ECOLOGY OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

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Charles L. Elliott

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Jerran T. Flinders, Committee Chairman

Kimball T. Harper, Committee Member

Hal L. Black, Committee Member

May 12, 1980
Date

Wilford M. Hess, Graduate Coordinator

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DIETARY AND HABITAT RELATIONSHIPS OF THE COLUMBIAN GROUND SQUIRREL IN THE IDAHO PRIMITIVE AREA

ABSTRACT-- The food habits of columbian ground squirrels in the Idaho Primitive Area are identified. The squirrels exhibited a sterotypic generalist dietary strategy, consuming food items with predictable levels of carbohydrates and fats. Habitat preferences were influenced by soil moisture and cover.

Geist (1978), when considering what information is necessary to properly manage wildlife species, pointed out that animal management ultimately must be based on the knowledge of local populations and their behaviors. He particularly noted the need for precise food habit data when referring to an animal's habitat preferences and ecological relationships.

In the Pacific Northwestern region of the United States members of the genus Spermophilus are an important component of the area's ecosystems. One member of this Spermophile group is the columbian ground squirrel (Spermophilus columbianus Ord). Although limited in geographical distribution (Manville, 1959), S. columbianus has been the subject of many ecological and behavioral investigations (Shaw, 1924; Steiner, 1970a, 1970b; Betts, 1974), but little information concerning the squirrels dietary habits and habitat relationships has been reported. This paper presents the results of a two year study of the columbian ground squirrel relative to habitat characteristics and dietary selection.

METHODS

The study was conducted in the Big Creek Ranger District, Idaho Primitive Area. A description of the Big Creek drainage, its geology, vegetation, and topography are described by Hornocker (1970) and Seidensticker et al. (1973). A preliminary examination of the Big Creek region showed two types of habitats were generally occupied by columbian ground squirrels.

Cold Meadows (elev. 2142 m) typified the mountain meadow habitat type utilized by S. columbianus. Meadow vegetation appeared to have developed through normal processes of hydroseral succession with the soil being maintained in a saturated or near saturated condition (Wing, 1969). Vegetation within the meadow exhibited a predominance of sedges with a wide variety of grasses and forbs. Hydromorphic and alluvial soils predominante, but sandy loams occur along the outer meadow edges (Wing, 1969).

Rush Point (elev. 1890 m) represented the Artemisia tridentata-bunchgrass association typical of the southeast-facing slopes occupied by columbian ground squirrels. The perennial dominated plant community occupies soils derived from basalt, granite, sedimentary deposits and metamorphosed variations of these materials (Mueggler and Harris, 1969).

Each study area was visited according to a monthly schedule; Cold Meadows 12-19 June, 17-24 July, and 14-21 August; Rush Point 1-8 June, 1-8 July, and 1-8 August, 1977 and 1978. Field work prior to 12 June at Cold Meadows was impractical because of bad weather and the inaccessibility of the area to aircraft.

A 90 m X 90 m grid with 36 trapping stations 15 m apart was established at each study site. One live trap (15 X 15 X 48 cm) was placed at each trapping station. Captured squirrels were classified by age (adult, young of the year=juvenile) and marked using the toe clipping sequence of Melchior and Iwen (1965). Population size was determined using the Jolly (1965) mark-recapture method.

Plant biomass was determined monthly at each site using the calibrated weight-estimate method (Tadmor et al., 1975). Using the northern boundary of the trap grid, north-south vegetation sampling transects were established. The starting location of each transect was determined by multiplying the boundary length (90 m) by a two digit random number. The random number was regarded as a percent. The resulting product designated a distance from the northwest corner of the trap grid, the endpoint of which served as a starting point for one sampling transect. Preliminary sampling in 1976 determined that ten transects at Cold Meadows and 14 transects at Rush Point were required to be 95% certain the vegetation sample mean was within 20% of the true mean for the single most abundant plant species at each site (Subcommittee on Range Research Methods of the Agricultural Board, 1962:230). A 50 X 50 cm sampling frame was placed every 9 m along a transect line, this size plot was used to reduce the "edge effect" encountered when sampling in tall vegetation (Tadmor et al., 1975).

After every ten vegetation plots, samples of each plant species that had occurred in amounts of one gram or more per plot were estimated by weight, clipped, weighed to the nearest gram in the field, stored, and returned to the laboratory. Here they were oven dried at 64°C for 72 hrs, weighed to the nearest gram and moisture content calculated. The individual plant samples were then combined, by species, for each month and analyzed for percent: fiber, protein, phosphorus (P), and calcium (Ca). A combined percent for crude fat and nitrogen free extract (NFE) was obtained by subtracting the sum of the experimentally determined nutrient categories from 100%.

Ground squirrels for use in diet determination were collected at each site (from locations outside the trap grid) using live traps in 1977 and a small caliber rifle in 1978. The collecting method change was necessary because of the reluctance of columbian ground squirrels to enter traps in August. Stomach contents were analyzed using the microtechnique procedure described in Flinders and Hansen (1972). One alteration was made in the procedure, stomach content slides were prepared using Naphrax high resolution diatom mounting medium (Northern Biological Supply, Martlesham Heath, Ipswich, England) instead of Hertwig's and Hoyer's solution. Indices of dietary similarity were calculated using Sorensen's similarity index (Sorensen, 1948). Indices of dietary preference were calculated using the procedure described by Hansen and Ueckert (1970).

Mean litter size was determined by examining female reproductive tracts and counting placental scars. Examination of placental scars during necropsy is an established technique for determining reproductive characteristics of mammals (Layne and McKeon, 1956; Henry and Bookhout, 1969; Martin et al., 1976).

The scientific nomenclature of plants follows Hitchcock and Cronquist (1973); mammals, Burt and Grossenheider (1976); birds, Peterson (1969).

RESULTS AND DISCUSSION

A total of 296 columbian ground squirrels were collected for dietary analysis. Similarity indices were calculated to compare the monthly diets, between years, for each sex and age class (Table 1). The resulting percents for each location indicated a high degree of dietary overlap between the two years. The dietary data were therefore pooled and a combined monthly diet determined (Tables 2 and 3).

The nutrient analyses for those plant samples having the greatest frequency of occurrence at each study site exhibited certain seasonal trends (Tables 4 and 5). Plant moisture content, crude protein, and phosphorus tended to decline as the season progressed while crude fiber, combined NFE-crude fat, and calcium increased with time. The calcium:phosphorus ratio increased in most plants as the season progressed.

The botantical communities of the two study sites were compared using Jaccard's community coefficient (Jaccard, 1912). The resulting index value of 22% indicated each site was a distinct vegetation community exhibiting little similarity in plant composition.

Mean monthly precipitation for 1977 and 1978 was not significantly different (unpaired t-test, $P>0.05$), but mean monthly temperatures were found to be significantly greater (unpaired t-test, $P<0.05$) in July, 1978, and August, 1977, for each study area.

Biomass production was not significantly different (unpaired t-test, $P>0.05$) between years for each study site (Table 6). The sex ratio for each colony (incorporating live trapped and shot squirrels) did not greatly differ from 1:1 (Table 6). Litter size did not differ statistically (unpaired t-test, $P>0.05$) between years (Table 6). Monthly population size between 1977 and 1978 was not significantly different (Chi square, $P>0.05$) for Cold Meadows or Rush Point (Table 7).

When using data gathered during different years to determine an animals food habits one question becomes of paramount importance; were the different years ecologically equivalent. If they were the dietary results can be assumed to represent the "typical" food habits of the animal in question. But if the time periods differ ecologically the food consumed in one season may be "atypical" and the determined diet misleading.

To determine if the sampling periods for each site in this study were similar, a number of parameters were measured. The monthly population size did not differ greatly between seasons indicating no apparent population fluxuations. The sex ratio of adults and juveniles remained 1:1 (Table 6). Verme (1967, 1969) reported undernourished white-tailed deer (Odocoileus virginianus) would conceive fawns that were predominantly males; but does receiving adequate prebreeding rations produced offspring of a nearly even sex ratio. The presence of a juvenile sex ratio of 1:1 for both years and a near constant litter size (Table 6), when intrepreted in light of Verme's findings, would indicate the two ground squirrel populations examined were not under nutritional stress. The consistency in the amount of biomass produced (Table 6) indicates the study sites did not vary dramatically in their productivity between seasons.

A count of columbian ground squirrel predators observed at each study site was made to provide a relative index of predatory pressure (Table 8). The assumption was made that a colony under heavy predator pressure one season and less pressure the next season may reflect the differential predator influence in their diet. Heavy predator pressure may cause the animal to make quick, abbreviated foraging trips, feeding as rapidly as possible to decrease the amount of time it would be exposed above ground. Conversely, light predator pressure would allow for more protracted feeding bouts and the opportunity to be selective (if that were the animals optimum feeding strategy). The relative predator pressure at each study site did not appear to vary significantly between years, implying a constant predator pressure.

The consistency exhibited by the population size, sex ratios, litter size, biomass, precipitation, and predator pressure when compared between years indicate the sampling periods were ecologically equivalent. The food habit data reported for each habitat type may thus be interpreted as representing a "typical" columbian ground squirrel diet.

