THE UNIVERSITY OF ALBERTA

ECOLOGY OF THE COLUMBIAN GROUND SQUIRREL IN THE SHEEP RIVER REGION

A DISSERTATION

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

by

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EDMONTON, Alberta

[illegible]

1962

Frontispiece. Columbian Ground Squirrel. Photo, C. Hampson.

ABSTRACT

This study of the ecology of the Columbian ground squirrel, *Citellus columbianus columbianus* (Ord), was undertaken during the summers of 1958, 1959 and 1960. The research was carried out in the vicinity of the Alberta Biological Station at Gorge Creek, 18 miles west of Turner Valley, Alberta. Four study areas were established at various elevations and features of the habitats such as the topography, soils, climate and vegetation were described. The composition and cover of the vegetation were sampled by randomly distributed square meter quadrats. In addition, the range condition or extent of grazing on the study areas was assessed by estimating forage yields from dry-weight-samples of clipped vegetation.

The squirrel populations on the four study areas were surveyed to obtain data on reproduction, growth and population statistics. The densities were estimated by three methods--counts, capture-recapture data, and by attempts to kill and obtain all resident squirrels within a 3-acre plot. The number of squirrels per acre on a 1.5 acre observation area, showed no significant changes during the springs of 1958, 1959 and 1960. In addition, the densities of adults and yearlings were fairly uniform on the four study areas. The sex and age composition of the populations were estimated from samples of live-trapped and dead squirrels. Information on reproductive success was obtained from autopsies of female squirrels and specimens were aged by skull and tooth characters. Also, capture-

recapture data were used in estimating mortality rates, movements, and home ranges.

Some attributes of the squirrel populations on the four study areas were related to features of the habitat. It was concluded that environmental factors such as climatic conditions and food supply ultimately regulate the seasonal activity, reproductive rate and growth of the Columbian ground squirrel. The length of the active season was about 3 weeks shorter at an elevation of 6,800 feet compared to an elevation of 5,000 feet. Low growth and reproductive rates were correlated with low yields and relative scarcity of preferred food plants.

ACKNOWLEDGEMENTS

The author is deeply indebted to the following men--Dr. J. E. Moore, who first inspired interest in this project, and to the late Dr. R. B. Miller who gave much valuable advice. Special recognition must also be paid to Dr. W. A. Fuller, who served as supervisor during the last year of the study. The generous assistance received from Dr. V. Lewin and D. A. Boag is gratefully acknowledged. Thanks are extended to Dr. J. C. Holmes and Dr. W. L. Jellison for identifications of parasites. The kind help received from Dr. R. G. H. Cormack, who identified many plant species, is appreciated.

The author is grateful for the cooperation and assistance donated by the rangers--R. Mustard, J. Machovec and A. Obourne, and by members of the Biological Station staff--P. Hochachka, D. Filion, W. Sharp, D. Hocking and J. Poulsen. Appreciation is also shown for the many suggestions and observations contributed by D. Stelfox, and the following ranchers--A. Murdoch, Col. Robinson, and L. Miller.

Financial assistance for the study was received from the University of Alberta in 1958, and subsequently from a Canadian Industries Fellowship granted in 1959 and 1960. Living and travel expenses were provided for by the Fish and Game Branch of the Department of Lands and Forests.

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INTRODUCTION

An ecological study of the Columbian ground squirrel, Citellus c. columbianus (Ord), 1815 was conducted at the Alberta Biological Station, 18 miles west of Turner Valley. The objective of this research was to make a comparative study of four colonies of ground squirrels, and relate the results to physical and biotic features of the environment. The research was concerned with three aspects--a description of the habitat, an analysis of a ground squirrel population, and other related information which is presented in the appendices.

Four study areas were set up, and the various features of the habitat such as topography, soils, climate, vegetation, and associated animals were described. Reproductive rates, growth, population size and composition, and mortality of the ground squirrels on the study areas, were compared. Differences in seasonal activity and population dynamics were related to variations in the habitats. In addition, aging methods, movements, and food habits were described.

DESCRIPTION OF THE COLUMBIAN GROUND SQUIRREL

Most of the following account of the taxonomic status of the ground squirrel was adopted from Howell (1938).

Citellus c. columbianus (Ord), 1815 was first recorded from a locality between the Clearwater and Kooskooskie rivers in Idaho by the Lewis and Clark expedition of 1804-1806. Ord described the species as Arctomys columbianus from specimens taken at the same locality. Oken in 1816 proposed Citellus as the generic name for the ground squirrels. The type for the genus is Citellus citellus from Hungary. Since 1816, the generic name has been changed many times. Cuvier in 1925 introduced Spermophilus and Merriam in 1891 upheld the name until Citellus was revived by Allen in 1902. Since 1902, the generic name Citellus has been widely accepted. Howell (1938) revised the genus Citellus and regarded C. columbianus as a member of the more highly evolved subgenus Citellus. He retained the name C. columbianus and recognized two subspecies: C. c. columbianus and C. c. ruficaudus. Recently, Hall and Kelson (1959) have resurrected the name Spermophilus because Citellus Oken was considered non-Linnaean in character, giving Spermophilus priority. However, the Committee on Nomenclature have recommended the retention of the generic name Citellus (Am. Soc. Mammal., 1960). Therefore, in this paper, Howell's classification will be used.

The Columbian ground squirrel is a large squirrel, exceeded in weight only by some males of the Arctic ground squirrel

(Citellus parryi group). Mean weights and measurements are given in Table I below.

Table I. Mean weights and measurements for adult male and female Columbian ground squirrels, 1960.

Sex	No.	Total length (mm.)	No.	Tail length (mm.)	No.	Weight (Gms.) (Late summer)
Male	52	350 (305-398)*	52	88 (56-109)	29	690 (555-1025)
Female	73	350 (322-392)	70	87 (66-102)	39	525 (415-740)

* Range in measurements

The following description is adopted from Howell (1938):

Summer pelage: Nose and front of face tawny or hazel; crown mixed with cinnamon buff and smokey grey; occiput, nape and cheeks smokey grey, eye ring buff; ears brown on outer surface and tawny on inner surface; upper parts including back, shoulders and rump, mottled grey brown, the underfur fuscous; flanks grey to buffy white; underparts cinnamon buff to ochraceous; front legs and feet fulvous; hind feet ochraceous tawny, the thighs hazel; tail black above with outer hairs white tipped and under fur fulvous; tail beneath, mixed fuscous black and greyish white.

Winter pelage: Fur thicker, upper parts sprinkled more heavily with grey. This pelage is present in April and May before the moult. Winter hairs appear again shortly before hibernation.

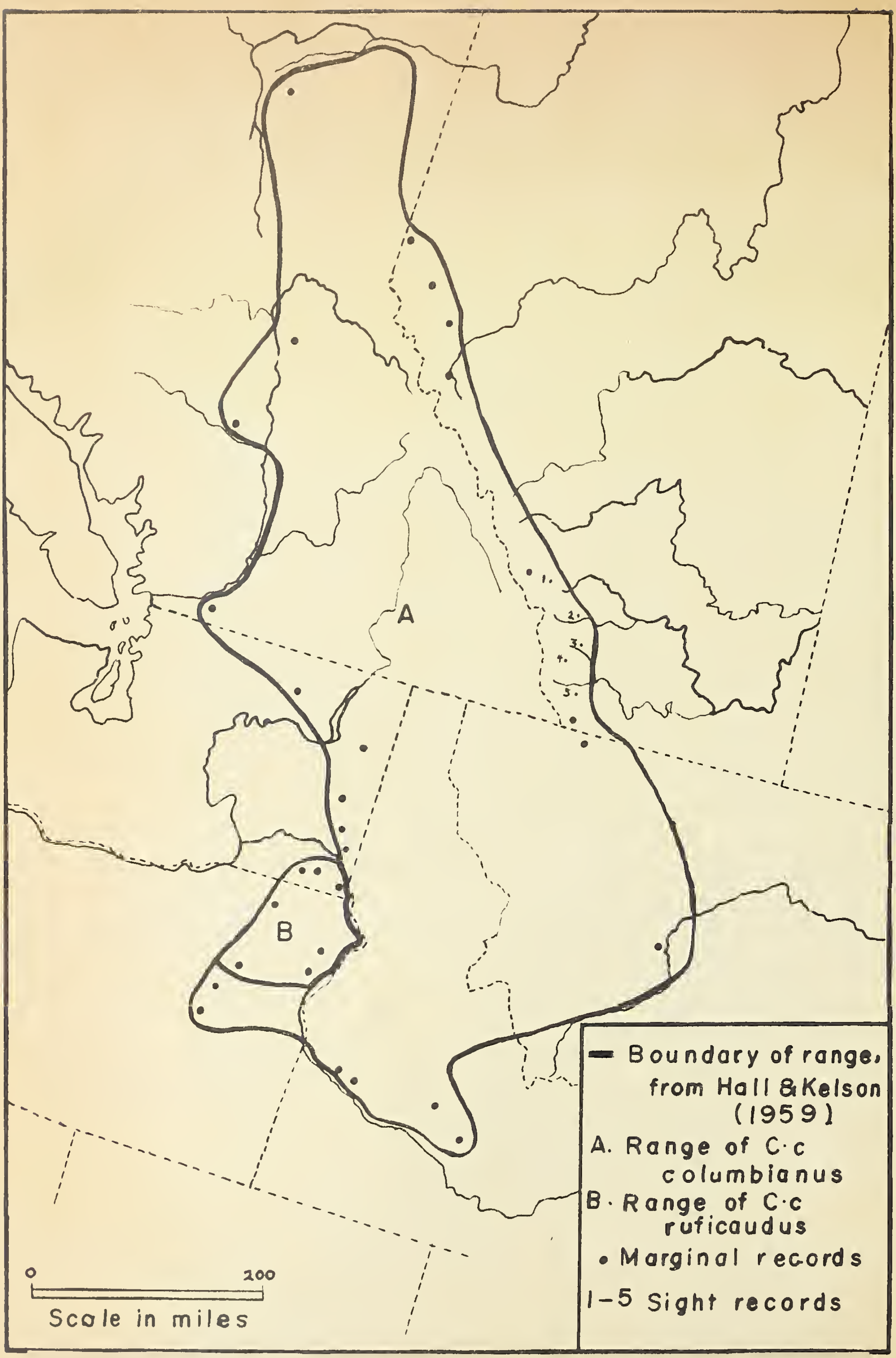


Figure 1. Distribution map of the Columbian ground squirrel.
1. Exshaw 2. Okotoks Mtn. 3. Willow Creek
4. N. Branch Oldman R. 5. 5 mi. S. Pincher Creek.

DISTRIBUTION

The Columbian ground squirrel occupies a rather limited range in comparison with other species. It is restricted to the Rocky Mountain region of eastern British Columbia; southwestern Alberta, western Montana and Idaho, west to eastern Oregon and Washington (Figure 1). The northernmost extent of the range is the headwaters of the South Pine River, east of the lower Parsnip River near the Peace River in British Columbia. The squirrels occur as far south as the Craters of the Moon, Idaho, and Harney county, Oregon (Howell 1938).

The subspecies Citellus columbianus ruficaudus is found only in the Blue Mountains region south of the Snake River in Oregon. An isolated population of C. columbianus columbianus is found south of the above area and the rest of the range is occupied by C. c. columbianus. In Montana and Idaho, the Columbian ground squirrel is extending its range southward and eastward into cultivated valleys (Howell 1938).

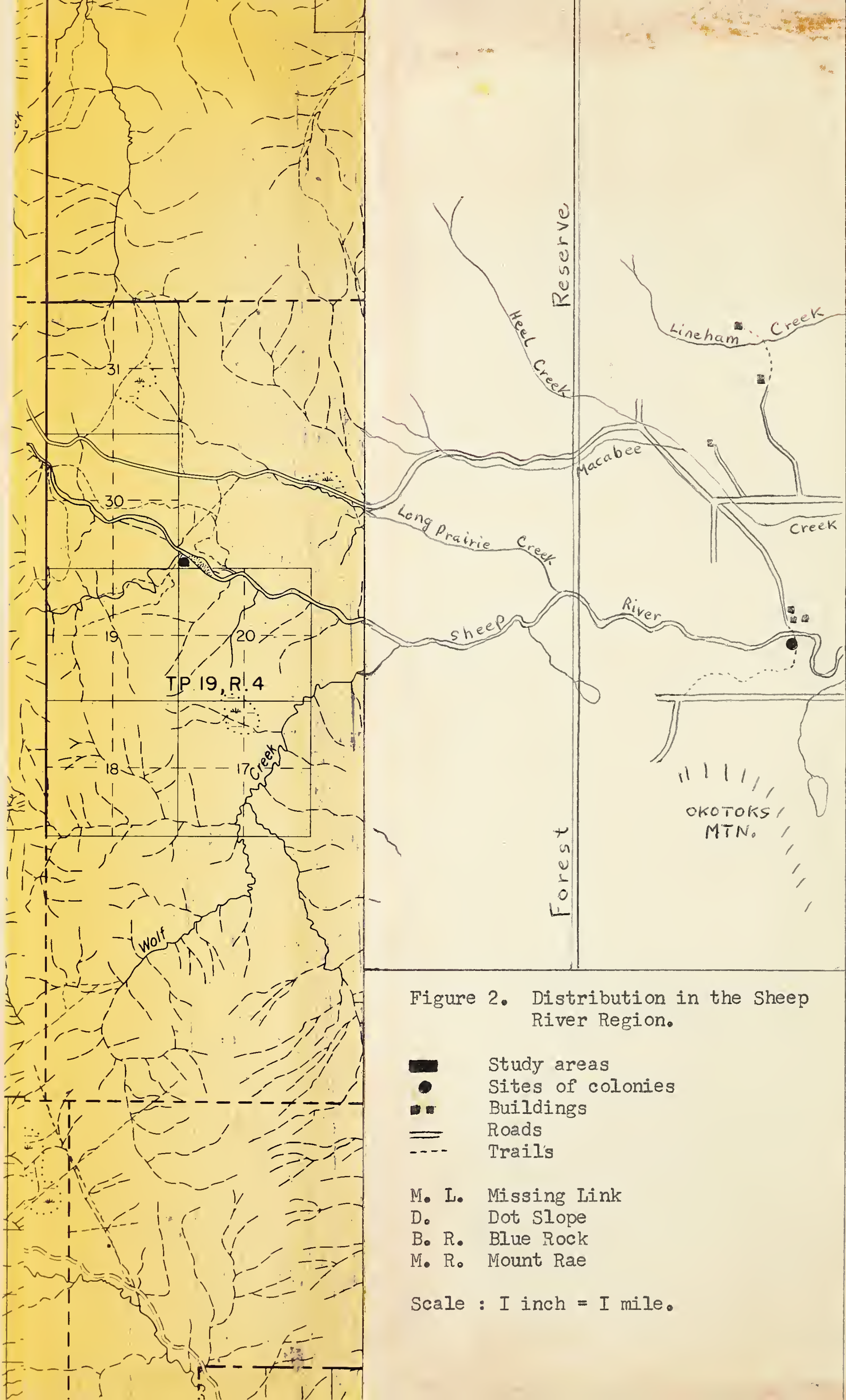
In Alberta, the squirrels are found in suitable habitats along the eastern slopes of the continental divide and in the foothills. The furthest northward extent of the range in Alberta is in the Torrens River region near the British Columbia-Alberta border, 70 miles southwest of Grande Prairie at latitude 54° 10' N. (Soper pers. comm.). Southeastward the ground squirrels occur


Elbow
12
M.R.
Cougar Creek
B.R.
32
Rae Creek
29
Bluerock
20
21
Creek
TP.19, R7
TP.19, R.6
Creek
16
15
Sheep Creek
Burns
Burns Lake
9
10
Creek
2
Cliff
35
36
31
Creek
25
30

Figure 2. Distribution in the Sheep River Region.

▬	Study areas
●	Sites of colonies
■■	Buildings
═	Roads
----	Trails
M. L.	Missing Link
D.	Dot Slope
B. R.	Blue Rock
M. R.	Mount Rae

Scale : I inch = I mile.



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all along the eastern slopes to Waterton Lakes Park and the international border (Figure 1). At Waterton Lakes, the columbians have reached the edge of the plains where they meet the Richardson's ground squirrels, C. richardsonii .

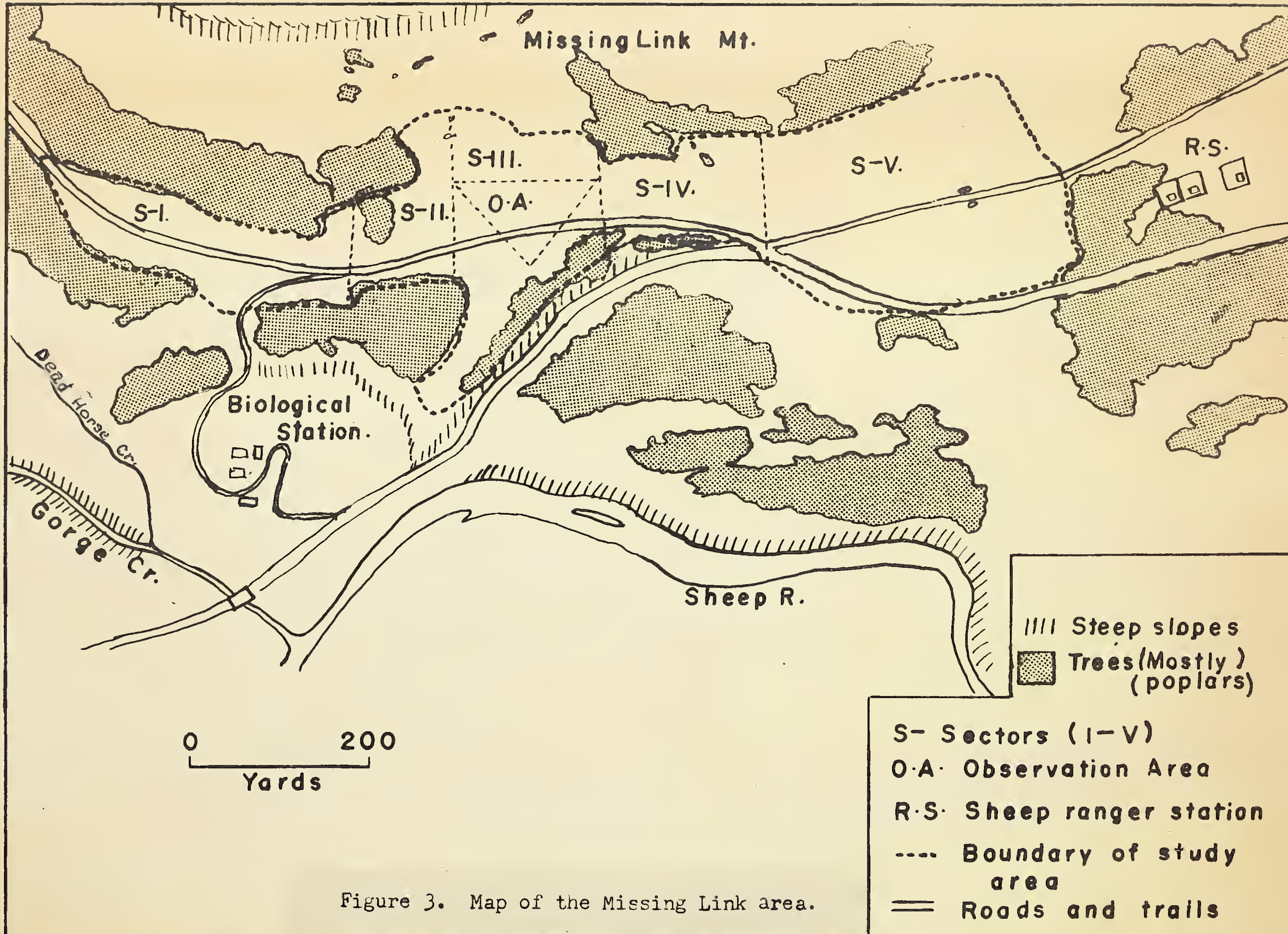

Figure 3. Map of the Missing Link area.

STUDY AREAS

Introduction

In the summer of 1958, a triangular 1.5-acre study plot was established on a rocky meadow below Missing Link Mountain at an elevation of 5,000 feet (Figure 3). This meadow was moderately grazed year round by horses (fewer than 10), mule deer, Odocoileus hemionus , and bighorn sheep, Ovis canadensis . The 1.5 acre area was designated as the observation area and was 1 quarter mile east of the Biological Station directly above the confluence of Gorge Creek and the Sheep River. Counts and live trapping were carried out within this plot and around the periphery in 1958. In 1959, the study area was extended east and west to occupy a flat 1,100 yards long and about 28 acres in area (Figure 4). For convenience in live-trapping, the study area was divided into five unequal sectors numbering from west to east. The observation area was a part of Sector III. Live-trapping and counts were continued over this enlarged study area in 1959 and 1960.

Three other study areas representing different habitats were selected in 1959 and 1960. Each was limited to plots 3 acres in size and each supported a high density of Columbian ground squirrels. One plot was located 200 yards west of Dead Horse Creek on an open south-facing slope of

Sector V.

Sector IV.

Sector III.

Sector II.

Sector I.

Figure 4. Missing Link Flat.

west Missing Link, locally known as Dot Mountain. This plot was in a zone ungrazed by domestic stock, although bighorn sheep and deer grazed there in winter and spring. Another plot, on the flat below Blue Rock Mountain at the headwaters of South Gorge Creek, was situated on a grazing lease and consequently was heavily grazed by cattle. The third plot was situated on a southwesterly slope below the north foot of Mount Rae on the summit between the Elbow and South Sheep Rivers. This slope, being at a higher elevation (6,800 feet) was sparsely vegetated and was heavily grazed by cattle and wapiti, *Cervus canadensis*.

Physical Features

Topography and Altitude. The Missing Link study area is an undulating rocky meadow, 28 acres in size at an approximate elevation of 5,000 feet. It extends in an east-west direction on a high bench land between Missing Link Mountain and the South Sheep River canyon (Figure 4). The area is bordered on three sides by trees, *Populus tremuloides* and *Pinus contorta*, and by a steep gravelly slope on the fourth. These features constitute a barrier to movement and only in the east is immigration and emigration of ground squirrels likely.

Although the Dot study area is situated only 1 quarter mile west of the western border of the Missing Link area (Figure 5), it is considered to support a distinct population

Figure 5. Dot Slope, showing study area.
Photo, B. Sharp.

Figure 6. Dot Slope study area.

because of a buffer strip consisting of forested slopes and a stream, Dead Horse Creek. The elevation of the 3-acre plot is about 5,100 feet. It is on a slope facing south-southwest at an angle of 17° to 20° from the horizontal. The steepness of this slope has a marked effect upon the moisture, vegetation and soil (see below). The nearest source of water is Dead Horse Creek, 200 yards east of the plot. A truck trail bisects the area and appears to have attracted squirrels by providing cut banks suitable for burrowing.

The Blue Rock Flat is situated 5 miles west of the Biological Station at an elevation of 5,900 feet (Figure 7). The area is a hummocky meadow, interlaced by branches of south Gorge Creek. In late summer the upper reaches of these streams are dry. The flat is bordered by a muskeg area on the east, a low forested ridge on the west, forested slopes of Blue Rock Mountain on the south and Mount Ware on the north. Cattle have caused erosion of stream banks bordering the study area, and have denuded a strip about 100 feet by 20 feet on the study area where salt had been placed.

