Elizabeth J. Dyni[1] and **Eric Yensen,**[2] Department of Biology and Museum of Natural History, Albertson College, Caldwell, Idaho 83605 USA

Dietary Similarity in Sympatric Idaho and Columbian Ground Squirrels (*Spermophilus brunneus* and *S. columbianus*)

Abstract

We studied diets of *Spermophilus brunneus*, a rare endemic species, and *S. columbianus*, a larger, widespread potential competitor, in two areas where they were sympatric to learn if competition for food might be a factor in *S. brunneus'* rarity. Because the diet of *S. brunneus* was unknown, we also wished to determine if dietary specializations might explain the species' limited distribution. Vegetation at the study sites was sampled using a point frame method. Fecal pellets were collected from live-trapped squirrels and analyzed using a microhistological technique; plant parts (leaves/stems, seeds/flowers, roots/bulbs) were tallied as separate categories for each species. At the two sites, *S. brunneus* consumed 45-50 species of plants in 55-75 categories, although only 18-20 categories comprised >1% of the diet and only 5-7 comprised >5%. Similarly, *S. columbianus* consumed 53-58 plant species in 74-75 categories; only 10-17 categories comprised >1% of the diet and only 4-6 comprised >5%. Idaho and Columbian ground squirrel diets were 30-52% similar at a site, whereas each species' diet was only 25-37% similar between sites. Diets were not correlated with plant abundance in the habitat, indicating that diet selection was taking place. The diet of *S. brunneus* appears typical of ground squirrels of the subgenus *Spermophilus*. Both species utilized similar resources, and habitat segregation probably accounted for most of the observed dietary differences. The results suggest that dietary overlap with *S. columbianus* relegates *S. brunneus* to less productive habitats and is a factor in *S. brunneus'* rarity.

Introduction

The Idaho ground squirrel (*Spermophilus brunneus*) is one of the rarest North American mammals. It has the smallest geographic range of any *Spermophilus*, and certainly one of the smallest ranges among North American mainland mammals (maps in Hall 1981). Further, it is rare within its limited range (pers. obs.). This research was part of an effort to determine why *S. brunneus* is so rare.

Ground squirrels of the subgenus *Spermophilus* have similar diets and habits, and their geographic distributions are almost always allopatric or parapatric (Howell 1938, Durrant and Hansen 1954, Turner 1972, Hall 1981). However, throughout much of its 125 x 90 km geographic range in west-central Idaho (Yensen 1991), the endemic Idaho ground squirrel is sympatric with the widely-distributed Columbian ground squirrel (*S. columbianus*).

Columbian ground squirrels are about one and a half times as large as Idaho ground squirrels (head and body 245-300 mm vs. 160-190 mm) and two to three times as massive (450 vs. 170 g, lean weight of adult males; E. Yensen, unpublished data) and thus would have an advantage in an aggressive interaction. Optimal foraging studies of *S. columbianus* found that they attempt to maximize energy intake rather than maximizing nutrient intake or minimizing feeding time (Belovsky 1986, Ritchie 1988, Ritchie and Belovsky 1990). If *S. brunneus* followed a similar strategy, and if diets were similar, then in order for the two species to coexist sympatrically we would predict that the larger species would utilize the most productive habitats, and relegate the smaller species to habitats too unproductive for the larger competitor.

Consistent with this expectation, in Adams County, Idaho, Columbian ground squirrels occupy mesic meadows, forest edges, sparsely-timbered areas with open canopies, and fields, but do not occur in the more sparsely vegetated, rocky, xeric meadows with shallower soils associated with *S. brunneus*. Some meadows have both xeric and mesic vegetation as a result of a mixture of deeper and shallower soils, and in these the two species may occur adjacent to each other, with *S. columbianus* always in the more mesic habitat. Plant species composition differs strikingly in the mesic and xeric portions of the meadow, with xeric areas having obviously less total plant cover, fewer grasses, more forbs, and plants of shorter stature (E. Yensen, unpublished data).

[1]Present address: Box 1665, Eastsound, WA 98245

[2]Address for reprints and correspondence.

At meadows with both species, we have occasionally observed them foraging within a few meters of each other in ecotones, and we have also observed individuals of each moving up to 100 m from nest burrows to forage. Thus, both species potentially had access to the same resources, although in actuality there was habitat segregation with only a small area of overlap (<500 m2).

The only published information on Idaho ground squirrel diets is one anecdotal foraging observation (Davis 1939:184). Columbian ground squirrels eat mostly grasses, herbs, fruits, and bulbs (Howell 1938). In central Idaho, Lambeth and Hironaka (1982) found 43 species in their diet, of which silky lupine (*Lupinus sericeus*), yarrow (*Achillea millefolium*), grasses and sedges were the most important, whereas Elliott and Flinders (1985) found balsamroot (*Balsamorhiza saggittata*), yarrow (*Achillea millefolium*), clover (*Trifolium* spp.), fleabane (*Erigeron speciosus*), silky lupine (*Lupinus sericeus*), alpine timothy (*Phleum alpinum*) and bluebunch wheatgrass (*Agropyron spicatum*) were most important. In British Columbia, clover (*Trifolium dubium*), bentgrass (*Agrostis alba*), Kentucky bluegrass (*Poa pratensis*), and dandelion (*Taraxacum officinale*) comprised 98% of the diet (Harestad 1986).

