of the National Oceanic and Atmospheric Administration located at Boise, Idaho (Boise Airport Weather Service Forecast Office; 43°34'N, 116°13'W; 865 m above mean sea level) to assess seasonal and annual climate patterns during 1991–1994. We examined monthly cumulative precipitation and monthly averages for maximum daily temperatures for January–June and total snowfall for January–February, and compared them to long-term means (1940–1990). Temporal patterns of climate were similar for Boise and the Birds of Prey Area, but actual precipitation at the Birds of Prey Area is ca. 84% of that at Boise (Van Horne et al., 1997).

Vegetation.—We sampled vegetation and plant phenology on each site to provide a context for assessing dietary differences. We estimated plant cover during two periods in 1991 (14 March–9 April, 17 April–2 May) and during three periods in 1992–1994 (19 February–10 March, 12–20 April, 22–30 May). We measured plant cover at 15–22 random locations in the trapping area on each site with point-intercept methods using a 3- by 0.5-m point frame as the sampling unit (Floyd and Anderson, 1982). In addition to recording the species encountered at each intercept, we noted if a grass blade or a forb leaf was green and succulent or brown and desiccated. We used this status variable (succulent or desiccated) to examine temporal changes in desiccation patterns for Sandberg's bluegrass, which was presumed to be the main perennial grass in the diet of the ground squirrels. For that analysis, we used sites as replicates and excluded those sites with $\leq 1.5\%$ total cover of Sandberg's bluegrass. We summarized mean coverage of common plant species ($>1\%$ horizontal coverage) for each habitat type using averages across years and sample periods. We also examined temporal changes in the coverage of the three most common annuals (Russian thistle—*Salsola iberica*, tansymustard—*Descurainia*

pinnata and *D. sophia* were not differentiated in sampling, and cheatgrass—*Bromus tectorum*).

Diet sampling.—We collected fecal samples from animals handled during regular trapping near the time at which we sampled vegetation; an early-season sample of adults collected between 20 February–10 March, a mid-season sample of both adults and juveniles collected between 10–24 April, and a late-season sample of juveniles collected between 18–31 May. Fecal samples were dried at 65°C for 48 h. Personnel at the Compositional Analysis Laboratory at Fort Collins, Colorado, quantified diets of squirrels using a microhistological technique (Sparks and Malechek, 1968) in which dried samples were ground over a 1-mm mesh screen, 20 fields were read from a prepared microscope slide, and plant species from the fecal samples were identified by matching epidermal patterns with those of plant tissues from reference material. Our ability to distinguish sources of seed material was variable, so we combined seed material into a single diet category for statistical comparisons.

Evaluation of diet methodology.—We used two approaches to assess reliability of our fecal analysis for estimating diet. First, we evaluated repeatability of the lab in estimating percent relative density of dietary items in our samples. In 1993, we selected three fecal samples from each of three habitats (grassland, sagebrush, and winterfat) during early and mid-season and three samples from two habitats (grassland, sagebrush) during late season. Thus, we used 24 samples in our evaluation. We divided each of the samples into three subsamples by splitting individual fecal pellets into three equal pieces and then placing each piece into one of the three subsamples. Choice of samples and placement of material into subsamples was done in a random manner. All subsamples were placed in sterile bags and labeled following normal procedures, except that two of the three subsamples were given false identification numbers. The lab was not notified of our evaluation, and thus it was a blind test. We calculated a similarity index (Anthony and Smith, 1977; Wydeven and Dahlgren, 1982) for each set of three subsamples as:

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

where Y_i was the lowest percentage value of a shared diet item and n was the total number of items. We tested for differences in mean simi-

larity indices among seasons with an analysis of variance (ANOVA) after arcsine-square root transformation of the data (SAS Institute Inc., 1989).

We were interested in the relationship between fecal samples and stomach contents. Westoby et al. (1976) detailed some of the problems with using particle counts from stomachs to estimate herbivore diets. In general, taxa are overestimated when abundant and underestimated when rare. Biases associated with differences in digestibility are likely to be magnified in fecal analyses, although Shalaway and Slobodchikoff (1988) and Wydeven and Dahlgren (1982) found a high positive association between particle frequencies in stomachs and in feces of Gunnison's (*Cynomys gunnisoni*) and black-tailed prairie dogs (*C. ludovicianus*), respectively. To compare similarity in diets from paired stomach and fecal samples from individual ground squirrels, we collected squirrels either through shooting or snap trapping in grassland and sagebrush habitats during early and late seasons in 1993. Samples from stomachs and feces were dried and analyzed following our normal procedures. We compared correspondence in diets estimated from paired stomach and fecal samples using the previously defined similarity index and ANOVA on arcsine-square root transformed data (proc GLM; SAS Institute Inc., 1989).

Diet analysis.—To investigate differences in estimated diet among habitats, sexes, and ages, we used multivariate ANOVA of arcsine-square root transformed values (SAS Institute Inc., 1989) of percent relative frequency for the most common fragment types. We report results only for analyses with $d.f. \geq 20$; in some years, individuals of a given sex or age class were too rare to provide sufficient numbers of fecal samples for robust analysis. To interpret significant results, we conducted separate ANOVA of diet items and used least squares-means for pairwise comparisons among years or habitats. We also measured similarities between male and female diets using the similarity index.

We used Savage's (1931) forage ratio and its associated variance (Manly et al., 1993:38) to examine preference among common foods and how preference changed with season and age class, a ratio >1 indicated a food was being consumed in higher proportions than its availability. Measures of preference based on differences in rank of available and consumed foods (e.g.,

Johnson, 1980) have been criticized for loss of quantitative information (Alldredge and Ratti, 1986). Ratios, however, may be particularly imprecise when resource availability is low. Also, when animals prefer to include a given food as a certain proportion in their diet regardless of availability, the preference value will nonetheless vary with the quantity available. Where this food is common, it may not be "preferred," even though it represents a large fraction of the diet. In contrast, a food that animals consume only in small quantities, even when it is abundant, may appear preferred where it is rare. We calculated preference patterns to aid in interpretation of dietary variation and thus did not test for differences in preference statistically. We used the six most common foods to measure preference. Because we had only one measure of vegetation, and hence availability, for each site, we used relative proportions of these six forages on each site as a measure of availability that we compared with the mean diet on that site. Each site rather than each animal was an observation. We thus report the mean ($\pm 1 SE$) of preference across sites within age classes, years, and sample periods (early-, mid-, and late-season). We restricted our measure of availability to percent cover of green (not woody or senescent) plants of a given species. This may have led us to underestimate availability, and thus overestimate preference, on the few occasions when animals consumed apparently senescent grasses.