Preference indices were calculated for each plant species occurring in the diet. No species exhibited a preference value greater than one. This lack of preference for any particular plant species characterizes the columbian ground squirrel as a generalist, an organism that utilizes several categories (in this case plant species) with considerable frequency (Morse, 1971). Schoener (1971) considered when the dietary generalist strategy is optimal and concluded "an animal can be said to be more generalized than a second if it is omnivorous, eating both animal and plant food...". Columbian ground squirrels are known to utilize animal matter (Betts, 1974; Elliott, 1978) in addition to vegetation. Furthermore, the types of habitat occupied by columbian ground squirrels in the Idaho Primitive Area indicate the generalist strategy would be expected. The ultimate pressures producing the specialist or generalist strategies have been considered in terms of what MacArthur and Levins (1964) referred to as "grain".

If an organism remains within a relatively homogeneous setting (a grain), it is said to occupy a coarse-grained environment; if it does not, then it occupies a fine-grained environment. All else being equal, the organism in a coarse-grained environment should attain a higher level of specialization than the one in a fine-grained setting. Therefore specialists should characterize coarse-grained environments and generalists fine-grained environments (Morse, 1971). Cold Meadows and Rush Point can best be described as fine-grained environments.

The dietary strategy of the columbian ground squirrel may be further delineated when considered in terms of sterotypy or plasticity. Stereotypy is the tendency to perform an act with high predictability; plasticity may be considered the opposite (Morse, 1971). Generalists may be either stereotyped or plastic. In the former case an individual would continually utilize a broad set of items with great predictability; in the latter the individual would utilize a wide variety of items with little long-term predictability (Morse, 1971). When the plant species that constitute a minimum 60% of each monthly diet (Tables 2 and 3) are multiplied by the monthly mean nutrient values (Tables 4 and 5) for those particular items, the nutritional plane of the diets can be determined. The category that remains predictable throughout the season is NFE-crude fat. The monthly means remain near constant levels for both adults and juveniles (Cold Meadows 34-40%, Rush Point 35-44%). The use of a number of food items that are predictable in their combined NFE-crude fat level indicate the dietary strategy of the columbian ground squirrel may be best described as that of a sterotypic generalist.

Columbian ground squirrels are hibernators, depending on the fat accumulated during the summer to sustain them while inactive. The inability to acquire sufficient fat stores before hibernating has been postulated to be a cause of over-winter mortality (Shaw, 1926). The optimal foraging theory assumes that the fitness associated with an animals foraging behavior has been maximized by natural selection (Pyke et al., 1977). One of the basic arguments of the theory is that behavior in general, and foraging behavior in particular, shows heritable variation; and this entails variation in the contribution to subsequent generations. Comparison of the seasonal diets of adult columbian ground squirrels versus juveniles indicates a significant degree of dietary similarity (Cold Meadows 66%, Rush Point 70%).

The argument may then be made that the sterotypic generalist strategy exhibited by the columbian ground squirrels in the Idaho Primitive Area is the optimum foraging strategy for those colonies. The selection of a number of food items that are predictable in carbohydrate-fat levels will enhance the over-winter survival chances, and directly the "fitness" of those individuals who practice the sterotypic generalist method. The strategy is perpetuated through the juveniles, those young squirrels that maximize the foraging process will acquire sufficient fat to over winter and take part in the immediate post-emergence breeding.

Wing (1969) defined three cover types for the Cold Meadows area. He classified the types according to soil moisture. Those areas exhibiting the highest moisture levels were designated as wet cover type, the driest areas were dry cover type and those areas intermediate were moist cover type. Using Wing's classification the three cover types were tested to determine if the vegetational composition of each type was different. The total production (in grams) for each species in each cover type was calculated. The cover types were statistically compared using the Mann-Whitney Wilcoxon test (Gibbons, 1976:159). The dry cover type did not differ significantly ($P>0.05$) from the moist type. The wet cover type was found to differ significantly ($P<0.05$) from both the dry and moist types. The number of ground squirrel burrow entrances in each cover type were counted (Table 9) to obtain an index of cover type use. Columbian ground squirrels at Cold Meadows exhibited a distinct habitat preference for the dry cover type and avoided the wet type. The wet cover type was dominanted by Carex aquatilis a plant used minimally by the squirrels as food (Table 2).

At Rush Point the soil moisture was constant throughout the study area (30% water holding capacity), but the amount of vegetative cover was not. Cover was determined by sampling 12 points (7.5 m apart) along each live-trap transect (N=72 plots). Using the vegetation sampling plot, the amount of aerial coverage was estimated and a cover map constructed. Ground squirrel burrow entrances were counted and plotted on the cover map. Columbian ground squirrels at Rush Point preferred those habitats that offered the greatest amount of cover (Table 9).

Habitat preferences of columbian ground squirrels in the Idaho Primitive Area varied. Squirrels at Cold Meadows were influenced by soil moisture, the wetter areas provided poor conditions for burrowing and offered less attractive food items. Squirrels at Rush Point were influenced by the amount of cover available. Placing burrows under the plant canopy would conceal the animals from predators and provide shade. The lack of readily available water at Rush Point (as opposed to Cold Meadows) would make bodily water loss and thermoregulation difficult problems. Prolonged exposure to high temperatures is deadly to columbian ground squirrels (Shaw, 1945), therefore it is probable that temperature regulation is the factor that dictates habitat use for ground squirrels at Rush Point.

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TABLE 1. Percent dietary similarity between 1977 and 1978 monthly diets for each sex and age class of columbian ground squirrels collected at Rush Point and Cold Meadows, Idaho Primitive Area.

	RUSH POINT			COLD MEADOWS		
Sex & Age class	June	July	August	June	July	August
Adult Males	78	62	88	56	65	62
Adult Females	67	77	66	65	68	65
Juvenile Males		58	68		65	67
Juvenile Females		68	64		51	60

TABLE 2. Mean percent dry weight of plants comprising at least 1% of the 1977 and 1978 combined monthly diets of columbian ground squirrels collected at Cold Meadows, Idaho Primitive Area.

	June		July				August			
	Adults		Adults		Juveniles		Adults		Juveniles	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Species	(23)[a]	(27)	(19)	(25)	(7)	(8)	(6)	(9)	(12)	(10)
				FORBS						
Achillea millefolium	11	25	14	20	19		25	65	40	41
Antennaria microphylla								2	4	5
Castilleja rusickii		2								
Dodecatheon pauciflorum			1							
Erigeron speciosus	13	7	7	9	36	51	6	14	32	23
Eriogonum umbellatum	1			5						
Fragaria virginiana				1			1			
Penstemon spp.[b]	1		3							
Polygonum bistortoides							1			
Potentilla gracilis		3		2						
Ranunculus alismaefolius	2	6	9	4						
Senecio serra	1	1	1	1						1
Taraxacum officinale	8	5	13	6		3	2			
Trifolium longipes	46	38	19	29	35	33		5		2
Valeriana officinalis			1				6			
			GRASSES & GRASS-LIKE							
Agropyron caninum				2						
Carex aquatilis	-	3	2	1	3		2	3	12	1
Danthonia intermedia	1					5	2	3		
Deschampsia caespitosa										5
Festuca idahoensis								3		
Phleum alpinum	9	8	31	16	6	4	42	7	6	21
Trisetum spicatum	6	1		6		4	12		5	
			SHRUBS & TREES							
Pinus contorta		1								
Vaccinium caespitosum							3			

a: total number of stomachs examined.

b: includes Penstemon procerus and P. rydbergii.

Note. Due to trace amounts and plant particles identified as unknowns, the columns will not total 100%.

TABLE 3. Mean percent dry weight of plants comprising at least 1% of the 1977 and 1978 combined monthly diets of columbian ground squirrels collected at Rush Point, Idaho Primitive Area.

	June		July				August			
	Adults		Adults		Juveniles		Adults		Juveniles	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Species	(11)	(27)	(22)	(22)	(15)	(16)	(8)	(8)	(12)	(10)
			FORBS							
Achillea millefolium	20	16	4	4			16	7	5	5
Balsamorhiza saggittata	59	56	38	54	30	33	31	39	40	21
Descurainia richardsonii		2	2	1	2		7			3
Erigeron speciosus				1	1			3		
Frasera montana						1				
Galium triflorum		1	1							
Hieracium albertinum	3	5	3	1	1	4	4			
Hydrophyllum capitatum		1								
Lithospermum ruderale		1	4	4	1	9	1			
Lomatium ambiguum										1
Lupinus sericeus	2	9	19	9	11	13	12	24	36	22
Machaeranthera canescens				1	1		5	4	1	5
Potentilla glandulosa		1			8	1		8	2	
Senecio integerrimus		3	2	1	1	1				
Smilacina racemosa		1								
Stellaria nitens						1	1			1
Trifolium repens		1								
			GRASSES & GRASS-LIKE							
Agropyron spicatum	2	2	13	20	38	4	13	8	9	29
Bromus marginatus			2							
Bromus tectorum			1	1		6				
Danthonia intermedia		1								
Festuca idahoensis		4	8	1	4	2	7	4	6	
Festuca ovina			1	1						
Koeleria cristata	1	1		2						
Poa sandbergii		3								
			SHRUBS & TREES							
Artemisia tridentata		2	3					1		
Berberis repens			1							
Physocarpus malvaceus	4		2			1	2	1	1	7
Purshia tridentata					3	5	1		1	7

a: total number of stomachs examined.

Note. Due to trace amounts and plant particles identified as unknowns, the columns will not total 100%.