The purpose of this investigation was to determine if indeed Idaho and Columbian ground squirrels had similar diets in areas where they co-occur as a step toward understanding the relations between the two species in areas of potential competition. A secondary goal was to determine if *S. brunneus* had any dietary specializations that might be responsible for its restricted distribution.

Study Sites

Two sites approximately 35 and 45 km NW of Council, Adams Co., Idaho where *S. brunneus* and *S. columbianus* foraged in close proximity were selected for study.

"Huckleberry." This site (Fig. 1) was in a 10-ha meadow surrounded by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) forest and was located 1.6 km N, 1.6 km E of Bear Guard Station, Adams Co., Idaho (45°05'N, 116°37'W, 1490 m elev.). The lower (southern) portion of the meadow was inhabited by Columbian ground squirrels, had soils >2 m deep, and was dominated by grasses and associated forbs. In the upper meadow there was a series of low, xeric, rocky ridges with shallow soils generally <1 m deep and intervening grassy swales that were inhabited by Idaho ground squirrels. There was a sharp contrast in vegetation cover between the xeric and mesic areas inhabited by the two species. Squirrel trapping and vegetation analysis were done in an area of ca. 2 ha that included both habitat types and the ecotone. The site was grazed by cattle in late summer. (See Yensen et al. [1991] for additional site description).

"Squirrel Valley." This site (Fig. 2) was at the SE edge of a 5 km^2 meadow between Bear and Steve's Creeks, 1 km S and 1 km E of Bear townsite (45°00'N, 116°39'W, 1320 m elev.). The study site spanned Steve's Creek. Columbian ground squirrels occupied most of the creek bottom and hillside to the east. The soils in the area occupied by *S. columbianus* were >2 m deep and the area supported a lush growth of mostly native and a few introduced grasses and forbs. Just east of the study site boundary was a hayfield with alfalfa (*Medicago sativa*). In the bottom west of the creek was an ecotone occupied by both species of ground squirrels. Further west was a steep bank about 8 m tall with well-drained, gravel soils. Above this was a grassy swale on shallower soils (<1 m deep to a clay layer) which supported a dense Idaho ground squirrel population. The vegetation analysis and squirrel trapping were done in an area of ca. 3 ha that included areas occupied by both squirrel species and an ecotone. The site was on a cattle ranch, and was moderately grazed at intervals throughout the growing season. Native vegetation had been partly replaced with introduced pasture grasses. There was much less contrast in vegetation structure or composition between the areas occupied by the two species of ground squirrels than at Huckleberry.

Methods

Ground squirrels were trapped using unbaited 14 x 14 x 41 cm Tomahawk traps or burrow entrance traps (Wobeser and Leighton 1979) set at burrow openings immediately after a squirrel's entrance. All other openings to the burrow system were blocked until the squirrel emerged into the trap. Trapped squirrels were weighed, marked with monel fingerling tags, and age (juvenile, yearling, or adult when these could be distinguished), sex,