The study plot at Mount Rae is located on a slope at an elevation of 6,800 feet (Figure 8). The slope declines south-westward to the bottom of a narrow draw, at an average of 20° from the horizontal. The slope varies in declination from 15° at its easterly edge to approximately 23° at the western border

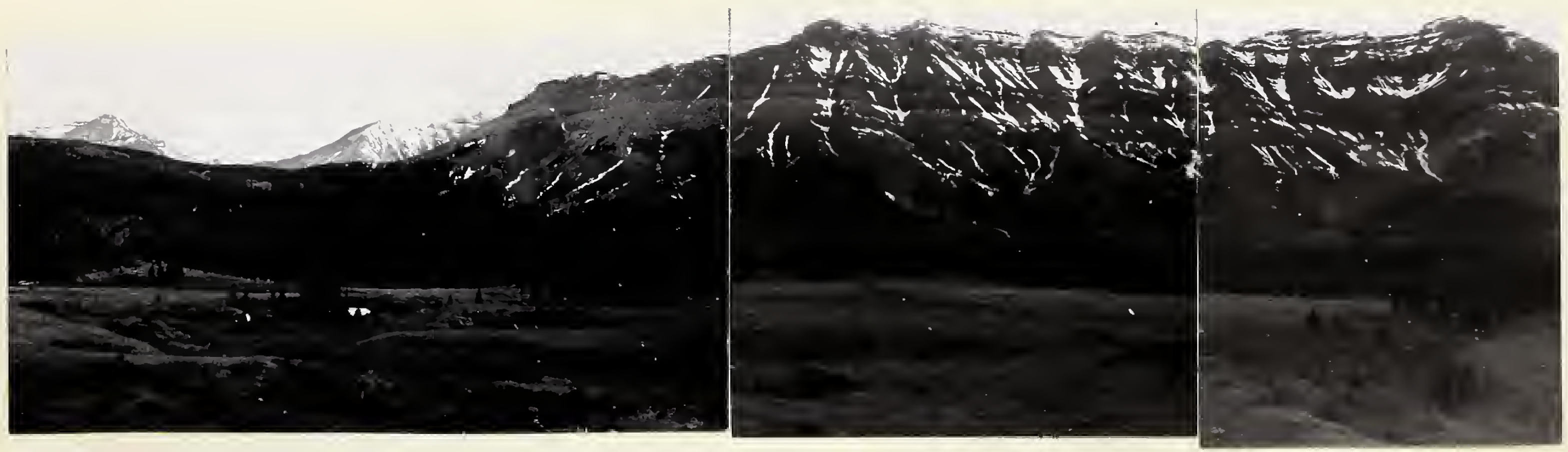

Figure 7. Blue Rock Flat.

of the area. A seasonal rivulet gathers melt waters from the snow and flows along the draw down into Rae Creek. The slope is a rocky, burnt-over area and is spotted with regenerating spruce, *Picea engelmanni*, fir, *Abies lasiocarpa*, and alpine larch, *Larix lyalli*. A small forested ridge on the south partially protects the area from winds. On the north, a forestry road parallels the upper border of the plot.

Soil. Most soils in the Sheep River region can be placed in one of two general categories. These are grey wooded soils if developed under forest, and chernozems if developed under grasslands. Soil profiles or vertical cuts were made in the soil to a minimum depth of 3 feet; and the horizons and subhorizons on the exposed profiles were measured and described. The texture of the soil and the occurrence of layers of gravel were also noted. Three profiles were examined from the Dot, Blue Rock and Mount Rae study areas, and five profiles were taken on the Missing Link Flat. The results are presented in Table II.

The characteristics of the soil profiles from the Missing Link area most closely fit the description of the chernozemic shallow black type. The soil depth as measured to the parent material layer or glacial till, varied from approximately 20 to 40 inches. The profiles of the Dot Slope illustrate the

Figure 8. Mount Rae study area.

Figure 9. Mount Rae study area.

influence of topography for the soil at the bottom of the slope is deeper and has a deep rich black A horizon (approximately 9 inches) as compared with the thin A horizon (less than 1 inch) on the slopes. Run off water has probably carried black soil from the slope and deposited it at the bottom. The soil at the base of the slope can be classed as an azonal deep black profile and on the slopes the soil best fits the chernozemic shallow black category. The depth of the soil layer above the gravelly till varies from 21 to 29 inches. At Blue Rock the A horizon is of moderate thickness, but is only dark grey in color. Probably the soil is a shallow black type and the suggestion of an A_2 horizon indicates that the soil is becoming degraded or podzolized. At a depth of about 2 feet, coarse limestone gravel is common.

The Mount Rae study plot in contrast to the other three areas, is situated on podzolic soil rather than chernozem. This indicates that the soil has developed under tree vegetation, although now the slope is open except for scattered alpine fir and Engelmann spruce. The presence of decaying burnt logs indicates that a fire swept the area many years ago. The parent material of the soil appears to be gravelly till and shale, found at depths varying from 17 to 36 inches, although gravel is found throughout the B horizon.

Table II. Soil characteristics of the four study areas, 1960.

Study Area	Profile Type	A Horizon Mean Thickness (in.) A_1	A Horizon Mean Thickness (in.) A_2	B Horizon Mean Thickness	B Horizon Structure	Mean Depth to Gravelly Till (in.)
Missing Link	Shallow black	5 (1-12)*	-	23 (18-28)	Compact silty clay	29 (19-40)
Dot Slope	Shallow black (slope)	1	-	22 (18-28)	Compact clay clay-loam	26 (21-29)
	Deep black (bottom)	9	-			
Blue Rock	Shallow black (degraded)	6 (4-8)	-	16 (15-18)	Silty clay	25 (23-27)
Mt. Rae	Grey wooded (podzolized)	1 (1-2)	5 (2-7)	18 (12-24)	Compact clay loam	25 (17-36)

* Bracketed numbers, range in thickness (inches).

Climate. In the cordilleran region which includes the study areas on the east slope, altitude rather than latitude is generally the climatic determinant (Dom. Bur. Statistics, 1959). As the westerly winds pass over the cordillera, they cool and lose moisture. Precipitation decreases eastward, especially in the lee of the successive mountain ranges. Usually a slightly heavier precipitation belt occurs in the region between the mountains and the prairies. High mountains often act to disperse or divert rain clouds and thus certain localities in a given region may receive more rain than others. Heavier precipitation seems to occur at the higher elevations such as the Blue Rock and Mount Rae study areas as compared to the other two areas.

Diurnal temperature variations are high, varying as much as 40° Fahrenheit, and summers are hot in the Sheep River region (Table III). Chinooks are also pronounced in southwestern Alberta and they occur in the Sheep River locality. Chinooks can cause a rapid temperature increase of as much as 60° Fahrenheit in one day. Consequently early spring thaws may result and thus affect the emergence times of the ground squirrels.

The prevailing wind in the Sheep River region during the summer, is largely from the west and is responsible for snow and rain. In spring and early summer at the higher elevations, strong cold winds blow down the valleys from the persisting snow on the high peaks such as Mount Rae, Blue Rock and the Highwood Range. The

high mountains disrupt the normal westerly circulation and can cause complete reversals of wind direction in minutes. In late summer when most of the alpine snow is gone, the winds have diminished little in velocity, but are usually warm and dry. During the hot and dry weather in July, these winds are largely responsible for extracting moisture from the soil and promoting ripening of the vegetation.

In 1960, daily records were kept of maximum and minimum temperatures and precipitation. Tables III and IV show these data in condensed form.

Table III. Mean weekly temperature (^{o}F) records at Gorge Creek, 1960.

Months	Weeks	Weekly Means Max.	Weekly Means Min.	Monthly Means Max.	Monthly Means Min.	Extremes Max.	Extremes Min.	Number of frost days
May	1-7	52.4°	30.0°	59.3	32.2	66	26	15
	8-14	68.0	35.0			82	29	
	15-21	54.7	33.3			62	26	
	22-28	59.0	39.2			66	21	
May 29 - June 4		67.4	39.2	69.6	37.9	74	32	4
June	5-11	70.0	35.3			78	31	
	12-18	68.6	35.0			76	32	
	19-25	69.0	39.0			78	32	
June 26-July 2		71.0	42.0			77	39	
July	3-9	80.0	39.3	83.4	44.1	87	34	0
	10-16	83.5	45.5			92	36	
	17-23	87.6	50.7			94	46	
	24-30	88.0	41.6			92	34	
July 31-Aug. 6		70.0	46.6			78	41	
August	7-13	79.7	44.0	72.4	42.0	86	38	2
	14-20	74.3	43.0			82	36	
	21-27	67.0	38.0			78	32	
Aug. 28-Sept. 3		72.4	36.8			85	32	
Sept.	7-14	79.0	35.0					

Table IV. Mean weekly precipitation for Gorge Creek, 1960.

Months	Weeks	Precipitation Snow (Inches)	Precipitation Rain (Inches)	Total Monthly Precipitation (Inches)	Days of Precipitation	Maximum 24 hour fall (Inches)
May	1-7		.08	1.19	15	.06
	8-14		-			-
	15-21	.56	.26			.56
	22-28		.22			.22
May 29-June 4			.28			.17
	5-11		.56	3.3	15	.54
	12-18		1.57			1.04
	19-25		.43			.41
June 26-July 2			.94			.39
July	3-9		-	.56	9*	.04
	10-16		trace			trace
	17-23		.01			.01
	24-30		trace			-
July 31-Aug. 6			3.38	4.24	14	1.11
August	7-13		.53			.48
	14-20		trace			trace
	21-27		.44			.16
August 28-September 3**			-			trace
September 7-14			.19			unknown

* During these nine days in July only trace amounts of rain fell.

** Some snow occurred but no records were taken.

Figure 10. Sighting quadrat line.

Figure 11. Chart quadrat.

Biotic Features

Vegetation.

(a) Methods of Analysis - A chart quadrat one meter square was selected as a convenient measuring device for recording the frequency of occurrence and the percent crown coverage of both the shrub and herb strata (Oosting 1958). The quadrat frame was divided by string into eight equal rectangles for convenience in mapping (Figure 11). Species occurrence was recorded and the approximate leaf and crown coverage of all but the most insignificant plant species was mapped to scale on ruled graph paper. Later the quadrat maps were analyzed and the area covered by each plant species in each quadrat was measured. The cover values of plant species covering less than 25 square centimeters of a given quadrat were not included in the data, but the occurrence was noted. The frequency of occurrence and percentage of total cover for each species in all the quadrats, were tallied and the means were calculated for the study areas (Tables V, VI, VII, and VIII).

The sampling quadrats were distributed randomly within a sampling square 100 yards in linear dimensions. A 100-yard-long transect string bisected the square and ran through the mid portion of the study area and at right angles to the slopes at Mount Rae and Dot. The string was divided into 10

intervals by markers spaced 10 yards apart. Every marker on the transect string indicated the midpoint of a 100 yard long quadrat line at right angles to the transect string. Therefore, in each sampling square there were 10 lines, 100 yards long, perpendicular to, and bisected by the transect string. Each quadrat line was sighted from the transect marker with a home made transit (Figure 10). Ten stations were located on each quadrat line at intervals of 10 yards. The stations were numbered and the station to be sampled was determined by drawing a number from a hat. The quadrat was placed at a site corresponding with the randomly selected number, by pacing off the required distance from the transect marker.

Four sampling squares were set up on the Missing Link flat. One square was established on each of the first four sectors and consequently 10 quadrats were mapped in each of the four sectors, making a total of 40 quadrats for the area. On the other 3-acre areas, only two sampling squares were utilized. The two squares were located adjacent to each other and thus 20 quadrats were mapped.

Vegetative sampling was carried out on the Missing Link study area in late July and early August of 1959. The Mount Rae study plot was sampled in the third week of August, 1959. In August, 1960, the quadrat analyses were continued on the Dot slope, and on Blue Rock flat.

Comparisons of the four study areas in regard to plant composition and percentage of cover is insufficient if the actual yields of forage produced on the areas are not considered. This is especially important when grazing, slope and altitude are critical factors.

The forage yields on the study areas were determined from square-meter samples of clipped vegetation. Ten square-meter quadrats were taken on each study area. The clip quadrats were laid out in a systematic fashion, and an attempt was made to distribute them evenly over the 3-acre study area. On the Missing Link flat only a 3-acre portion of sectors II and III was sampled. A line was paced off through the middle of the plot. Ten positions on the line were determined and were spaced equal distances apart; the lengths of the intervals varied with the length of the study plot. At each position on the line the meter frame was tossed either to one side or the other. The sample was clipped wherever the frame landed.

The vegetation occurring within the meter frame was clipped level with the ground surface and raked into a bag. Later, after the samples had thoroughly dried over a 2-week period, the litter or previous year's growth of forbs and grass was screened out, and the remaining plants were sorted into three categories--grass and sedge, forbs, and shrubs. These sortings of plants were then weighed to an accuracy of 5 grams (Table IX).

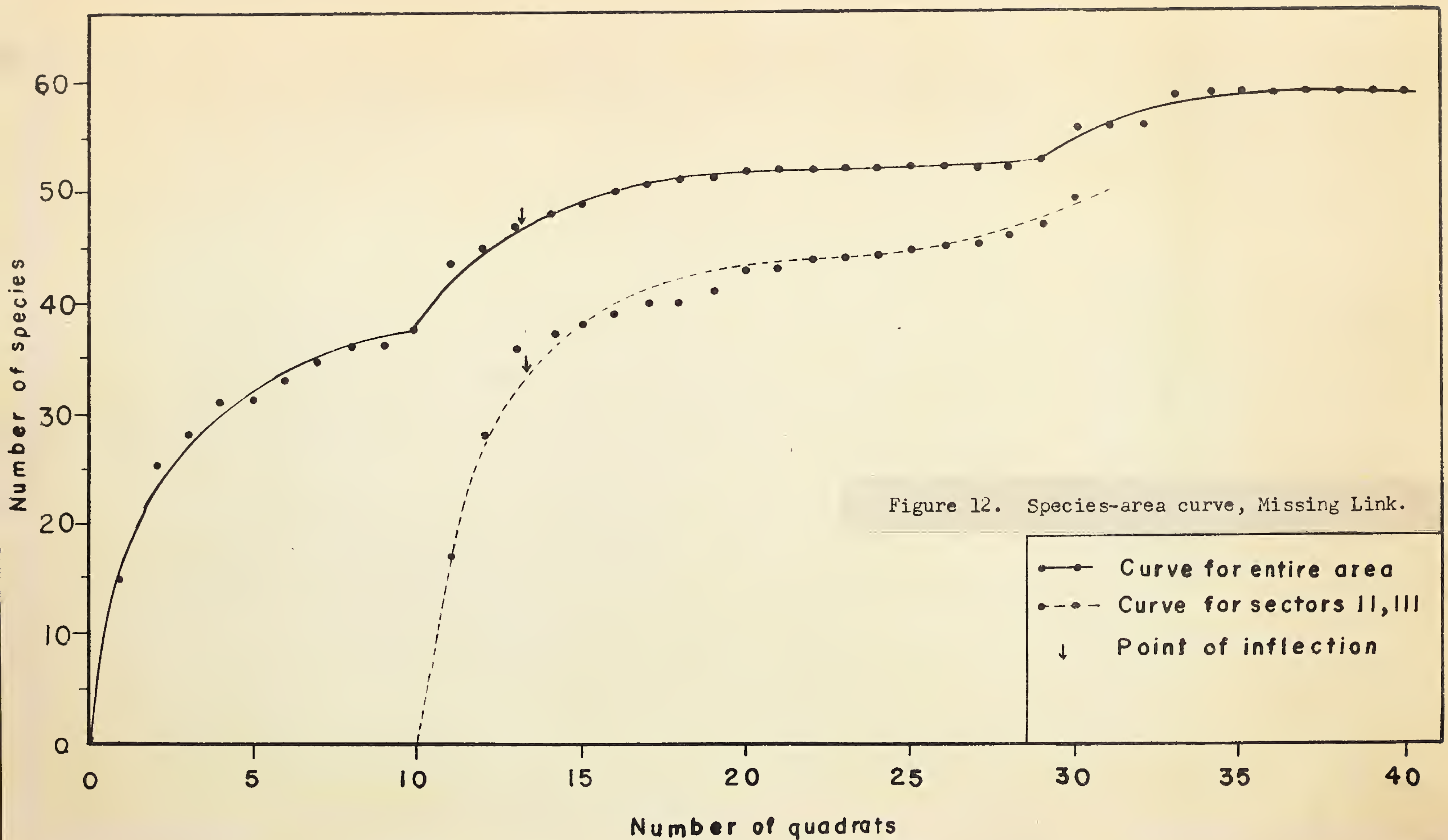

Figure 12. Species-area curve, Missing Link.

In early June of 1959, an exclosure plot 50 feet square was built adjacent to the study area on Blue Rock Flat (Figure 21). Rail fences 7 feet high were erected around the plot to prevent ingress by cattle and big game mammals. Half of the plot was fenced 3 feet above ground and 3 feet below ground level with 1-inch-mesh wire. This was done to keep out ground squirrels. At the top, the wire was bent outward for 6 inches to discourage squirrels from climbing the fence.

The exclosure plot was to serve as an ungrazed control area. The squirrel proof section and the section allowing free access to the squirrels was set up in an attempt to show the effects of forage use by the squirrels. Only one squirrel was seen within the squirrel-proof section and it was discouraged from returning by stopping up the burrow openings. Five quadrats were mapped and two were clipped in each section of the exclosure plot in 1960, two growing seasons after its erection.

Species-area curves were constructed to determine whether the number of map-quadrat samples was adequate to include variation and to show a sufficient representation of species (Oosting 1958). The curve first rises steeply and then flattens out as the first few quadrats record up to 80 percent of the species and additional quadrats record a diminishing number of plant species. According to Oosting, the break in the curve represents the point beyond which extra effort is required to

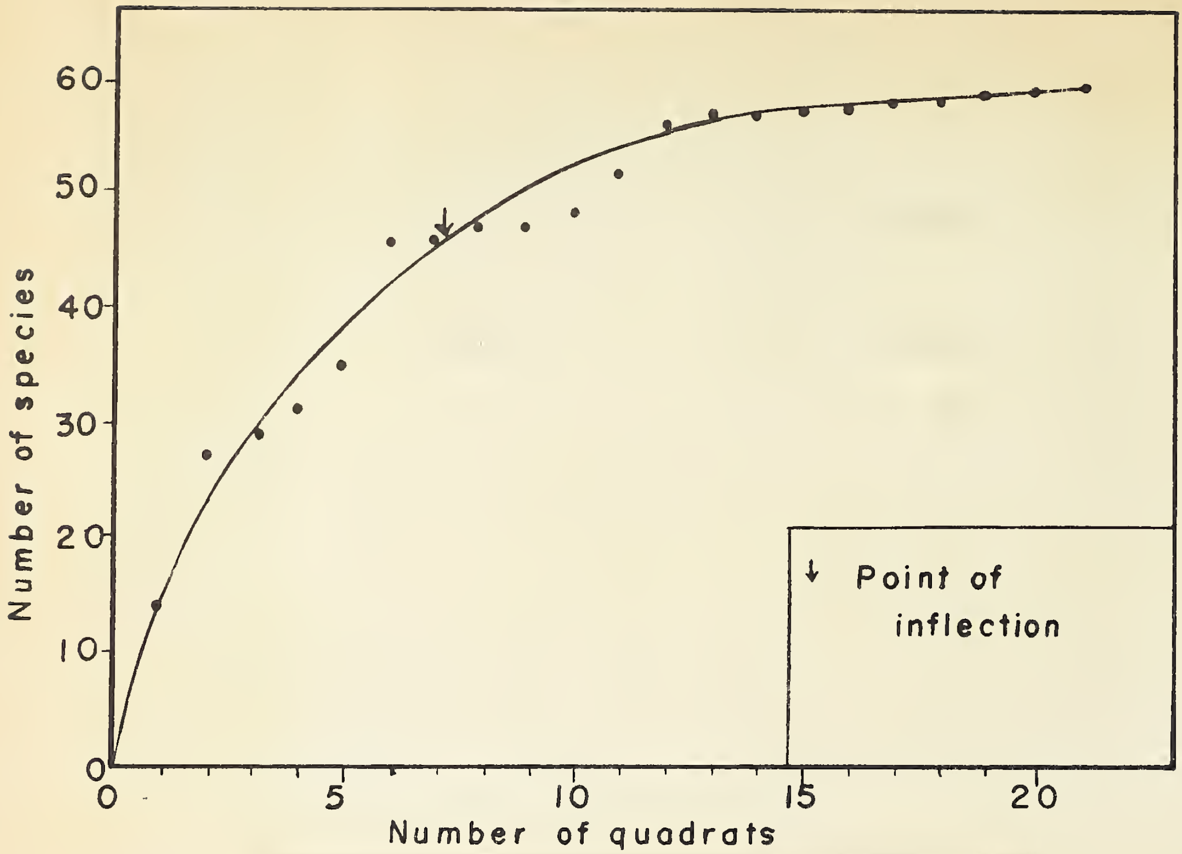

Figure 13. Species-area curve, Dot Slope.

obtain data on these less common species. This point can be assumed to represent the minimum number of quadrats needed to include a representative sample of species. Actually, in practice the number of quadrats should exceed the minimum number. The point of inflection for each curve was determined by plotting a straight line tangent to the curve and parallel to a straight line running through the origin and a point representing 10 percent of the species and 10 percent of the number of quadrats used (Oosting 1958).

The species-area curves of the four study areas show definite leveling off (Figures 12, 13, 14, 15). Only on the Missing Link area do definite breaks occur in the curve. These breaks represent an abrupt accumulation of new species. The first break coincides with a shift in sampling from the ungrazed and partially wooded Sector I, to the open, grazed Sector II. The second break coincides with the change from Sector III to Sector IV which is more heavily grazed.

The points of inflection of the four curves are all well within the sample number of quadrats for each area. Therefore the number of sampling quadrats used on each study area can be assumed to be adequate to sample most of the plant species. Curves for all four study areas show the inflection point corresponding to about 80 percent of the sampled plant species.

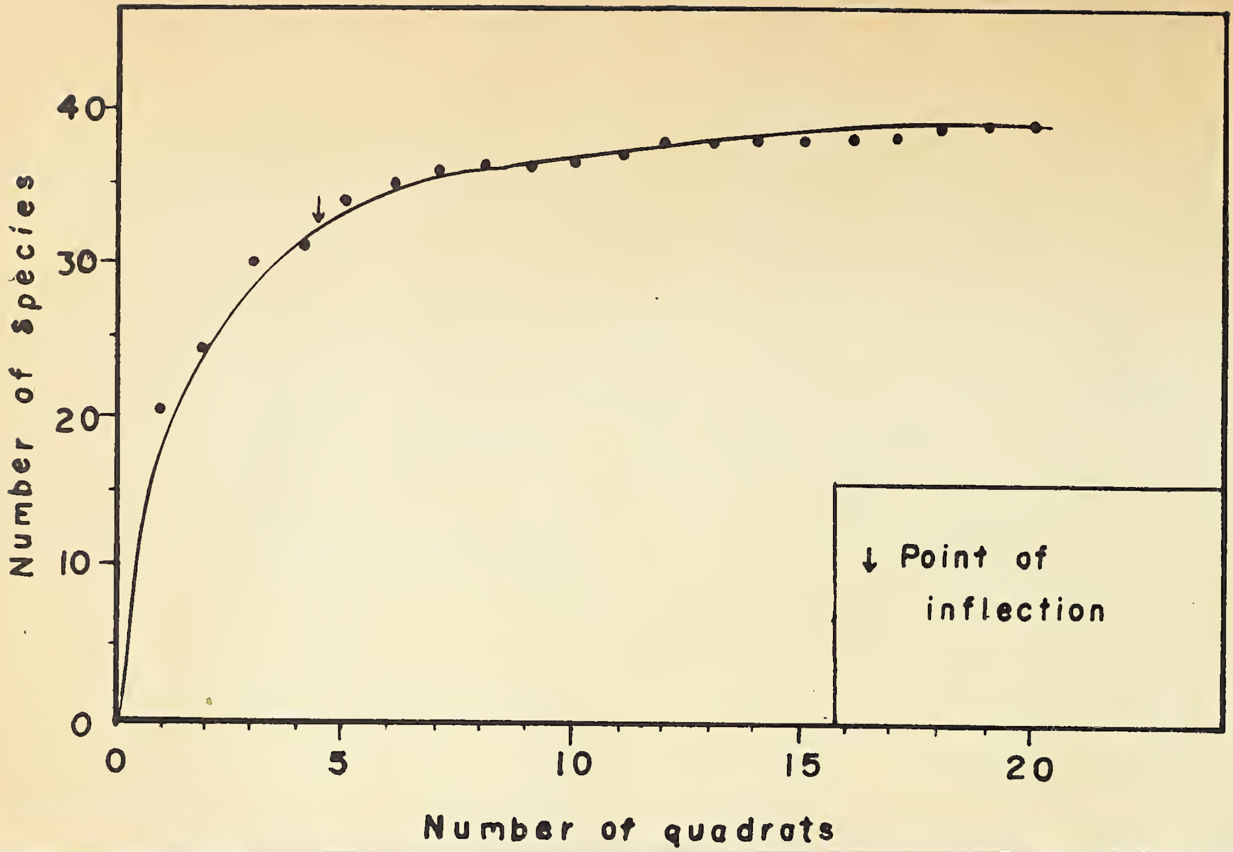

Figure 14. Species-area curve, Blue Rock.