TABLE 4. Monthly mean percent nutrient and moisture levels of plant species exhibiting the highest frequency of occurrence at Cold Meadows, Idaho Primitive Area, 1977 and 1978.

Species	Fiber	Protein	P	Ca	NFE-Fat	Moisture
			JUNE			
Achillea millefolium	22	20	0.19	0.52	57	78
Agropyron caninum	25	9	0.06	0.14	66	61
Carex aquatilis	28	15	0.12	0.26	57	54
Erigeron speciosus	18	19	0.16	0.56	62	75
Festuca idahoensis	28	15	0.09	0.25	55	60
Fragaria virginiana	17	16	0.10	0.68	66	72
Penstemon spp.	26	15	0.15	0.57	59	72
Phleum alpinum	28	17	0.08	0.18	55	64
Potentilla gracilis	19	20	0.18	0.65	61	75
Senecio serra	22	14	0.15	0.62	63	78
Trifolium longipes	15	27	0.44	1.70	56	70
			JULY			
Achillea millefolium	24	17	0.20	0.90	58	64
Agropyron caninum	33	11	0.07	0.14	56	59
Carex aquatilis	29	13	0.12	0.33	58	55
Erigeron speciosus	20	16	0.16	0.65	63	69
Festuca idahoensis	36	13	0.07	0.19	52	59
Fragaria virginiana	28	13	0.18	0.85	59	66
Penstemon spp.	33	9	0.13	0.58	58	68
Phleum alpinum	34	9	0.07	0.17	57	54
Potentilla gracilis	17	16	0.18	0.69	66	65
Senecio serra	29	10	0.19	0.78	61	75
Trifolium longipes	20	22	0.40	1.70	56	55
			AUGUST			
Achillea millefolium	25	14	0.20	1.05	60	58
Agropyron caninum	35	8	0.04	0.14	57	50
Carex aquatilis	30	10	0.12	0.32	59	30
Erigeron speciosus	24	13	0.20	1.03	63	58
Festuca idahoensis	37	10	0.07	0.20	53	31
Fragaria virginiana	16	12	0.18	0.83	71	52
Penstemon spp.[a]	31	10	0.14	0.92	58	47
Phleum alpinum	34	7	0.09	0.20	59	27
Potentilla gracilis	19	12	0.19	1.07	69	58
Senecio serra	30	8	0.21	0.91	62	50
Trifolium longipes	27	14	0.34	1.05	57	35

Note. Due to rounding the nutrient categories may not equal 100%.

a: Includes *Penstemon procerus* and *P. rydbergii*.

TABLE 5. Monthly mean percent nutrient and moisture levels of plant species exhibiting the highest frequency of occurrence at Rush Point, Idaho Primitive Area, 1977 and 1978.

Species	Fiber	Protein	P	Ca	NFE-Fat	Moisture
			JUNE			
Achillea millefolium	29	16	0.25	0.96	54	70
Agropyron spicatum	36	15	0.11	1.15	48	61
Balsamorhiza saggitata	29	20	0.26	2.45	49	31
Eriogonum umbellatum	27	15	0.22	0.79	57	66
Festuca idahoensis	35	13	0.12	0.36	52	61
Frasera montana	22	17	0.15	0.42	61	78
Hieracium albertinum	25	18	0.22	0.45	56	77
Koeleria cristata	38	11	0.08	0.12	49	57
Lithospermum ruderale	34	19	0.19	1.71	46	73
Lupinus sericeus	24	19	0.35	1.58	55	74
Purshia tridentata	41	15	0.09	0.63	43	55
			JULY			
Achillea millefolium	30	14	0.23	0.76	55	60
Agropyron spicatum	38	12	0.09	0.51	52	41
Eriogonum umbellatum	27	13	0.15	1.66	58	56
Festuca idahoensis	32	13	0.18	0.21	55	43
Frasera montana	27	13	0.17	1.11	58	60
Hieracium albertinum	27	11	0.20	1.08	60	63
Koeleria cristata	40	9	0.06	0.20	51	38
Lithospermum ruderale	30	14	0.25	1.95	55	57
Lupinus sericeus	26	17	0.21	1.09	55	62
Purshia tridentata	32	14	0.10	0.93	53	49
			AUGUST			
Achillea millefolium	31	12	0.20	1.13	56	53
Agropyron spicatum	36	7	0.06	0.41	56	36
Balsamorhiza saggittata	29	10	0.19	1.48	59	52
Eriogonum umbellatum	31	8	0.15	0.87	60	43
Festuca idahoensis	34	12	0.16	0.48	53	42
Frasera montana	28	8	0.10	0.36	64	38
Hieracium albertinum	32	8	0.13	1.10	58	57
Koeleria cristata	47	3	0.06	0.17	50	8
Lithospermum ruderale	30	9	0.16	2.03	58	49
Lupinus sericeus	35	8	0.12	0.97	55	59
Purshia tridentata	34	11	0.11	0.78	55	47

Note. Due to rounding the nutrient categories may not equal 100%.

TABLE 6. Mean litter size and sex ratio (male:female) of columbian ground squirrels and biomass (kg/ha) for Cold Meadows and Rush Point, Idaho Primitive Area, 1977 and 1978.

	COLD MEADOWS		RUSH POINT	
Item	1977	1978	1977	1978
Litter size	3.60	4.00	3.25	3.17
Sex ratio				
Adults	1:1.3	1:1	1:1.2	1:1.1
Juveniles	1.4:1	1:1.3	1:1.5	1.4:1
Biomass	1919	1822	1195	1086

TABLE 7. Monthly population size for columbian ground squirrels at Cold Meadows and Rush Point, Idaho Primitive Area, 1977 and 1978.

	COLD MEADOWS			RUSH POINT		
Year	June	July	August	June	July	August
1977	35	72	24	26	42	20
1978	32	69	22	28	39	21

TABLE 8. Columbian ground squirrel predators observed at Cold Meadows and Rush Point, Idaho Primitive Area, 1977 and 1978.

RUSH POINT

Species	1977 June	1977 July	1977 August	1978 June	1978 July	1978 August
Aquila chrysaetos (Golden Eagle)	2	3	2	2	2	2
Buteo jamaicensis (Red-tailed Hawk)	1			1	2	1
Canis latrans (Coyote)	1	2	2	1	3	2
Mustela frenata (Long-tail Weasel)		1				
Taxidea taxus (Badger)			1			
Ursus americanus (Black Bear)	2	1	1	2	2	1

COLD MEADOWS

Species	1977 June	1977 July	1977 August	1978 June	1978 July	1978 August
Buteo jamaicensis	2	4	2	2	3	2
Canis latrans	1	1	1	1	1	1
Circus cyaneus (Marsh Hawk)	1	1		1	1	
Taxidea taxus	1	1	1	2	2	1

TABLE 9. Columbian ground squirrel burrow placement in relation to habitat parameters in Cold Meadows and Rush Point, Idaho Primitive Area.

COLD MEADOWS

Cover type	Burrows counted	Percent of study sites per cover type	Percent burrows per cover type	Expected number of burrows per cover type
Dry	116	50	80	72.5
Moist	29	17	20	24.7
Wet	0	33	0	47.9
				Chi square= 74.74

RUSH POINT

Cover category (%)	Burrows counted	Percent of study site per cover category	Percent burrows per cover category	Expected number of burrows per cover category
0-25	3	20	5	11.2
25-50	10	60	18	33.6
50-75	12	10	22	5.6
75-100	31	10	55	5.6
				Chi square= 145.08

SEASONAL ACTIVITY PATTERNS OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

ABSTRACT-- Data are presented on the seasonal activity pattern of a population of columbian ground squirrels (*Spermophilus columbianus*) in the Idaho Primitive Area. Adult females were significantly more active in June of all years than were adult males. A relationship between activity and temperature is postulated in which squirrels alter their activity to avoid high temperatures and possible heat stress.

Members of the genus Spermophilus are typically characterized by a short period of summer activity and a long period of hibernation. During the period of surface activity ground squirrels must establish territories, breed, reproduce and gain sufficient weight to survive the winter. The annual cycle of activity for various species of ground squirrels has been reported (Skryja and Clark, 1970; Michener, 1974; Loehr and Risser, 1977), but data are limited for columbian ground squirrels.

METHODS

The study was conducted at Cold Meadows, an 87 ha meadow (elev. 2010 m) located in the northeastern portion of the Big Creek Ranger District, Idaho Primitive Area. A description of the Big Creek area has been documented (Wing, 1969; Hornocker, 1970; Seidensticker et al., 1973). Ground squirrels were trapped from 12-19 June, 17-24 July and 14-21 August, 1976-1978. Field work prior to 12 June was impractical because of bad weather and the inaccessibility of the study area to aircraft. A 90 m X 90 m grid with 36 trapping stations 15 m apart was established on the central portion of the meadow. One live trap (15 X 15 X 48 cm) was placed at each trapping station. Traps were baited with carrot and checked every hour. Captured squirrels were marked using the toe clipping sequence of Melchior and Iwen (1965), sexed, measured, weighed, time of capture recorded and released back onto the grid. Vegetation was collected using the procedure of Tadmor et al. (1975). All plant samples were weighed to the nearest gram in the field and then taken back to the laboratory where they were oven dried at 64°C for 72 hrs. The specimens were then weighed to the nearest gram and percent moisture content calculated. Daily ambient temperatures were obtained using a Taylor Maximum-Minimum thermometer.