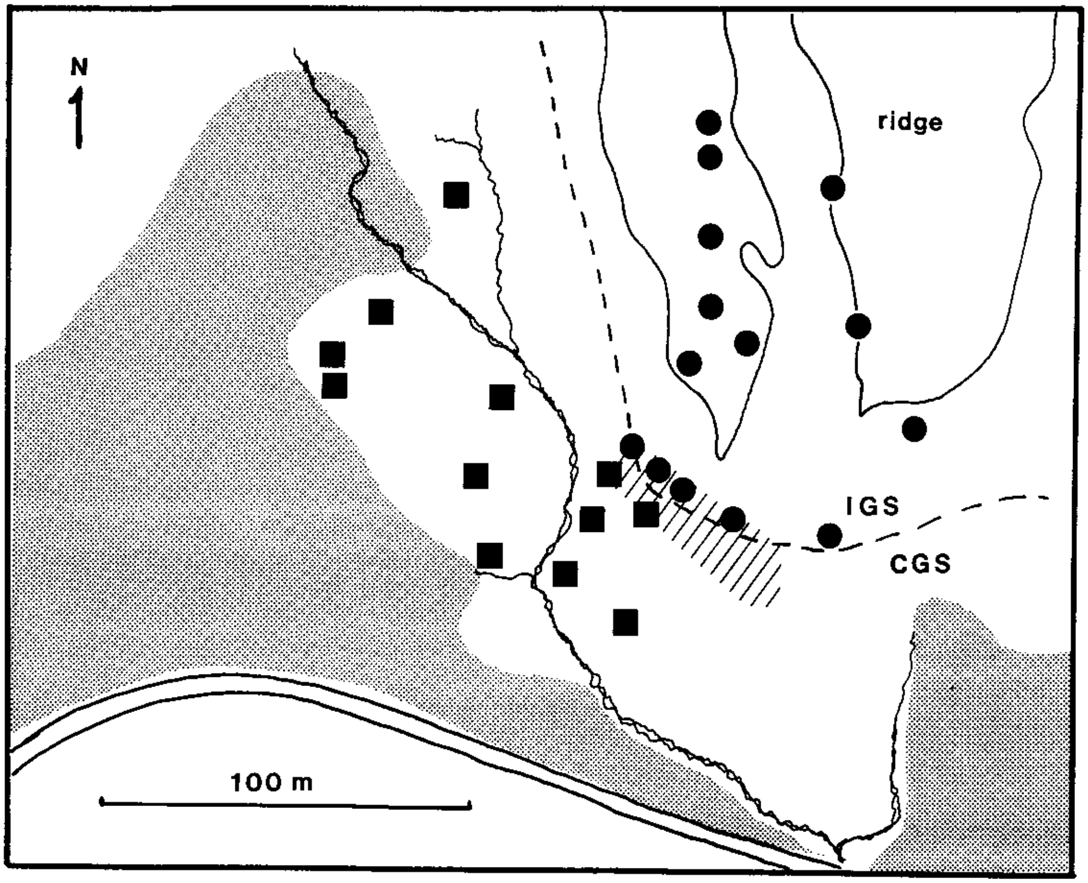

Figure 1. Map of Huckleberry study site, Adams Co., west-central Idaho showing capture locations of *Spermophilus brunneus* (circles) and *S. columbianus* (squares) for fecal pellet analysis. Cross-hatching indicates an area where both species foraged, although burrow locations were in areas separated by the dashed line; IGS = Idaho ground squirrel area, CGS = Columbian ground squirrel area. The shaded area indicates forested areas; forest also occurs south of the road, but is not shown. The two ridges (upper right) have shallow soils and xeric vegetation.

reproductive condition, and trap location were noted. Fecal pellets were collected from each animal and stored in paper envelopes with salt until processed. Voucher specimens of *S. brunneus* and *S. columbianus* were deposited in the Albertson College Museum of Natural History.

Fecal pellets were collected at Squirrel Valley on 9-17 June 1988 (soon after the pups were weaned) and at Huckleberry on 30 June-8 July 1988 (prior to onset of estivation of males). Huckleberry is at higher elevation and the growing season lags about two weeks behind Squirrel Valley (E. Yensen, unpublished data), but at the time of pellet collection the squirrels' active season at Huckleberry was about one to two weeks more advanced than when pellets were collected at Squirrel Valley. Both squirrel species have similar seasonal activity cycles, emerging from hibernation in late March or early April and reentering seasonal torpor in late July or early August, always within a few days of each other at a site (E. Yensen and P.W. Sherman, unpublished data).

We collected 181 herbarium sheets at Huckleberry and 97 at Squirrel Valley as part of a larger collection of 925 sheets from the general area. These specimens were deposited in the Harold M. Tucker Herbarium at Albertson College. Plant collections at the two sites were made between 28 March-7 August 1987, 26 March-30 July 1988, and 27 April-6 May 1989, and should be reasonably complete inventories of the species at each site.