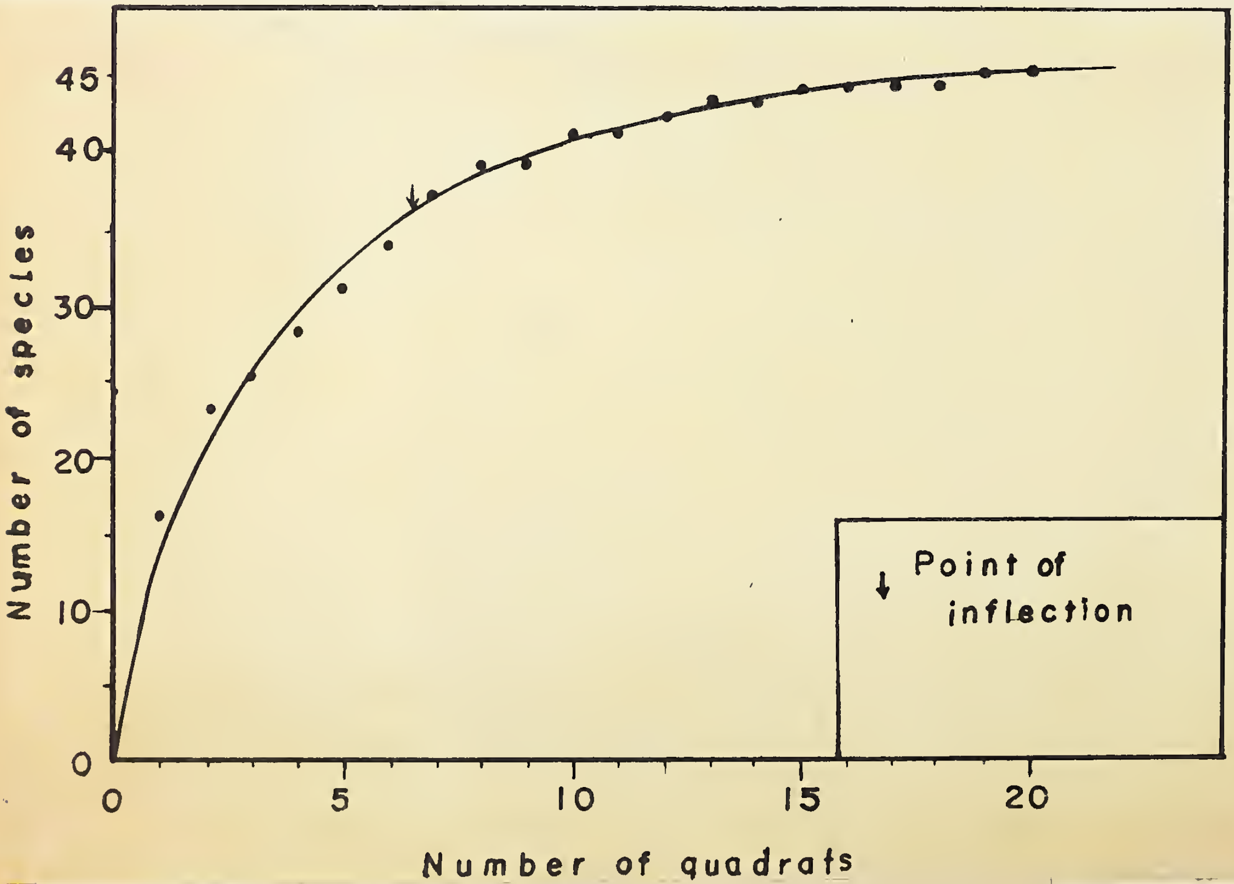

Figure 15. Species-area curve, Mount Rae.

(b) Major Forest Communities - Two broad phytogeographic zones occur in the upper portion of the South Sheep River drainage--the boreal-cordilleran transition and the subalpine forest. The study areas are associated with forest communities within these zones. The white spruce association is the chief climax forest community of the transition zone; and Engelmann spruce and alpine fir are the dominant climax species in the subalpine zone at elevations of 6,000 to 7,000 feet (Moss 1955). At lower elevations, from 4,000 to 6,000 feet, aspen groves are found in the moister soils and in the ravines and draws of the higher foothills. Aspens appear to be invading grasslands in this region. However, only on local protected sites, do aspens appear to compete successfully with conifers.

Lodgepole pines are common on gravelly sites or on burnovers, usually in even-aged stands. Mature, climax white spruce stands are only found in areas which have escaped severe fires for a considerable period of time. Usually these stands are found along streams or in sheltered valleys in the Sheep River region. Other minor forest communities are found in close proximity to the study areas. Douglas fir, *Pseudotsuga taxifolia*, and limber pine, *Pinus flexilis*, are found along the Missing Link Mountain escarpment just above the Missing Link and Dot Slope study areas. Engelmann spruce, alpine fir and alpine larch are

dominant trees on the Mount Rae study plot.

(c) Major Grassland Communities - The characteristic climax grassland community of the submontane mixed prairie in south-western Alberta is the Festuca scabrella-Danthonia association described by Moss (1955). Festuca idahoensis and Danthonia parryi are the two grass species often associated with Festuca scabrella, and the former two species are considered as subclimax to the latter. Danthonia parryi dominates in local areas and is found usually on exposed south facing slopes such as on Missing Link Mountain. Further west on the Blue Rock flat, D. intermedia appears to have replaced D. parryi. Moss lists other grasses such as Koeleria cristata, species of Agropyron and Stipa columbiana as members of the association. These grasses are all abundant in the region studied. However, the composition of the grasslands in the Sheep River region has been altered by utilization and by the introduction of new plant species, so that virtually no virgin climax fescue prairie is left.

(d) Vegetation of the Study Areas

Missing Link Flat: The Missing Link meadow is a grassland undergoing a recent invasion by aspen. The effects of grazing and fire have considerably altered the composition of the vegetation. The abundance of fire weed , Epilobium

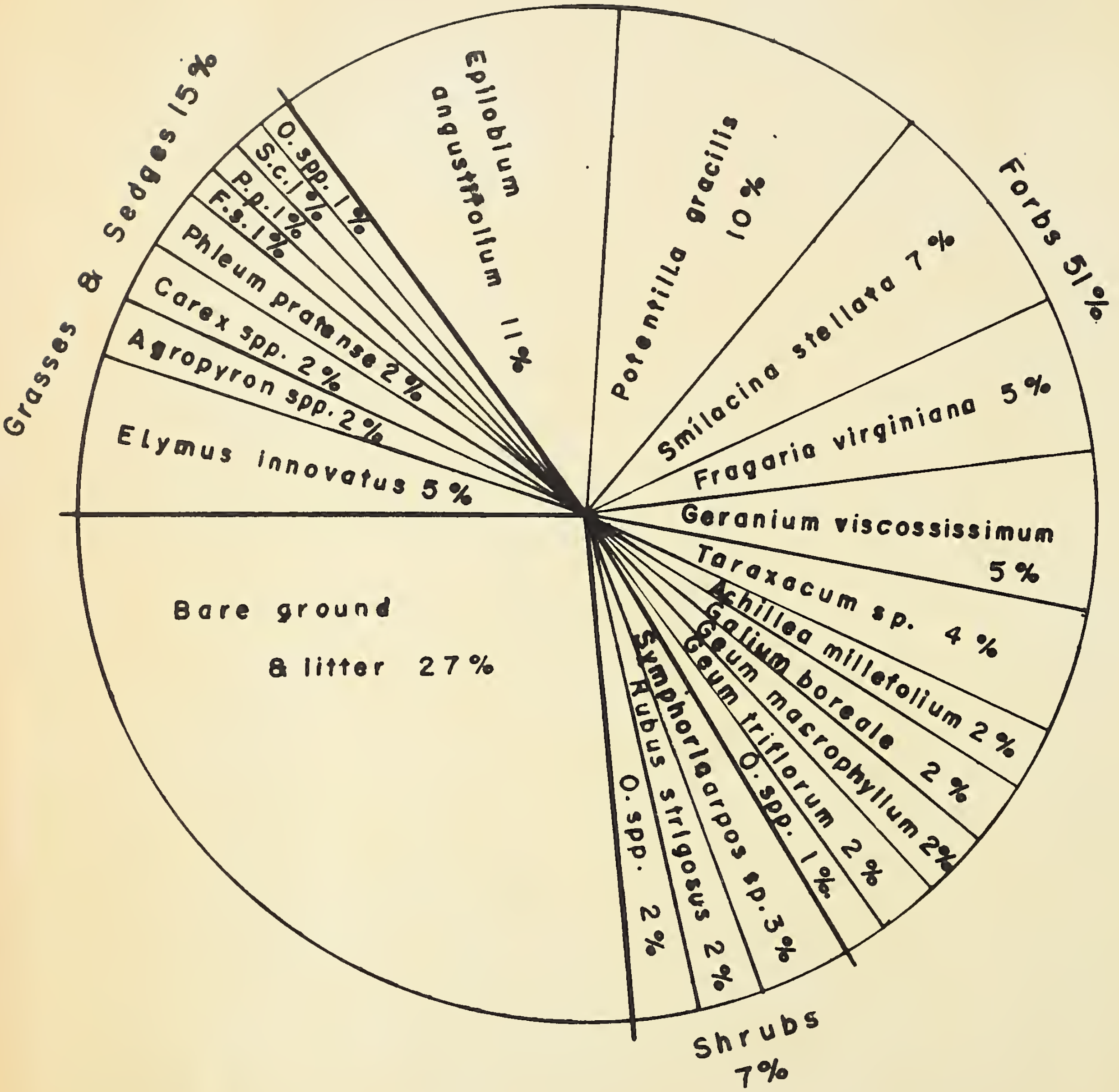

Figure 16. Relative cover of dominant plant species, Missing Link, 1959.

F.s. Festuca scabrella

P.p. Phleum pratense

S.c. Stipa columbiana

O.spp. Other species

angustifolium, indicates that a disturbance such as fire has occurred. Grass and sedge species make up over 13 percent, forbs comprise 48 percent and shrubs make up 4 percent of the total vegetation on the study area. The remaining 33 percent of the sampled area is litter and bare earth.

Grasses typical of the submontane mixed prairie are present on the area, but are not abundant. Festuca scabrella occupies only about 1 percent of the area and Danthonia, Koeleria and Stipa altogether make up only 2 percent of the vegetative cover. The only abundant grass is Elymus covering 6 percent, while Agropyron species cover 2 percent of the sample area (Table V).

Dominant forbs are Epilobium, Fragaria, Geranium, Geum, Potentilla gracilis, Smilacina and Taraxacum (Figure 16). The most common shrub is Symphoricarpos, although Rosa and Rubus are also present. Several introduced plants such as Bromus inermis, Cirsium, Hackelia, Phleum and Hordeum are present, but only show as trace amounts in the sampling.

Dot Slope: The two grass species that are characteristic of the Festuca-Danthonia association are represented on the Dot study area. Danthonia parryi is the most abundant grass occupying about 7 percent of the study area, whereas Festuca only covers

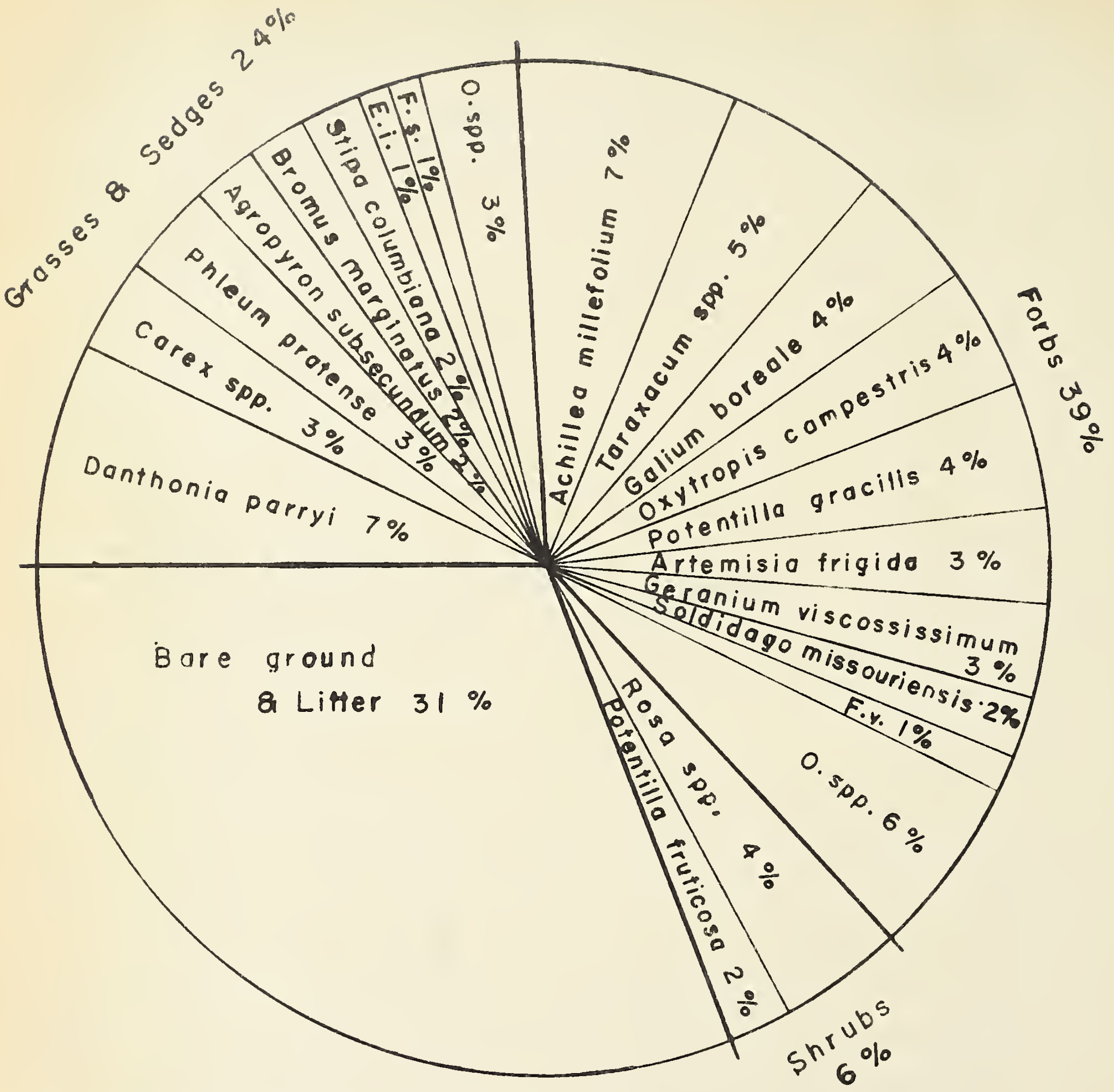

Figure 17. Relative cover of dominant plant species, Dot Slope, 1960.

E. i. Elymus innovatus

F. s. Festuca scabrella

F. v. Fragaria virginiana

O. spp. Other species

1 percent of the area (Figure 17). The comparative scarcity of fescue is probably caused by its intolerance to the southern dry exposure and thin soil, for overgrazing is not a problem on this study area. Danthonia in contrast, does well on such sites and can be maintained as an edaphic subclimax species (Moss 1955). Both Agropyron and Stipa species that are typical of the climax community are common, comprising 4 percent and 2 percent of the area respectively (Table VI).

Grass and sedge species comprise 24 percent of the ground area. Forbs and shrubs occupy 39 and 6 percent respectively (Figure 17). Dominant forbs arranged in decreasing order are Achillea, Taraxacum, Galium, Potentilla gracilis, Geranium, Artemesia frigida and Soldidago. The shrubs Rosa and Potentilla fruticosa are scattered over the slope. Aspen groves border three sides of the study plot.

Introduced species that have invaded the study area are Cirsium, Hackelia, Phleum, Plantago and Taraxacum. The most abundant of these non-native species are Phleum and Taraxacum, comprising 3 percent and 5 percent of the cover area.

Blue Rock Flat: The typical submontane prairie association as described by Moss (1955) has been considerably altered by local edaphic conditions and grazing on Blue Rock Flat. The most abundant grass is Deschampsia caespitosa, a

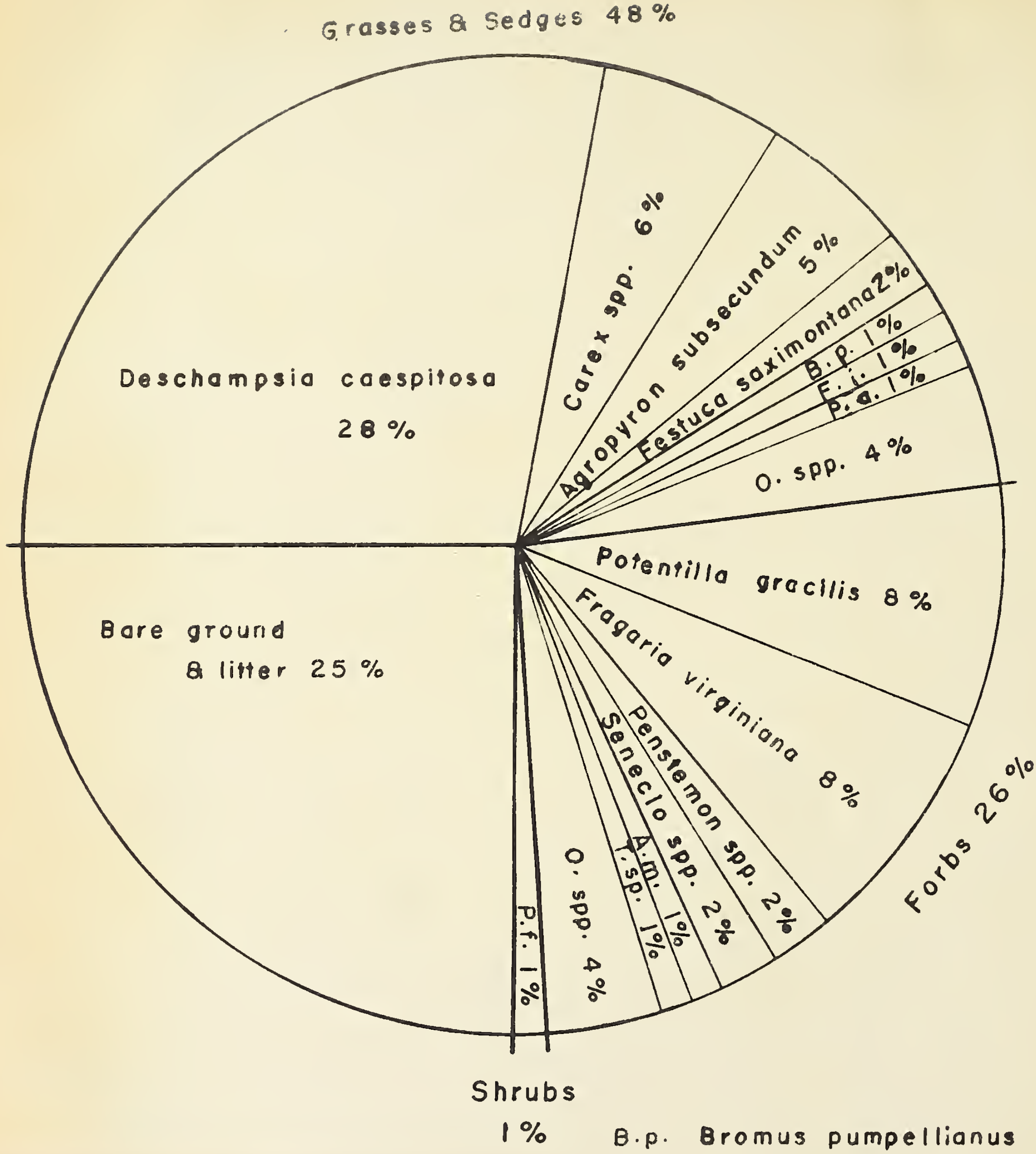

Figure 18. Relative cover of dominant plant species, Blue Rock, 1960.

B.p. Bromus pumpellianus
F.i. Festuca idahoensis
P.a. Phleum alpinum
A.m. Achillea millefolium
P.f. Potentilla fruticosa
T.sp. Taraxacum sp.
O.spp. Other species

species resistant to grazing. It covers 28 percent of the sampled area (Figure 18). New growth sprouts from the dead dry tussocks of previous years growth of the grass, giving the whole flat a hummocky appearance. Deschampsia is chiefly a species inhabiting wet places or moist meadows. The eastern edge of the flat is boggy due to seasonal flooding by springs, and it is possible that this grass spread out from that centre to occupy the drier portion of the flat on which the study area is situated. Heavy cattle-grazing may have enabled Deschampsia to compete successfully with other species.

Several grass species that are typical of the submontane prairie are present, but only Agropyron subsecundum is reasonably abundant, making up 5 percent of the sampled area. Festuca scabrella and Festuca idahoensis are both present but idahoensis is more abundant. In the non-grazed exclosure plot. F. scabrella was absent or very scarce as the species did not occur in the sampling. F. idahoensis covered 4 percent of the area within the plot compared to only 1 percent outside (Table VII). No change in cover area for Deschampsia was noted within the exclosure plot. It is possible that with grazing excluded on the flat, the vegetation would revert to a subclimax state with Festuca idahoensis, being the dominant grass. Moss (1955) regards this species as a subclimax to F. scabrella.

Other grasses such as Koeleria cristata and Danthonia

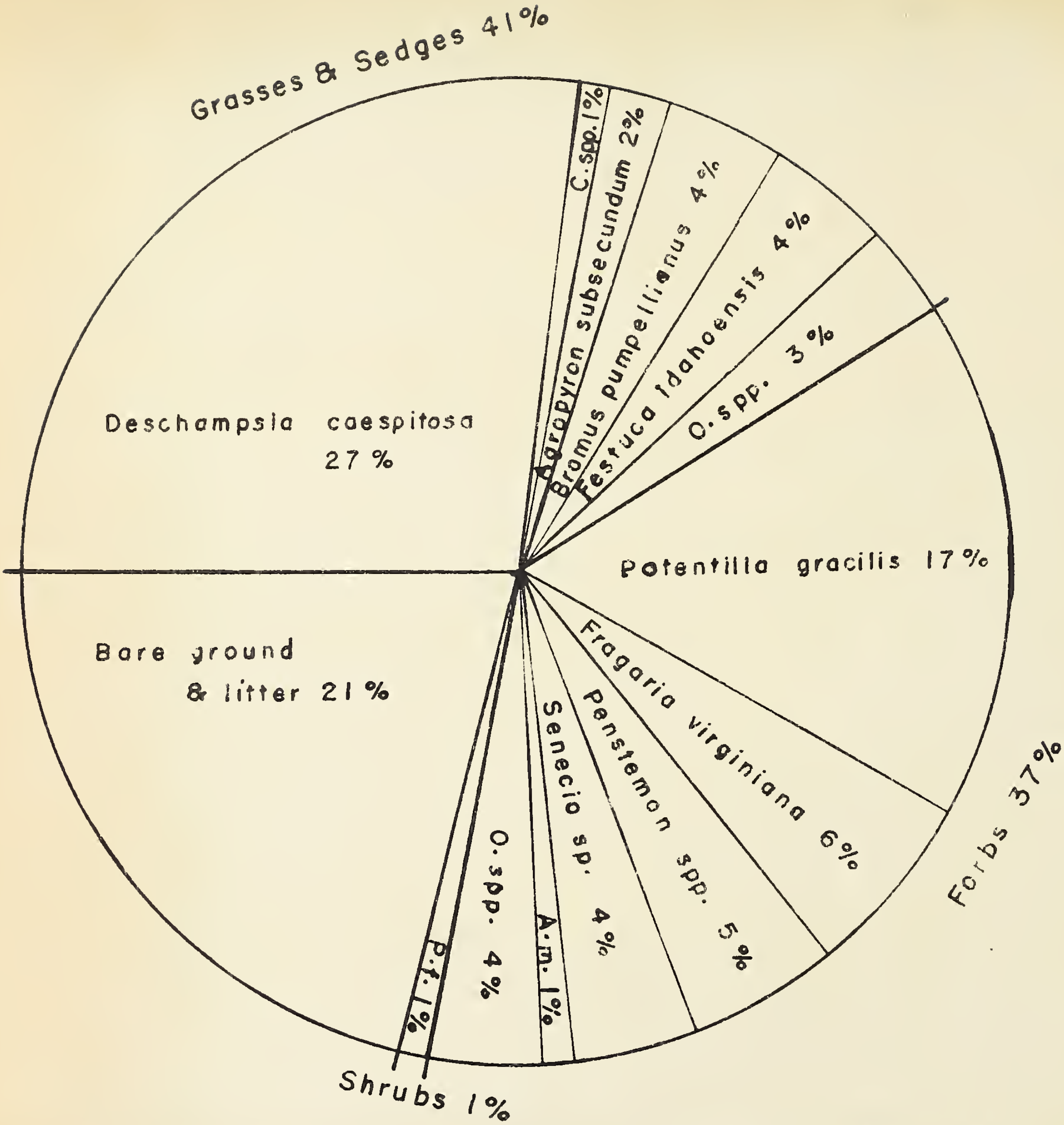

Figure 19. Relative cover of dominant plants in the exclosure plot, 1960.

A·m· Achillea millefolium

C·spp· Carex spp.

P·f· Potentilla fruticosa

O·spp· Other species

intermedia are present, but are not abundant. *D. intermedia* probably has replaced *D. parryi* at this higher elevation.

Grass and sedge species occupy approximately 48 percent of the study area; forbs cover 26 percent and shrubs, 1 percent (Figure 18). The total vegetative cover is about 75 percent with bare ground occupying the remainder of the sampled area. The common forbs are *Fragaria virginiana*, *Penstemon*, *Potentilla gracilis*, *Senecio* and *Taraxacum*. The most abundant shrub on the study area is *Potentilla fruticosa*.