To investigate effects of the 1992 drought on diet, we restricted analyses to sagebrush and grassland habitats, in which we had more sites and thus larger numbers of samples. We analyzed dietary composition separately for habitat types, ages, and sampling periods so that year was the only classification variable.

Forage quality and quantity.—To estimate forage quality in different habitats and at different times of the year, we used stomach contents from ground squirrels collected for the stomach-feces similarities. Contents were analyzed for acid detergent fiber, neutral detergent fiber, lignin, nitrogen, gross energy, and lipid content by the Nutritional Analysis Laboratory at Colorado State University. We used the resulting data to determine the proportion of the sample composed of nearly or completely indigestible cell-wall components (hemicellulose, cellulose, and lignin) and highly digestible components (pro-

tein, lipids, digestible carbohydrates—Robbins, 1983; Van Soest, 1963, 1967).

Assimilation depends on both forage quality and the quantity consumed. Dry mass of gut contents is an indicator of the latter when movement through the digestive system is constant. Unusually large gut capacity may be an indicator of low forage quality (Gross et al., 1985) and perhaps vulnerability to food limitation. We calculated wet masses of gut contents for four squirrels by subtracting wet mass of the empty digestive tract (stomach, cecum, intestines) from mass of the full digestive tract. Mean mass of empty digestive tracts was $7.3\% \pm 1.0\%$ of body mass. We compared the measured wet mass of gut contents with that predicted by the interspecific equation for herbivores: wet mass of contents (kg) = $0.0936 W^{1.03}$ where W was body mass in kg (Demment and Van Soest, 1985; Gross et al., 1985). For 29 squirrels, we had only summer weights of digestive tracts and gut contents. For those individuals, we assumed that empty digestive tracts weighed 7.3% of total body mass, and we compared estimated wet mass of gut contents to that predicted by the interspecific equation.

RESULTS

Climatic patterns.—Extreme differences in climate among years should influence vegetation in this dry region. In 1991, precipitation was somewhat below average, but maximum temperatures were near normal, except in February (Fig. 1). In 1992, a severe drought occurred during the active season of ground squirrels; there was little precipitation from February through May, and maximum temperatures were above average for January–June (Fig. 1). Precipitation that occurred in June 1992 fell after perennial grasses were dormant and nearly all of the ground squirrels had immersed. In 1993, cumulative precipitation was above average for March–June, and maximum temperatures were generally below average (Fig. 1). Cold temperatures in early 1993 were associated with above average snowfall in January (371 mm, 50-year mean = 168 mm) and February (264 mm, 50-year mean = 88 mm). Monthly snowfall during January and February was ≤ 96 mm

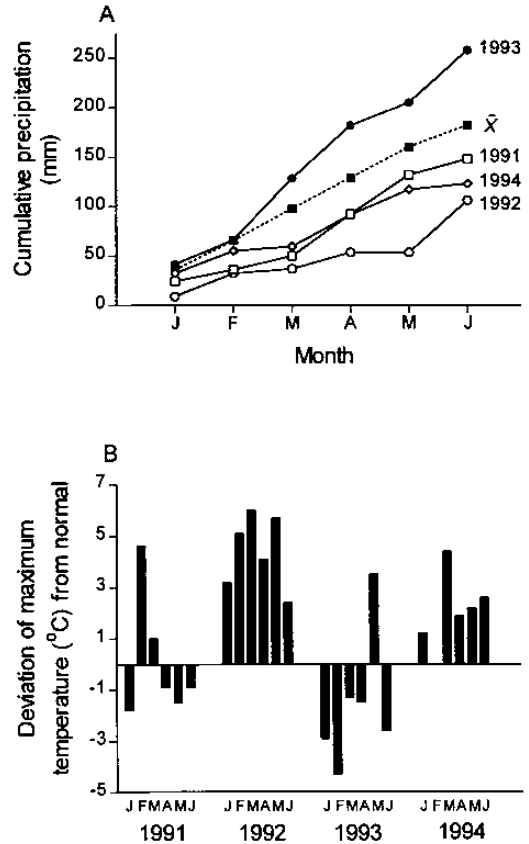


FIG. 1.—Climatic patterns for January–June 1991–1994 from data recorded at the weather station located at Boise, Idaho: A) monthly cumulative precipitation relative to the long-term mean (1940–1990), and B) deviation from normal (1940–1990 mean) for monthly means of daily maximum temperatures.

in the other 3 years. In 1994, precipitation was below normal and maximum temperatures were above normal, but conditions were not as severe as in 1992 (Fig. 1). Therefore, the main climatic patterns during our study were a severe drought in 1992, prolonged winter weather in early-season 1993, and unusually high precipitation during most of 1993.

Plant cover.—On the two winterfat sites, winterfat was the most common vegetation type ($\bar{X} = 16\%$) followed by mosses (*Tortula ruralis* and others; 10%), Sandberg’s bluegrass (5%), and budsage (*Artemisia*

spinescens; 1%). On the six sagebrush sites, big sagebrush was the most common groundcover ($\bar{X} = 23\%$), followed by mosses (15%), Sandberg's bluegrass (9%), bur-buttercup (*Ranunculus testiculatus*; 5%), cheatgrass (5%), and squirreltail (*Sitanion hystrix*; 3%). Big sagebrush was also the most common groundcover on the sagebrush-winterfat mosaic sites ($\bar{X} = 19\%$), followed by Sandberg's bluegrass (12%), winterfat (10%), mosses (9%), and tansymustard (*Descurainia*; 8%). Common species on grasslands, including reseeded sites, were Sandberg's bluegrass ($\bar{X} = 17\%$), cheatgrass (6%), Russian thistle (4%), and bur-buttercup (3%). Reseeded winterfat covered $<0.6\%$ of the area on the reseeded sites.