Ground squirrel activity in this study was equated with the animals presence in the traps. Bias due to "trap-shy" or "trap-happy" squirrels may be present but an alternative visual census proved progressively unreliable as the height of vegetation increased.

RESULTS AND DISCUSSION

Adult female squirrels were significantly more active in June of each year than were adult males (Table 1) (Kolmogorov-Smirnov Two Sample Test, $P < 0.05$). Activity for July and August was not significantly different between sexes of adult and juvenile columbian ground squirrels.

Male columbian ground squirrels are territorial during the breeding season (Steiner, 1970a), exhibiting aggression toward other males and occasionally "raiding" the colonies of adjacent males (Steiner, 1970a, 1970b, 1971, 1972). These observations of aggressive behavior and Lambeth's (1977) findings that columbian ground squirrels utilize an arena of activity between 21 and 40 m in size may account for the greater number of females captured in June, dominant males would have been excluding other male squirrels from the trapping grid.

The entry sequence into hibernation described by Manville (1959) and Michener (1977) for S. columbianus (adult males disappear first, then adult females) was not displayed by the Cold Meadows colony. This disparity may be artificial because adult ground squirrels during August became very lethargic and inactive and were extremely difficult to trap.

Shaw (1925) suggested early spring activities of columbian ground squirrels are largely controlled by temperature alone, whereas hibernation is induced by the drying of the vegetation. Howell (1938) wrote "the date of beginning estivation was determined chiefly by the ripening of the vegetation and consequent reduction of the moisture content in their (ground squirrels) food, and in part also by the accumulation of fat in the body". Nansel and Knoche (1972) observed columbian ground squirrels and postulated that hibernation was a response to drought prior to a decrease in temperature. The moisture content of plants at Cold Meadows declined as the season progressed (Table 2) as did above ground activity of ground squirrels (Table 1).

Changes in diurnal temperature appear to determine the peak period of daily activity. The mean maximum daily temperature for June 1976 (Table 3) was significantly greater (unpaired t-test, $P < 0.05$) than June 1977 or June 1978. The maximum percent of activity for June 1976 occurred later in the day than for June 1977 or June 1978 (Table 4). This same shift in activity in relation to significantly greater maximum temperatures was also evident for July 1978. Mean daily maximum temperature in August 1977 was significantly greater (unpaired t-test, $P < 0.05$) than August 1976 or August 1978, yet the expected shift in peak activity did not occur. The smaller sample of activity in August 1977 may have influenced the conclusion.

The relationship of temperature to activity of columbian ground squirrels indicates the higher the average daily maximum temperature, the earlier or later in the day peak period of activity will occur. If this hypothesis is valid then during those sampling periods when the average maximum temperatures were not significantly different the timing of peak activity should be similar. This relationship was observed for June 1977 and June 1978, as well as for July 1976 and July 1977 (Table 4).

Shaw (1945) noted that columbian ground squirrel activity in the agricultural region around Pullman, Washington, seemed to be controlled largely by climatic conditions, especially those relating to sunlight, lack of moisture and temperature. He observed that a change in late summer, from a high to a low temperature, resulted in an increase in squirrel activity. Betts (1976) observed a colony of S. columbianus in western Montana and reported that with the increase in daily diurnal temperatures during lactation and post-lactation periods there was an increase in morning and late afternoon activity and a decrease in mid-day activity. He postulated that temperature or solar radiation limited the amount of consecutive time columbian ground squirrels could spend above ground.

The observations of Betts (1976) and Shaw (1945) and data reported here indicate the scheduling of surface activity for the columbian ground squirrel is an apparent behavioral response designed to escape heat induced stress.

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TABLE 1. Live trapping results for columbian ground squirrels reported by age and sex for Cold Meadows, Idaho Primitive Area, 1976-1978.

	June		July				August			
	Adult		Adult		Juvenile		Adult		Juvenile	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1976	12	25	15	32	15	13	5	5	13	5
1977	15	39	7	12	11	8	3	2	2	4
1978	24	32	18	13	6	7	2	6	7	6

TABLE 2. Mean (±SD) percent moisture content of plant species having the highest frequency of occurrence at Cold Meadows, Idaho Primitive Area.

	1976		1977			1978		
Species[1]	July	August	June	July	August	June	July	August
Achillea millefolium	66±1	72±4	72±1	72±5	58±1	82±3	77±2	60±4
Carex aquatilis	65±5	63±6	61±7	51±4	30±1	67±2	58±3	45±5
Fragaria virginiana	67±8	66±2	65±8	65±7	52±1	76±1	67±2	55±1
Penstemon procerus	68±6	65±2	72±3	66±5	47±1	73±1	69±2	63±2
Phleum alpinum	63±5	57±7	57±1	49±8	27±1	72±2	59±4	30±1

1: n=10 samples/species/month

TABLE 3. Monthly mean (±SD) maximum daily temperatures at Cold Meadows, Idaho Primitive Area.

	1976	1977	1978
June 12-19	22±2	20±2	20±2
July 17-24	22±1	22±1	24±1
August 14-21	17±2	25±1	17±2

TABLE 4. Peak times of activity for adult columbian ground squirrels at Cold Meadows, Idaho Primitive Area.

	1976	1977	1978
June 12-19	1700-1800 hrs	1400-1500	1400-1500
July 17-24	1300-1400	1200-1300	1000-1100
August 14-21	1600-1700	1200-1300	1300-1400

SEASONAL HOME RANGE OF A COLONY OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

ABSTRACT-- Mean seasonal home range for a colony of columbian ground squirrels in the Idaho Primitive Area was 1532 square meters. Density was 13 adult squirrels per hectare.

The columbian ground squirrel (Spermophilus columbianus) is an endemic sciurid in the northwestern mountain states (Manville, 1959). Although much is known regarding its behavior (Betts, 1976) and life history (Steiner, 1970a, 1970b) little has been published concerning its home range requirement.

The concept of home range has been criticized by Hayne (1949) who noted it is important to recognize that when trapping data are interpreted in terms of home range, the assumption is implicit, but not always valid, that the animal will be trapped over all of the "ecologically significant" area of its home range. In a discussion concerning the activity of the California ground squirrel (Spermophilus beecheyi), Linsdale (1946) criticized the interpretation of activity in terms of area. He noted the activities of an animal are seldom within a two-dimensional space, yet we calculate the animals activity on a single plane in order to assess its movements. He further stated that a boundary drawn upon a map detailing activity sites is our own abstraction and of no meaning to the animal itself. Stickel (1954) cautioned that boundaries of a home range must be considered diffuse and general rather than sharply or definitely outlined. It is therefore necessary to interpret home range data cautiously, bearing in mind the many criticisms concerning the concept of home range. Home range is often considered to represent the living area of an animal; its size being related to the animals living requirements (Stickel, 1954). Home range data are often essential for population estimations, it was for this reason the data reported here were collected.

METHODS

The study was conducted at Cold Meadows, an 87 ha meadow (elev. 2010 m) located in the northeastern portion of the Big Creek Ranger District, Idaho Primitive Area. A description of the Big Creek area has appeared elsewhere (Wing. 1969; Hornocker, 1970). Ground squirrels were trapped for three summers, from 12-19 June, 17-24 July, and 14-21 August, 1976-1978. Data reported here concern the 1977 and 1978 field seasons. A 90 m X 90 m grid with 36 trapping stations 15 m apart was established on the central portion of the meadow. One live trap (15 X 15 X 48 cm) was placed at each trapping station. Traps were baited with carrot and checked every hour. Captured squirrels were marked using the toe clipping sequence of Melchior and Iwen (1965). Each recaptured squirrel was identified and the trap location plotted to determine individual seasonal home range. The term "seasonal" home range is used because adult male columbian ground squirrels are known to be territorial during the breeding season (Murie and Harris, 1978) but the data reported here represent trapping results for the entire summer period (pre- and post-breeding time).

RESULTS AND DISCUSSION

Analysis of the trapping data showed three adult squirrels had been captured five times or more each summer. Following Hayne's (1949) method the "center of activity" was determined for the three repetitively captured squirrels. The centers of activity were found to coincide for each squirrel for both seasons. The center of activity is equivalent to the geographic center of all points of capture (Hayne, 1949). It was assumed that if the centers of activity remained constant for each year the data gathered would reflect the mean seasonal home range.

A problem in utilizing home range data reported in the literature is the variation in techniques used for determining home range. These differences in methodology make it difficult to compare data obtained from other geographic locations (Mohr, 1947). Table 1 lists the mean estimations of home range determined for individual columbian ground squirrels at Cold Meadows. Home ranges were determined using the methods indicated (Table 1), calculation procedures for each method are described in Hayne (1949) and Stickel (1954). Means obtained for each technique were compared between individual squirrels using unpaired t-tests (P=0.01). No significance differences were noted, suggesting that the mean home range reported for a particular home range determination method is the same for both sexes.

Stickel (1954), using an artificial population, reviewed various techniques and reported that the boundary strip method of calculating home range area gave results closest to the true value. Calculations using the exclusive boundary strip method were reported the most accurate. Using the mean home range derived by calculating the exclusive boundary strip (Table 1) the density of columbian ground squirrels at Cold Meadows was 0.15 adult squirrels per hectare or 13 resident adult squirrels.

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Table 1. Mean (±SD) individual estimations of home range for columbian ground squirrels, Cold Meadows, Idaho Primitive Area, 1977-1978.