Mount Rae Study Area: The vegetation of the Mount Rae study area is best characterized as an alpine meadow community at the verge of the transition zone between subalpine spruce-fir forest association and the Krummholz, an altitudinal belt in which small groves and individual stunted trees occur (Moss 1955). Species that are included in this meadow type and also found on the study area are *Anemone* spp., *Festuca ovina*, *Poa alpina*, *Potentilla* spp., *Sibbaldia procumbens* and *Trisetum* spp.

This area was once forested and is now undergoing a slow vegetative succession (Page 13). Young Engelmann spruce and alpine larch are invading the open slope. Approximately 16 percent of the area is occupied by shrubby plants such as *Arctostaphylos*, *Potentilla fruticosa* and *Salix*. Forbs cover 29 percent of the area and grass and sedge species make up about

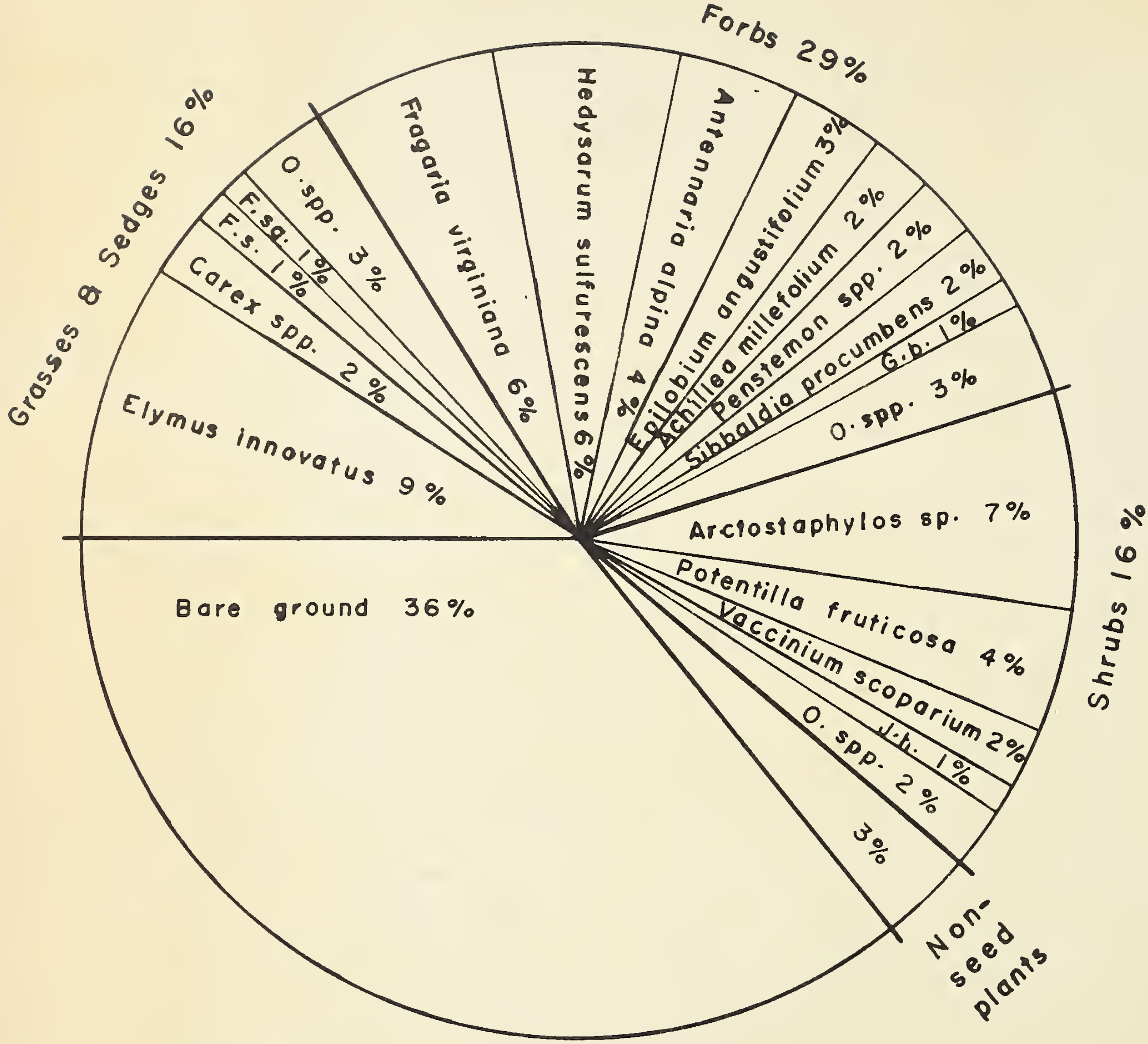

Figure 20. Relative cover of dominant plant species, Mount Rae, 1959.

F.s. Festuca scabrella
F.sa. Festuca saximontana
G.b. Galium boreale
J.h. Juniperus horizontalis
O.spp. Other species

16 percent (Figure 20). Other "trace species" cover 5 percent of the area. The dominant forbs are Antennaria, Achillea, Epilobium, Fragaria, Hedysarum, Penstemon and Sibbaldia. Elymus is the most abundant grass with 9 percent coverage, followed by Carex (a sedge), Festuca and Koeleria, (Table VIII). The relative abundance of Elymus and Epilobium may be related to the effects of grazing and fire, because both species grow well on denuded sites. Bare ground covered approximately 36 percent of the sampled area.

(e) Results of Vegetation Analysis

Table V. Missing Link Flat - composition and relative cover of Vegetation, 1959.

No.	Species	Common Name	Frequency (%)[1] Sectors 2 & 3	Total Sectors	% Cover[2] Sectors 2 & 3	Total Sectors
Grasses and Sedges						
1.	Elymus innovatus	Hairy wild rye	90	90	5.0	6.0
2.	Agropyron spp.	Wheat grass	85	80	2.0	2.0
3.	Carex spp.	Sedge	90	87.5	2.0	2.0
4.	Bromus marginatus	Awned brome	25	35	Tr	1.0
5.	Festuca scabrella	Rough fescue	45	35	1.0	1.0
6.	Phleum pratense	Timothy	40	37.5	2.0	1.0
7.	Poa pratensis	Kentucky blue grass	80	55	1.0	1.0
8.	Stipa columbiana	Columbia needle grass	45	37.5	1.0	1.0
9.	Agrostis scabra	Hair grass	35	30	Tr*	Tr
10.	Bromus spp.	Brome	-	12.5	Tr	Tr
11.	Bromus inermis	Awnless brome	15	10	Tr	Tr
12.	Bromus pumpellianus	Northern awnless brome	35	25	Tr	Tr
13.	Danthonia parryi	Parry's oat grass	5	-	Tr	Tr
14.	Festuca ovina	Sheep fescue	-	5	-	Tr
15.	Helictotrichon hookeri	Hooker's oat grass	5	5	Tr	Tr
16.	Hordeum jubatum	Foxtail barley	-	2.5	-	Tr
17.	Juncus sp.	Rush	5	12.5	Tr	Tr
18.	Koeleria cristata	June grass	25	35	Tr	Tr
19.	Poa compressa	Canada blue grass	5	2.5	Tr	Tr
20.	Poa sp.	Blue grass	40	37.5	Tr	Tr
21.	Unknown grass		5	17.5	Tr	Tr
Forbs						
1.	Potentilla gracilis	Graceful cinquefoil	95	92.5	10.0	10.0
2.	Epilobium angustifolium	Fire weed	60	72.5	11.0	8.0
3.	Fragaria virginiana	Wild straberry	95	95	5.0	6.0
4.	Smilacina stellata	Solomons seal	75	52.5	7.0	4.0
5.	Geranium viscossissimum	Sticky purple geranium	90	67.5	5.0	4.0
6.	Archillea millefolium	Yarrow	95	95	2.0	4.0
7.	Taraxacum sp.	Dandelion	40	47.5	4.0	2.0

1. Proportion of the total number of sampling quadrats in which a given plant species occurs.
2. Proportion of the sampled area covered by a given plant species.

Table V. (Continued)

No.	Species	Common Name	Frequency (%) Sectors 2 & 3	Frequency (%) Total Sectors	% Cover Sectors 2 & 3	% Cover Total Sectors
Forbs						
8.	Geum macrophyllum	Yellow avens	50	62.5	2.0	2.0
9.	Artemisia ludoviciana var. gnaph.	Prairie sagewort	40	35	1.0	2.0
10.	Galium boreale	Northern bedstraw	90	77.5	2.0	1.0
11.	Geum triflorum	Prairie smoke	60	32.5	2.0	1.0
12.	Aster sp.	Aster	10	15	Tr	1.0
13.	Geranium richardsonii	White flowered geranium	10	27.5	Tr	1.0
14.	Lathyrus ochroleucus	Vetchling	5	22.5	Tr	1.0
15.	Thalictrum sp.	Meadow rue	15	15	Tr	1.0
16.	Agoseris sp.	False dandelion	-	5	-	Tr
17.	Allium textile	Wild onion	5	5	Tr	Tr
18.	Anemone multifida	Cutleaf anemone	10	15	Tr	Tr
19.	Cirsium arvense	Canada thistle	5	2.5	Tr	Tr
20.	Castilleja sp.	Indian paint brush	-	2.5	-	Tr
21.	Erigeron speciosus	Fleabane	-	5	-	Tr
22.	Gaillardia aristata	Gaillardia	5	2.5	Tr	Tr
23.	Hackelia floribunda	Stickseed	5	5	Tr	Tr
24.	Heracleum lanatum	Cow parsnip	5	7.5	Tr	Tr
25.	Lithospermum ruderale	Puccoon	10	10	Tr	Tr
26.	Mitella sp.	Bishop's cap	-	2.5	-	Tr
27.	Plantago major	Plantain	5	5	Tr	Tr
28.	Potentilla pennsylvanica	Cinquefoil	20	15	Tr	Tr
29.	Senecio sp.	Groundsel	-	5	-	Tr
30.	Soldidago spp.	Goldenrod	5	10	Tr	Tr
31.	Urtica sp.	Nettle	-	2.5	-	Tr
32.	Vicia sp.	Vetch	5	-	Tr	-
33.	Zizia aptera	Meadow parsnip	5	5	Tr	Tr
34.	Unknown forbs		10	15	Tr	Tr
Shrubs and Trees						
1.	Symphoricarpos occidentalis	Snowberry	15	15	3.0	1.0
2.	Rubus strigosus	Wild raspberry	15	15	2.0	1.0
3.	Rosa sp.	Wild rose	10	10	1.0	1.0
4.	Ribes sp.	Wild currant	10	5	1.0	Tr
5.	Populus tremuloides	Quaking aspen	15	22.5	Tr*	Tr
6.	Potentilla fruticosa	Shrubby cinquefoil	5	5	Tr	Tr

Tr* = Trace less than 1% of cover.

Table VI. Dot Slope - Composition and relative cover of Vegetation, 1960.

No.	Species	Common Name	Frequency (%)	% Cover
Grasses and Sedges				
1.	Danthonia parryi	Parry's Oat grass	40	7.0
2.	Carex spp.	Sedge	80	3.0
3.	Phleum pratense	Timothy	30	3.0
4.	Agropyron subsecundum	Bearded wheat grass	85	2.0
5.	Stipa columbiana	Columbia needle grass	60	2.0
6.	Bromus marginatus	Awned brome	40	2.0
7.	Elymus innovatus	Hairy wild rye	50	1.0
8.	Festuca scabrella	Rough fescue	40	1.0
9.	Poa pratensis	Kentucky blue grass	50	1.0
10.	Agropyron smithii	Western wheat grass	45	1.0
11.	Agropyron dasystachyum	Northern wheat grass	30	1.0
12.	Agropyron spp.	Wheat grass	25	Tr
13.	Agropyron trachycaulum	Slender wheat grass	20	Tr
14.	Agrostis scabra	Hair grass	10	Tr
15.	Bromus spp.	Brome	10	Tr
16.	Bromus anomalus	Nodding brome	5	Tr
17.	Bromus pumpellianus	Northern awnless brome	10	Tr
18.	Danthonia intermedia	Timber oat grass	5	Tr
19.	Festuca saximontana	Sheep fescue	5	Tr
20.	Helictotrichon hookeri	Hooker's oat grass	30	Tr
21.	Koeleria cristata	June grass	75	Tr
22.	Poa spp.	Blue grass	20	Tr
Forbs				
1.	Achillea millefolium	Yarrow	85	7.0
2.	Taraxacum sp.	Dandelion	85	5.0
3.	Galium boreale	Northern bedstraw	85	4.0
4.	Potentilla gracilis	Graceful cinquefoil	60	4.0
5.	Oxytropis campestris	Loco weed	45	4.0
6.	Artemesia frigida	Pasture sagewort	55	3.0
7.	Geranium viscossissimum	Sticky purple geranium	40	3.0
8.	Soldidago missouriensis	Goldenrod	60	2.0
9.	Artemesia ludoviciana gnaphalodes	Prairie sagewort	40	1.0
10.	Potentilla pennsylvanica	Cinquefoil	40	1.0
11.	Geum macrophyllum	Yellow avens	30	1.0

Table VI. (Continued)

No.	Species	Common Name	Frequency (%)	% Cover
Forbs				
12.	Fragaria virginiana	Wild strawberry	25	1.0
13.	Monarda fistulosa	Horse mint	15	1.0
14.	Cirsium arvense	Canada thistle	5	1.0
15.	Agoseris sp.	False dandelion	35	Tr
16.	Allium cernuum	Wild onion	10	Tr
17.	Androsace septentrionales	Fairy candelabra	15	Tr
18.	Anemone multifida	Cutleaf anemone	25	Tr
19.	Antennaria spp.	Everlasting	5	Tr
20.	Artemisia campestris	Green sagewort	10	Tr
21.	Aster sp.	Aster	5	Tr
22.	Campanula rotundifolia	Bluebell	5	Tr
23.	Epilobium angustifolium	Fireweed	5	Tr
24.	Erigeron speciosus	Fleabane	20	Tr
25.	Gaillardia aristata	Gaillardia	30	Tr
26.	Geum triflorum	Prairie smoke	20	Tr
27.	Hackelia floribunda	Stickseed	10	Tr
28.	Haplopappus lyalli		10	Tr
29.	Hedysarum sp.		30	Tr
30.	Lactuca pulchella	Common blue lettuce	10	Tr
31.	Lithospermum ruderale	Puccoon	5	Tr
32.	Plantago major	Plantain	10	Tr
33.	Potentilla arguta	White cinquefoil	15	Tr
34.	Rhinanthus crista-galli	Yellow rattle	20	Tr
35.	Thalictrum sp.	Meadow rue	10	Tr
36.	Thlaspi arvense	Stinkweed	15	Tr
37.	Unknown forbs		60	Tr
Shrubs				
1.	Rosa sp.	Wild rose	55	4.0
2.	Potentilla fruticosa	Shrubby cinquefoil	20	2.0

Table VII. Blue Rock Flat -- Composition and relative cover of vegetation, 1960.

No.	Species	Common Name	Frequency (%) Main Flat	Frequency (%) Exclosure Plot	% Cover Main Flat	% Cover Exclosure Plot
Grasses and Sedges						
1.	Deschampsia caespitosa	Tufted hair grass	100	100	28.0	27.0
2.	Carex spp.	Sedge	95	80	6.0	1.0
3.	Agropyron subsecundum	Bearded wheat grass	100	100	5.0	2.0
4.	Festuca saximontana	Sheep fescue	65	-	2.0	-
5.	Festuca idahoensis	Idaho fescue	40	100	1.0	4.0
6.	Bromus pumpellianus	Northern awnless brome	45	80	1.0	4.0
7.	Poa spp.	Blue grass	65	40	1.0	Tr
8.	Koeleria cristata	June grass	60	30	1.0	Tr
9.	Phleum alpinum	Alpine timothy	45	-	1.0	-
10.	Agrostis scabra	Hair grass	40	10	1.0	Tr
11.	Elymus innovatus	Hairy wild rye	60	90	Tr	2.0
12.	Helictotrichon hookeri	Hooker's oat grass	55	80	Tr	1.0
13.	Agropyron trachycaulum	Slender wheat grass	25	40	Tr	Tr
14.	Danthonia intermedia	Timber oat grass	40	-	Tr	-
15.	Festuca scabrella	Rough fescue	40	-	Tr	-
16.	Juncus sp.	Rush	40	40	Tr	Tr
17.	Muhlenbergia richardsonii	Matmuhly	5	-	Tr	-
18.	Poa alpina	Alpine blue grass	5	-	Tr	-
19.	Unknown grass		30	10	Tr	Tr
Forbs						
1.	Potentilla gracilis	Graceful cinquefoil	100	100	8.0	17.0
2.	Fragaria virginiana	Wild strawberry	80	90	8.0	6.0
3.	Penstemon spp.	Beard tongue	80	100	2.0	5.0
4.	Senecio sp.	Groundsel	80	90	2.0	4.0
5.	Achillea millefolium	Yarrow	85	90	1.0	1.0
6.	Galium boreale	Northern bedstraw	90	70	1.0	1.0
7.	Aster sp.	Aster	55	40	1.0	1.0
8.	Taraxacum spp.	Dandelion	55	40	1.0	Tr

Table VII (Continued)

No.	Species	Common Name	Frequency (%) Main Flat	Frequency (%) Exclosure Plot	% Cover Main Flat	% Cover Exclosure Plot
Forbs						
9.	Potentilla diversifolia	Diverse leaf cinquefoil	45	20	1.0	Tr
10.	Geum macrophyllum	Yellow avens	20	50	Tr	1.0
11.	Agoseris sp.	False dandelion	25	-	Tr	-
12.	Androsace septentrionales	Fairy candelabra	15	10	Tr	Tr
13.	Anemone multifida	Cutleaf anemone	15	20	Tr	Tr
14.	Antennaria sp.	Everlasting	20	-	Tr	-
15.	Gentiana sp.	Gentian	15	-	Tr	-
16.	Geum triflorum	Prairie smoke	5	-	Tr	-
17.	Soldidago sp.	Goldenrod	5	10	Tr	Tr
18.	Thalictrum sp.	Meadow rue	55	80	Tr	1.0
19.	Vicia sp.	Vetch	5	-	Tr	-
20.	Unknown forbs		20	30	Tr	Tr
Shrubs						
1.	Potentilla fruticosa	Shrubby cinquefoil	20	20	1.0	1.0

Table VIII. Mount Rae Study Area - Composition and relative cover of vegetation, 1959.

No.	Species	Common Name	Frequency (%)	% Cover
Grasses and Sedges				
1.	Elymus innovatus	Hairy wild rye	95	9.0
2.	Carex spp.	Sedge	90	2.0
3.	Festuca scabrella	Rough fescue	75	1.0
4.	Festuca saximontana	Sheep fescue	60	1.0
5.	Koeleria cristata	June grass	40	1.0
6.	Bromus pumpellianus	Northern awnless brome	30	1.0
7.	Poa spp.	Blue grass	50	Tr
8.	Poa rupicola		40	Tr
9.	Poa alpina	Alpine blue grass	35	Tr

Table VIII. (Continued)

No.	Species	Common Name	Frequency (%)	% Cover
10.	Deschampsia spp.	Tufted hair grass	5	Tr
11.	Juncus sp.	Rush	5	Tr
12.	Phleum alpinum	Alpine timothy	5	Tr
13.	Trisetum spicatum	Spike trisetum	5	Tr
14.	Unknown grass		15	Tr
Forbs				
1.	Fragaria virginiana	Wild strawberry	85	6.0
2.	Hedysarum sulfurescens		75	6.0
3.	Antennaria alpina	Alpine everlasting	80	4.0
4.	Epilobium angustifolium	Fireweed	75	3.0
5.	Achillea millefolium	Yarrow	90	2.0
6.	Penstemon sp.	Beards tongue	85	2.0
7.	Sibbaldia procumbens		10	2.0
8.	Galium boreale	Northern bedstraw	60	1.0
9.	Anemone multifida	Cut leaf anemone	50	Tr
10.	Pyrola sp.	Wintergreen	50	Tr
11.	Potentilla gracilis	Graceful cinquefoil	45	Tr
12.	Mitella sp.	Bishop's cap	30	Tr
13.	Antennaria pulcherinna	Showy everlasting	30	Tr
14.	Anemone sp.	Anemone	20	Tr
15.	Androsace septentrionales	Fairy candelabra	15	Tr
16.	Oxytropis sp.	Loco weed	15	Tr
17.	Senecio sp.	Groundsel	15	Tr
18.	Androsace chamaejasme	Sweet flowered androsace	10	Tr
19.	Arnica cordifolia	Heart leaf arnica	10	Tr
20.	Unknown forbs		40	Tr
Non seed plants				
1.	Unidentified Bryophyte	Moss	35	2.0
2.	Cladonia spp.	Lichen	5	Tr
3.	Equisetum scirpoides	Horsetail	20	Tr
4.	Unidentified Lichen		20	1.0
Shrubs and Trees				
1.	Arctostaphylos sp.	Bearberry	40	7.0
2.	Potentilla fruticosa	Shrubby cinquefoil	55	4.0
3.	Vaccinium scoparium	Grouse-berry	20	2.0
4.	Juniperus horizontalis	Juniper	10	1.0

Table VIII. (Continued)

No.	Species	Common Name	Frequency (%)	% Cover
5.	Salix sp.	Willow (Mountain)	5	1.0
6.	Artemisia michauxiana	Sage wort	20	Tr
7.	Vaccinium myrtilis	Low bilberry	10	Tr
8.	Larix lyalli	Alpine larch	5	Tr
9.	Picea engelmanni	Engelmann spruce	5	Tr

Table IX. Comparative yields of the vegetation on the four study areas, 1960.

	Missing Link Sectors II & III	Dot Slope	Blue Rock Main Flat	Blue Rock Exc. Plot	Mt. Rae
Grass and Sedge	180[1] (46)[2]	150 (70)	40 (67)	320 (90)	15 (8)
Forbs	175 (45)	50 (23)	10 (16.5)	35 (10)	15 (8)
Shrubs	35 (9)	15 (7)	10 (16.5)	- -	160 (84)
Mean Forage Production (Gms.)	390	215	60	355	190
Estimated yield per Acre (kilograms)	1,650	900	250	1,500	800

1. Mean dry weight (gms.) of vegetation per square meter.
2. Percentage by weight of the various vegetation types

Figure 21. Exclosure plot, Blue Rock Flat.

Figure 22. Vegetation inside exclosure.

Figure 23. Comparison of vegetation inside exclosure with vegetation on the grazed main flat, Blue Rock.

(f) Study Areas, Comparisons

The Missing Link and Dot study areas both exhibit richer flora than the other two areas. A maximum of 59 and 60 species were recorded in the sampling for Missing Link and Dot, and only 39 and 45 species were found on the Blue Rock and Mount Rae areas. Only 12 species of plants are constant on all four areas (Table X). Twenty-seven species are concurrent on three areas and 59 species are represented on at least two of the study areas.

Table X. Comparisons of the cover values (%) of plant species common to all study areas.

Species	Missing Link	Dot Slope	Blue Rock Main Flat	Blue Rock Exc. Plot	Mt. Rae
1. Achillea millefolium	2.0	7.0	1.0	1.0	2.0
2. Anemone multifida	Tr	Tr	Tr	Tr	Tr
3. Bromus pumpellianus	Tr	Tr	1.0	4.0	1.0
4. Carex spp.	2.0	3.0	6.0	1.0	2.0
5. Elymus innovatus	5.0	1.0	Tr	2.0	9.0
6. Festuca scabrella	1.0	1.0	Tr	-	1.0
7. Fragaria virginiana	5.0	1.0	8.0	6.0	6.0
8. Galium boreale	2.0	4.0	1.0	1.0	1.0
9. Koeleria cristata	Tr	Tr	1.0	Tr	1.0
10. Poa spp.	Tr	Tr	1.0	Tr	Tr
11. Potentilla fruticosa	Tr	2.0	1.0	1.0	4.0
12. Potentilla gracilis	10.0	4.0	8.0	17.0	Tr

An interesting comparison of the vegetation composition can be made between the squirrel-proof and the unfenced portion of the exclosure plot (Table XI). Eight species were selected and an

analysis of variance was made on the percentage cover data. The "F" value calculated was 12.38 at 39 degrees of freedom. This value is significant at the .01 probability level and one can assume that the two sections show differences in vegetation composition over and above sampling error.

Table XI. Comparison of cover values (%) and frequency of selected*** plants in the two sections of the Exclosure Plot, 1960.