Vegetation dynamics.—Any pronounced temporal changes in timing and coverage of vegetation would be expected to influence diet of the largely herbivorous Townsend's ground squirrels. There were substantial among-year differences in the temporal patterns of desiccation of Sandberg's bluegrass (Fig. 2). The drought of 1992 was associated with early drying of Sandberg's bluegrass; a mean of 43% of Sandberg's bluegrass was classified as desiccated in April of 1992 compared with $\leq 12\%$ in the other 3 years. Late winter of 1993 was associated with a delayed green-up of Sandberg's bluegrass compared with other years (Fig. 2). The above-normal precipitation during the spring of 1993 also was related to a delay in the desiccation of Sandberg's bluegrass; a mean of 71% of Sandberg's bluegrass was classified as desiccated in late May 1993 compared with 99% in 1992 and 1994 (Fig. 2).

Several species of annual plants had a growth flush during the wet spring of 1993. The coverage of succulent tansymustard was typically $\leq 1.5\%$, but by late season 1993, it averaged 10.2% on winterfat sites, 3.4% on sagebrush sites, 21.0% on mosaic sites, 10.7% on grassland sites, and 16.8% on reseeded sites. Coverage of succulent Russian thistle also was generally $<1.5\%$,

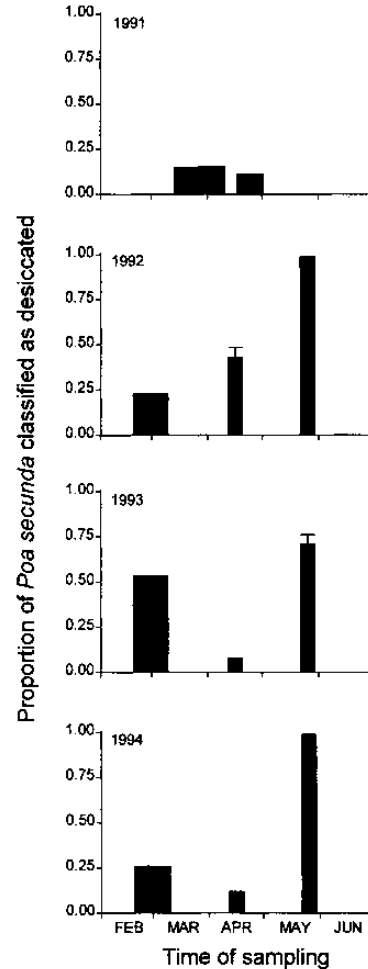


FIG. 2.—Seasonal and annual patterns in the proportion of *Poa secunda* that was classified as desiccated at the Birds of Prey Area, 1991–1994. Each bar represents a mean ($+1$ SE) for multiple study sites ($n = 16$ in 1991; $n = 18$ in 1992–1994); most SEs were ≤ 0.03 and are not displayed; width of each bar along the x-axis indicates the time period when sampling was conducted.

but by late season in 1993, it averaged 14.8% on grassland sites and 8.0% on reseeded sites. The only other time with moderate coverage of Russian thistle was in late season of 1994 (grassland = 5.6%, reseeded = 7.2%). Russian thistle did not exhibit a growth flush on any of the shrub-dominated habitats. Coverage of succulent cheatgrass also peaked in late season of 1993 on

TABLE 1.—Similarity indices (SI) for comparisons of diet items of *Spermophilus townsendii* during early-, mid-, and late-season in 1993. Comparisons are for triplicate subsamples of individual fecal samples and for paired stomach contents and feces.

Season	SI (%) for triplicates of fecal samples				SI (%) for stomach-feces comparisons			
	\bar{X}	SE	Range	n	\bar{X}	SE	Range	n
Early	86	4.8	64–100	9	92	5.3	55–100	7
Mid	86	3.9	59–98	9				
Late	58	9.6	22–85	9	67	6.4	41–97	10

both grassland ($\bar{X} = 10.8\%$) and sagebrush sites (8.1%).

Evaluation of diet methodology.—The mean similarity index for triplicate subsamples of individual fecal samples was $72 \pm 4.1\%$ ($n = 24$). Repeatability of dietary determinations was similar in early- and mid-season, but it declined in late season ($P = 0.008$; $F = 6.10$, $d.f. = 2,21$; Table 1). Total number of dietary items in fecal samples was similar in early season ($\bar{X} = 2.4$, range = 1–5) and in mid-season (3.0, range = 2–5), but it increased in late season (7.8, range = 6–9). There was a negative association between total number of diet items in fecal triplicates and their similarity ($r_s = -0.76$, $P = 0.0001$, $n = 24$).

The mean similarity index of dietary items in stomach contents and feces of ground squirrels was $82 \pm 5.0\%$ ($n = 17$). However, similarity in diets between stomachs and feces was greater in early season than in late season ($F = 11.92$, $d.f. = 2,14$, $P = 0.004$; Table 1). Average number of dietary items in stomachs increased from early season ($\bar{X} = 1.2$, range = 1–2) to late season (4.0, range = 2–6). Number of items in fecal samples also increased from early season ($\bar{X} = 2.3$, range = 1–4) to late season (5.0, range = 3–7). Overall, there was a negative correlation between total number of dietary items in a paired sample and the similarity index ($r_s = -0.90$, $P = 0.0001$, $n = 17$).

Fecal samples of Townsend's ground squirrels tended to have more species of forage items than did stomach samples. Wydeven and Dahlgren (1982) found a sim-

ilar pattern and reported a mean similarity of 63% between stomach and fecal samples, which was lower than ours. However, their samples contained more species than our samples (averages of 9.1 and 9.7 species in stomach and fecal samples, respectively), so we would expect their similarities to be lower if similarity declines with increased numbers of species.

Dietary variation.—We analyzed 457 fecal samples in 1991, 403 in 1992, 264 in 1993, and 308 in 1994 for a total of 1,432 samples. More than 80% of the mean diet across years and seasons in each habitat consisted of four plant species: Sandberg's bluegrass, winterfat, big sagebrush, and Russian thistle (Appendix I).

To assess overall differences in diets among habitats, sample periods, and drought and non-drought years, we used broad classifications of dietary items to develop a summary graph (Fig. 3). Statistical tests for differences were conducted on distinct dietary items, not on those broad classifications. There was little indication of dietary differences between drought and non-drought years in early-season samples (Fig. 3); effects of the severe drought of 1992 appeared in mid-season and were most pronounced by late-season. By mid-season, consumption of annuals was relatively low in grassland habitats during the drought, and by late-season, the decrease in consumption of both annuals and seeds was pronounced, except in winterfat habitats where those items were always rare in the diet.