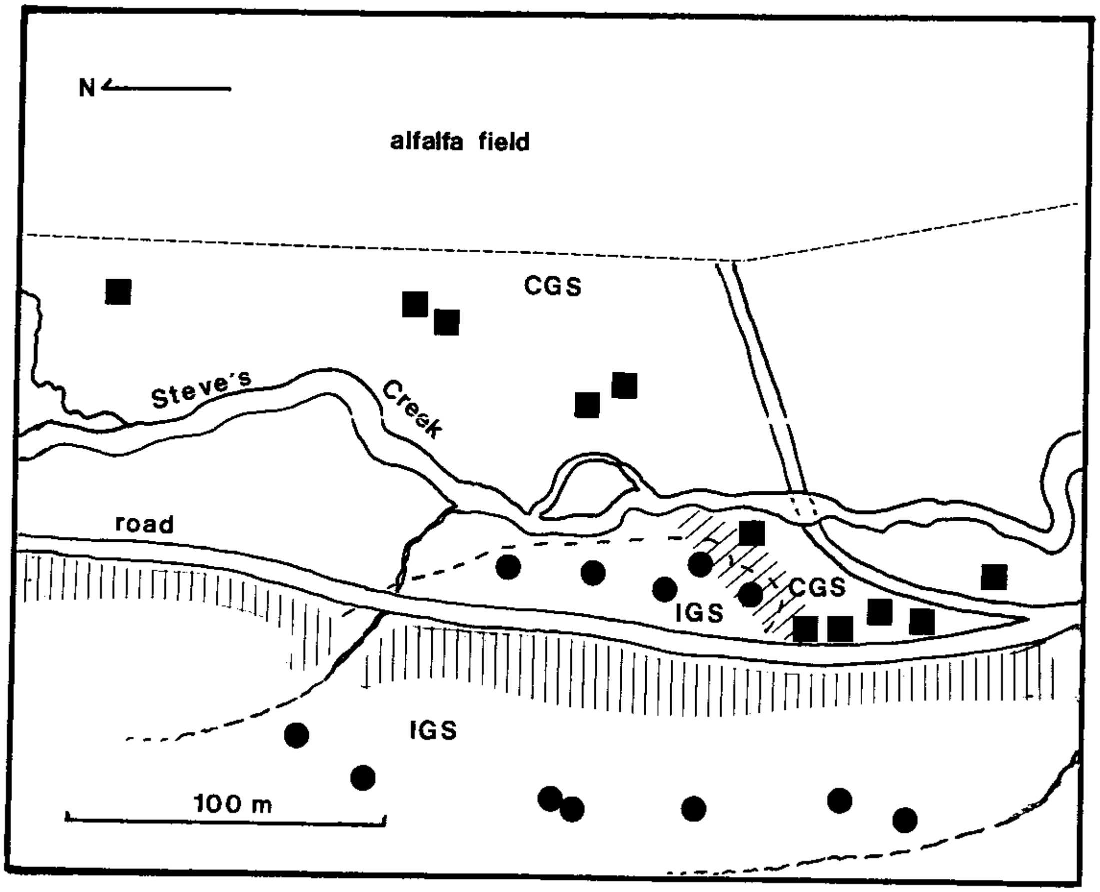

Figure 2. Map of Squirrel Valley study site, Adams Co., west-central Idaho showing capture locations of *Spermophilus brunneus* (circles) and *S. columbianus* (squares) for fecal pellet analysis. Cross hatching indicates an area where both species foraged, although burrow locations were in areas separated by the dashed line; IGS = Idaho ground squirrel area, CGS = Columbian ground squirrel area. Vertical hatching indicates a steep bank up to 8 m tall.

In the laboratory, each group of pellets from a single squirrel was soaked in water 5-15 min to remove salt, diluted with water, and homogenized 1 min in a Waring blender. Following Hansen's (1978) method, the homogenate was washed through a 1 mm sieve and collected below on a 0.1 mm sieve. A portion of the homogenate was placed on each of five microscope slides, cleared with Hertwig's solution, and mounted using Hoyer's medium (Sparks and Malechek 1968).

Plant species in the diet were identified using microhistological characters by comparisons to a collection of reference slides of leaves/stems, flowers, seeds, and roots. These were prepared from mounted, catalogued specimens in the Harold M. Tucker Herbarium at Albertson College using the technique above. The plant specimens used were collected at the study sites or in the general area, and the sheets were so annotated. Botanical taxonomy and nomenclature follows Hitchcock and Cronquist (1973).

Plant fragments in fecal samples were identified and categorized as leaves/stems, flowers, seeds, and roots/bulbs. Frequency of occurrence of food categories was recorded from 20 microscope fields per slide using a phase-contrast microscope at 100X. Five slides were examined per fecal cluster. Frequency of items in 100 fields was then converted to percent relative density (Sparks and Malechek 1968) using a table developed for frequency-to-density conversion (Fracker and Brischle 1944). Accuracy and precision of the technique were calibrated using test slides with known mixtures of plant species found at the sites (Holechek and Gross 1982). Accuracy of identification of slide contents was >99% and precision of frequency of items averaged 90.9% (83-96%, s=4.02) in 35 tests.

After collecting the fecal pellets, vegetation at each site was sampled using a point frame method which measured cover at 36 points in a 0.5 x 1 m area (Floyd and Anderson 1987). Four to six transects were established which crossed each area where foraging squirrels had been captured (hereafter, Idaho ground squirrel area, Columbian ground squirrel area). Point frame sampling was done at 8-11 random intervals on each of the transects.

Dietary preferences were analyzed by comparison of a plant species' rank order of abundance in the diet with its abundance in the vegetation sampling. This was done for all species with >1% importance values in the vegetation analysis. However, we did not use Johnson's (1980) rank preference indices because of the large number of rare dietary categories which could not be reliably ranked.

Dietary and vegetation similarity were quantified using the Bray-Curtis similarity index (C=2w/a+b) with a computer routine provided in Ludwig and Reynolds (1988). SYSTAT 5.0 (Wilkinson 1990) was used for statistical analyses; P<0.05 was accepted as the level of statistical significance.

Results

Vegetation Analysis

We recorded 98 species of vascular plants from Squirrel Valley and 125 species from Huckleberry. Only 38 species occurred at both, a 34.1% similarity in species composition between sites.

At Squirrel Valley, the Columbian ground squirrel area was dominated by grasses (graminoid importance value = 70.4) with 96% total plant cover (Table 1). The Idaho ground squirrel area had fewer grasses (importance value = 56.2) but more forbs (42.1) and high total plant cover (91%). At Huckleberry, the contrast between Idaho and Columbian areas was greater. The Columbian area was again dominated by grasses (62.7) with 97% cover, while the Idaho ground squirrel area had fewer grasses (33.1) and less cover (59%).