Species	Frequency Control*	Frequency Non Control	% Cover Control	% Cover Non Control
1. Potentilla gracilis	5**	5	20.0	14.0
2. Fragaria virginiana	4	5	5.0	6.0
3. Bromus pumpellianus	4	4	2.0	6.0
4. Festuca idahoensis	5	5	5.0	3.0
5. Agropyron subsecundum	5	5	3.0	1.0
6. Elymus innovatus	5	4	3.0	Tr
7. Carex spp.	4	4	1.0	1.0
8. Taraxacum officinale	4	-	Tr	-

* Control - Squirrel-proof section
** Frequency - Total sample plots in each section were five.
*** Plants selected on basis of food and as range indicators.

The mean yields of vegetation for the four study areas were compared by an analysis of variance (Table IX). A separate test was conducted for grasses-sedges and for forbs. In both cases the analysis showed a significant difference at the .01 probability level in the mean yields of the four study areas. Therefore, the differences in the sample means probably cannot be attributed to errors in sampling.

The Missing Link Flat produced the most forage by weight,

and the Blue Rock Flat produced the least (Table IX). The exclosure plot yielded the most grass per unit area (320 gm.), whereas the Mount Rae area yielded only 15 grams. The yield of forbs was highest on the Missing Link area (175 gm.) and lowest on the grazed Blue Rock Flat (10 gm.). The Mount Rae area shows the highest yield of shrubs (160 gm.) per unit area whereas Blue Rock shows the least (10 gm.). Almost six times the weight of forage was produced in the exclosure plot compared to the main flat at Blue Rock (Table IX). A higher yield of grasses and a lower yield of forbs occurred in the exclosure plot.

Animal Associates

A number of mammals and birds utilize the study areas for habitation or food. These animals can be classed into three groups--the competitors, the buffer species, and the predators. The competitors actively compete with ground squirrels for food and living space whereas buffers do not necessarily compete, but serve as alternate prey for predators.

The chief competitors of ground squirrels on the study areas are large ungulates and pocket gophers, *Thomomys talpoides*. On the Missing Link Flat, the only domestic stock present are horses that belong to the local rangers. The horses averaged about six in number and grazed the area, with the exception of Sector I, throughout the year. The Dot Slope and Missing Link

areas are also part of the essential winter range of bighorn sheep (Wishart 1958), and are grazed by those animals in winter and spring. Deer also utilize grass in the spring before foliage appears on the choice browse species. Herds of deer and flocks of sheep, numbering as high as 50 individuals, have been seen on or near the two study areas. In the last few years, wapiti have occasionally been seen on the areas, but the numbers have been too few to affect the forage seriously. However, a herd of about 50 wapiti was seen in the vicinity of the Mount Rae plot in June, 1959, and the abundance of droppings on this area indicates they exert considerable grazing pressure. On the Blue Rock study area occasional sightings of deer, wapiti, and moose, Alces americana, were made. However, only the latter two species are known to be common on the flat.

In 1960, 108 cattle were pastured on Blue Rock Flat, beginning on June 10. These cattle were left for 4 months to graze three flats. They occupied the study area and vicinity for about a month before being moved to another pasture. Similarly 49 cows and 2 bulls were moved to the Rae Creek area, which includes the Mount Rae study plot, on June 17. Presumably these cattle were left there the whole summer.

Pocket gopher diggings were prevalent in Sectors I and II of the Missing Link area and at the bottom of the Dot Slope. On the Blue Rock and Mount Rae study areas, no evidence of

pocket gopher activity was found.

Common buffer species found on the Missing Link area are red squirrels, Tamiasciurus hudsonicus, chipmunks, Eutamias amoenus, and deer mice, Peromyscus maniculatus. Birds such as magpies, Pica pica, sparrow hawks, Falco sparverius, blue grouse, Dendragapus obscurus, and ruffed grouse, Bonasa umbellus, were abundant on the Dot Slope and Missing Link Flat.

The most important predator of the Columbian ground squirrel in the Sheep River region is the golden eagle, Aquila chrysaetos. The badger, Taxidea taxus, probably is second in importance. Badgers, or their fresh diggings, and eagles have been seen regularly on the four study areas. In fact, a pair of eagles have nested on Missing Link Mountain for several years. Only once, during the period of study, did the eagles successfully raise an eaglet. This was during 1958, and a food study made that year and during 1955, will be discussed later.

The importance of the weasels Mustela frenata, as ground squirrel predators is unknown. Probably weasels can be ranked as one of the three chief predators. Several weasels have been seen on the Dot area and Missing Link Flat. The presence of weasels causes great alarm among the ground squirrels indicating that weasels are greatly feared. In 1960, three weasels were accidentally trapped on the southeast edge of the Dot study area in a three-day period. Also one weasel was live-trapped in

Sector IV on the Missing Link Flat. Therefore, the weasel population is undoubtedly higher than observations alone would indicate. Weasels may be more effective than other predators because of their ability to enter ground squirrel burrow systems.

Coyotes, Canis latrans, are not very abundant in the upper Sheep River region due to persecution by man. However, coyotes have been seen on all four study areas. A pair of coyotes was seen on Blue Rock Flat in 1959 and two were seen on the Missing Link Flat in 1958. Also in 1958, one young cinnamon bear, Euarctos americanus, was observed several times about Missing Link mountain and the adjacent study areas. On the Dot Slope, it attempted to dig out ground squirrels.

Other potential ground squirrel predators were raptors that occasionally visited the study areas. Peregrine falcons, Falco peregrinus, goshawks, Accipiter gentilis, marsh hawks, Circus cyaneus, red-tailed hawks, Buteo jamaicensis, and Swainsons hawks, Buteo swainsoni, were seen on Missing Link Flat. Marsh hawks were observed on all the study areas and red-tailed hawks appeared on the Mount Rae area and nested within 2 miles of Blue Rock Flat.

Figure 24. Adult Columbian ground squirrel.

Figure 25. Young Columbian ground squirrel.

POPULATION DYNAMICS

Reproduction

Breeding Activity. The adult male Columbian ground squirrels usually emerge from hibernation in the spring as much as a week earlier than the females (Shaw 1925c). Specimens collected by Assistant Ranger J. Machovec, showed that the testes were not descended in males that had recently emerged in late April, 1959. In another sample about a week later, the testes were scrotal. Therefore, it can be concluded that the breeding season does not begin until at least a week after the first emergence of adults. The testes remain scrotal for a period of 3 to 4 weeks and then they are withdrawn into abdomen. This period marks the extreme duration of the breeding season. The onset and duration of the breeding season can be affected by weather conditions and the spring thaw.

Columbian ground squirrels breed but once a year. The gestation period is 24 days; the mean litter size is 3.5 and the young emerge at 21 to 29 days of age (Shaw 1925a). The beginning of the breeding season can be estimated from the date on which the first young emerge. If 25 days is taken as the mean age of young squirrels at emergence, then the approximate date of the onset of the breeding season can be determined by back-dating. This has been done for the seasons of 1958, 1959, and 1960 (Table XII), on the Missing Link Flat.

Table XII. Comparisons of Breeding Dates for the three summers, 1958 to 1960.

Year	Date of First Adult Emergence	Date of First Emergence of Young	Estimated onset of Breeding Season	Estimated Beginning of Parturition
1958	April 28	June 22	May 4 ± 4*	May 28 ± 4
1959	April 12	June 26	May 8 ± 4	June 1 ± 4
1960	April 12	June 18	April 30 ± 4	May 24 ± 4

* four days

Some idea of the duration of the breeding season for the year 1958 can be gained from direct observation. A pair of squirrels was seen copulating on May 18 and on May 22. Also the last adult male exhibiting scrotal testes was trapped on May 21. Therefore, the breeding season must have lasted at least 18 days if May 4 is assumed to be the beginning date (Table XII). In 1960, the last sexually active adult male, as determined by the presence of scrotal testes, was trapped on May 7. The duration of the breeding season, if estimated by the method outlined above, would be 7 to 11 days. The brevity of this breeding period may have been related to the early emergence (April 12) and the late heavy snowfall (about 12 inches) during the last week in April

During the breeding period much chasing and fighting occurred among individuals in the Missing Link colony. Members of

mated pairs were observed to wrestle and chase each other on occasion. Serious fighting probably took place between adult males only, for they most frequently had combat scars on the cheeks and muzzle. Females were seldom scarred.

Towards the end of May, 1960, female squirrels were observed carrying nesting material (grass) to the burrows. By June 4 or 5, the adult females were lactating. Therefore the parturition period probably began in the last week in May and the peak may have occurred on or before June 4 (Table XII). The lactation period lasted about 4 weeks and by July 7, the mammary glands were beginning to regress. One adult female was observed suckling a young squirrel within a day or two after emergence of the young. Shaw (1925a) states that the nursing period for this species lasts 30 days. The young squirrels emerge during the third week in June on the Missing Link area (Table XII).

On the four study areas, only about half of the females aged 1 year or older (Appendix A), had reproduced. Of 76 adult and subadult females trapped in 1960, only 47 percent were known to have bred. On the Dot Slope area, 11 out of 20 or 55 percent bred. Similarly at Blue Rock and Mount Rae respectively, 54 percent and 43 percent of the females 1 year or older had given birth to young. Those females that did not breed were usually small in size. In samples from Blue Rock and Mount Rae, the specimens of non-breeding

females were aged as yearlings on the basis of tooth wear (Appendix A). Fewer data are available for males because trapping did not begin early enough to sample a sufficient number of males during the peak of the breeding season. Those males that did not show scrotal or inguinal testes during the short breeding season were small in size averaging 50 to 100 grams less than the breeding males.

Twelve males, weighing 280 to 395 grams were collected from the Blue Rock and Mount Rae areas during the first two weeks of June. These squirrels were classed as non-breeders by the presence of undeveloped scrota and abdominal testes; and they were aged as yearlings by tooth wear (Appendix A). During the same period, in another sample of 13 assumed adult males (Appendix A), all weighing in excess of 500 grams, six were undergoing testicular involution. Therefore, from this evidence, I conclude that yearlings of both sexes do not breed.

Reproductive Success.

(a) Missing Link Flat: In 1958, insufficient information on reproductive success was collected to warrant any interpretations. In 1959, considerably more squirrels were live-trapped and collected on the Missing Link area. Of 44 adult and yearling females live-trapped in 1959, 23 (52%) were in breeding condition. The number of breeding females was obviously greater than the number trapped. Trap and sight counts on the study area revealed

at least 40 litters.

Despite the early emergence of adults on April 12, 1959, the squirrels did not breed until about the first week of May (Table XII). Parturition probably occurred during the end of May since lactating females were not seen until June 2. Young squirrels emerged during the last week in June. Placental scar and embryo counts made on 10 adult females collected in or near the study area, showed a mean of 3.7 per litter with a range of 2 to 6. The maximum number of young squirrels observed per natal burrow was four. Assuming 40 litters of 3.7 each, the annual increment on the study area was about 150 squirrels or 5.2 per acre (Table XIII).

The ground squirrels emerged early in 1960 as they did in 1959. Breeding took place during the first week of May or earlier, and parturition occurred at the end of May (Table XII). The parturition period was marked by the absence of breeding females in the traps. By June 4, the first lactating females were trapped. The first young of the year was trapped two miles west of the Dot Slope on June 18. It weighed only 80 grams and may have emerged prematurely. The first juvenile was observed on the Missing Link Flat on June 25.

There were 76 adult and yearling females trapped in 1960, and 36 (47%) were breeding. Counts of litter sites in 1960 showed that at least 45 females had given birth to young.

Thus, a population of 45 breeding females was assumed for the 28-acre study area. The mean litter size was 3.5, ranging from 2 to 6, as determined from placental scar counts on 12 specimens. The potential annual increment based upon the 45 females was approximately 160 juvenile squirrels or 5.7 per acre (Table XIII).

(b) Dot Slope Study Area: Twenty adult and yearling females were either live-trapped or shot on the 3 -acre area, but only 11 had reproduced. Assuming the mean litter size to be 3.5 as on the Missing Link Flat, then the potential increment was about 40 young squirrels or 13 per acre. This estimate is supported by the fact that 31 juveniles or 10 per acre were recorded by the capture-kill method (See below). However, the latter value is minimal since some juveniles were neither trapped nor killed.

(c) Blue Rock Flat: Out of a sample of 42 adult and yearling squirrels collected in the 3 -acre area, 26 were females (Page 63). Fourteen (54 %) of the females had bred. However, an additional 12 squirrels on the area were not recovered in the sample (Page 63). Assuming the same ratio of females in the unrecovered portion as in the sample, then an estimated 18 breeding females were present on the area. The mean litter size as determined from autopsying the 14 females in the sample, was 4.0 (3-6). The potential increment

for 18 breeding females would have been 72 juveniles or 24 per acre (Table XIII).

Two pregnant females were collected on June 1, and the other 12 breeding females were collected on June 7 and 8. Nine of the 12 collected on the latter dates had recently given birth to young squirrels. Therefore the peak of parturition presumably occurred between June 1 and 8 (Table XIII).

(d) Mount Rae Study Area: On the Mount Rae area, it was assumed that all the breeding females were accounted for in the sample of 46 animals collected (Page 63). Only seven squirrels were not recovered. Twelve of the females or 43 percent had bred. The mean litter size as determined from autopsying the 12 females, was 2.8 (1-4). Therefore the estimated annual increment for the Mount Rae study plot would have been 34 juveniles or about 11 per acre (Table XIII).

The collecting dates of June 17, 18 and 19, coincided with the period when the young were being born. Only 5 out of 12 breeding females still contained embryos. The peak of the parturition period can then be assumed to be the week of June 15 to 21 (June 18 ± 3 days).

Table XIII. Comparisons of Reproductive data for the four study areas.

Area	Year	Estimated Parturition Dates	Females in Sample		Litter Size	Estimated Total Females		Increment	
			No.	Breeding	% Breeding	No.	Breeding	Total	per/acre
Missing Link	1959	May 28-June 5	44	23	52	3.7 (10)*	77	40	148	5.2
Missing Link	1960	May 20-28	76	36	47	3.5 (12)	96	45	158	5.7
Dot Slope	1960	May 23-31	20	11	55	3.5 (12)	20	11	39	13.0
Blue Rock	1960	June 1-8	26	14	54	4.0 (14)	33	18	72	24.0
Mount Rae	1960	June 15-21	28	12	43	2.8 (12)	28	12	34	11.0

* Sample number of autopsied breeding females.

The proportions of breeding females in the samples from the four study areas, including Missing Link Flat 1959, were compared by means of a homogeneity chi square test. The mean of the ratios of breeding to non-breeding females was almost 1:1. This ratio was taken as the theoretical ratio and a chi square value of 1.84 at 4 degrees of freedom was calculated. The chi square indicates that there are no significant differences at the .05 probability level, among the proportions of breeding females on the four study areas.

The mean litter sizes for the four study areas were also compared. The Dot and Missing Link samples were combined to increase the sample size. "T" tests conducted on the raw data, showed no significant differences between the Dot-Missing Link sample and that of the Blue Rock and Mount Rae areas at the .05 probability level. However, a demonstrable statistical difference at the .05 level did show between the Mount Rae and Blue Rock litter sizes.

Growth

Comparisons of Mean Weights.

Introduction: Weight records were obtained from captured squirrels on the Missing Link area throughout the summer period. However the other three study areas were not sampled continuously and therefore no comparisons of growth rates could be undertaken. Nevertheless, the mean weights of the adult-yearling age groups for

Figure 26. Weighing squirrel.

Figure 27. Young ground squirrel showing clipped toe.

the four areas could be compared if samples were taken in phenological periods. Since the populations of the Blue Rock and Mount Rae areas were sampled during the peaks of the parturition periods (Page 52), samples were also taken from Dot and Missing Link areas during their corresponding parturition periods (Table XIII). Data were obtained from live captures on the Dot and Missing Link areas and weights were recorded from specimens collected on the Blue Rock and Mount Rae areas.

Comparisons.

Table XIV. Comparisons of Mean Weights of the Adult-Yearling Age Groups on the four study areas, 1960.

Study Area	Sample Period	Adults and Yearlings No.	Mean Weight (Gm.)
Missing Link	May 25 - June 5	21	470
Dot Slope	May 27 - June 1	31	510
Blue Rock	June 1 - 8	42	450
Mount Rae	June 13 - 19	46	410

These mean weights were compared by unpaired t tests to judge whether there were any significant statistical differences between the localities. The .05 probability level of significance was selected. The weights attained by the squirrels on the Dot Slope were significantly greater than the weights recorded in the Blue Rock and Mount Rae samples. Similarly, the Missing Link sample is statistically

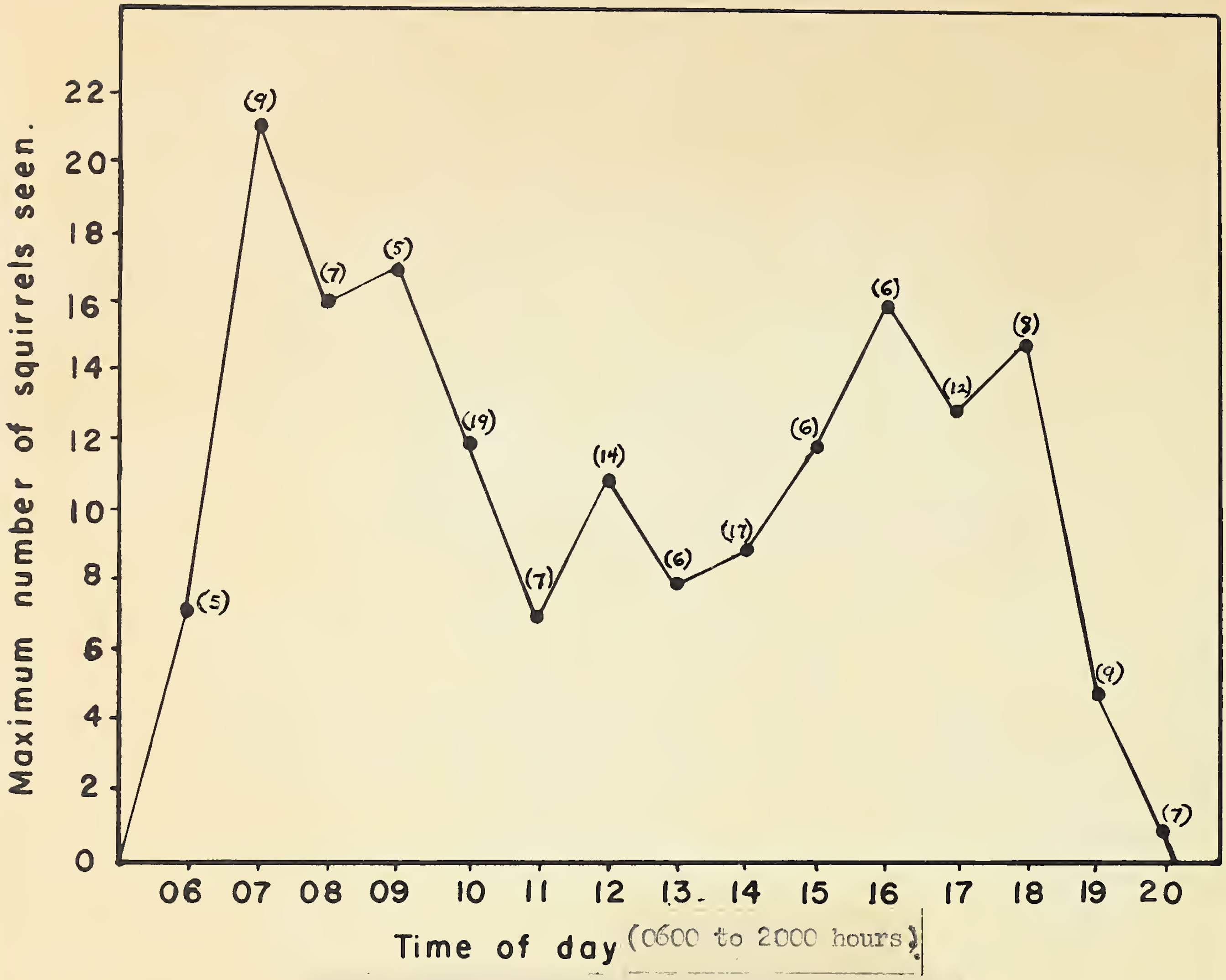

Figure 28. Daily activity periods of the Columbian ground squirrel.

Figures in brackets are the number of counts made at given times during a 19- day period.

different from the sample from the Mount Rae area. The mean weights of the squirrels on the Missing Link area did not show a significant departure from the means on the Dot Slope and Blue Rock areas. However the differences between the Blue Rock and Mount Rae samples are almost significant as the probability lies between .05 and .10 percent. Therefore the squirrels appear to gain weight more rapidly on the Dot and Missing Link areas as compared with the Blue Rock and Mount Rae areas.

Populations.

Techniques.

(a) Counts: In 1958, a triangular 1.5 acre plot, known as the "observation area", was staked out in Sector III of the Missing Link study area (Figure 3). Counts were made on the area by using 7 x 50 binoculars from a high vantage point on the slope of Missing Link Mountain. The binoculars were swept systematically from one edge of the plot to the other, and all squirrels seen within the confines of the area were counted. The duration of the counts lasted 2 to 3 minutes. The counts were made during May and early June before the vegetation grew tall enough to obscure vision. Since it was too early for juveniles to appear, only adults and yearlings were counted. In 1958, counts were conducted at various times of the day in order to establish a daily activity pattern (Figure 28). In 1959 and 1960, the observations were restricted to early morning periods that corresponded to the activity peak. More ground squirrels were active between 0600 and 0900 hours than at any other time of the day. The second activity peak occurred between 1600 and 1800 hours (Figure 28).

In order to determine population density from these counts, it has to be assumed that only the total number of residents within the observation area, was counted. Movements of squirrels onto, or off the area would tend to give either a higher or lower estimate of density. However, since the counts were taken in the morning shortly after the squirrels emerged, most of the squirrels were observed in close proximity to their burrows. It appears that the squirrels are at first hesitant about moving far from the safety of the burrows. Therefore it was less likely that counts would be biased by movements.

On the Missing Link area, shortly after the emergence of young ground squirrels, counts were made to ascertain the number and location of all the litters present. Locations of litters were plotted whenever seen during transect walks throughout the area. Young ground squirrels range only a limited distance from the natal burrow during the first few weeks and hence there was little possibility of duplicating counts. A minimum distance of 20 yards between natal sites was considered sufficient to eliminate overlap.

(b) Burrow Counts: Burrow sampling was carried out on the Missing Link study area in 1958, 1959 and 1960. Only the observation area was sampled in 1958, but in 1959 and 1960, the whole flat, including the observation area was sampled. In addition, the other three study areas were surveyed in 1960.

Burrow sampling was conducted by employing a 50 foot cord attached to a central stake, to describe a circle 100 feet in diameter. All burrow openings within this circle were counted. A systematic system was adopted in the laying out of these circular plots. The observation area was sampled by nine circular plots fitted side by side in a triangular arrangement. The same number and arrangement of plots was used in 1959, and 1960. The other four sectors (I, II, IV and V) were sampled in 1959 and 1960, only, by running a series of adjacent circular plots along a midline through the 1,100-yard-long study area. Thirty-two sample plots were surveyed in 1959, and 33 in 1960 on the Missing Link area. The other three study areas were sampled by nine circular plots arranged in two rows of four or five plots each, on the 3 -acre study areas. The number of burrow openings with mounds, and badger diggings were also tabulated along with the total entrances (Table XV). The total number of sampled burrow openings was later converted into holes per acre.

The number of burrows per acre could be a fairly reliable index of ground squirrel densities. However, since not every burrow entrance represents a burrow system, the average number of openings per system will have to be deduced. Five burrow systems ranging in approximate lengths from 15 to 120 feet, and possessing from two to eight entrances were excavated in 1958.

The excavations revealed that the number of burrow openings

was highly variable, usually depending upon the length and complexity of the burrow system. Therefore the average number of openings per burrow system could not be determined from this small sample. However, burrow mounds only varied from two to four per burrow system in the sample. The fact that certain mounds, which were observed over three summers had increased in size, whereas no new mounds appeared in the immediate vicinity, suggests that most of the excavated earth is usually concentrated into one or two mounds. If two mounds per burrow system is assumed to be the average, then density indices can be estimated for each study area by dividing the number of mounds by two (Table XV).

Table XV. Comparisons of burrow counts and estimates of burrow indices for the four study areas.

Study Area		Burrow Openings per Acre	Estimated Mounds per Acre	Number Openings per Mound	Burrow Index	Badger Diggings per Acre
Observation Area	'58	195	-		-	
Observation Area	'59	200	-		-	
Observation Area	'60	185	30	6	15	7
Missing Link Flat	'59	120	-	-	-	-
Missing Link Flat	'60	115	25	5	12	4
Dot Slope	'60	205	45	4	22	5
Blue Rock	'60	135	45	3	22	25
Mount Rae	'60	255	90	3	45*	28

* Index may be too high because of a great number of badger holes.