We expected that diets might vary be-

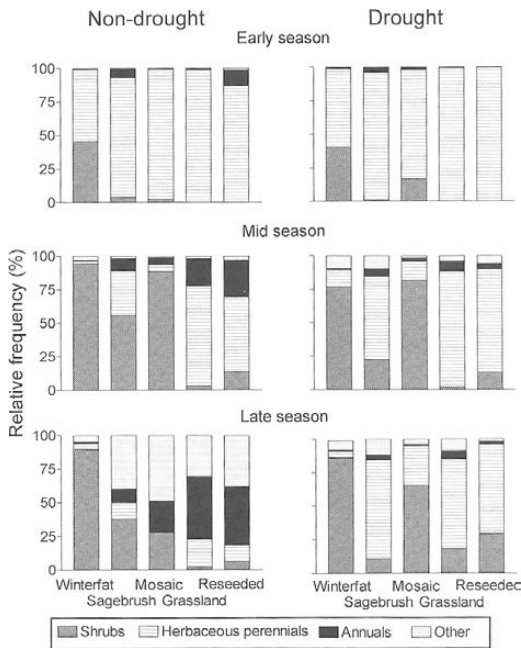


FIG. 3.—Mean relative frequencies of general food categories in diets of individual Townsend's ground squirrels in different habitat types on the Birds of Prey Area, Idaho, during non-drought (1991, 1993, and 1994) and drought (1992) years; low-moisture conditions associated with the 1992 drought were most pronounced during the mid- and late-season.

tween sexes because males are larger than females (adult males averaged 310 g prior to estivation in 1991; adult females averaged 220 g), and because females have high reproductive demands during the active season (\bar{X} litter size = 9—Rickart, 1987). To test for such a difference in diet, we performed a MANOVA (SAS Institute Inc., 1989) using the six most common mid-season diet categories (Sandberg's bluegrass, winterfat, big sagebrush, seed, Russian thistle, and cheatgrass) on individual samples within age classes (adult and juvenile), years (1991–1994), sampling periods (early, middle, and late; no late samples in 1991), and habitat types (winterfat, sagebrush, winterfat-sagebrush mosaic, grassland, reseeded grassland). We also calculated similarities of mean male and female diets for

all habitats in each of these groups based on all 12 dietary categories. We detected no differences in diets between either adult males and females ($P \geq 0.205$ for 15 comparisons, $d.f. \geq 20$) or juvenile males and females ($P \geq 0.179$ for 13 comparisons). Mean similarity of male and female diets was 74.4% for adults and 60.8% for juveniles. Inspection of the mean diets revealed no systematic differences, so we concluded that male and female diets were similar and combined them for all remaining analyses.

To compare diets of adults and juveniles, we performed a MANOVA using the six most common mid-season dietary categories (tansymustard replaced cheatgrass as the sixth most common item) for individuals blocked by habitat in each of the years separately. Diet differed significantly in each year ($P < 0.0001$). Separate ANOVA for those dietary items revealed that adults ate more big sagebrush, winterfat, and tansymustard and less Sandberg's bluegrass than juveniles in each year; differences in consumption of Russian thistle and seed were inconsistent among years.

Relationship between diet and habitat.—Habitats differed markedly and consistently through time in vegetation cover of the six plants most commonly found in the diet, except that cover was similar in the grassland and reseeded-grassland habitats (Fig. 4). Diets were considerably more variable through time than was vegetation cover, probably as a result of seasonal differences in succulence or chemical composition, and seasonal changes in availabilities of other foods such as seeds and insects.

There was clearly a relationship between coverage of a plant species on a site and its consumption; such concordance was evident for winterfat in winterfat habitats, big sagebrush in big-sagebrush habitats, and Russian thistle in grassland habitats (Fig. 4). Temporal linkage also was evident in limited instances; tansymustard appeared in both vegetation and diet in mosaic habitats at mid-season 1993, and consumption of Russian thistle increased when coverage in-