At Squirrel Valley, the vegetation of areas occupied by *S. brunneus* and *S. columbianus* were more similar (52%) than at Huckleberry (13%). Correspondingly, the lush meadows used by Columbian ground squirrels at Huckleberry and Squirrel Valley were 37% similar, whereas the Idaho ground squirrel areas at the two sites were only 25% similar. Thus, the mesic areas used by *S. columbianus* were more similar to each other at the two sites than the xeric areas used by *S. brunneus*.

The Columbian ground squirrel areas were floristically less diverse. They had about half as many species in the vegetation analysis as areas occupied by Idaho ground squirrels (25 vs. 52 species for Squirrel Valley and 17 vs. 35 at Huckleberry). Point frame sampling found only one species (*Poa praetensis/compressa*) common to all four areas (Table 1).

Diet Analysis

We analyzed fecal pellets from 49 ground squirrels: 14 *S. brunneus* and 12 *S. columbianus* from Huckleberry and 12 and 11 individuals, respectively, from Squirrel Valley. Four *S. brunneus* and two *S. columbianus* from Huckleberry were sampled from the common foraging area, as were two of each species at Squirrel Valley (Figs. 1 and 2).

There were a minimum of 68 species belonging to 55 genera of plants in the fecal pellets of *S. brunneus* and *S. columbianus* at the two sites. Including the leaves/stems, flowers, seeds, and roots/bulbs of each species as separate categories, and adding insects, fungi, bryophytes, and *Equisetum* sp., we found a total of 141 food categories in the fecal pellets (Table 2; a complete list is available from the authors).

At Squirrel Valley, *S. columbianus* had a more diverse diet (74 categories and 58 plant species in the fecal samples) than *S. brunneus* (55 categories and 45 plant species). Leaves of two bunch grasses, *Poa bulbosa* and *Bromus commutatus/tectorum*, were important for both species, as were Asteraceae seeds, and leaves of lupine and alfalfa (Table 2).

At Huckleberry, each species of squirrel consumed 75 dietary categories, consisting of a minimum of 50 and 52 plant species for *S. brunneus* and *S. columbianus*, respectively (Table 2). Seeds

TABLE 1. Vegetation analysis of areas used by Idaho (IGS) and Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho. Data are importance values from point frame sampling. Species with importance values <1 are not listed, but are included in totals.

	Squirrel Valley		Huckleberry	
Species	IGS	CGS	IGS	CGS
Agropyron cristatum	2.59	—	—	—
Agropyron intermedius	3.78	14.60	—	1.40
Agropyron spicatum	—	1.64	—	—
Agrostis tenuis	—	—	5.51	—
Bromus commutatus	2.92	1.86	2.12	—
Bromus inermis	2.36	10.09	4.82	—
Festuca ovina	3.65	—	—	—
Koeleria nitida	1.12	—	—	—
Phleum pratense	4.64	—	—	—
Poa praetensis/compressa	13.57	27.49	3.66	14.22
Poa bulbosa	8.44	10.63	4.71	—
Poa scabrella	—	—	4.61	—
Poa sp.	3.76	—	—	—
Stipa columbiana	—	3.06	2.80	25.14
Sitanion jubatum	1.12	—	—	—
Carex spp.	—	0.81	—	14.09
Juncus spp.	4.13	—	2.51	7.09
Total Graminoids	56.22	70.39	33.06	62.65
Achillea millefolium	1.80	1.52	6.36	—
Allium tolmiei	—	—	1.83	—
Antennaria spp.	2.17	—	4.72	—
Balsamorhiza sp.	1.97	—	—	—
Cirsium spp.	—	0.92	—	1.58
Clarkia pulchella	1.31	—	—	—
Erigeron pumilus	—	—	—	3.87
Erigeron sp.	2.42	2.07	—	—
Eriogonum heracleoides	—	—	—	6.18
Eriogonum sphaerocephalum	—	—	7.64	—
Eriogonum umbellatum	—	—	4.05	—
Frasera albicaulis	1.11	—	1.26	—
Gayophytum diffusum	—	—	7.31	0.89
Geranium viscosissimum	—	3.84	—	4.58
Lomatium grayi	—	—	9.76	—
Lupinus laxiflorus	2.72	—	—	—
Lupinus leucophyllus	1.43	0.94	—	—
Madia gracilis	—	—	1.44	—
Microseris sp.	1.68	—	—	—
Navarretia intertexta	—	—	1.44	—
Penstemon spp.	—	—	—	2.11
Potentilla glandulosa	0.87	—	1.54	—
Potentilla gracilis	14.26	12.16	0.77	11.95
Potentilla recta	—	—	5.41	2.80
Potentilla sp. seedlings	—	—	3.68	—
Sedum stenopetalum	—	—	1.83	—
Sidalcea oregana	1.11	0.48	3.65	—
Spergularia rubra	—	—	—	2.03
Taraxacum spp.	—	—	—	0.71
Total forbs	42.11	24.85	65.40	37.41
Symphorocarpus oreophilus	—	2.52	0.48	—
Total shrubs	1.73	2.94	0.48	—
Equisetum sp.	—	1.88	—	—
moss	—	—	1.07	—
Total non-vascular	—	1.88	1.07	—
TOTAL	100.06	100.06	100.01	100.06
Total cover (%)	91.23	96.42	59.03	97.05
Total species	52	25	35	17

TABLE 2. Food categories comprising >1% of diet of Idaho ground squirrels (IGS) and/or Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho. Symbols: + = <0.1%, lv = leaves, st = stems, fl = flowers. Because of omitted categories, totals may be higher than sum of amounts shown in table. A complete list of dietary categories is available from the authors.