Sq.#	Sex	Observed range length (m)	Adjusted range length (m)	Minimum area (m^2)	Inclusive boundary strip (m^2)	Exclusive boundary strip (m^2)
7	F	40.5±27	55.5±27	319.7±293	1332.0±770	1181.2±715
30	F	52.5±10	67.5±10	572.7±332	2027.0±809	1729.5±695
12	M	49.5±6	64.5±6	956.2±238	2020.5±642	1687.5±795
MEAN		47.5±6	62.5±14	616.2±364	1739.1±678	1532.7±632

POST-EMERGENCE DEVELOPMENT AND INTERYEAR RESIDENCE OF JUVENILE COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

ABSTRACT-- A colony of columbian ground squirrels in the Idaho Primitive Area was observed from 1976-1978. Seven body measurements were recorded for juveniles obtained in 1978. Measured body dimensions were compared with corresponding adult squirrels. There was a lack of sexual dimorphism among developing juveniles. The hind foot was the fastest developing feature. Juveniles obtain adult size their second year. Juvenile males exhibited the lowest interyear residency of either sex or age group examined.

Pengelley (1966), in a comparison of developmental patterns of four species of ground squirrels (Genus: Spermophilus), noted developmental rates appeared to have an adaptive value to particular habitats occupied by each species. Thus an understanding of growth patterns for a particular species may provide insight into the basic ecology of that species. Information on various aspects of growth and development for several species of Spermophilus has been reported (Wade, 1927; Svihla, 1939; Blair, 1942; Mayer and Roche, 1954; Denniston, 1957; Tomich, 1962; McKeever, 1964; Clark, 1970; Iverson and Turner, 1972; Zimmerman, 1972; Turner et al., 1976) but little data have been compiled for the columbian ground squirrel (Spermophilus columbianus). Shaw (1925) traced the development of S. columbianus from birth to emergence from the den but information concerning post-emergence development is lacking.

METHODS

The study was conducted at Cold Meadows, an 87 ha meadow (elev. 2010 m) located in the northeastern portion of the Big Creek Ranger District, Idaho Primitive Area. A description of the Big Creek area has appeared elsewhere (Wing. 1969; Hornocker, 1970; Seidensticker et al., 1973). Ground squirrels were trapped from 12-19 June, 17-24 July and 14-21 August, 1976-1978. Field work prior to 12 June was impractical because of bad weather and the inaccessibility of the study area. A 90 m X 90 m grid with 36 trapping stations 15 m apart was established in the central portion of the meadow. One live trap (15 X 15 X 48 cm) was placed at each trapping station. Traps were baited with carrot and checked every hour. Squirrels were toe clipped using the method of Melchior and Iwen (1965), sexed, measured, weighed to the nearest gram and released back on the grid. Additional specimens were collected from outside the trap grid with a small caliber rifle. Post-emergence development reported here is based on data acquired during the 1978 field season.

RESULTS AND DISCUSSION

Seven body measurements were taken on each sex of juvenile (=young of the year) columbian ground squirrel live trapped or shot (Table 1). No significant difference (unpaired t-test) was found between measurements of males and females (excluding body weights) for July or August. This lack of sexual dimorphism in developing ground squirrels has been observed for other Spermophiles (Kiell and Millar, 1978).

The body dimensions were compared (Table 2) with corresponding measurements of 76 adult squirrels taken in the same collection period. The hind foot was the fastest developing item measured, a feature also noted in S. richardsonii (Clark, 1970), S. lateralis (Clark and Skryja, 1969), S. parryii (Kiell and Millar, 1978), S. tereticaudus (Neal, 1965) and S. harrisii (Neal, 1965). All measurements except tail length and condylobasal length were significantly larger (unpaired t-test, $P<0.01$) during August than July. Shaw (1925) noted columbian ground squirrels did not complete their growth cycle until the second season. Based on 12 juveniles captured in 1977 and recaptured in 1978, ground squirrels at Cold Meadows also reach adult size their second year of life. The combined proportions for both sexes in August (Table 2) indicate approximately 90% of the adult dimensions (excluding body weight) are obtained by the end of the first season. This delaying of maturity has been observed in other species of Spermophilus (Bridgwater, 1966; Morton and Tung, 1971). Morton et al. (1974) noted that in S. beldingi fattening and overall growth were concurrent at first but that caloric intake was then diverted primarily toward lipid synthesis and storage for catabolism during hibernation. This caloric diversion resulted in a late season slowing of increase in linear dimensions. The columbian ground squirrels at Cold Meadows are active approximately 3-4 months out of the year, hibernating for the remaining period. The necessity to "trade off" calories for growth to develop greater body reserves for hibernation may account for the inability of juveniles to attain adult size their first season.

Utilizing capture-recapture data acquired during 1976-1978, the percent interyear residence for each sex and age group of S. columbianus was calculated (Table 3). Juvenile males exhibited the lowest rate of fidelity. Michener and Michener (1971) observed the same residency pattern in S. richardsonii. Reasons for the reported absence of juveniles have been postulated to be the result of predation, dispersal, or winter mortality (Michener and Michener, 1971). Juvenile male dispersal has been reported for a number of ground squirrel species (Evans and Holdenried, 1943; Fitch, 1948; McCarley, 1966; Quanstrom, 1971; Yeaton, 1972; Morton et al., 1974). Adult male columbian ground squirrels are territorial during the breeding season exhibiting aggression toward other males (Steiner, 1970). Although predation and winter mortality affect the population, it is probable the aggressive behavior of territorial males accounts for the low interyear residency exhibited by juvenile males in Cold Meadows. Numerous observations of chases and fights, plus the presence of scars on 42% of the juveniles examined indicates a high level of aggression occurred in the Cold Meadows colony. Rapid post-emergence development in relation to adult size has been reported for many species of ground squirrels (Neal, 1965; Clark, 1970) and is also exemplified by *Spermophilus columbianus*.

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TABLE 1. Mean measurements (±SD) of juvenile columbian ground squirrels collected at Cold Meadows, Idaho Primitive Area, 1978.

Date	Sex	N	Foot Length	Ear Length	Tail Length	Total Length	Body Weight	Zygomatic Breadth	Condylobasal Length
July 17-24	M	4	47±1 mm	17±1	82±5	258±14	200±34 g	27±2	49±3
	F	8	46±2	17±1	82±7	258±15	173±34	27±1	51±3
	Combined	12	46±1	17±1	82±6	258±14	182±35	27±1	50±3
August 14-21	M	9	50±1	18±1	82±4	280±7	311±43	30±2	52±3
	F	9	49±1	17±1	81±3	276±11	264±31	29±3	49±1
	Combined	18	49±1	18±1	82±3	278±9	288±44	29±2	50±2

TABLE 2. Size of juvenile columbian ground squirrels expressed as a percent of the size of adults taken during the same collection period in Cold Meadows, Idaho Primitive Area, 1978.

Date	Sex	Foot Length	Ear Length	Tail Length	Total Length	Body Weight	Zygomatic Breadth	Condylobasal Length
July 17-24	M	92	85	87	78	33	80	84
	F	93	86	92	81	34	83	90
	Combined	92	85	89	79	32	82	88
August 14-21	M	98	89	87	84	53	88	89
	F	99	89	91	87	51	89	87
	Combined	98	89	89	86	52	89	88

TABLE 3. Percent interyear residence of columbian ground squirrels at Cold Meadows, Idaho Primitive Area, 1976-1978.

	1977 recaptures/1976 captures	Percent	1978 recaptures/1977 captures	Percent
Adult males	10/16	62.5	5/13	38.4
Adult females	16/22	72.7	7/20	35.0
Juvenile males	3/14	21.4	2/12	16.6
Juvenile females	4/9	44.4	3/9	33.3

ORGAN WEIGHTS AND THE CONTRIBUTION OF VARIOUS ORGANS TO THE TOTAL BODY MASS OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

ABSTRACT-- Seven internal organs were examined in adult and juvenile columbian ground squirrels. No significant organ weight differences were detected between sexes within each age category. The liver and lungs contributed the greatest percent of total body mass of organs examined.

Organ weight data have been reported for Spermophilus lateralis (McKeever, 1964; Skryja and Clark, 1970) and S. beldingi (McKeever, 1963) but to the best of my knowledge no information concerning organ weights for the columbian ground squirrel (S. columbianus) has been published. This paper compares organ weights of male and female adult and juvenile columbian ground squirrels.

METHODS

The study was conducted at Cold Meadows an 87 ha mountain meadow (elev. 2010 m) located in the northeastern portion of the Idaho Primitive Area. A description of the vegetation and physiography of the Primitive Area has appeared elsewhere (Hornocker, 1970; Seidensticker et al., 1973). Squirrel specimens were collected 18 August 1978 and flown to the University of Idaho's Taylor Ranch Field Station. The samples were immediately frozen and later transported to the Wildlife and Range Resources Laboratory at Brigham Young University. Squirrels were measured, aged (adult, young of the year=juvenile), weighed and autopsied. The excised organs were cleaned of excess tissue and weighed on a Sartorius 3705 top-loading electric balance. Unpaired t-tests were used to determine if a significant difference existed for the average organ weight between adult and juvenile male and female ground squirrels. The same test was used to compare the average weight of left and right organs of an organ pair within the same sex.