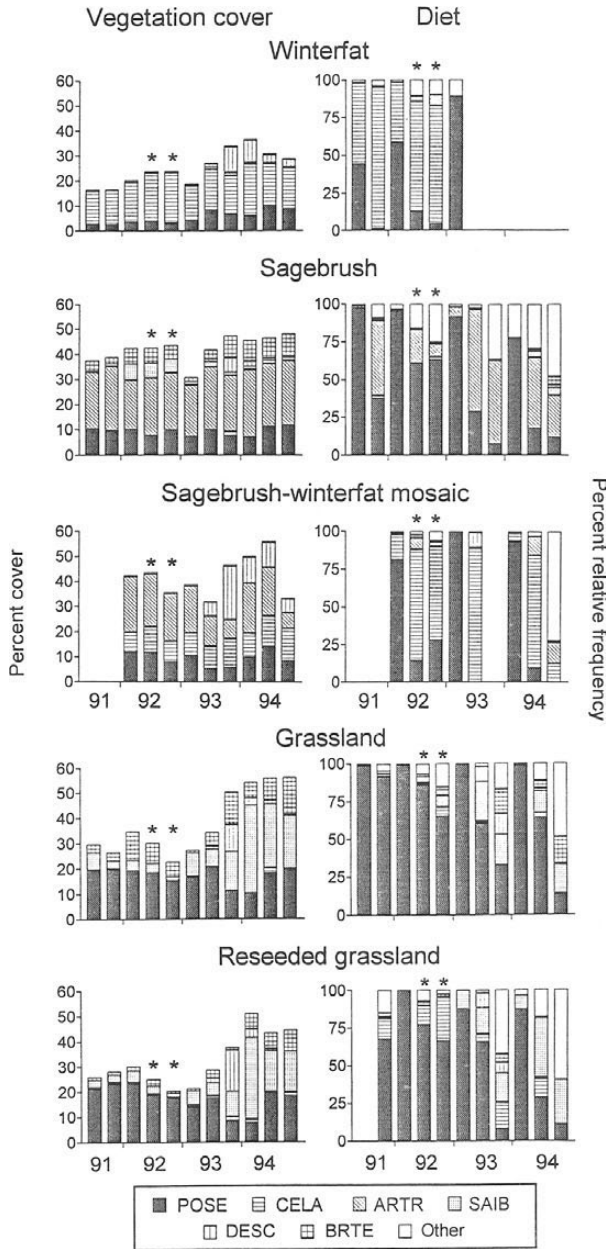


FIG. 4.—Mean percentage of vegetation cover across sites within habitat types for the six most common plants (POSE = Sandberg's bluegrass, CELA = winterfat, ARTR = big sagebrush, SAIB = Russian thistle, DESC = tansymustard, and BRTE = cheatgrass) found in diets of Townsend's ground squirrels in the Birds of Prey Area, Idaho, and relative frequency of these items and all other dietary items combined (Other); bars represent vegetation and dietary samples for early- and mid-season in 1991, and early-, mid-, and late-season in all other years; bars are omitted where low densities precluded diet estimation; age classes were pooled for calculating diet means; mid- and late-season samples in 1992 when drought effects were most severe are indicated with asterisks.

TABLE 2.—Dietary preference (means and standard errors) across sites for the six most common food items of adult and juvenile Townsend's ground squirrels at different times in the 1991–1994 active seasons in the Birds of Prey Area. Foods with means >1 (asterisk) comprised a higher mean proportion of the diet than their mean proportionate coverage among the six food types on sites and may have been preferred. "High" and "low" indicate the item was apparently preferred, but the mean available resource covered <0.1% of the ground so that we have little confidence in the actual preference value. "High" items comprised >10% and "low" items <10% of the mean diet for a given age class, time, and year.

Age	Season	Year	Sandberg's bluegrass (perennial)		Winterfat (perennial)		Big sagebrush (perennial)		Russian thistle (annual)		Cheatgrass (annual)		Tumble-mustard (annual)		
			\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	
Adult	Early	1991	1.3*	0.04	1.4*	1.24	0.2	0.02	1.0	0.71	0.0				low*
		1992	1.6*	0.03	0.6	0.13	0.0		0.0		0.0				low*
		1993	1.8*	0.08	0.1	0.01	0.2	0.01	0.1	0.01	0.0				low*
		1994	4.3*	1.12	0.1	0.00	0.0		0.0		low*				0.0
	Mid	1992	1.3*	0.03	1.5	0.14	0.6	0.01	0.2	0.01	0.0			0.8	0.12
		1993	0.8	0.02	4.8*	10.87	2.3*	0.20	1.5*	0.08	0.0			1.6*	1.14
		1994	0.1	2.58	3.7*	0.18	3.1*	1.01	1.1*	0.01	low*			0.3	0.03
Juvenile	Mid	1991	0.9	0.01	1.6*	0.16	0.9	0.01	low		0.4	0.08			low*
		1992	1.5*	0.01	1.3*	0.07	0.2	0.00	0.2	0.00	0.0			0.5	0.06
		1993	1.0	0.03	3.2*	10.04	1.4*	0.04	1.9	0.15	0.0			0.9	0.04
		1994	7.4*	7.53	2.8*	0.20	0.4	0.03	0.2	0.01	2.4*	3.39		0.1	0.00
	Late	1992	high*		1.4*	0.05	0.2	0.00	0.1	0.00	0.0				low*
		1993	3.8*	1.19	3.2*	1.43	1.1*	0.00	1.0	0.10	0.7	0.38		0.4	0.02
		1994	high*		0.5	0.13	0.9	0.09	0.7	0.02	1.4*	0.44		0.3	0.04

creased in 1993 and 1994 in grassland and reseeded-grassland habitats.

Some of the dietary variance may have indicated preference or avoidance. In sagebrush-winterfat mosaic habitats, winterfat was relatively more common than big sagebrush in diets, although coverage of those plants was similar (Fig. 4). The perennial plants—Sandberg's bluegrass, winterfat, and big sagebrush, tended to be more common in diets than annual plants—Russian thistle, cheatgrass, and tansymustard.

Formal calculations of preference were consistent with those patterns. Among foods common in the diet, mean preferences for perennials generally were higher than those for annuals (Table 2), although it was likely that annuals had a shorter period in which they were commonly eaten (and we may not always have sampled precisely at this time). Among the plants used in preference calculations, availabilities of perennials were greater than those of an-

nuals (Fig. 4), so preference for perennials reflected higher consumption rather than lower availability. Winterfat and big sagebrush were preferred by adults at mid-season in 1993 and 1994 and juveniles in 1993 when Sandberg's bluegrass was not preferred (Table 2). Preference patterns for perennial shrubs may have been associated with relatively wet years and timing of new shrub growth. During the drought of mid- and late-season in 1992, winterfat was preferred food.

Effects of drought on diet.—During the drought, Townsend's ground squirrels did not follow normal patterns of mass gain. Compared to 1991, pre-immersion masses at the end of the above-ground season in 1992 were 43% less for adult males, 44% less for adult females, 52% less for juvenile males, and 35% less for juvenile females. Fewer animals were recaptured between 1992 and 1993 than between 1991 and 1992. We measured persistence of individ-