	Huckleberry (early July)		Squirrel Valley (early June)	
Food Category	IGS	CGS	IGS	CGS
n	14	12	12	11
Agropyron lv	0	0	0	5.6
Bromus commutatus/tectorum lv	0.5	0	7.7	12.3
Bromus sp. fl/seed	1.5	0.9	0	0.3
Danthonia californica fl/seed	1.9	0	0	0
Poa bulbosa fl	1.9	0.9	21.4	19.6
Poa pratensis lv	0	8.0	1.5	4.0
Poa sp. lv	0.6	+	0	1.0
Poa sp. fl	+	0.9	2.8	0.4
Stipa sp. seed	17.4	55.3	0	+
grass fl	2.0	0	0	+
Carex sp. fl/seed	+	2.0	0	0
TOTAL GRAMINOIDS	26.3	68.4	34.7	43.5
Allium sp. lv	+	+	2.3	0
Allium sp. seed	2.0	+	0	0
Calochortus eurycarpus seed	0	0	1.9	0
TOTAL OTHER MONOCOTS	3.1	+	4.2	0
Achillea millefolium lv/fl	0	0	0	1.2
Artemisia arbuscula lv/fl	0	0	0	1.0
Artemisia ludoviciana lv	0	0	0	2.2
Erigeron pumilis lv/st	0	0.6	1.2	0.9
Madia sp. seed	5.9	+	0	0
Microseris nigrescens lv/st	0	0	13.9	0.2
Tragopogon dubius seed	0	0	4.0	+
Asteraceae seed	0.4	0.6	8.7	5.9
Cryptantha sp. lv	0.2	0.1	+	1.3
Cryptantha sp. seed	13.6	0.4	+	0
Plagiobothrys scouleri seed	3.5	0	0	0
Descurainia sp. lv/st	+	+	0.1	1.2
Scrophulariaceae seed 1*	9.1	0	+	0
Polygonaceae? lv	0.5	0.1	0	2.0
Collomia linearis fl/st	0	0	1.0	0
Collomia linearis seed	0.6	1.2	0	0.1
Gilia aggregata seed	3.9	0.3	0	0
Microsteris nutans lv/st	0.2	0	1.8	+
Microsteris nutans seed	2.0	0.8	1.0	1.7
Polemoniaceae seed	1.4	2.8	0	0
Amelanchier alnifolia lv	0.3	1.8	0	0
Potentilla/Fragaria seed	0	1.8	0	+
Viola sp. lv/st	+	1.4	0.2	0.5
Lupinus sp. lv/st	0	5.9	9.3	4.4
Lupinus sp. fl/seed	0	+	+	8.6
Medicago sp. lv/st	0	0	7.3	13.2
Lomatium sp. seed	4.5	0.3	0	0
Silene menziesii lv/st	0	0.2	0	1.4
unk 2 lv	0	0	1.3	0.8
unk 3 root	0	0.4	1.4	0.2
unk 4 root/stem/bulb	11.6	0.1	1.8	+
unk 5 root/stem	0	0	1.5	0
unk 7 seed	2.8	+	+	0
unk 22 dicot tissue	1.2	0	0	0
TOTAL DICOTS	66.2	26.1	56.1	55.7
insects	4.3	5.4	5.1	0.7
TOTAL MISC.	4.4	5.4	5.2	0.7
TOTAL	100.0	100.0	100.0	100.0

**Castelleja* sp., *Orthocarpus* sp., and/or *Penstemon* sp.

of needlegrass (Stipa sp.) were the only food category utilized heavily by both species (Table 2).

The diets of the two species were more similar to each other at the vegetatively more homogeneous Squirrel Valley (52%) than at Huckleberry (30%). *S. brunneus*' diet was only 10% similar between sites whereas *S. columbianus*' diet was 15% similar.

Although both species of ground squirrels at both sites ate a large number of food categories, most were present in small quantities. For example, at Huckleberry, Idaho ground squirrels ate 75 categories of foods, but only 18 comprised >1% of the diet, and only 5 comprised >5% of the diet (Table 2). The patterns for Columbian ground squirrels at Huckleberry and both squirrels at Squirrel Valley were similar, although Idaho ground squirels tended to have more food sources comprising >1% of the diet (18 and 20) than Columbian ground squirrels (10 and 17). Only 44 of the 141 (31%) of the food categories were shared between Squirrel Valley and Huckleberry.