RESULTS AND DISCUSSION

Average organ and body weights of collected adult and juvenile S. columbianus are given in Table 1. Percent contribution of each organ to the total body weight is shown in Table 2. No significant organ weight differences were detected between sexes within each age category. There was no relationship found between organ weights and body weight.

Hakonson and Whicker (1971) investigated the contribution of various tissues and organs to the total body mass of mule deer (Odocoileus hemionus). They found liver and lungs contributed the greatest percent of total body mass of the organs examined, a trend also noted in the columbian ground squirrel (Table 2).

The lack of a significant difference in adult male vs female liver, kidney, lung, and spleen weights has been reported for other mammals (Terman, 1969; Chapman, 1971; Havera, 1977).

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TABLE 1. Mean (±SD) organ and body weights (g) of adult and juvenile columbian ground squirrels.

Organs	Adult Males (n=5)	Adult Females (3)	Adults combined (8)	Juv. Males (4)	Juv. Females (3)	Juv. Combined (7)
Liver	10.535±2.201	11.247±2.878	10.802±2.296	7.658±2.113	5.981±1.352	6.955±1.916
Lung	5.148±1.164	4.369±0.526	4.856±1.008	2.654±0.311	3.027±0.144	2.814±0.308
Heart	1.964±0.374	2.072±0.438	2.005±0.371	1.202±0.180	1.008±0.168	1.119±0.191
Spleen	0.857±0.270	0.575±0.221	0.751±0.279	0.394±0.119	0.290±0.088	0.349±0.112
Left Kidney	1.017±0.201	1.202±0.198	1.087±0.208	0.745±0.193	0.681±0.118	0.718±0.156
Right Kidney	0.964±0.204	1.013±0.118	0.982±0.169	0.700±0.160	0.630±0.051	0.670±0.123
Left Adrenal	0.036±0.020	0.029±0.016	0.033±0.017	0.015±0.001	*	---
Right Adrenal	0.034±0.010	0.018±0.006	0.028±0.011	0.014±0.003	*	---
Left Testes	0.160±0.112	---	---	0.020±0.002	---	---
Right Testes	0.178±0.122	---	---	0.021±0.003	---	---
Body Weight	585±58	530±26	564±54	322±63	255±13	293±58

* organs damaged while collecting and not included in calculations.

TABLE 2. Mean (±SD) percent of total body mass of selected organs from adult and juvenile columbian ground squirrels.

Organ	Adult	Juvenile
Liver	1.80±0.30	2.32±0.35
Lung	0.76±0.27	0.98±0.21
Heart	0.35±0.06	0.38±0.05
Spleen	0.21±0.24	0.11±0.03
Left Kidney	0.18±0.03	0.24±0.03
Right Kidney	0.17±0.03	0.22±0.02
Left Adrenal	0.005±0.003	*
Right Adrenal	0.004±0.001	*

* organs damaged while collecting and not included in calculations.

CANNIBALISM EXHIBITED BY THE COLUMBIAN GROUND SQUIRREL

ABSTRACT-- A case of cannibalism is reported for the columbian ground squirrel.

Betts (1976) while observing a Montana colony of columbian ground squirrels (Spermophilus columbianus Ord) noted that the squirrels would eat dead ground squirrels in much the same manner as grass. Although cannibalistic behavior of Spermophiles has been noted for many species (Bailey, 1926; Shaw, 1926; Alcorn, 1940; Hawbecker, 1944; Edwards, 1946; Cade, 1951; Mayer, 1953; Musacchia, 1954; Hansen and Ueckert, 1970) Betts observation appears to be the only reported case of cannibalism for S. columbianus. I would like to report another case of cannibalism for this species.

During the summers of 1976-1978 I have been involved in a food habit study of the columbian ground squirrel in the Idaho Primitive Area. On 26 July 1978, I was collecting stomach samples from a ground squirrel colony located on the south slope of Rush Creek Point (2354 m), Valley County, Idaho. I had shot a ground squirrel (female, 465 g) and placed the body at the base of a douglas fir tree (Pseudotsuga menziesii), intending to reclaim it after I had obtained another sample. I returned to the spot approximately 25 min later. The dead squirrel was gone but I observed a squirrel, lying on its back, disappearing down a burrow. When I pulled the squirrel out I noted that the skin and superficial facial muscles posterior of the right eye, and the right eye itself, had been eaten.

I placed the dead animal 1 m from the burrow entrance where I had recovered it and waited. Five minutes later an adult columbian ground squirrel emerged from the burrow and started eating the dead squirrel. I collected this squirrel (male, 580 g).

Shaw (1924) noted that the reduction of litter size in the columbian ground squirrel may be effected by the cannibalistic instinct of the mother, although he had no direct evidence of cannibalistic behavior to support his hypothesis. With this additional observation the possible use of cannibalistic behavior as a natural population control means by the columbian ground squirrel must be considered.

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MAMMALIAN SPECIES: *SPERMOPHILUS COLUMBIANUS* (ORD, 1815) COLUMBIAN GROUND SQUIRREL

Spermophilus *columbianus* (Ord, 1815)

Columbian Ground Squirrel

Arctomys *Columbianus* Ord, in Guthrie's Geography (2nd. Amer. ed.) 2:292 (described on p. 303), 1815. Based on Lewis' and Clark's description of animals taken on a camas prairie between the forks of the Clearwater and Kooskooskie rivers, Idaho.

Anisonyx *brachiura* Rafinesque, 1817:45. Based on same source as *Arctomys* *Columbianus* Ord.

Arctomys *parryi* var. *β*., *erythrogluteia* Richardson, 1829:161 Type locality, "Rocky Mountains, near the source of the Elk River" (= Wolf Plain, 30 miles west of Rock Lake, Alberta, Canada).

Cynomys *columbianus* True, 1884:593. Proc. U. S. Nat. Mus. 7 (App. Circ. 29), apparently based on *Arctomys* *Columbianus* Ord, 1815).

Spermophilus *columbianus* Merriam, 1891:39. Type locality Moscow, Idaho.

Citellus *columbianus* *albertae* Allen, 1903:537. Type locality Canadian National Park, Banff, Alberta, Canada.

Citellus (Colobotis) *columbianus* Preble, 1908:164. Type locality Smoke Valley, 50 miles north of Jasper House, Alberta, Canada.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Spermophilus*. There are eight recognized living species of *Spermophilus* and two recognized subspecies of *S*. *columbianus* (Howell, 1928:85-90; Hall and Kelson, 1959:341-342) as follows:

S. c. columbianus ((Ord) in Guthrie, 1815:303). see above.

S. c. ruficaudus (Howell, 1928:212). Type locality Wallowa Lake, Wallowa Co., Oregon.

DIAGNOSIS. The subgenus Spermophilus is separated from the other subgenera of ground squirrels by having the metaloph on P4 continuous and the upper body parts exhibiting reddish or fine white spots on a gray background. Within the subgenus, S. columbianus differs from other species by having buffy dorsal spots and hind feet greater than 43 mm in length (Hall and Kelson, 1959).

GENERAL CHARACTERS. Hall and Kelson (1959) described S. columbianus as follows: "Nose and face tawny or hazel; occiput, nape, and sides of neck smoke gray; upper parts cinnamon buff or sayal brown, shaded with fuscous and in winter with smoke gray; hind legs and feet tawny or hazel; front feet ochraceous buff; tail gray or tawny; underparts ochraceous buff or tawny. Skull resembling that of S. richardsonii but longer and zygomatic arches less expanded posteriorly; dorsal outline more nearly flat; supraorbital margins of frontals not elevated or thickened; rostrum and nasals longer; upper tooth-rows nearly parallel instead of appreciably divergent anteriorly." Howell (1938) described the summer and winter pelages plus the molt pattern. Spermophilus columbianus is one of the largest members of the subgenus Spermophilus, being second in length to only S. undulatus. External measurements (millimeters) range as follows: total length, 327 to 410; length of tail, 80 to 116; length of hind foot, 49.5 to 57 (Hall and Kelson, 1959). Average cranial measurements taken from 12 specimens of S. c. columbianus by Howell (1938) are: greatest length of skull, 51.7; palatilar length, 25.1; zygomatic breadth, 31.8; cranial breadth, 20.8; interorbital breadth, 10.6; postorbital constriction, 11.3; length of nasals, 19.4; and maxillary toothrow, 10.9. For a detailed morphological comparison between S. c. columbianus and S. c. ruficaudus see Howell (1938). The skull of S. c. columbianus is illustrated in Figure 1.

DISTRIBUTION. The columbian ground squirrel is found in the Rocky Mountain region of western Montana, Idaho, northeastern Washington, southeastern British Columbia and western Alberta; also the plains of eastern Washington and mountains of east-central Oregon (Dice, 1919; Howell, 1938; Davis, 1939; Rust, 1946; Hall and Kelson, 1959; Manville, 1959; Larrison and Baxter, 1960; Larrison, 1967, 1970; Cowan and Guiguet, 1975) (Figure 2).