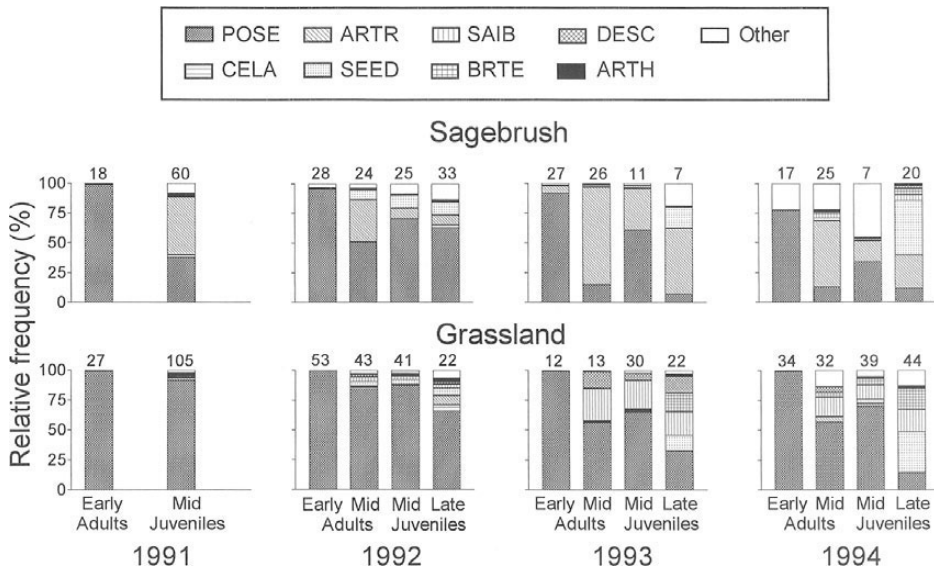


FIG. 5.—Mean relative frequencies of food types in diets of adult and juvenile Townsend's ground squirrels in the Birds of Prey Area, Idaho, during 1991–1994 in sagebrush and grassland habitats (POSE = Sandberg's bluegrass, CELA = winterfat, ARTR = big sagebrush, SEED = seed material, SAIB = Russian thistle, BRTE = cheatgrass, DESC = tansymustard, ARTH = arthropods, and Other = other fragment types); sample sizes are indicated above bars.

uals through the inactive period as the percentage of marked individuals present during the immergence period that were recaptured in the following season; that number reflected both survival and emigration from study plots (Van Horne et al., 1997). Persistence declined from 55% to 34% for adult males, from 69% to 12% for adult females, from 29% to 1% for juvenile males, and from 51% to 1% for juvenile females (Van Horne et al., 1997).

Because effects of drought on change in body mass and plant phenology began to appear in mid-season of 1992 and were most evident by late-season that year, we were interested in dietary differences between 1992 and other years during those periods. We did not expect to see drought effects on early-season samples. Because we used only sagebrush and grassland habitats that were not reseeded to test for among-year differences in diet, winterfat was rare. We used Sandberg's bluegrass, big sagebrush, seed, and Russian thistle as dependent variables in MANOVA. For each

habitat, age, and sample period, the MANOVA with year as an effect was significant ($P < 0.0001$). All differences discussed below had $P < 0.05$ for least-squares means comparisons of separate ANOVA for each dietary item. Early in the season, consumption of Sandberg's bluegrass by adults in sagebrush habitats was relatively low in 1994, but consumption of Sandberg's bluegrass in grassland habitats was relatively high in 1992 and consumption of Russian thistle was relatively low in 1992 and 1994 (Fig. 5). In mid-season, consumption of Sandberg's bluegrass and seeds by adults in sagebrush habitats was relatively high in 1994. Similarly, adults in grassland habitats ate relatively more Sandberg's bluegrass and less Russian thistle in both 1991 and 1992, and more seeds in 1992.

Differences in diet for juveniles in mid-season of 1992 were similar to patterns of adults. Juveniles in sagebrush habitats in mid-season also ate more seeds in 1992 than in the other years, and they ate more Sandberg's bluegrass in both 1992 and

1993 than in 1991 and 1994. They ate less Russian thistle in both 1991 and 1992 than in 1993 and 1994 and more big sagebrush in 1991 than in the other years. Juveniles in grassland habitats ate more Sandberg's bluegrass and less Russian thistle in 1991 and 1992 than in 1993 and 1994. High seed consumption by adults in both habitat types and juveniles in sagebrush at mid-season of 1992 may have been related to earlier phenology, especially of grasses, associated with the warm early spring and subsequent onset of drought. High consumption of Sandberg's bluegrass, given its high coverage value in these habitats, was probably associated with lower availability of alternate foods such as new growth of big sagebrush, and Russian thistle, a moisture-sensitive annual whose coverage was reduced by dry conditions.

Late-season samples in 1992–1994 continued the same trends, except that seed consumption was lower than in 1991. Consumption of seeds was lower on both habitats in 1992 and 1993 than in 1994. Less Russian thistle was consumed in 1992 than in 1993 and 1994 on grassland sites, but consumption was lower on sagebrush sites in both 1992 and 1993 in comparison to 1994. Consumption of Sandberg's bluegrass by juveniles late in the season was higher in 1992 than in the other years in both habitats. Again, this likely was associated with shortage of alternative foods.

Forage quality.—Although ground squirrels in grassland and sagebrush sites had different diets, they selected diets of similar quality in 1993 (Table 3). Nutritional quality of the stomach samples did not differ ($P > 0.20$) between ground squirrels collected in grassland and sagebrush sites in 1993, although the percentage of lignin increased ($P = 0.0012$) and protein decreased ($P < 0.0001$) between March and May (Table 3). Caloric values of stomach contents (gross energy) also were similar to those reported by Rickart (1982) for Townsend's ground squirrels in Utah ($\bar{X} = 3.8$ – 4.6 kcal/g).

TABLE 3.—Composition of forage removed from stomachs of Townsend's ground squirrels in the Birds of Prey Area, Idaho, 1993. Sample sizes are 14 for early season (March) and 9 for late season (May). Means that differ significantly between early and late season have an asterisk.

Component	Early season		Late season	
	\bar{X}	SE	\bar{X}	SE
Cellulose (%)	11.3	0.23	12.9	1.40
Lignin (%)	3.2*	0.32	6.2*	0.76
Hemicellulose (%)	22.9	0.49	22.5	3.54
Silica (%)	2.6	0.45	2.0	0.46
Protein (%)	34.9*	0.82	19.7*	1.90
Lipid (%)	7.4	0.71	7.8	1.07
Gross energy (kcal/g)	4.45	0.04	4.32	0.14

Gut contents.—For the four ground squirrels with actual weights of gut contents, wet masses of gut contents were $144 \pm 9.4\%$ higher than those predicted using the interspecific equation based upon body mass (e.g., actual mass 37 g, predicted mass 15 g). For the remaining 29 squirrels for which we had estimated weights of gut contents, gut contents weighed 84% more than would be predicted by body mass (e.g., actual mass 27 g, predicted mass 15 g). Actual increases in gut capacity over predicted values were probably higher than those reported because it was unlikely that all digestive tracts were filled to capacity.