Although the details were different, the two squirrels consumed similar sets of dietary categories at Squirrel Valley in early June. Leaves/stems were most important, followed by flowers and seeds. At Huckleberry in late June-early July, both squirrels also used similar dietary categories, although Idaho ground squirrels ate more seeds, roots/bulbs, and fewer leaves/stems, than Columbian ground squirrels (Table 3).

Within a species at the same site, fecal pellet content varied considerably from squirrel to squirrel. Food categories sampled from individual squirrels varied from 0 to 83% ($\bar{X}$=34.3%) similar. Content of fecal pellets of individual *S. columbianus* was most similar at Huckleberry (60%) and most dissimilar at Squirrel Valley (25.4% similarity), whereas similarity among *S. brunneus* individuals was low at both sites (27.1% similarity at Huckleberry and 34.1% at Squirrel Valley).

Rank order comparisons of ground squirrel diets with plant abundance at each site indicated that although the squirrels fed in small amounts upon many plant species at each site, they were selective feeders. There was no correlation (Spearman $r_s = 0.086$, $P>0.5$) between a plant species' rank in the vegetation analysis and its rank in the diet. Although several plant species were common in the diets, most of these were rare in the habitat, and many were too rare to appear in the vegetation analysis. Of the 44 species in the diets, half (22) had ranks >25 in the vegetation analysis.

TABLE 3. Major patterns of resource utilization (percentage use) by Idaho (IGS) and Columbian ground squirrels (CGS) at two study sites in Adams Co., Idaho.

	Huckleberry (early July)		Squirrel Valley (early June)	
Category	IGS	CGS	IGS	CGS
Leaves/stems	3.4	24.4	47.8	57.9
Flowers	5.4	2.0	24.3	30.1
Seeds	73.6	67.7	18.0	9.6
Roots/bulbs	13.2	0.5	4.7	0.2
Insects	4.3	5.4	5.1	0.7
Non-vascular plants	0.1	0.0	0.1	1.5
TOTAL	100.0	100.0	100.0	100.0

Discussion

Vegetation analysis confirmed what was apparent to the eye: Columbian ground squirrels inhabit areas with more luxuriant vegetation. Either squirrel may be able eat plants in the area occupied by the other species, but the low density of food resources may make it unprofitable for *S. columbianus* to attempt to maximize energy intake (Belovsky and Schmitz 1994) in more xeric areas, leaving those areas open to exploitation by *S. brunneus* with one-third the body mass. In addition, the shallower soils in the xeric areas may not allow enough depth for Columbian ground squirrel burrows. Foraging at a distance from a burrow should increase the risk of predation for a ground squirrel. Thus, the larger Columbian ground squirrels would have higher energetic requirements and should forage more efficiently and safely in more productive habitats.

There was no indication of unique dietary specialization in *S. brunneus* which would suggest reasons for its rarity. Idaho ground squirrels ate 45 and 50 species of plants at the two study sites, and the dietary categories differed more between sites than between ground squirrel species.

Idaho and Columbian ground squirrels appear to select the same types of food resources. Of the 49 food categories that comprised >1% of the diet, 37 (75%) were consumed by both species, despite the differences in plant composition of the areas and limited sample sizes. Further, the dietary similarities within and between species and sites paralleled vegetation similarities, indicating that more similar resources were consumed when they were available.

The dietary differences between species thus appear to be the result of food plant availability in xeric vs. mesic meadows rather than inherent dietary preferences. Small pockets of mesic vegetation in the xeric areas gave Idaho ground squirrels access to nearly all of the species available to Columbian ground squirrels, although the amounts were different. With one exception at Squirrel Valley, xeric areas were no more than 100 m from the burrow of any Columbian ground squirrel captured, so they would thus have access to the resources there.

The growing season was about two weeks later at Huckleberry than Squirrel Valley because of elevation, but sampling at Huckleberry was done three to four weeks after Squirrel Valley. This time difference should not have affected the vegetation analysis, but the xeric areas at Huckleberry were already drying out by late June when green vegetation would have been losing its nutritional value (Murray et al. 1978), but more seeds were available. This may explain the higher proportion of seeds consumed at Huckleberry. Thus, the dietary differences between sites was due partly to season and partly to species composition. Idaho ground squirrels ate more dicot seeds, roots and bulbs whereas *S. columbianus* ate more dicot leaves, grass seeds and flowers, and grass leaves at Huckleberry, but these foods are green longer in wet meadows (E. Yensen, unpubl. data). Lambeth and Hironaka (1982) and Elliott and Flinders (1985) found that Columbian ground squirrel diets varied considerably from one site to another, sometimes with little overlap among sites.

Both species concentrated on a few important species, and also ate a little of a great many species. Given the high degree of individual dietary variation (34% similarity), our sample sizes were too small to determine if the differences among particular squirrels reflected individual dietary preferences, or were simply an artefact of the sampling process. However, like other studies of ground squirrel diets (e.g., Fitch 1948, Hansen and Johnson 1976, Yensen and Quinney 1992), we did not find any sex- or age-related differences in resource utilization patterns.