FORM AND FUNCTION. Howell (1938) described two pelage types and one annual molt for S. columbianus. The molt pattern has been described as a 'diffuse type' by Hansen (1954). Adults emerge from hibernation in winter pelage; the summer coat is attained in June in Idaho. The integumentary glands of columbianus have been examined histologically (Kivett, 1978) and compared with other members of the genus Spermophilus (Kivett et al., 1976). Pitcher (1926) described the development of the endochondral bone. Layne (1954) and Burt (1960) described the configuration and dimensions of the baculum. Nunemarker (1933) traced cell division in the embryo of the columbian ground squirrel and reported where histologically possible, every cytological structure previously identified in the chicken embryo. Stone (1925) examined the development of the central nervous system and reported it very similar to the development of the nervous system of other mammals. He also observed that in its early stages the developing nervous system compared very favorable with that of aves. Howard (1924) described spermatogenesis of the columbian ground squirrel noting the testis undergo an annual cycle, the greatest activity occurring during hibernation. The relationship between renal function and hibernation for S. columbianus has been examined by Pengelley and Fisher (1961), Pfeiffer and Moy (1968), Lesser et al. (1970), Moy (1971), Moy and Pfeiffer (1971), Moy et al. (1972) and Passmore et al. (1975). Blood changes in torpid and aroused S. columbianus have been reported by Nansel and Knoche (1972). The effects of centrally injected noradrenaline on new-born columbian ground squirrels were studied by Glass and Wang (1978) to provide data on the ontogeny of thermoregulatory pathways.

ONTOGENY AND REPRODUCTION. Breeding in S. columbianus commences shortly after the adult females have appeared from hibernation and continues actively for a period of about three weeks (Shaw, 1924). The reproductive cycle of the male columbian ground squirrel was described by Shaw (1926a) and Smith (1947). The gestation period is 24 days (Shaw, 1925d). There is one litter per year (Shaw, 1924; Michener, 1977). Michener (1977) noted columbian ground squirrels delay breeding until two years of age but Shaw (1924) and Smith (1947) observed that females would breed as yearlings. Moore (1937) noted the effect of altitude in delaying sexual maturation of juveniles. Shaw (1924) found the average number of fetal scars to be 5.09. The mean number of embryos per female has ranged from 4.9 (Couch, 1932) to 5.4 (Shaw, 1924). Average litter size at birth has been reported to be 5.3 (Shaw, 1924), 3.5 (Cowan and Guiguet, 1975:126) and 3.3 (Michener, 1977). The brood den is frequently an old summer den, a portion of which is used for the brood nest (Shaw, 1924). Shaw (1925d) observed breeding and development of a colony of captive columbian ground squirrels and described the development of young ground squirrels from birth to 28 days. The growth of young S. columbianus is arrested at the end of the first summer of life; the animal reaching adult size the second year (Shaw, 1924). Michener (1977) reported juvenile columbians attained about 60% of adult prehibernation weight before entering hibernation, whereas the juveniles of S. richardsonii reached about 80-90% of adult prehibernation weight. Levenson (1979) documented the rate of growth of S. columbianus from birth to 50 days. Although juvenile columbians enter hibernation at a lighter weight (in proportion to adult weight) and at a younger age than richardsonii juveniles, Michener (1977) observed S. columbianus had a higher recovery rate as yearlings. Betts (1973) reported between-year recovery rates of 44-71% for juvenile columbian ground squirrels in Montana.

ECOLOGY. Spermophilus columbianus is a mountain species typically found in alpine or subalpine meadows (Steiner, 1970a). In Oregon S. columbianus occurs in the Hudsonian, Canadian, and upper edges of the Transition life zones, but rarely in heavy timber (Bailey, 1936), thus their distribution is usually discontinuous. Similar habitat is occupied in Idaho (Davis, 1939), Montana (Manville, 1959), and Washington (Dice, 1919). In the Blue and Wallowa mountains of Oregon Turner (1972) reported columbian ground squirrels occupied meadows that are frequently flooded. Here the ground squirrels occurred only around meadow edges or on mounds within the meadows. Durrant and Hansen (1954) rated S. columbianus second to S. beldingi as the least adapted to dry conditions, emphasizing the squirrels need for a moist habitat. Shaw (1920), during seven successive years of trapping, reported a ground squirrel population density of 5.9 squirrels per hectare. He also noted densities of 24.7 squirrels per ha on wheat fields and 61.7 animals per ha on agricultural bottom lands. Lambeth (1977) reported 32 squirrels per ha on subalpine openings in central Idaho while Adams (1961) recorded 34.6 squirrels per ha in Alberta. Barash (1973) and Tyser (1978) made interspecific comparisons of the foraging behaviors of S. columbianus, Ochotona princeps and Marmota caligata in a sympatric situation in Montana. Turner (1972) examined the interspecific relationship between S. columbianus and S. beldingi on an area of sympatry in Oregon. Lambeth (1977) determined that the columbian ground squirrel was not a direct dietary competitor with domestic sheep but could become one where range conditions were poor. Murie and Harris (1978) reported the average home range for 22 resident male columbian ground squirrels was 4200 m^2. Males were noted to range widely during the breeding season but restricted their activities to a small area thereafter. Shaw (1945) reported an emigration of immature squirrels occurs shortly after the yearlings emerge in spring. Columbian ground squirrels have been reported as prey for many mammalian predators (Preble, 1908; Wright, 1913; Rust, 1946; Weckwerth and Hawley, 1962; Taylor, 1964; Ogle, 1969; Seidensticker et al., 1973; Barash, 1971; Koehler and Hornocker, 1977). The golden eagle (Aquila chrysaetos) (Boag, 1977; Thurow and Peterson, 1978) and red-tailed hawk (Buteo jamaicensis) (Munro, 1929; Miller, 1931) appear the principal avian predators. S. columbianus has shown cannibalistic behavior (Betts, 1976; Elliott, 1978). Dietary observations were recorded by various authors (Shaw, 1925g, 1926c; Howell, 1938; Martin et al., 1951; Manville, 1959). Lambeth (1977) used the microhistological method to examine contents of 39 columbian ground squirrel stomachs. He found silky lupine (Lupinus sericeus) to be the most abundant item in the diet. The columbian ground squirrel has been regarded as a major host of the Rocky Mountain spotted fever tick (Dermacentor andersoni) (Birdseye, 1912; Bishopp and Trembley, 1945). Because of this association the ectoparasties of S. columbianus have been extensively examined (Baker, 1904; Jellison and Good, 1942; Hubbard, 1947; Holland, 1949; Bacon et al., 1959; Hilton and Mahrt, 1971a). Hilton and Mahrt (1971b, 1972a, b) reported Trypanosoma otospermophili, Eimeria bilamellata, Eimeria callospermophili and Eimeria lateralis as endoparasites of S. columbianus. Plague (Yersinia pestis) was recorded in columbians by Twigg (1978). McLean et al. (1969, 1970) detected the presence of hemagglutinin inhibiting antibodies to Powassan and/or St. Louis encephalitis viruses in columbian ground squirrels from British Columbia. They postulated that S. columbianus may function as a natural reservoir for the viruses. Wobeser and Gordon (1969) observed columbians infected with a dermatitis, Dermatophilus congolensis. Members of the genus Spermophilus have been subjected to various control measures (Record, 1978). Shaw (1916, 1920, 1925e) concluded that uncontrolled ground squirrel populations on pasture lands may be competitors with domestic livestock. He reported 385 squirrels would consume the same amount of forage required by one cow per day; 96 squirrels would consume the equivalent forage used by one sheep per day. Record (1978) evaluated the results of zinc phosphide, Compound 1080, and strychnine grain as controls for columbian ground squirrels in Montana.

BEHAVIOR. Shaw (1945), Steiner (1970a, 1970b, 1971, 1972, 1973, 1974, 1975), Betts (1976), and Murie and Harris (1978) examined and described the behavior and social organization of S. columbianus. Acoustical behavior of S. columbianus and four other ground squirrel species in an area of sympatry was discussed by Koeppl et al. (1978). Burrowing and burrow construction was described by Shaw (1920, 1924, 1925a, 1925h, 1926b), Steiner (1970b) and McLean (1978). Shaw (1925a, 1925c, 1925e, 1925f) described hibernation and breeding behavior. Behavioral responses to various weather conditions were noted by Shaw (1925b, 1926a, 1936) and Manville (1959). Postures and behavior of young columbian ground squirrels were documented by Steiner (1970a, 1970b). Greeting behavior between individual columbians and this activity as it relates to scent marking was reported by Steiner (1975), Kivett et al. (1976) and Thiessen and Rice (1976). Steiner (1970a) noted the columbian ground squirrel usually moves by bounding, giving the gait a characteristic "bumpy" appearance. Spermophilus columbianus is basically a terrestrial mammal but has been noted exhibiting aquatic behavior (Manville, 1959; Dagg and and Windsor, 1972) and arboreal tendencys (Manville, 1959; Steiner, 1970b).

GENETICS. The columbian ground squirrel has a diploid chromosome number of 32 (Pechanec, 1926; Nadler, 1966) the fundamental number is 60 (Nadler, 1966). The karyotype contains 18 metacentrics, 12 submetacentrics, a submetacentric X and a minute metacentric Y chromosome (Nadler, 1966). Nadler et al. (1975) developed an idiogram of G-band patterns for chromosomes of S. columbianus based on 18 metaphase cells. Pechanec (1926) examined the oogenesis of the columbian ground squirrel and found the nucleus of the definitive oocytes do not pass through a complicated chromosomal history. Schwarz (1927) determined the sex of embryo columbians through investigation of somatic cells. She found a dimorphic condition exists in the chromosome number of male and female somatic cells. Embryos with 33 chromosomes were considered males; embryos with 34 chromosomes were female. Nadler and Hughes (1966) electrophoretically examined the serum protein of S. undulatus, S. columbianus, and S. beldingi. They found the serum patterns of the three species exhibited an overall similarity in the number of protein fractions and their respective mobilities. Nadler (1968) examined the serum proteins and transferrins of the subgenus Spermophilus and found each species, except S. beldingi and certain subspecies of S. townsendi, could easily be identified by characteristics of their proteins. Johnson and Wicks (1964) showed an electropherogram of several members of the family Sciuridae including S. columbianus. Albinism has been observed in the columbian ground squirrel by Svihla (1932, 1933), Davis (1937) and Howell (1938).