DISCUSSION

General dietary patterns.—The importance of *Poa secunda* in diets of Townsend's ground squirrels in the Birds of Prey Area, especially early in the season, is consistent with indications from other researchers that Townsend's ground squirrels are highly dependent on grasses. Rogers and Gano (1980) found *Poa*, *Descurainia*, and *Lupinus* to be the most common foods of Townsend's ground squirrels in southcentral Washington. Koehler and Anderson (1991) reported that Townsend's ground squirrels ate a large proportion of crested wheatgrass (*Agropyron desertorum*) at a site in south-

eastern Idaho (this grass was not similarly available in the Birds of Prey Area).

Yensen and Quinney (1992) reported that grasses comprised 37–87% of the diet of Townsend's ground squirrels in the Birds of Prey Area, with winterfat and sagebrush also being important components. As we found for juveniles, animals in their study consumed more seeds prior to torpor. Our data also are consistent with their suggestion that seed consumption decreased under drought conditions. We did not, however, find consumption of cheatgrass as high as that reported by Yensen and Quinney (1992). Because cheatgrass is an annual, its coverage varies greatly with rainfall patterns. Coverage was higher during their study, averaging 11% in 1987 and 33% in 1988 on sites dominated by native perennial bunch grasses. In contrast, mean coverage of cheatgrass during our study varied from 3% to 14% on native grass sites during 1991–1994.

Leaves of shrubs are consumed by Townsend's ground squirrels when available, although it appears that consumption of big sagebrush is limited largely to new growth. Cook (1977) reported that ether extract (essential oils), protein, and gross energy of big sagebrush and winterfat in the Great Basin of western Utah were higher in April and May when those browse species were actively growing than in January or July when they were maturing or quiescent. New growth of shrubs may provide some nutrient value not available from Sandberg's bluegrass. According to Cook (1977), those browse species were higher in protein, lignin, and phosphorus than were grass species (Indian ricegrass, *Oryzopsis hymenoides*, and squirreltail grass), which were higher in cellulose.

Shrubs also may provide more fat than grasses. Linoleic acid can decrease energy costs of hibernation in marmots (Florant et al., 1993), and the polyunsaturated fatty acids linoleic and alpha-linolenic may be essential for successful hibernation in ground squirrels (J. C. Corn, in litt.). Those poly-

unsaturated fatty acids cannot be synthesized endogenously, except from specific fatty-acid precursors (J. C. Corn, in litt.). Animal adipose tissue content of these essential fatty acids is correlated closely with dietary content, although somewhat higher (J. C. Corn, in litt.). Winterfat and sagebrush are similar in linolenic acid content but higher relative to Sandberg's bluegrass. Those shrubs are likely to be a better source of essential fatty acids than are grasses.

Lack of difference between male and female diets is somewhat surprising, given the size dimorphism between sexes and the need for females to bear most of the energetic and nutrient costs of reproduction late in their short active season. However, males have high energy demands associated with early arousal and searching for mates early in the active season and may need to store extra fat late in the previous active season to meet those demands. Variation in availability among years, seasons, and habitats also may constrain the optimal diet for males and females in a similar fashion.

In contrast to the male-female pattern, there were differences in diet between ages shortly after juvenile emergence—the only time at which we sampled both adults and juveniles. Such differences could result from a lack of foraging experience causing juveniles not to be selective or to respond more directly to availability than did adults, or they may be reluctant to forage widely from the burrow entrance because of extra predation risk caused by lack of experience and physical immaturity. It is also possible that their diet is no less optimal than that of adults, but they are either relatively intolerant of the secondary chemistry in sagebrush leaves, or they avoid protein-complexing properties of secondary chemistry of sagebrush during their rapid growth phase.

Effects of the drought on diet.—Differences in nutrient levels of foods may help explain continued low reproduction and survival during and immediately following the drought (Van Horne et al., 1997). New

growth of grass is a better source of essential fatty acids than mature grass. Linolenic acid is higher in green plants than in senescent plants and is also relatively high in seeds (J. C. Corn, in litt.). Both new growth of grasses and numbers of seeds were at low levels late in the 1992 season. Plants in 1993 had relatively low content of linoleic acid compared with pre-drought conditions.

Effects of drought on diet varied with habitat type. Alternative foods were an important component of the diet in winterfat, sagebrush, and mosaic habitats when Sandberg's bluegrass senesced early and seeds matured early in the drought year of 1992. Juvenile ground squirrels consumed relatively high amounts of Sandberg's bluegrass late in the season despite its senescent state, and did not gain mass as they did during non-drought years. Only a few juveniles in sagebrush habitats and none in grassland habitats were recaptured after the intervening inactive season; clearly, the diet of senescent Sandberg's bluegrass was inadequate. Adults in sagebrush habitats were recaptured the year following the drought at relatively higher rates than in grassland habitats (30% for adult males and 28% for adult females in sagebrush; 17% for adult males and 10% for adult females in grassland excluding reseeded and food-supplemented sites; Van Horne et al., 1997). Loss of annuals as a major diet component, especially on grassland and reseeded sites during the mid-season period of the drought year, may explain the relatively low persistence of animals on these sites as compared to sagebrush sites, where animals consumed more shrub and other foods during the mid-season of the drought year.

Animals in sagebrush habitats consumed relatively more shrub material in both drought and non-drought years than those in grassland habitats. This alternative food source may have provided an important source of water and nutrition during drought. Because animals in sagebrush ate more shrub material, diets in sagebrush habitats in 1993 appeared to meet physio-

logical requirements for essential fatty acids, but diets in grasslands apparently did not (J. C. Corn, in litt.). Consumption of annuals was always relatively lower for both adults and juveniles in these shrubby habitats, so that rarity of annuals during drought had relatively less effect on overall diet. During drought, proportions of foods in the diet were least affected on the winterfat sites, and individuals on the mosaic sites sought out shrub material (mostly winterfat) under drought conditions. It thus appears that habitats dominated by native shrub species may support a more stable food source under drought conditions than habitats dominated by Sandberg's bluegrass and exotic annuals.

Our study indicates that ground squirrels are dependent on perennial plants, especially early in the active season, and that drought may drastically decrease availability and consumption of annual plants late in the active season. As a consequence, we believe that any habitats dominated by annual plants that lack substantial coverage of perennial plants cannot support stable, increasing, or source populations of ground squirrels for any substantial time period. Regional extinctions of ground squirrels are likely to occur, especially during drought, if such habitats become widespread. These annual-dominated habitats are a product of human disturbance and mixing of biotas, and ground squirrels may not be able to adapt to them. Even if large blocks of shrub-steppe habitat are not converted to annual-dominated grassland, we predict that increased coverage by annuals and decreased coverage by perennials will increase sensitivity of Townsend's ground squirrel populations to low moisture conditions.