The relationship of burrow indices to actual densities is difficult to determine especially when information concerning the numbers of squirrels inhabiting burrow systems is lacking. Several squirrels were known to inhabit the largest excavated burrow, but the actual number was not known. Also, there may be seasonal variation in the number of occupants of a burrow system. Therefore, no attempt was made to convert burrow indices to squirrel densities. However, the burrow indices of the four study areas were compared with the estimated squirrel densities of the same areas (Page 70).

(c) Live-trapping: A program of live-trapping was initiated on and around the periphery of the observation area in 1958. At that time only four traps were available and only 53 squirrels were live-trapped. In 1959 and 1960, 20 aluminum folding Sherman live traps (16" x 4" x 4") were used. No definite grid trapping pattern was adopted for it did not appear to be as efficient as locating traps at burrow entrances. Fitch (1948) also reported better success by placing traps at burrows or along runways. The squirrels tend to restrict their travels to well-beaten pathways through the vegetation and thereby could miss many traps that are employed in a grid. Also the squirrels appeared more vulnerable to trapping when traps were placed at entrances, for frequent encounters with traps made the squirrels

more accustomed to them.

The traps were baited with salted,rolled oats, sunflower seeds, or a mixture of both. All types of bait were effective, but sunflower seeds were preferred in the spring. Trapping was carried out by moving the traps in waves over the entire study area, intensively covering a portion at a time. More intensive live-trapping was undertaken in Sectors II and III than in the other sectors. Traps were spaced a minimum distance of 5 yards apart and whenever a squirrel was captured, the site was marked by a numbered stake. Later, the positions of the numbered stakes were plotted on a map. Each captured squirrel was weighed on a Cave triple beam balance to an accuracy of 5 grams. Individual squirrels were permanently marked by a system of toe-clipping. In addition, some were marked with standard fur dyes and Du Pont Rhodamine B and fast-red dyes, fixed with hydrogen peroxide. However, the dyeing attempts failed. Dyed squirrels that were subsequently recaptured showed that the dye faded considerably in a few days and consequently the marked animals could not be readily distinguished in the field. Other information such as age, moult patterns, and reproductive condition was obtained from captured squirrels.

There are disadvantages in using trapping results as a census technique. The greatest bias is caused by the trap repeaters. These trap-susceptible animals probably reduce the opportunities for

warier squirrels to enter the traps at any particular site. Also some trap-shy animals are never caught. In a few instances, squirrels were seen nosing about a trap, but they were never caught, even after several attempts. Juvenile ground squirrels were generally difficult to trap, especially during the first few weeks above ground. Seasonal differences in trap susceptibility were also noted in adults and subadults. Few adult females were trapped during late May, a period corresponding to the peak of parturition. However, in the first week of June, increasing numbers of adult females were trapped. This is probably related to the females requiring more nourishment to sustain a litter of young. In early May there was a great response to the traps. In an 8-day period in early May, 64 squirrels were captured or recaptured. This excellent success is probably related to the shortage of new green food plants and the corresponding attractiveness of the bait.

The trapping success varied over the three summers. The number of trap days (traps x days set) was 216 in 1958, 780 in 1959 and 1280 in 1960. The number of trapped animals, including recaptures, was 108, 171, and 356 in the three years. These totals yield calculated trapping successes of 50, 22, and 28 percent respectively.

Live-trapping was undertaken on the Dot Slope study area for two short periods of time. The two periods lasted from

May 27 to June 1, and from July 17 to July 25, 1960. Forty-six squirrels were trapped for the first time and there were 26 re-captures. The trapping success was 24 percent.

(d) Shoot-out Census: This technique was devised for accurate counting of the populations on three study areas over a convenient period of time. Basically, the census was an attempt to remove the entire population of squirrels from each of the 3-acre plots--Dot Slope, Blue Rock and Mount Rae. To achieve this end, squirrels were shot and trapped using a .22 calibre rifle, shotguns and Oneida steel traps (#0). An attempt was made to procure as specimens every squirrel thus shot or trapped. Most of the animals were recovered, but some were hit and escaped down burrows. Also a few wary squirrels avoided "capture" by these two methods. Counts were made after periods of shooting to determine how many were still present on the area. The number of squirrels shot but not retrieved, or counted on the area after the sampling ceased, were accounted for as unknowns. There were 12 such unknowns on the Blue Rock area and seven on the Mount Rae plot (Pages 51, 52).

The population of the Blue Rock area was sampled by the above methods on June 1, and during the period from June 6 to 8, 1960. The Mount Rae area was sampled during June 17 to 19 of the same year. These two periods coincided with the parturition

dates (Table XIII), and therefore only adults and yearlings were obtained. The Dot Slope area was sampled, after the two live-trapping periods, from July 24 to 31, 1960. Specimens collected on the Dot area consisted of the three age groups--adults, yearlings, and juveniles. The specimens that were obtained by the shoot-out census were weighed, measured and examined for reproductive condition. Embryos and placental scars were counted, and many skulls were saved for later age determinations (Appendix A).

The shoot-out census appears to be a more accurate method than live-trapping. All age and sex groups of squirrels were susceptible to the sampling as long as they could be approached within gun-shot range. No personal bias in discriminating between such groups of squirrels was involved. Counts made on the Blue Rock and Mount Rae areas were not hindered by high vegetation since both areas were well grazed (Page 11). Therefore it is extremely unlikely that any squirrels would have escaped notice from two observers over a 2-day period.

However, the sampling carried out on the Dot Slope plot was inadequate. The presence of high grass and forbs on the Dot Slope greatly limited visibility and thus several squirrels, especially juveniles, were missed. Also an unfortunate bias was introduced. The absence of certain previously marked adults (Page 73) in the sample and the presence of newly-plugged burrow entrances attested to the fact that some adults and yearlings had

entered into hibernation just previous to, and during the sampling period.

Density

(a) Missing Link Flat: Density values were determined for the observation area only, in 1958 and 1959. Density was estimated from counts made during the morning activity peak (Figure 28) in May and early June (Table XVI). The estimates cannot be applied to the entire Missing Link Flat because trapping results and burrow counts (Table XV) indicate a higher density on the observation area than on the flat considered as a whole.

Table XVI. Densities on observation area.

Year	Squirrels Counted	Number/Acre
1958	21	14
1959	20	13
1960	24	16

The 1960 population of Sectors II and III of the Missing Link area was estimated from capture-recapture data by Hayne's method (1949a). The estimate was based only upon the two sectors because more thorough trapping was conducted there, and a higher proportion of marked squirrels occurred in the trapping samples.

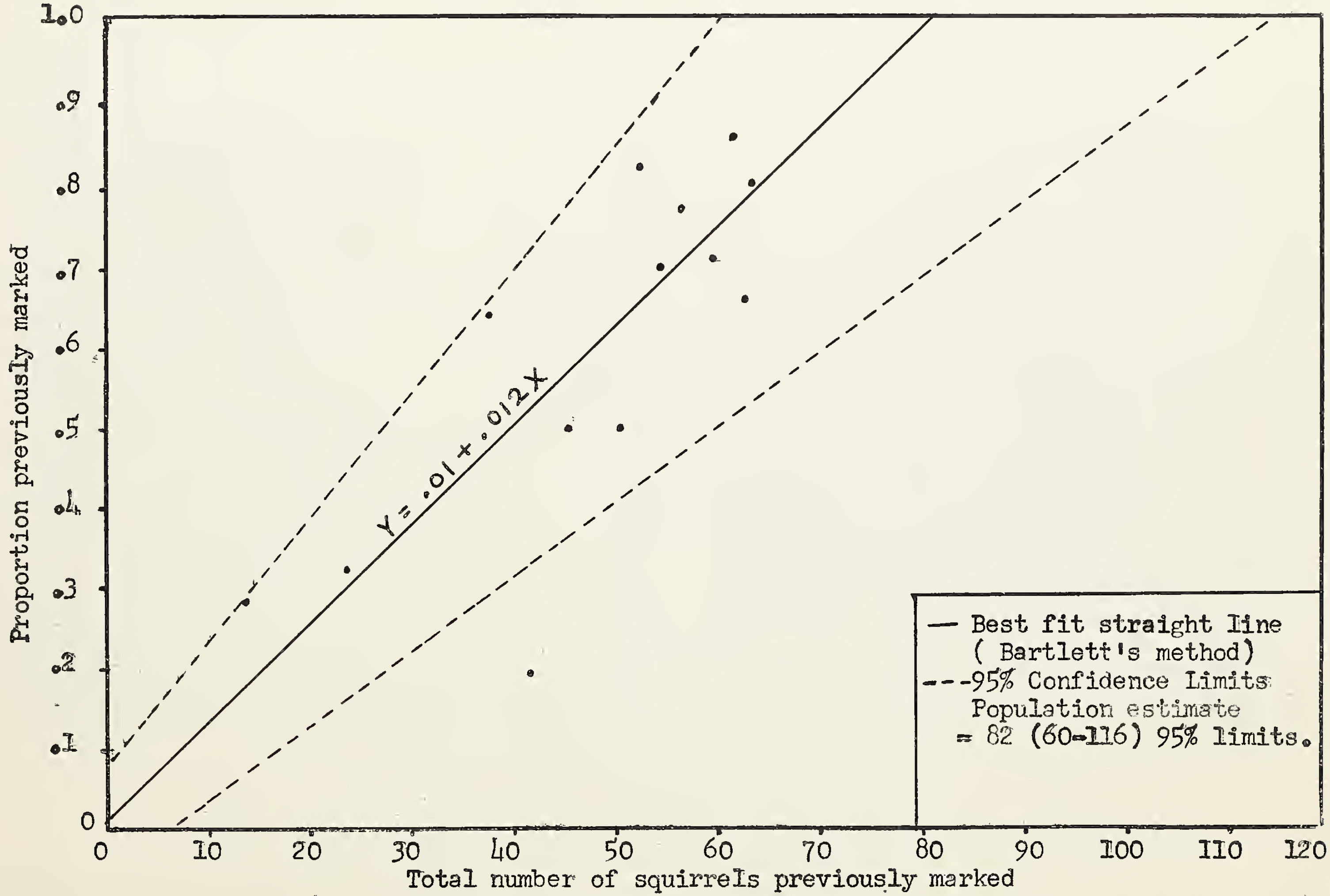

Figure 29. Population estimate for sectors 11 and 111, Missing Link Flat, 1960.

Only adults and yearlings in the sample were considered because the juvenile trapping success was poor. The trapping days were grouped into 2 -day periods. Squirrels that were previously marked in 1958 and 1959 were regarded as new captures when they were caught for the first time in 1960. Subsequent captures in 1960 of these previously marked squirrels were considered as recaptures. The estimate was based upon 64 captured squirrels, in the trapping period, May 4 to July 15.

The data were plotted and a straight line was fitted by Bartlett's method as described by Simpson et al. (1960). The slope of the line and the Y intercept were estimated by the above method and confidence limits at the 95 percent level were determined for both the slope and Y intercepts (Figure 29). A "Y" value of 1.0 indicates that the entire population was marked, and the slope intersecting this value gives the corresponding population estimate on the X-axis.

The population estimate of sectors II and III is 82 using the above method, and the 95 percent confidence limits give a range of 60 to 116 animals (Figure 29). Since the two sectors are about 8 acres in size, the mean density of the area is 10 (7.5 - 14.5)* per acre.

The population of juveniles can be estimated with more reliability from the litter counts. In 1959, about 40 litters were counted giving an estimate of 150 juveniles on the

* Confidence limits (95%) for number per acre.

entire Missing Link Flat. The mean litter size was 3.7 (Table XIII). In 1960, 160 young squirrels were estimated to have been produced on the study area. The approximate juvenile mean densities were 5.2 per acre in 1959 and 5.7 per acre in 1960 (Table XIII). Therefore, assuming the juvenile density of 5.7, the mean density of all age groups in 1960 was about 16 per acre in Sectors II and III of the Missing Link Flat (Table XVII).

(b) Dot Slope: The population of squirrels on the Dot Slope was estimated by three methods--live-trapping, counts, and shoot-out sampling. Thirty-eight adults and yearlings were captured, marked and released. Later a sample of 25 adults and yearlings were collected by shooting and trapping. Of these 25 squirrels, only 14 were unmarked in the live-trapping period. Therefore at least 52 adults and yearlings were accounted for on the area.

Counts that were made on a 1-acre portion of the Dot study area indicated a maximum of 16 adults and yearlings, yielding an estimated population of 48. This estimate agrees with the total number of squirrels handled (see above). The population as estimated by Lincoln's index is about 86 squirrels with a range of 66 to 140 at the 95 percent confidence limits (Adams 1951). However, the estimate by the latter method is probably too high when compared with actual counts of individuals

(see above). Therefore, the population estimate based upon the trap and shoot-out sample was selected, and the estimated density for the Dot Slope was approximately 17 per acre.

The number of juveniles produced on the area can be determined from the number of breeding females present. Eleven breeding females were sampled and if a mean litter size of 3.5 is assumed, then an estimated 40 juveniles or 13 per acre were present on the area (Page 51). Therefore, the total density of all age groups was about 30 per acre (Table XVII).

(c) Blue Rock Flat: Fifty-four adults and yearlings were accounted for in the shoot-out sampling on the Blue Rock Flat (Page 63). However, only 42 squirrels were recovered for age and sex determination. The approximate population size was therefore 54 adults and yearlings or 18 per acre. Since the sampling was not carried out continuously as in live-trapping, no confidence interval can be estimated for the data. However, the accuracy of the sampling method and the reasonably short sampling period indicates that the population estimate is probably quite accurate (Page 64). The estimated expected population of juvenile squirrels was about 72, or 24 per acre (Table XIII). Hence the post-breeding density per acre would have been about 42 squirrels on the Blue Rock Flat (Table XVII).

(d) Mount Rae Study Area: The population on the Mount Rae area was also estimated only by the shoot-out census. Forty-six squirrels were collected and only an additional seven were unretrieved. Therefore, the estimated population was 53 or 18 adults and yearlings per acre. Confidence limits could not be applied (see above), but the estimate is believed to be close to the true population size.

Since at least 12 breeding females were present on the area, the expected number of juveniles would have been 34 or about 11 per acre (Mean litter size = 2.8)(Table XIII). Thus the total density on the Mount Rae area would have been approximately 29 per acre (Table XVII).

(e) Comparisons and Summary of Densities:

Table XVII. Densities on the four study areas, 1958-1960.

Area	Year	Density (Squirrels per Acre) Adult-Yearling	Juveniles	Total
Missing Link	1960			
1. Sectors II & III		10 (7.5-14.5)*	5.7**	16
2. Observation Area				
	1958	14		
	1959	13		
	1960	16		
Dot Slope	1960	17	13	30
Blue Rock	1960	18	24	42
Mount Rae	1960	18	11	29

* Figures represent 95% confidence limits

** Estimate of 5.7 for entire area

The adult-yearling and juvenile densities of the four study areas in 1960 were compared by means of a homogeniety chi square test. A fixed theoretical ratio of .56 adult-yearlings to the total density was assumed. This ratio was obtained by taking the mean of the ratios from the four study areas. The chi square value for homogeneity is 3.43 at three degrees of freedom and it is not significant at the .05 probability level.

In addition to the above test, a chi square test for goodness of fit was conducted on the total densities of the four study areas. A standard value of 29 squirrels per acre, or the mean of the four densities was assumed. The total chi square value at three degrees of freedom is 11.72. This is significant at P=less than .01. The densities of the Missing Link and Blue Rock areas show the greatest departures from the mean and these two areas can be assumed to show real differences in total density, from the densities on the Dot Slope and Mount Rae areas. However, there is no obvious difference in adult-yearling densities on the Dot, Blue Rock and Mount Rae areas (Table XVII).

The densities were compared with burrow indices (Table XV). There was no evident correlation between the indices or burrow counts and the estimated densities. However, the burrow indices do indicate a comparatively low density for the Missing Link area which has a lower population than the other three study areas. However, the unusually high index for Mount Rae is

not comparable with the Dot and Blue Rock areas which support similar densities. Burrow counts may indicate both present and past density, for many burrow systems may be unused if the population has declined. Therefore burrow counts are not necessarily a good criterion for indicating relative abundance of ground squirrels.

Although the densities of adult and yearling squirrels on the four study areas are very similar, real differences in total density do exist. These differences can be attributed to variations in breeding success. The Blue Rock population would attain the highest density because a greater number of young are produced. The Missing Link area supports the lowest density and the total population densities of the Dot Slope and Mount Rae are virtually the same. The possible causes of the variation in the number of young produced on the study areas may be related to food supply (Page 96), but the reason for the uniformity in the adult-yearling densities is not known.

Population Composition

(a) Sex Ratios: Sex ratios were determined from samples of live-captured squirrels on the Missing Link Flat, from both live-caught and dead squirrels on the Dot Slope, and from dead squirrels only, at Blue Rock and Mount Rae. Juveniles were collected only on the Missing Link and Dot areas and they could be aged easily

(Appendix A). Live squirrels could not be satisfactorily aged as yearlings or adults since there was considerable overlap in weights. Therefore the yearling and adult data were combined. However, on the Blue Rock and Mount Rae areas, the adults were segregated from yearlings by criteria set out in Appendix A.

Table XVIII. Sex Ratios.

Study Area	Year	Combined Adults and Yearlings No.	% ♂	Adults No.	% ♂	Yearlings No.	% ♂	Juveniles No.	% ♂
Missing Link	1959	76	42	-	-	-	-	42	43
Missing Link	1960	126	44	-	-	-	-	58	53
Dot Slope	1960	52	60	-	-	-	-	29	41
Blue Rock	1960	42	39	22	38	20	40	-	-
Mount Rae	1960	46	39	25	48	21	29	-	-

The sex ratios of the adult-yearling group on the four areas, were compared by means of a homogeneity chi square test. A 1:1 ratio was assumed. The chi square value of 6.16 has a probability between .10 and .25 . Therefore, the deviations in the sex ratios from the expected 1:1 ratio are not significantly different from one another. The samples of all the areas, with the exception of the Dot Slope, show an excess of females compared to males. The actual proportions of males and females may be roughly 44 to 56,

as shown by the large sample from the Missing Link area, 1960. The apparently greater proportion of males in the Dot Slope sample was probably caused by a greater number of females retiring underground for the season (Page 64). Shaw (1925c) claimed that adult females entered hibernation at least a week earlier than the adult males.

The sex composition of adults and yearlings on the Missing Link area remained about the same in 1960 as compared with 1959. A slight increase in the proportion of juvenile males occurred in the 1960 sample relative to 1959. However, this increase was obviously not significant. The sex ratios of juveniles on the Missing Link and Dot Slope are also not significantly different from each other ($P > .25$).

(b) Age Ratios: The ground squirrels were aged by methods mentioned above and in Appendix A. The data are presented in Table XIX.

Table XIX. Age Ratios and Proportions of the Age Groups.

Study Area	Year	Combined Adults & Yearlings	Juveniles	Proportion of Juveniles	Adults	Yearlings
Missing Link	1959	76	42	36%		
Missing Link	1960	126	58	32%		
Dot Slope	1960	52	29	36%		
Blue Rock	1960	42	-	-	22(52)*	20(48)
Mount Rae	1960	46	-	-	25(54)	21(46)

* Figures in brackets are percentages.

The relative proportions of juveniles on the Missing Link and Dot areas are obviously so similar that there is no need for a statistical comparison. Similarly, there is no difference between the proportions of the adult-yearling age groups on the two areas.
The adults and yearlings outnumber juveniles by two to one. The proportions of adults and yearlings on the Blue Rock area show close agreement with the same age classes on the Mount Rae area. Hence the evidence suggests that the age composition of the populations is quite uniform on the study areas. Also there may be a tendency for ground squirrel populations to maintain a fairly constant age ratio from year to year as shown on the Missing Link area.

Survival and Mortality

Longevity.

Since it has been established that the Columbian ground squirrels in the Sheep River region do not breed until they attain about 2 years of age (Page 49), a life span considerably longer than 2 years is expected. A population of marked squirrels on the Missing Link study area was traced through a 2-year period from 1958 to 1960. In 1958, eight breeding females were captured and subsequently in 1960, three of the eight squirrels were recaptured. Therefore the three squirrels must have been at least 4 years old. A juvenile female was one of 19 squirrels marked in 1955 by Boag (Moore 1955). This individual was subsequently recovered in the shoot-out sample on the Dot Slope in 1960. Consequently, at least 5 years can be assumed to be the life span of this species. According to Shaw (1925a) the oldest known Columbian ground squirrel reached 4 years of age.

Trap Revealed Mortality.

It was possible to estimate the approximate proportion of survivors and conversely the mortality over a 2-year period, from a population of marked squirrels on the Missing Link study area. The basic assumption made was that all the surviving marked individuals were trapped in the year following the marking. This assumption is probably not strictly true because some animals, when trapped once,

Figure 30. Composite survival curve for marked female squirrels on the Missing Link Flat.

became trap-shy and were never recaptured. Also there is the possibility that some marked squirrels moved off the study area. However, any such movement was unknown and was likely to be minimal because of the natural barriers hindering colonization of adjacent areas (Figure 4).

The mortalities of the different age and sex groups were estimated and are presented in Table XX. Mortality was estimated on a yearly basis, that is, from one year to the next. Over the 1958-59 period, males of both age groups experienced higher mortality than the females. In 1959-60, the juveniles appeared to undergo a higher mortality than adults. The difference was tested by means of a contingency table and was found to be significant (chi square = 6.55, $P < .05$. This is to be expected as juveniles usually experience greater mortality than adults. A contingency chi square value of .266 indicates no significant difference between the mortality of the two sexes (1959-60) at a probability greater than .50.

The survival of marked female squirrels on the Missing Link area was traced over a 2-year period. Only females were selected for they could be aged more accurately than males. The squirrels were classed into juveniles, yearling and adult age groups by size and breeding status (Appendix A), and the proportion of females of each age group surviving an additional year was determined. The results are presented in a composite survival curve (Figure 30).

Table XX. Estimated Mortalities of the Sex and Age classes of Columbian Ground Squirrels from 1958-60.

Period	Age Class (Years)	Sex	Total Previously Marked	Subsequently Recovered	Presumed Dead	Mortality %
1958-59	0-1	♂	13	5	8	62
		♀	12	6	6	50
	> 1	♂	14	4	10	71
		♀	14	8	6	43
	Total		51	23	30	59
1959-60	0-1	♂	18	4	14	78
		♀	24	6	18	75
	> 1	♂	34	15	19	56
		♀	44	22	22	50
	Total		120	47	73	60
1958-60	2	♂	27	6	21	78
		♀	24	9	15	63
	Total		51	15	36	71

In the first year of life about a third of the marked squirrels survived. Of the marked yearlings, about 50 percent survived to the second year, and 53 percent of the adults survived an additional year. Thus the curve demonstrates the relationship between age and survival. The juveniles suffer a much higher mortality than yearlings or adults and the mortality rate appears to decrease with age.

Predation Losses

Predation probably accounts for most of the mortality suffered by the Columbian ground squirrel. The predators involved have been mentioned above. A direct assessment of the results of predation is difficult. However, some interpretations can be made from a food habit study conducted on golden eagles for the years of 1955 and 1958, by Boag (1955, 1958). Observations were made of an eagle's nest located on the Missing Link escarpment just above Sector IV of the Missing Link study area. The species and numbers of prey animals that were carried to the eaglet by the adult birds were recorded. In 1955, in a 69 day period, 68 ground squirrels were carried to the nest. The sex composition of these squirrels was 24 females, 41 males and 3 of unknown sex. Hence the results strongly suggest a selective mortality factor operating against males. However, no sex-discriminating mortality was statistically upheld in the trap-revealed mortality of 1959-60 (see above). Nevertheless, this does not disprove that such sex-selective mortality does exist.

In 1958, there was no reference to the number of squirrels taken; but in both years, almost 80 percent of the total prey items procured were Columbian ground squirrels. Observations made in 1958, indicated that a large but unknown proportion of the prey were juvenile squirrels.

The eagles were seen to hunt over other areas besides the

Missing Link Flat. These areas adjoined the Missing Link Flat and included a hayfield, a pasture and an open slope of west Missing Link which included the Dot Slope study area. Columbian ground squirrel colonies occupied the above areas which covered approximately 130 acres. Judging from observations, the populations of the adjoining areas appeared to be comparable with the populations on the Missing Link Flat. Therefore, if the mean density of adults and yearlings for the entire 130 acres is assumed to be about 10 per acre as in sectors II and III, and if six juveniles per acre is assumed (Table XVII), then roughly 16 squirrels occupied an acre. If eagles killed at least 70 squirrels per season (see above), then mortality due to eagle predation would be about 4 percent per year.

Badgers are also important specialized predators and such predation is not limited to the active ground squirrel season. Fresh badger diggings were found in November at Gorge Creek, 6 weeks after all squirrels had begun the hibernation period. A comparison of the badger burrow counts reveals much greater predation on Blue Rock Flat and the Mount Rae Slope (Table XV). Roughly 4 times as many badger diggings were found in the latter two areas as compared with the Missing Link Flat and the Dot Slope. Badgers were seen on all areas but the Mount Rae area in 1959 and 1960.