In summary, we found broad dietary overlap between *S. brunneus* and *S. columbianus* suggesting that the two are competitors for the same food resources. Because of its larger body size, we would expect *S. columbianus* to win any aggressive encounter and thus restrict *S. brunneus* to less productive sites not used by *S. columbianus*. However, many less productive sites lack pockets of deep, well-drained soils (pers. obs.) needed for nest burrows (Yensen, et al. 1991), limiting the number of sites that could be occupied by *S. brunneus*. Thus, dietary overlap with *S. columbianus* suggests that competition could be an important factor in *S. brunneus*' rarity.

Acknowledgements

This project was made possible by grants from the National Geographic Society (#3485-86 to Paul W. Sherman and Eric Yensen), Mr. George C. "Tim" Hixon, the Nongame Program of the Idaho Department of Fish and Game, and Albertson College. All trapping was carried out under scientific collecting permits granted by the Idaho Department of Fish and Game. We thank Scott Estergard and Sandy Launt for field assistance; Marc Luscher for assistance with slide preparation; John Dyer and Tim Hixon (OX Ranch) for access to the Squirrel Valley study site and providing welcome logistical support; and the Council Ranger District, Payette National Forest, for permission to work at the Huckleberry study site; Theresa M. Foppe for helpful discussion of various aspects of the dietary analysis technique; and Donald R. Johnson, Eric A. Rickart, Paul W. Sherman, and Karen Steenhof for helpful comments on an earlier draft of the manuscript. Finally, we owe a special debt to Patricia L. Packard for help with so many plant identifications.

Literature Cited

Belovsky, G. E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70:35-52.

Belovsky, G. E., and O. J. Schmitz. 1994. Plant defenses and optimal foraging by mammalian herbivores. Journal of Mammalogy 75:816-832.

Davis, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho. 400 pp.

Durrant, S. D., and R. M. Hansen. 1954. Distribution patterns and phylogeny of some western ground squirrels. Systematic Zoology 3:82-85.

Elliott, C. L., and J. T. Flinders. 1985. Food habits of the Columbian ground squirrel, *Spermophilus columbianus*, in southcentral Idaho. Canadian Field-Naturalist 99:327-330.

Fitch, H. S. 1948. Ecology of the California ground squirrel on grazing lands. American Midland Naturalist 90:334-340.

Floyd, D. A., and J. E. Anderson. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221-228.

Fracker, S. B., and J. A. Brischle. 1944. Measuring the local distribution of Ribes. Ecology 25:283-303.

Hall, E. R. 1981. Mammals of North America. second edition. John Wiley & Sons, NY. 2 vols., 1181 pp.

Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave. Arizona. Paleobiology 4:302-319.

Hansen, R.M., and M.K. Johnson. 1976. Stomach content weight and food selection by Richardson ground squirrels. Journal of Mammalogy 57:749-751.

Harestad, A. S. 1986. Food habits of Columbian ground squirrels: a comparison of stomach and fecal samples. Murrelet 67:75-78.

Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle and London. 730 pp.

Holechek, J.L., and B. Gross. 1982. Training needed for quantifying simulated diets from fragmented range plants. Journal of Range Management 35:644-647.

Howell, A. H. 1938. Revision of the North American ground squirrels, with a classification of the Sciuridae. North American Fauna 56:1-256.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Lambeth, R., and M. Hironaka. 1982. Columbia [sic] ground squirrel in subalpine forest openings in central Idaho. Journal of Range Management 35:493-497.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. John Wiley & Sons, New York. 337 pp.

Murray, R. B., H. F. Mayland, and P. J. Van Soest. 1978. Growth and nutritional value to cattle of grasses on cheatgrass range in southern Idaho. USDA Forest Service, Research Paper INT-199. 58 pp.

Ritchie, M. E. 1988. Individual variation in the ability of Columbian ground squirrels to select an optimal diet. Evolutionary Ecology 2:232-252.

Ritchie, M. E., and G. E. Belovsky. 1990. Sociality of Columbian ground squirrels in relation to their seasonal energy intake. Oecologia 83:495-503.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21:264-265.

Turner, L. W. 1972. Habitat differences between *Spermophilus beldingi* and *S. columbianus* in Oregon. Journal of Mammalogy 53:914-917.

Wilkinson, L. 1990. SYSTAT, version 5.0. Systat, Inc., Evanston, Illinois.

Wobeser, G. A., and F. A. Leighton. 1979. A simple burrow entrance live trap for ground squirrels. Journal of Wildlife Management 43:571-572.

Yensen, E. 1991. Taxonomy and distribution of the Idaho ground squirrel, *Spermophilus brunneus*. Journal of Mammalogy 72:583-600.

Yensen, E., M. P. Luscher, and S. Boyden. 1991. Structure of burrows used by Idaho ground squirrels, *Spermophilus brunneus*. Northwest Science 65:93-100.

Yensen, E., and D. L. Quinney. 1992. Can Townsend's ground squirrels survive on a diet of exotic annuals? Great Basin Naturalist 52:269-277.

Received 2 March 1995
Accepted 12 January 1996