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APPENDIX I

Fragment types identified in fecal samples from Townsend's ground squirrels in the Birds of Prey Area, Idaho. The mean percentage of total fragments for individuals within habitat types across years (1991-1994) and across sampling periods (early, middle, late) is given. Columns represent mean total diet for a habitat and thus sum to 100. P = number of sample periods and n = mean number of ground squirrels sampled per sampling period. Items are listed in decreasing order of mean percentage across habitat types. Items comprising <0.1% of mean total fragments are indicated as "trace".^a

Dietary component	Category	Habitat				
		Winterfat (P = 7; n = 10)	Sage- brush (P = 11; n = 30)	Mosaic (P = 8; n = 18)	Grassland (P = 11; n = 52)	Seeded (P = 10; n = 18)
Sandberg's bluegrass (<i>Poa secunda</i>)	Perennial	30.8	53.7	40.8	73.6	59.9
Winterfat (<i>Ceratoides lanata</i>)	Shrub	61.2	0.4	42.1	0.8	9.2
Big sagebrush (<i>Artemisia tridentata</i>)	Shrub	1.7	26.2	4.7	1.4	0.2
Russian thistle (<i>Salsola iberica</i>)	Annual	trace	0.9	0.0	8.0	13.0
Grass seed	Annual, Perennial	1.1	5.8	2.5	3.9	4.1
Pinnate tansymustard (<i>Descurainia pinnata</i>)	Annual	trace	0.6	1.7	2.8	2.1
Boraginaceae seed	Perennial	0.0	0.0	2.7	0.8	2.2
Unidentified seed	Annual, Perennial	0.0	2.0	1.4	0.7	1.3
Cheatgrass (<i>Bromus tectorum</i>)	Annual	0.0	0.7	0.1	3.5	0.6
<i>Lappula occidentalis</i>	Perennial	trace	trace	2.8	0.2	1.3
Unidentified arthropod	Other	1.1	0.4	0.5	0.6	0.4
Unidentified forb	Annual, Perennial	0.0	2.8	0.0	trace	trace
Crested wheatgrass (<i>Agropyron desertorum</i>)	Perennial	trace	1.2	0.2	0.2	0.6
Thistle (<i>Cirsium arvense</i>)	Annual	0.0	0.9	0.0	0.7	0.5
<i>Medicago sativa</i>	Perennial	0.0	0.0	0.0	0.3	1.5
<i>Atriplex</i>	Shrub	1.6	0.1	0.0	0.1	0.0
Thurber's needlegrass (<i>Stipa thurberiana</i>) or Indian ricegrass (<i>Oryzopsis hymenoides</i>)	Perennial	0.1	1.3	trace	0.1	trace
Rabbitbrush (<i>Chrysothamnus viscidiflorus</i> or <i>C. nauseosus</i>)	Shrub	0.0	1.0	0.0	0.1	0.5
Tumblemustard (<i>Sisymbrium altissimum</i>)	Annual	0.1	trace	trace	0.2	
Coleoptera	Other	0.7	trace	trace	0.2	0.1
<i>Kochia scoparia</i>	Shrub	0.0	0.0	0.1	0.6	trace
Horsebrush (<i>Tetradymia glabrata</i>) or spiny horsebrush (<i>T. spinosa</i>)	Shrub	0.0	0.6	0.0	trace	trace
Squirreltail (<i>Sitanion hystrix</i>)	Perennial	0.0	0.1	0.0	trace	0.4
Prairie junegrass (<i>Koeleria pyramidata</i>)	Perennial	0.0	trace	0.0	trace	0.4
Coleoptera or Hymenoptera	Other	0.4	0.0	0.0	0.0	0.0
Tapertip hawksbeard (<i>Crepis acuminata</i>)	Perennial	0.2	0.2	trace	0.0	trace
Moss (<i>Tortula ruralis</i>) and other mosses	Perennial	0.2	trace	trace	trace	trace
Orthoptera	Other	0.2	trace	0.1	trace	trace
Phlox (<i>Phlox aculeata</i>)	Perennial	0.0	0.2	0.0	0.13	trace
Flower	Annual, Perennial	0.0	0.3	0.0	trace	0.0
Greasewood (<i>Sarcobatus vermiculatus</i>)	Shrub	0.1	0.1	0.0	trace	trace
<i>Endogone</i> -fungus	Other	0.0	0.1	0.0	0.0	0.2

APPENDIX I.—Continued.

Dietary component	Category	Habitat				
		Winterfat (<i>P</i> = 7; <i>n</i> = 10)	Sage- brush (<i>P</i> = 11; <i>n</i> = 30)	Mosaic (<i>P</i> = 8; <i>n</i> = 18)	Grassland (<i>P</i> = 11; <i>n</i> = 52)	Seeded (<i>P</i> = 10; <i>n</i> = 18)
Shadscale (<i>Atriplex confertifolia</i>)	Shrub	0.2	trace	0.0	trace	0.0
Blazing star (<i>Mentzelia albicaulis</i>)	Perennial	0.0	0.0	0.2	0.0	0.0
Unidentified bark	Shrub	0.0	0.1	0.0	trace	trace
Compositae	Annual, Perennial	0.0	trace	trace	0.1	trace
Brassicaceae seed	Perennial	0.0	0.1	0.0	trace	0.0
Diptera	Other	0.0	0.0	0.0	0.0	0.1
Lepidoptera	Other	0.0	0.0	0.0	0.0	0.1

* Items that comprised <0.1% of the mean diet in all habitat types included, in decreasing order of commonness; the annuals storksbill (*Erodium cicutarium*), *Lepidium perfoliatum* or *L. papilliferum*, *Panicum*, *Draba verna*, six weeks' fescue (*Vulpia octoflora*), and *Medicago* or *Melilotus*; annual or perennial unidentified plant material; the perennials *Sphaeralcea munroana*, lichens, prickly lettuce (*Lactuca serriola*), and unidentified Umbelliferae; *Artemisia* seed; and lepidoptera larvae.