The effects attributed to other predators are unknown.

Hawks were observed on many occasions attempting to capture ground squirrels, but they were unsuccessful. In a few cases, carcasses of ground squirrels were found, suggesting weasel predation.

Miscellaneous Mortality Factors

Mortality due to such factors as disease and parasites is unknown. No obviously sick or diseased individuals were recovered in the trapping samples. Heavy infections of external parasites were seldom found. Only sucking lice were ever abundant on ground squirrel specimens. These lice were identified as Neohaematopinus laeviusculus by Jellison, 1961. Unidentified fleas and mites were other ectoparasites. It is extremely unlikely that deaths could be caused by such infections. No thorough investigations for internal parasites were conducted, but large stomach nematodes were found in two specimens examined from the Mount Rae plot. These nematodes were identified as Physaloptera sp. (Holmes pers. comm.).

Mortality from human interference was prevented. Only one known case of shooting occurred on the Missing Link Flat and only two squirrels were killed. Extremes of weather such as heavy rains may cause deaths of young squirrels due to exposure. For example, heavy rains occurred in 1960, during mid June (Table IV) a period when young ground squirrels are relatively unfurred and

helpless underground. Also mortality may occur during hibernation. Hibernation is such a taxing physiological state that it has serious effects on teeth and tissues of the body (Mayer 1960). Some squirrels may not have sufficient liver and muscle glycogen stored to meet their needs during the winter. It is possible that a few succomb to freezing temperatures despite the insulation provided in their hibernating cell.

Deaths of individuals could conceivably result from fights during the breeding season. Also the possibility of cannibalism as a mortality factor in juveniles should be considered. No direct evidence of this was found, although it was suspected. Alcorn (1940) reported that adult male Townsend ground squirrels, *Citellus townsendii*, ate their young. Possibly this is an important cause of pre-emergent juvenile mortality.

DISCUSSION

The four study areas are situated at various elevations and as a result corresponding differences in seasonal activity occur. The lengths of the active seasons of Columbian ground squirrels on the study areas were estimated from known dates of emergence, parturition, and hibernation. The squirrels were active for about 18, 17, 17 and 15 weeks respectively on the Missing Link, Dot, and Blue Rock and Mount Rae areas. The shorter season at the higher elevations is probably related to more severe climatic conditions such as persisting snow, lower mean temperatures and fewer frost free days. Also the soil probably remains frozen for a longer period at the higher altitudes, keeping the squirrels underground longer (see below). These conditions delay the growth of vegetation upon which the ground squirrels depend for food.

There is a variation of up to 3 weeks between parturition periods for the Missing Link and Mount Rae populations (Table XIII). The Blue Rock population showed a delay of 1 week compared to the Missing Link colony. Thus similar corresponding delays probably occurred in the emergence of ground squirrels on the study areas. Moore (1937) and Manville (1959) observed similar altitudinal differences in the active season of Columbian ground squirrels in Idaho and Montana. Moore (op. cit.) postulated that an increase of 100 feet in altitude results in a delay of 1 day in the emergence of

young squirrels.

On emergence dates, soil temperatures varied from 45.5° to 57° Fahrenheit at a depth of 20 inches (Wade 1950). Since the lower temperature was similar to soil temperatures encountered during hibernation, Wade concluded that soil temperature was not the major factor controlling the emergence. The thawing and loosening of the soil correlated closely with the emergence of ground squirrels and appreciable rises in temperature above 32° Fahrenheit occurred for almost 10 days prior to the emergence dates. Warm chinook winds can cause premature thawing of the ground in late winter and this may account for some early emergence records such as March 26, 1959 in the Porcupine Hills (Miller pers. comm.).

The active season is terminated when the squirrels go into hibernation. Probably the squirrels do not become torpid immediately for signs of activity were detected in two hibernation burrows excavated at least 2 weeks after all squirrels had gone underground. One squirrel was heard within a burrow and two nests were found vacant. Also fresh earth plugs appeared in a burrow and stores of cut dandelion and poplar roots were found.

The squirrels on the Dot Slope study area went underground at least one week before the Missing Link population disappeared. Shaw (1925b) discovered that Columbian ground squirrels emerge earlier, breed earlier, and go underground earlier in the fall on

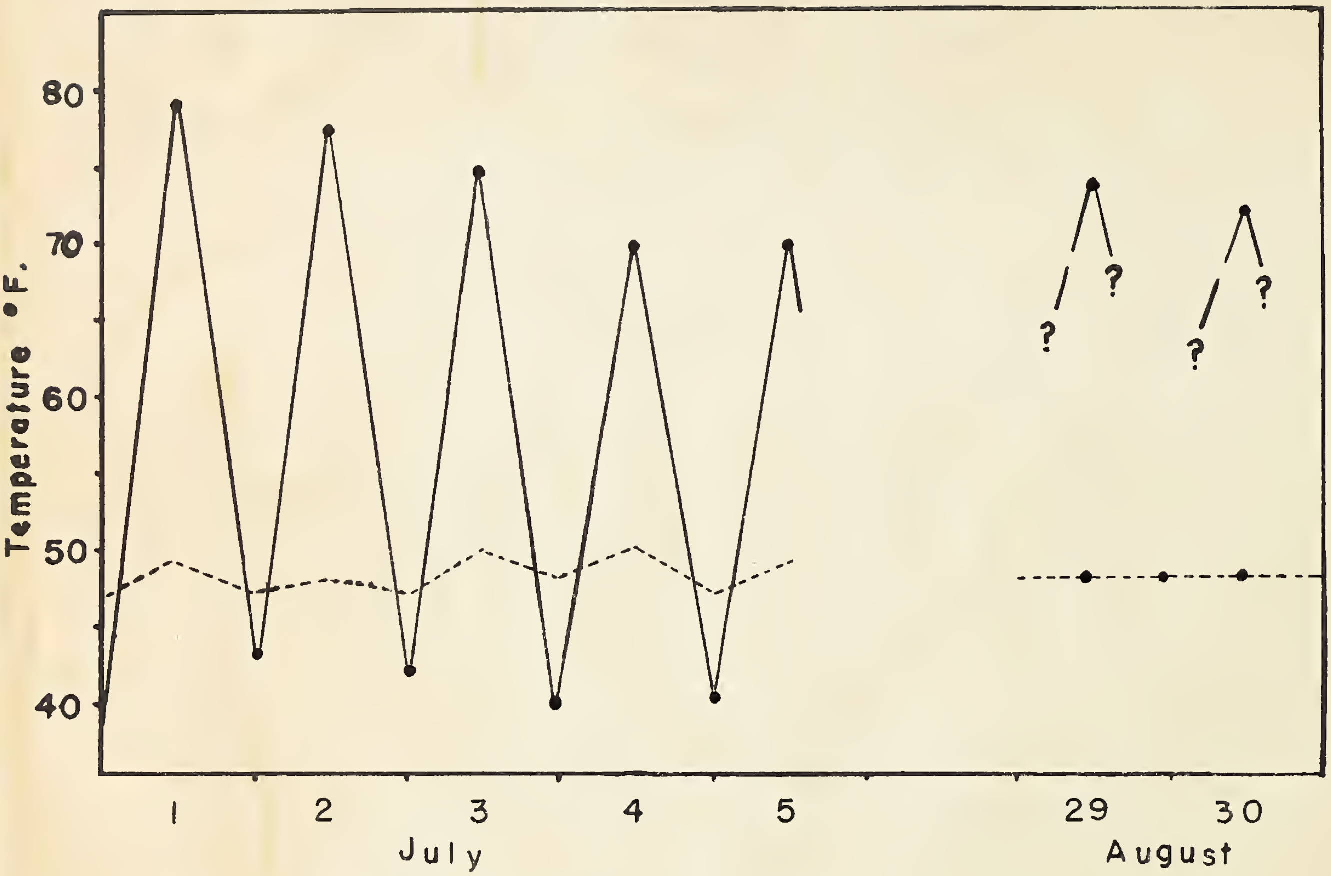

Figure 31. Relationships between burrow and air temperatures taken during periods in July and August, 1959.

Burrow temperatures were taken at a depth of 2 feet with a constant-recording thermometer.

- - - - - - burrow temperature

———— air temperature

Air temperatures were taken with a maximum- minimum thermometer. In August the thermometer failed to record minimum temperatures.

southwest slopes compared to populations on the north-facing slopes. A difference of 10 days was noted between emergence of squirrels on the northeast and southwest slopes of the same hill.

In 1959, all squirrels had disappeared below ground on or before September 4, on the Missing Link Flat. However, one squirrel was still active on the Mount Rae plot on September 12. In 1960, the squirrels in a small colony just 1 mile northeast of Okotoks Mountain, along the south side of the Sheep River (elevation 4,400 feet) (Figure 2), were underground before August 8. On the Missing Link Flat in 1960, the squirrels had disappeared on September 2. Squirrels on the Mount Rae area had denned up earlier than usual by September 5. During the above period a 3-inch snowfall occurred, accompanied by low temperatures and strong cold winds. All squirrels had gone under at this elevation, and a later warming trend did not cause any squirrels to emerge again. However, ground squirrels were still active as late as September 12, 1960, at Burns Lake (elevation 7,500 feet) (Figure 2).

During late August and early September, 1960, when the squirrels on the Missing Link area retired underground, the temperatures were similar to temperatures taken in June when the squirrels were very active (Table III). In 1959, burrow temperatures remained constant (about 48° Fahrenheit) during the first week in July and in late August, despite daily fluctuations in air temperature (Figure 31). On the Dot Slope, adults and yearlings retired as early as the third week of July after a

hot dry 3-week period (Table III). Therefore, there does not appear to be a definite correlation between high or low temperatures and dates of seasonal disappearance.

Shaw (1925c) observed that ground squirrels remained active above ground 2 weeks later in a wet year compared with a year of light snow and rainfall. The warm dry winds during mid summer may increase the transpiration rate of plants and thereby promote ripening by extracting moisture. The loss of available moisture from succulent plants could seriously deprive squirrels of their source of water. On south-facing slopes such as the Dot area, the effects of drought would be accelerated due to longer exposure to the sun. At higher elevations such as Mount Rae, the increased precipitation may delay the ripening period of the vegetation.

The south-facing slopes of the Dot and Mount Rae areas decline on a 36 percent gradient (20°), whereas the Missing Link and Blue Rock areas are undulating to flat. Above the study area, the slope of Dot mountain ascends on a steeper gradient of almost 50 percent, to the escarpment (Figure 5). The density of squirrels on the study area on the lower portion of the slope was high (30 per acre). Definite expansion of the colony occurred in the period from 1959 to 1960, but the squirrels populated only the lower half of the slope and only scattered individuals were found higher. Koford (1958) observed that slopes with a gradient more than 30 percent, were barriers to the expansion of colonies of prairie dogs,

Cynomys ludovicianus.

Squirrels inhabiting the Dot and Mount Rae slopes are not endangered by excess run-off water for natural drainage occurs. On the relatively flat Missing Link and Blue Rock areas lack of drainage is more critical. Heavy rains which are common in June (Table IV) could conceivably drown the occupants, especially pre-emergent juveniles. In order to prevent flooding, squirrels on flat terrain dig burrows with drains to conduct surplus water away from the nesting chambers. In contrast, burrows on slopes lack drains and are usually shorter in length compared to burrows in level ground (Shaw 1926). Three of five excavated burrows on the Missing Link Flat had definite drains or blind tunnels leading to depths of 27 and 40 inches. Nesting chambers were present at depths of 12 to 25 inches. The chambers were usually situated on a higher level than the main burrow to which they were connected.

Soil on slopes is usually shallower than soil in swales or on flat terrain. The depths of soil profiles on the slopes of the Dot and Mount Rae areas were 21 and 17 inches whereas at the bottom of the slopes, the soil layers were 29 and 36 inches deep (Table II). In comparison the average depths of the profiles on the Missing Link and Blue Rock areas were 29 and 25 inches. On the Missing Link Flat the mean depth of five excavated burrows was about 30 inches (18-40 inches), thereby corresponding to the mean thickness of soil above the gravelly till.

The thin soil on the Dot Slope is reflected in a thin humic layer or A horizon and a hard impervious B horizon. Therefore the moisture holding capacity of the soil is limited. On the Dot Slope many of the plants such as Parry's oat grass, needle grass, western wheat grass, the three species of sage and shrubby cinquefoil are tolerant of xeric conditions. Less tolerant plants such as rough fescue are not very abundant and timothy grows on the more level terrain near the bottom of the slope (Table VI). The yields of grasses and especially forbs are higher on the Missing Link Flat compared to Dot (Table IX), although the Dot Slope is the only area free from grazing by domestic stock. The probable cause of the poor range condition on the Dot Slope is related to drought conditions and erosion from run off water. On the Mount Rae area, erosion also affects the character of the vegetation.

The relative yields of grasses and forbs are a good indication of the range condition of the study areas. The areas, arranged in decreasing order from the least to the most depleted range are Missing Link, Dot, Blue Rock and Mount Rae. The vegetation is tallest and more dense on the Missing Link area and the corresponding depletion in forage on the remaining study areas is related chiefly to drought and heavy grazing. The most grazing pressure has been exerted on the Blue Rock Flat where 108 cattle were pastured. Fewer cattle (51) grazed on the Mount Rae area (Page 43). The effects of grazing by big game animals can not be separated from the effects

of total use. However, the poor yield of grasses on the Mount Rae area probably is not entirely due to grazing, but is also related to the less vigorous growth at the high elevation, the competition from shrubs, and erosion caused by trampling. Despite the heavier grazing, the Blue Rock Flat is probably in better condition because of the abundance of Deschampsia, a grass very resistant to grazing (Page 29).

Cattle grazing tends to favor increases of certain plants (see below) while conversely, these plants may decline on undisturbed grasslands where the vegetation is allowed to proceed towards a climax type. On protected grasslands the yield of grasses and sedges may increase by eight fold compared to heavily grazed areas. This is evident in the exclosure plot (Table IX). The increase in height and cover of grasses such as fescue, oat grass, needle grass and June grass may discourage ground squirrels by decreasing visibility and reducing the relative cover of preferred grasses and forbs. Bond (1945) claimed that stands of tall grasses discouraged squirrels and increased their vulnerability to predators. Koford (1958) observed that over-grazing by cattle resulted in an increase of prairie dogs. California ground squirrels thrived best on moderate to heavily grazed areas and total exclusion of grazing led to the disappearance of the squirrels from an area in six years time (Linsdale 1946). According to Phillips (1936), Citellus tridecemlineatus was most abundant in mowed hayfields and in moderately

overgrazed areas. On the study areas the net densities of ground squirrels are highest on the Blue Rock Flat and lowest on Missing Link (Table XVII).

The effects of grazing and the introduction of new plant species tend to hold back plant succession, preventing the attainment of the vegetative climax stage. In fact, the grass, *Festuca scabrella*, which is the potential dominant climax species on at least two of the study areas (Missing Link and Dot), decreases noticeably under grazing pressure (Campbell *et al.* 1956). Rough fescue occupies only 1 percent of the cover on the two areas. Other plants such as bearded wheat grass, needle grass, sedges, yarrow, dandelion and strawberry tend to increase under moderate grazing by livestock (Moss and Campbell 1947). Most of the above-mentioned plants are good forage for ground squirrels. These trends are evident on the Blue Rock Flat where the vegetation in the ungrazed exclosure may be compared with the grazed main flat (Table VII). The absence of rough fescue in the exclosure may be the result of increased competition with a related species, Idaho fescue.

Certain introduced species such as awnless brome, timothy, dandelion and stinkweed, tend to provide good forage or edible seeds for ground squirrels. According to Bond (1945) the increase of annuals and weeds which is typical of early successional stages, tends to provide more food, favoring the increase of spermophilous

rodents. Evans and Holdenried (1943) observed that the California ground squirrel preferred plants related to early vegetative succession.

The utilization of forage by ground squirrels is superimposed upon the effects of grazing by large ungulates. The ground squirrels favor more forb species than grass (Appendix C) and thus may increase the effective cover of certain grasses by eliminating competing forbs. According to Koford (1958) prairie dogs in mixed vegetation tend to decrease the proportions of forbs and annual grasses, favoring the increase of perennial grasses. The effects of ground squirrel utilization may be noticeably enhanced on an over-grazed area like Blue Rock or Mount Rae. Presumably a heavy population of squirrels on the Mount Rae area could eliminate most of the food plants in a dry year, resulting in a drastic reduction in the carrying capacity of [illegible] squirrels on the area.

In the exclosure plot the following species showed noticeably lower cover values in the section allowing free access to the squirrels, compared to the squirrel-proof section (Table XI)--*Potentilla gracilis*, *Festuca idahoensis*, *Agropyron subsecundum*, and *Elymus innovatus*. *Taraxacum* was present in four of five plots in the control section, but did not occur in the non-control sample. All the above-mentioned plants with the possible exception of *Festuca*, are eaten by the ground squirrels.

The four study areas were compared in regard to the total

cover area of preferred food plants as shown in Appendix C. Only species with cover values of one percent or more were considered. The relative cover areas can serve as indexes to the suitability of the habitat in relation to the abundance of food. The Blue Rock area has the highest coverage (30%), the Missing Link area (26%), the Dot Slope (24%), and the Mount Rae area (17%). The higher yields of forbs and grasses on the Missing Link and Dot study areas probably tends to compensate for the lesser coverage of preferred plant species.

The ground squirrels probably compete with big game and cattle for certain plant species. Because of their small size, Columbian ground squirrels probably can select the preferred food plants with more precision than the larger ungulates. The following plants are eaten by Columbian ground squirrels (Appendix C), and are good cattle forage according to Campbell _et al._ (1956):

Grasses

Agropyron trachycaulum
Agropyron subsecundum
Bromus inermis
Phleum pratense
Phleum alpinum
Poa compressa
Poa pratensis

Forbs

Lathyrus spp.
Aster spp.
Taraxacum spp.

Other valuable forage grasses or sedges that are eaten by

cattle but not preferred by ground squirrels are:

Agropyron dasystachyum
Carex spp.
Deschampsia caespitosa
Festuca scabrella
Stipa columbiana

The effects of competition between ground squirrels and pocket gophers are undetermined. It may be significant that abundant gopher diggings were never found in the more densely populated portions of the Missing Link Flat. Possible competition between the two species exists only on the Missing Link and Dot areas. One squirrel burrow excavated on the Missing Link area was connected to a shallow pocket gopher tunnel. Fitch (1948) also observed a connection between the burrow systems of California ground squirrels and gophers.

Buffer species such as red squirrels, chipmunks, deer mice, and grouse appear to be more numerous within or near the Missing Link and Dot areas compared to Blue Rock and Mount Rae. However, the interrelations between ground squirrels and these species are poorly understood. A ground squirrel and a red squirrel were observed feeding on oats a few feet from each other. Both species appeared to tolerate each other without showing animosity. On one occasion a dead and partly eaten deer mouse was found on a squirrel burrow mound, suggesting that ground squirrels may catch and kill mice. One ground squirrel ignored a hen blue grouse and brood only about 10 yards away. However, the squirrels did show

alarm if any large birds such as blue grouse or magpies flew over the colony.

The following predators or their signs have been observed on all four study areas--eagles, buteos, and badgers. Weasels seem to frequent areas where the vegetation is dense. They have been observed in tall grass only on the Missing Link and Dot areas.

Predation by raptors such as golden eagles is usually regarded as being density dependent (Koford 1958), but predation by specialized predators such as weasels and badgers probably acts independently of density. According to Koford, losses to specialized predators may not be compensated for, and numbers of prey can be reduced below the normal environmental capacity.

Badgers probably can limit the expansion of ground squirrel colonies. Large numbers of weasels could exert drastic effects upon a small ground squirrel population. However, the squirrels have evolved certain behavior patterns that serve as a defence against weasel predation. When weasels are near, the squirrels utter a peculiar alarm call and show little inclination to enter burrows where they would be more vulnerable. Manville (1959) observed adult ground squirrels searching for and heading the young away from burrow entrances. On the Dot Slope in 1960, two squirrels were seen chasing a weasel while others gave alarm.

Weather conditions strongly influence the seasonal activity of the Columbian ground squirrel. The emergence of the squirrels

in the spring is coincident with the thawing and loosening of the soil so that the squirrels are able to dig out. The presence of frozen soil undoubtedly would present a real barrier to emergence. At higher elevations the seasons are delayed and thus squirrels emerge later. The squirrels compensate for late emergence by remaining active later in the fall at higher elevations, unless severe weather conditions force them underground prematurely. Early snows or heavy frost could prevent access to a food supply if the vegetation is covered or frozen, and thus cause early retirement as on Mount Rae in 1960. Temperature does not appear to be the only factor involved in the termination of seasonal activity. Squirrels have gone underground when the temperatures were high during July (Table III) and during cool weather in early September. The lack of moisture appears to be an important factor. The ripening of vegetation, particularly during a drought period can be correlated with the cessation of activity.

The active season of the Columbian ground squirrel is longest on the Missing Link and Dot study areas and shortest on the Mount Rae area. The difference in elevation is 1,800 feet. The breeding period and presumably the emergence is delayed three weeks on the Mount Rae area compared to Missing Link. In regard to the longer season, the Dot, Missing Link and Blue Rock areas are probably more suitable habitats. The long season enables the squirrels to feed longer and to accumulate more fat in preparation for hibernation.

Also young squirrels can complete more of their growth during their first summer. Since the squirrels on the latter three study areas are in better condition as the mean weights would indicate (Table XIV), they may experience less mortality during the hibernating period (Page 81).

In the Sheep River region slopes steeper than 36 percent appear to limit the expansion of ground squirrel colonies. The Dot and Mount Rae areas are situated on slopes averaging about 36 percent. As a result the drainage is good and the populations on these two areas are not endangered by floodings of burrows. However, the soil is shallow on the slopes compared to the Missing Link and Blue Rock areas and thus the former two areas are not as suitable for burrowing. The depths of the burrows are limited, especially wherever layers of coarse gravel occur. Otherwise the squirrels do not prefer any soil type as long as it is suited for burrowing and is of a moderate depth.

The numbers of squirrels on the study areas are influenced by the range condition. The lowest total density (16 per acre) is found on the lightly grazed Missing Link Flat which supports the highest yield of vegetation. The remaining study areas arranged in decreasing order in relation to yields of grasses and forbs, are the Dot, Blue Rock and Mount Rae areas which support densities of 30, 42, and 29 per acre respectively (Table XVII). The density is highest on the heavily grazed Blue Rock Flat and lower on the

more depleted Mount Rae area. Therefore a certain intensity of grazing use appears to favor the increase of ground squirrels. Under-utilization or extreme over-utilization of the range are probably less preferable. The grazed areas are probably preferred because of the elimination of tall grass and the increase of preferred grasses and forbs. Tall grass obstructs the view of the ground squirrels making them less secure.

The greater abundance of preferred food plants on the Blue Rock area can be correlated with the highest breeding rate and the highest increment per acre (Table XIII). Similarly the scarcity of food plants on the Mount Rae area can be related to the lowest growth rate (Table XIV) and breeding rate (Table XIII). The mean weight for squirrels on the Blue Rock area is somewhat lower than is expected, but it is not significantly different from the Missing Link sample (Page 56). Squirrels on an area with more abundant food would be expected to show greater weight gains. However, the squirrels from the Dot area weigh significantly more than the Blue Rock squirrels. This may have been related to a delay in the timing of the sampling period since no allowance was made for a possible earlier emergence of squirrels on the Dot area compared to Missing Link (Page 83). With an earlier start in feeding, squirrels on the Dot Slope would have had a longer period to accumulate fat and thus outweigh squirrels on the other areas. Also there is a possibility that the greater yields of vegetation would have

contributed more bulk to the diets of squirrels on the Dot and Missing Link areas.

The ground squirrels do compete with cattle and big game for certain forage plants, especially on the Blue Rock and Mount Rae areas. However, at least five common species of grasses and sedges that are eaten by cattle are not touched by ground squirrels (see above). One of these grasses is Deschampsia. Therefore on the Blue Rock Flat where Deschampsia is abundant (28% coverage), there is probably little competition between cattle and ground squirrels until the cattle have grazed down the palatable shoots of grass.

Other animal associates are tolerated by the ground squirrels. There appears to be little competition between ground squirrels and pocket gophers. The presence of three important ground squirrel predators on the Missing Link area and the Dot Slope means that the populations suffer higher predation than on the other two study areas. Only two predators--eagles and badgers--are common on the Blue Rock and Mount Rae areas. Judging from the great number of old badger holes (Table XV), Blue Rock and Mount Rae had once experienced severe badger predation. On the Missing Link and Dot areas, the tall vegetation may conceal the ground squirrels from certain predators, but it also limits the visibility of ground squirrels. Thus in tall grass the squirrels may be more vulnerable to weasel predation. On grazed areas the ground squirrels responded quickly to the

Figure 32. Ground squirrel habitat in open spruce woods.