REMARKS. There is no known reported fossil record for S. columbianus but recent studies have hypothesized the origin of the species. Rand (1954) postulated a relationship existed between S. undulatus and S. columbianus. He suggested the two species evolved from a common ancestral stock as a result of separation by a continental glacier during the Pleistocene. Holland (1958) also suggested a close evolutionary relationship existed between S. undulatus and S. columbianus based on the fleas that parasitize the two species. Lyapunova and Vorontsov (1970) also held that S. undulatus and S. columbianus had a common ancestor or descended one from the other. Examination of chromosomes (Nadler, 1966, Nadler et al., 1975; Vorontsov and Lyapunova, 1969, 1970), serum proteins (Nadler et al., 1966, 1968), transferrins (Nadler, 1968; Nadler et al., 1973, 1974), and location of scent-glands (Kivett et al., 1976) tend to support the theory that S. columbianus is closely related to S. undulatus but Robinson and Hoffmann's (1975) analysis of cranial morphology for the genus Spermophilus discount an evolutionary relationship.

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FIGURE 1. Views of the skull and mandible of *Spermophilus columbianus columbianus* (female, from Cold Meadows, Big Creek Ranger District, Valley Co., Idaho), from top to bottom, dorsal view of skull, lateral view of skull, lateral view of mandible, and ventral view of skull. Scale represents 7 mm. Drawings by Sharon I. Steigers.

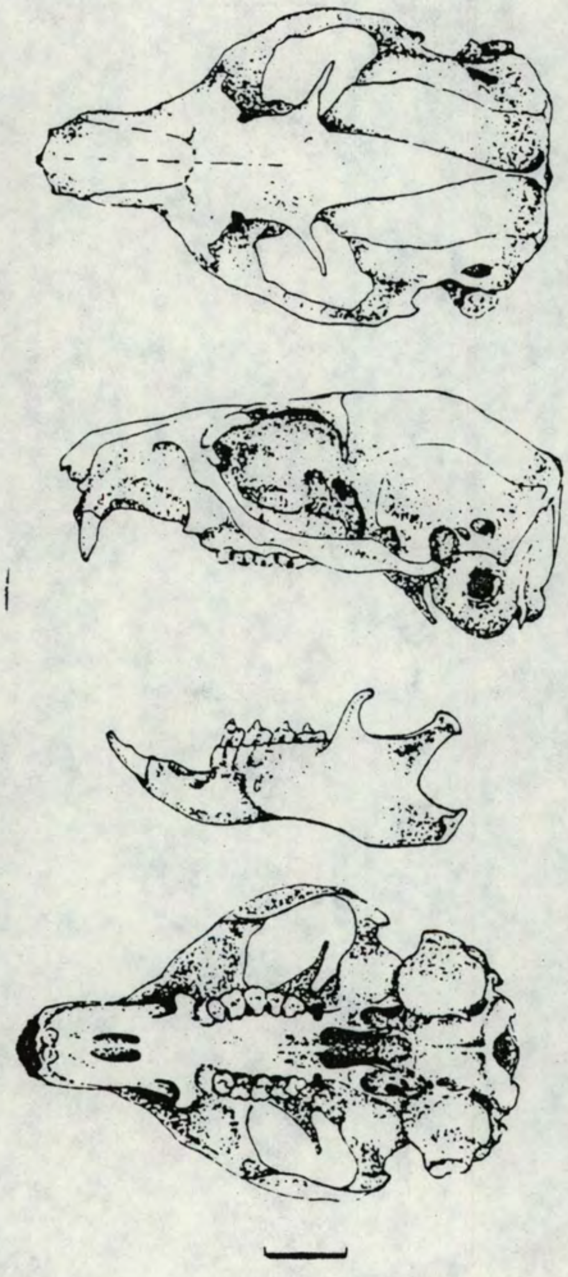
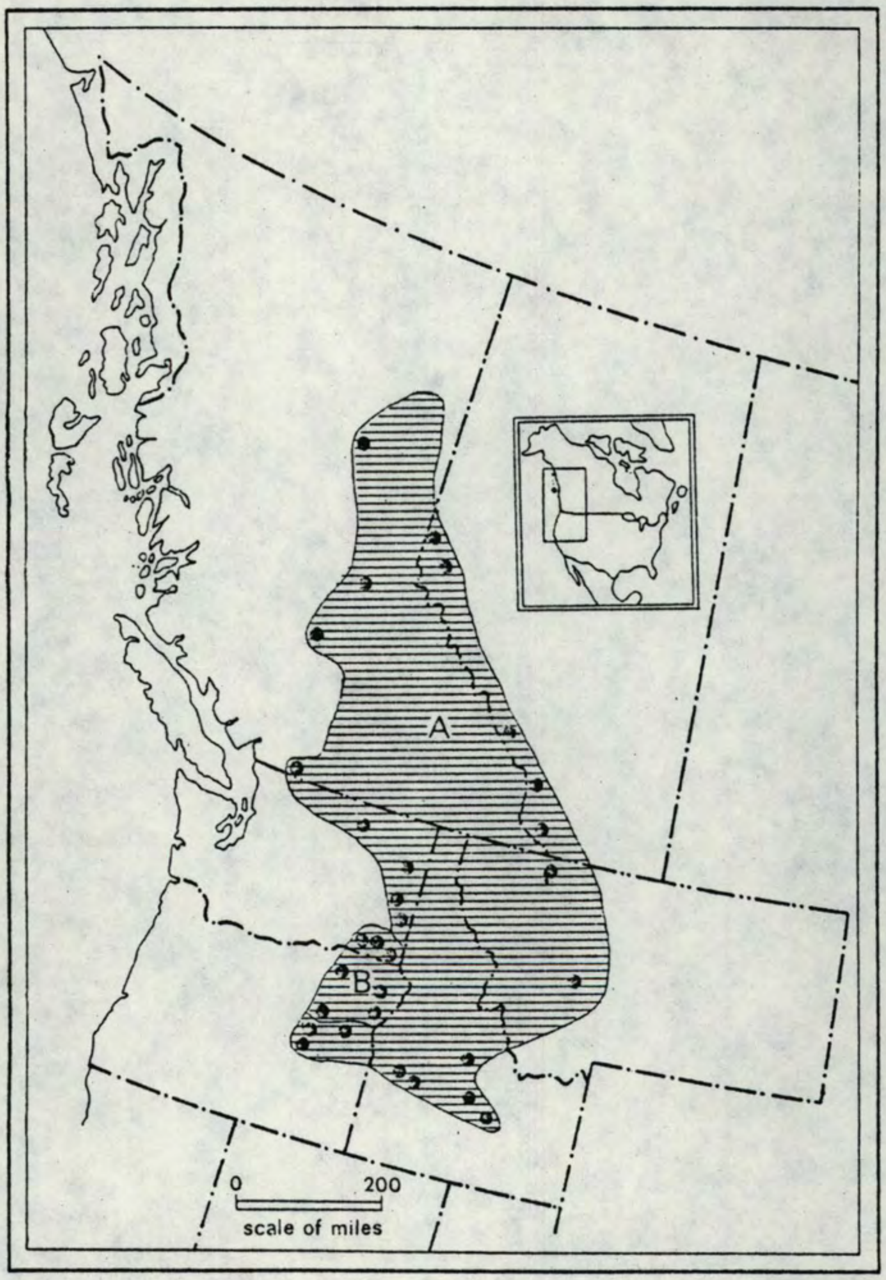


FIGURE 2. The geographic range of Spermophilus columbianus and its subspecies: A, S. c. columbianus; and B, S. c. ruficaudus. Adapted from Hall and Kelson, 1959. The dots coincide with the marginal records reported in Hall and Kelson (1959:342).


A
B
0
200
scale of miles

ECOLOGY OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

Charles L. Elliott

Department of Botany and Range Science

M.S. Degree, August 1980

ABSTRACT

Included in this thesis are seven manuscripts dealing with the columbian ground squirrel, titled as follows: (1) Dietary and habitat relationships of the columbian ground squirrel in the Idaho Primitive Area; (2) Seasonal activity patterns of columbian ground squirrels in the Idaho Primitive Area; (3) Seasonal home range of a colony of columbian ground squirrels in the Idaho Primitive Area; (4) Post-emergence development and interyear residence of juvenile columbian ground squirrels in the Idaho Primitive Area; (5) Organ weights and the contribution of various organs to the total body mass of columbian ground squirrels in the Idaho Primitive Area; (6) Cannibalism exhibited by the columbian ground squirrel and (7) Mammalian species: Spermophilus columbianus (Ord, 1815) Columbian ground squirrel.

COMMITTEE APPROVAL:

Jerran T. Flinders, Committee Chairman

Kimball T. Harper, Committee Member

Hal L. Black, Committee Member

Wilford M. Hess, Graduate Coordinator