Figure 33. Ground squirrel habitat in burnt over pine.

approach of raptors whereas on the Missing Link area the squirrels often did not see the raptors until they were directly above the squirrels.

In summary, the most suitable ground squirrel habitat was judged to be the Blue Rock area. The remaining areas, arranged in decreasing order of suitability were the Dot, Missing Link and Mount Rae areas. The differences in the first three areas were not great, but the Mount Rae slope was definitely the poorest habitat. The factors considered in evaluating the study areas were densities, weights, breeding rates, lengths of seasons, range conditions, the relative abundance of food plants and the presence of various predators.

Thus an ideal Columbian ground squirrel habitat appears to be a grazed grassland situated on a gentle slope near water, at an elevation between 4,000 and 6,000 feet. The soil of this habitat would probably be deep and vegetation would consist of an abundance of forbs and succulent grasses.

SUMMARY

1. This study of the population and habitat ecology of the Columbian ground squirrel was carried out during the summers of 1958, 1959 and 1960, at the Alberta Biological Station, Gorge Creek.

2. The average weights and total lengths for adult Columbian ground squirrels in July and August, were 690 grams and 350 millimeters for males, and 525 grams and 350 millimeters for females.

3. Of the 4 study areas, located at elevations from 5,000 to 6,800 feet, the Missing Link area was moderately grazed, the Blue Rock and Mount Rae areas were heavily grazed and the Dot area was ungrazed by domestic stock.

4. At higher elevations such as at Mount Rae (elevation 6,800 feet), the breeding season was delayed up to 3 weeks compared with the season at an elevation of 5,000 feet.

5. On south-facing slopes like Dot mountain, squirrels retired for the season at least a week earlier than on more level terrain such as the Missing Link Flat.

6. The depths of the soil profiles on the study areas varied from 17-40 inches.

7. The occurrence of strata of coarse gravel appeared to limit the maximum depth of burrows.

8. The ground squirrels avoided the high temperatures of the day by limiting their activity to periods between 0600 and 0900 hours and between 1600 and 1800 hours.

9. The high mean maximum temperature (83.4° F.) for July, 1960, and the drought conditions probably hastened adult squirrels into hibernation earlier than usual on the Dot Slope.

10. The Missing Link, Dot, and Blue Rock study areas were classed as modified fescue grasslands whereas the Mount Rae area was termed a modified alpine meadow community,

11. The vegetation covered approximately 67 percent of the sampled area on the Missing Link Flat, 69 percent on the Dot, 75 percent on Blue Rock and 64 percent on the Mount Rae area.

12. The yields of grasses were highest in the ungrazed exclosure (320 gm. per square meter) compared to 40 grams per square meter on the Blue Rock Flat and only 15 grams per square meter on the Mount Rae area.

13. The yields of forbs ranged from 175 grams per square meter on the Missing Link area to 10 grams per square meter on the Blue Rock area.

14. The preferred food plants of the Columbian ground squirrel were *Achillea*, *Aster*, *Fragaria*, *Lathyrus*, *Phleum*, *Poa*, *Potentilla gracilis*, *Taraxacum*, and *Vicia*.

15. The scarcity of preferred food plants was correlated with smaller litter size and lower weight gains in the Mount Rae population.

16. The chief competitors of the Columbian ground squirrels in the Sheep River region were cattle, horses, and wapiti.

17. The most important predators were golden eagles, badgers and weasels.

18. Columbian ground squirrels did not breed until they attained two years of age.

19. The mean litter size varied from 2.8 to 4.0.

20. In 1960, the increment of juveniles per acre was about 5.7 on the Missing Link Flat, 13 on the Dot Slope, 24 at Blue Rock, and 11 at Mount Rae.

21. The mean weights of adult and yearling squirrels were lowest on the Mount Rae area (410 gm.) and highest on the Dot Slope (510 gm.).

22. On the observation area, counts indicated that spring densities did not change much from 1958 through to 1960.

23. The 1960 densities of adult and yearling squirrels on the four study areas were fairly uniform; the estimated densities per acre were--the Missing Link area, 10; the Dot Slope, 17; and the Blue Rock and Mount Rae areas, 18.

24. The sex ratio of Columbian ground squirrels aged more than 11 months, was about 44 males : 56 females.

25. The ratio of adult and yearling squirrels to juveniles 4 to 6 weeks old, was about 2:1.

26. The average age ratio from the Blue Rock and Mount Rae areas was approximately 53 adults : 47 yearlings.

27. The longevity record for the Columbian ground squirrel is 5 years.

28. The 1959-60 mortality rate for squirrels aged more than 11 months was males (56 percent), and females (50 percent).

29. The juvenile mortality rates were 77 percent and 75 percent for males and females in 1959-60.

30. About 65 percent of the ground squirrels did not traverse distances greater than 50 yards.

31. The Blue Rock area was selected as representing the best ground squirrel habitat as judged by an appraisal of the physical and biotic features of the area.

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APPENDIX A

Aging Methods

Introduction

The Columbian ground squirrels were grouped as accurately as possible into three age categories by a combination of criteria. These categories were juveniles, aged 0-3.5 months, yearlings, aged 10 to 14.5 months, and adults, aged 22 months or more. For example, a yearling squirrel was considered an individual living in its second summer. The gaps in these age classes are due to the 7- to 9-month hibernation period when squirrels could not readily be obtained. The aging methods used were size and pelage characters, the condition of the reproductive organs and accessories, and skull and dental characters. Also some individuals were marked as juveniles and thus were of known age when recaptured in subsequent years. Dead specimens were aged with greater confidence than live specimens, since skulls could be obtained and autopsies made. No distinction between yearlings and adults was possible in the live-trapped squirrels except in the case of breeding females.

Size and Pelage

Juvenile squirrels were readily distinguished from the other two age groups by smaller size, especially during the first 2 months of life. By mid August, some juvenile males reached weights over-

lapping the weights of smaller yearlings or adults. The heaviest juvenile recorded, was a male weighing 480 grams. However, despite this overlap, juveniles could be determined by lighter colored pelage, less pronounced fulvous coloration on the nose and hind quarters, and by bushier tails.

Yearling squirrels could not be differentiated from adult squirrels by size or pelage characters, although some individuals that attained extreme weights of 800 or more grams, were presumably adults.

Reproductive Organs

Adult males could be differentiated from yearlings only during the short breeding period from late April until the end of the first week in May. Those squirrels with scrotal testes were assumed to be adults whereas those with undescended testes were classified as yearlings (Page 49). In the first week of May, 1960, the adult testes had begun to involute and before mid May the testes were inguinal in position or completely withdrawn into the abdomen.

Breeding females, assumed to be adults, could be detected by the presence of prominent mammary glands from late May until at least July 7, 1960 (Page 48). Even after this date, the mammary glands could be detected although they were regressing in size. Breeding females could be easily determined during the 3-month period from May 20 until August 15, by internal examination of

the reproductive tract. Of course, this could not be done with live-trapped animals. Recognizable embryos were present in the uterus by the former date, if not earlier, and after parturition placental scars were evident, lasting for at least 2.5 months. The scars did not accumulate from year to year since they regressed in size until scarcely discernable by August 15.

Skull and Dental Characters

Skull measurements were found to be inadequate criteria for segregating the three age-classes, but certain features of the cranium helped identify juveniles. Eighteen skulls of juveniles aged by methods previously mentioned, showed prominent fronto-parietal sutures and the lack of sagittal crests. In contrast 83 adult and yearling skulls showed fusion of the sutures and prominent sagittal crests.

Fifteen of the 18 juvenile skulls showed signs of tooth eruption or renewal, as the permanent teeth were pushing up under the deciduous teeth. The deciduous third and fourth premolars (p^3 and p^4) were the teeth being replaced. The third molar (M^3) was erupting in some skulls. In specimens as young as 1 month of age, M^1 and M^2 had already grown in. Therefore the molars must grow in during the first month of life and somewhat later the premolars are replaced. One out of 42 skulls of yearlings aged by dental wear, showed tooth renewal. Thus the premolars are not always replaced before the second summer. In a sample

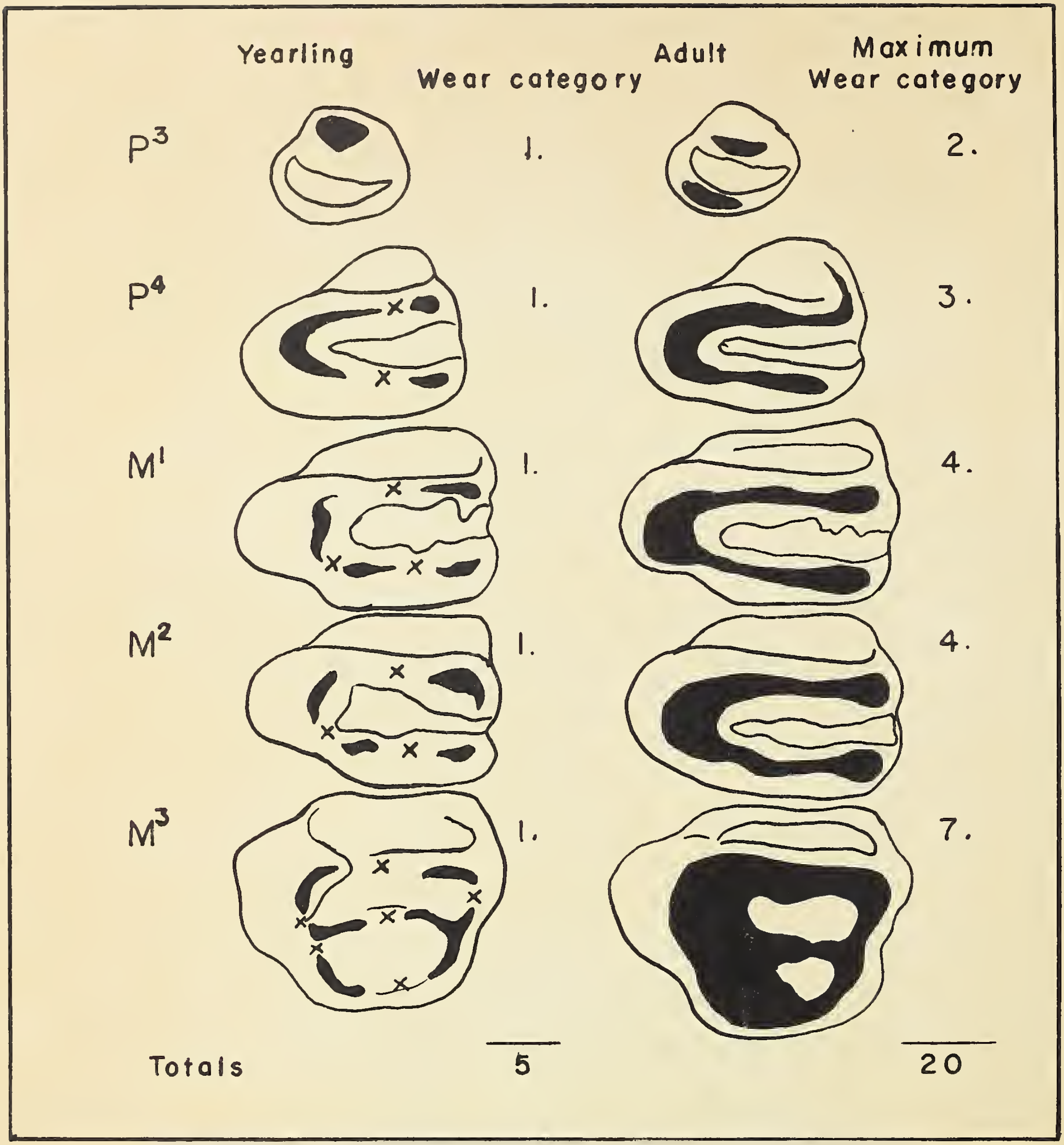

Figure 34. Illustration of tooth wear aging technique. Black areas are dentine patches. X=sites of potential fusions of dentine.

of 54 skulls of adult squirrels aged by dental wear counts, there was no sign of tooth replacement. Hence evidence of tooth renewal appears to be a valid criterion for separating juveniles from yearlings and adults.

An attempt was made to see if adult and yearling teeth showed a sequence of enamel wear that could be classed objectively into age categories as was shown by Fuller (pers. comm.) for caribou. Examination of maxillary tooth rows showed that there were three types of enamel wear patterns depending upon the type of tooth. P^3 showed simple spot wear, whereas P^4, M^1 and M^2 showed dentine appearing in a horseshoe shaped pattern around the infundibulum. M^3 developed an irregular figure eight pattern of wear (Figure 34). In the typical cheek tooth (P^4, M^1 and M^2) three or four wear patches first appeared. These were located on the protocone, paracone, metacone and the netaconule (Figure 34). Later as the animal aged, these wear patches fused together to form the horseshoe shape. A maximum of 3 fusions occurred in M^1 and M^2, and 2 fusions occurred in P^4. M^3 showed the development of five wear patches with a resulting six possible fusions.

Wear classes of 0-20 were assigned for describing the cheek teeth of a maxillary row. The assigned wear class was 0, if no patches of dentine showed on any teeth, and 20, if all teeth showed maximum wear as determined by counts of the fusions of dentine. The unfused condition of a worn tooth was designated as 1, and 1

point was added for each fusion of any two dentine patches. Figure 34 demonstrates the method used. The maximum wear designations from P^3 to M^3 were 2, 3, 4, 4, and 7.

The effectiveness of the above method was tested by examining cheek teeth of 20 known-age yearlings and adults, and determining the range of wear counts for each class. The known-age adult skulls were obtained from 11 previously marked squirrels. The yearlings were 9 females selected from the Blue Rock sample and aged by non-breeding status. The wear counts for the yearlings ranged from 3 to 6 with a mean of about 4. Similarly the adult sample showed a range from 6 to 19 with a mean of 13. The obvious separation is between category 6 and 7, with adults classed in the categories from 7 to 20. One known-age adult had a rating of 6, indicating about a 5 percent overlap between the two age groups. Confidence intervals at 95 percent for the mean wear counts of the two age groups were calculated. The intervals ranged from 0-11 for yearlings and 11-15 for adults.

APPENDIX B

Movements

Greatest Distance Between Capture Sites

The best method of determining the extent of movements of individuals is by actual observations of marked animals. Attempts at dye-marking the squirrels were unsuccessful (Page 61). Also the high vegetation in June and July, greatly hindered observations of movements of individual ground squirrels. Hence only information derived from live-trapping could be used. The movements of squirrels were assessed by determining the greatest distance measured in a straight line between capture sites for each animal captured more than once (Hayne 1949b).

Certain qualifications must be considered when interpreting trap-revealed movements. A greater number of recaptures of an individual is more likely to reveal greater movements than a lesser number of recaptures. In determining the greatest distances between trap sites, data for all animals captured more than once had to be used. Exclusion of those individuals with only two or three captures would have introduced a bias. However, two individuals were captured only two (No. 185) or three (No. 208) times; yet they travelled distances of 240 and 330 yards.

The greatest distances between trap sites were recorded on a yearly basis for each age and sex group. The movement data for 1958, 1959 and 1960 were grouped and the juvenile sexes were combined.

Yearlings are not included because of the poor returns and the difficulty in age determinations. The adults are of known age (Appendix A). The results are presented in Table XXI.

Table XXI. Greatest Distances Between Capture Sites. Movements of Columbian Ground Squirrels, 1958-60.

Range (Yards)	Frequency		
	Adult ♂♂	Adult ♀♀	Juveniles
0-50	14	25	22
51-100	6	13	8
101-150	3	1	4
151-200	1	-	-
201-250	2	-	-
251-300	1	-	-

Columbian ground squirrels are not mobile animals. They usually restrict their movements to the vicinity of burrow systems, and utilize well-worn pathways between burrow openings. One such network of pathways was partially mapped out and it extended over a distance of 70 yards. In the Missing Link colony, the squirrels were seldom observed to travel over any distance further than 100 yards. In all cases the majority of individuals showed movements of 50 yards or less. Adult males travelled the greatest distances (285 yards) although one yearling male traversed 330 yards. The greatest normal movement made by an adult female in one season was only 105 yards. Yearling females were only recorded to move a maximum distance of 80 yards, but the sample was small (n=15).

Two juvenile ground squirrels ranged over distances of 120 and 150 yards, but most individuals confined their movements to less than 50 yards. The long movements made by juveniles were only recorded in August.

Homing

During August, 1960, 11 squirrels were captured, marked and experimentally released at distances varying from 100 to 375 yards from the capture site, in order to ascertain homing distances. The results were somewhat inconclusive since four of 11 squirrels were recovered. Nevertheless the information obtained from these four squirrels was valuable.

One male (No. 205) that had been released 200 yards from the capture site, traversed a distance of 350 yards, the longest recorded movement of a Columbian ground squirrel on the Missing Link study area. One female (No. 85) moved 170 yards. All four of the squirrels that were recovered, returned to the vicinity of the capture site from distances of up to 200 yards. The movements of No. 85 and No. 205 were greater than any recorded in the normal trap-revealed movements (Table XXI). The results of these homing experiments were thus considered separate from normal movements.

Home Ranges

A home range is defined as an area traversed by an individual animal in its normal activities such as feeding and mating (Burt

1943). Long exploratory movements should be considered apart from home range movements. There are probably no discrete boundaries to a home range unless the animal is territorial in behaviour. Also seasonal as well as yearly changes in home ranges may occur.

Trap-revealed minimum home ranges were calculated for individual squirrels captured at four or more sites during a 4-month period. Data from 10 females and 8 males of the three age groups were utilized. No information was available for yearling males, but one yearling female was captured a sufficient number of times for home range measurements. The capture sites were connected by straight lines to form a polygonal home range enclosing the maximum area (Hayne 1949b). The area of the minimum home range for each individual was then calculated to an accuracy of 10 square yards (Table XXII).

Hayne (1949b) mentions three problems concerned with home range measurements. There is no evidence that an animal will reveal the actual area of its home range by appearing in traps, and it is not known whether the frequency of capture at certain sites corresponds to the intensity of use of those sites. Also Hayne states that the traps nearer the home sites may interfere with the normal activities and produce an apparently smaller home range. Nevertheless, the selection of the minimum home range method has an advantage over other methods in that it reveals a known area which the animal has traversed.

Table XXII. Trap Revealed Minimum Home Ranges of Selected Columbian Ground Squirrels (Combined Data), 1958-60.

Age	Sex	No.	No. of Trap Sites	Size of Home Range Square Yards	Acres
Adult	Females	15	5	1540	.32
		149	6	950	.20
		27	4	800	.16
		67	5	600	.12
		8	4	580	.12
		4	4	450	.09
		32	5	320	.07
		21	4	230	.04
Adult	Males	58	6	4560	.94
		39	4	1550	.32
		69	4	680	.14
Yearling	Female	276	4	2250	.46
Juveniles	Female	35	4	800	.16
	Males	231	4	3900	.80
		29	4	960	.20
		143	4	360	.08
		41	5	300	.06
		37	4	110	.02

Adult males appear to cover larger home ranges than either juveniles or adult females. The largest home range of .94 acres was an area traversed at least 3 times during the 1959 season by a male (No. 58). Therefore it is more likely that these movements occurred within a home range, rather than being exploratory in nature. A yearling female (No.276) occupied a larger home range than any of the 8 adult females. Also juveniles traversed surprisingly large areas in comparison with the adults. A juvenile

male (No. 231) occupied a home range of .8 acres, an area only exceeded by the home range of one adult male. A few litters of juvenile squirrels, that were under observation over a 6-week period, showed virtually no long movements away from the natal burrow system. Hence some of the long movements made by juveniles may have been exploratory, in search of more succulent food plants or hibernation sites. Exceptional movements such as distances of 240, 285, and 330 yards, traversed by adult and yearling males, were considered apart from normal home range movements.

Considerable overlap occurred among home ranges, especially with adult and yearling females and juveniles. Adult male ranges also overlapped somewhat. Trapping did not begin until early May 1960, and since the breeding season was almost over (Table XII), no comparisons of adult male home ranges during the breeding period, could be made. Hence no evidence of territorial behaviour of adult males could be found. There were no signs of territorial behaviour expressed by either sex of ground squirrels after the breeding season. However, aggressiveness among individual squirrels was noticed in early May. Several adult males were kept in confinement along with yearlings and adult females over a 1-year period. During the spring, no particularly aggressive behaviour was noted between the males, although a male and female continually fought.

Definite shifts in home range were not detected from the available data, but the transient movements mentioned above may

have been related to changes in range. One adult female (No. 8) appeared to have shifted its home range slightly west in 1960 as compared with 1958. However, since the home ranges for the two years lay adjacent, it is more probable that more recaptures would have revealed that both ranges overlapped. An adult female (No. 15) was captured a sufficient number of times in 1958, 1959 and 1960 to compare the home ranges. Although the sizes of the areas varied from year to year, the three areas did overlap considerably. Centers of activity, determined by averaging the points of capture on the vertical and horizontal axes (Hayne 1949b), coincided very closely. Therefore it is quite likely that adult females, at least, generally occupy much the same home range year after year.

Literature Cited

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal., 24: 346 - 352.

Hayne, D. W. 1949 b. Calculation of size of home range. J. Mammal., 30: 4 - 18.

APPENDIX C

Food Habits of the Columbian Ground Squirrel

Introduction

A knowledge of the food habits of the ground squirrels was necessary in order to relate their adaptations to the vegetative composition on the study areas. Observations were made in the field with the aid of binoculars and a telescope, but it was difficult to identify various species of plants eaten. Therefore this technique was limited in use. In 1958, stomach contents were collected from a small sample of specimens. Analysis of the contents proved difficult, for much of the green material in the stomachs was unidentifiable and only certain seed hulls and insect remains could be identified.

In 1960, feeding trials were conducted on a group of 15 captive ground squirrels. Twelve of the squirrels had been in captivity for a period of a year and had been fed laboratory food. Nevertheless, the squirrels still readily accepted native plant food. These squirrels were quite tame and while feeding they could be observed from nearby. Three wild juvenile squirrels were captured and placed in a separate cage so that comparative feeding trials could be undertaken. If the diet of the 12 squirrels had changed considerably under prolonged captivity, then it would be expected that the diet of the three wild squirrels would differ

from the former. However, this was not the case.

The feeding trials were only conducted on a qualitative basis, to determine whether the squirrels would accept or reject certain plant species. The squirrels were given water and the diet was supplemented with certain preferred foods such as dandelions so there was no necessity to eat undesirable foods. Altogether 48 species of fresh forbs, shrubs and grasses were given to both lots of squirrels.

The following table lists the plant species observed eaten in the field and accepted or rejected in feeding trials by the ground squirrels. Unless stated otherwise, the plant parts eaten were leaves, and also the shoots and rhizomes of grasses. Several species of plants were given to the ground squirrels at one time, and a given plant was presented more than once in combination with various species. Those plants that were always eaten first in preference to other species present, were classed as preferred species. Also, the palatable parts of the preferred plants were always completely consumed.

Table XXIII. Results of Field Observations and Feeding Experiments on the Food Habits of the Columbian Ground Squirrel, 1960.

Tests \ Field		Observed Eaten		Not Observed Eaten
Accepted	*	Achillea millefclium		Agoseris sp.
		Epilobium angustifolium		Agropyron trachycaulum
	*	Fragaria virginiana		Agropyron subsecundum
	*	Phleum pratense		Agrostis scabra
	*	Poa alpina	*	Aster sp.
		Populus tremuloides[1]		Bromus inermis

Table XXIII. (Cont'd)

Tests \ Field	Observed Eaten	Not Observed Eaten
Accepted	* Potentilla gracilis	Bromus marginatus
	Ribes sp.[2]	Carex sp.
	* Taraxacum sp.[4]	Danthonia parryi
		Elymus innovatus
		Erigeron sp.
		Gaillardia aristata
		Heracleum lanatum
		* Lathyrus ochroleucus
		Poa pratensis
		Potentilla pennsylvanica
		Soldidago sp.
		Thalictrum sp.
		* Vicia sp.
		Zizia aptera
Rejected		Agropyron dasystachyum
		Agropyron smithii
		Artemisia ludoviciana gn.
		Artemisia frigida
		Deschampsia sp.
		Festuca scabrella
		Galium boreale
		Geranium viscossissimum
		Geranium richardsonii
		Geum macrophyllum
		Geum triflorum
		Hackelia floribunda
		Koeleria cristata
		Monarda fistulosa
		Potentilla fruticosa
		Rosa sp.
		Rubus strigosus
		Symphorocarpos occidentalis
		Smilacina stellata
Not Tested	Lithospermum ruderale[3]	
	Poa compressa	
	Salix sp.	
	Thlaspi arvense[3]	
	Vaccinium sp.	

1. roots 2. fruit 3. seeds 4. whole plant
* Preferred species