Population status, social habits, movements and habitat relationships of the summer resident elk of Jackson Hole Valley, Wyoming

by Clifford Johnson Martinka

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Fish and Wildlife Management
Montana State University

Abstract:
A study was conducted from June through September 1963 and from May through November 1964 to obtain quantitative data on the distribution, population status, social habits, movements and habitat relationships of the relatively non-migratory elk of Jackson Hole Valley, Wyoming, The physiography of the area was described. The eight major plant communities, sagebrush-bunchgrass, coniferous forest, aspen, cottonwood-spruce, willow, bunchgrass-shrub, sedge-bluegrass and agricultural were described from measurements of 31 representative stands. A total of 42,237 elk observations was recorded during 302 observation trips. The locations of elk observed indicated resident population segments for the Refuge, Central Valley, Uhl Hill and Moran Meadows, Total population estimates were 1,162 in 1963 and 1,793 in 1964. Classifications of 1,302 elk in 1963 and 1,356 in 1964 indicated different sex and/or age structures for the Refuge and Central Valley segments, A disproportionate occurrence of yearling males and, to a lesser extent, yearling females apparently resulted from numbers of these animals from the herd that migrates from Jackson Hole in summer becoming a part of the resident herd. Proportions of adult males in 1964 did not reflect the high occurrence of yearling males in 1963. Five periods relative to elk social habits were recognized on the basis of grouping and association data: June 1-15, calving; June l6 - August 15, aggregation; August 16 - September 15, dispersal; September l6 - October 15, breeding; October 16-31, reaggregation. Movements were analyzed from 1,240 relocations of 383 marked elk. The percentage of migratory elk that were associated with resident elk declined from a maximum in May to a minimum in early July indicating the period of movement for migratory elk. The movement patterns of resident elk were discussed from the records of representative animals. During early summer the yearling male group showed the most extensive movements. The movements of females with calves and yearling females increased in late summer while those of yearling males decreased. Average home ranges varied from 3.6 square miles for females with calves to 5.7 square miles for yearling males. Fall movements suggested that hunting may have been effective in restraining resident elk within or influencing movements to areas closed to hunting. Sagebrush-bunchgrass was the most important vegetation type used for feeding during all months of the study. Relatively high use of the bunchgrass-shrub type in May was related to the earlier development of green vegetation on south exposures. Food habits were studied from 24,240 instances of plant use at 172 feeding sites. Forbs averaged 50 percent, grasses and grass-like plants 29 percent and browse 21 percent of the diet for the May - October period. Forage-class use varied on the different vegetation types but important seasonal and in-season differences occurred only on the sagebrush-bunchgrass and bunchgrass-shrub types. Rumen analysis for September - October specimens supplemented the data from feeding site examinations.

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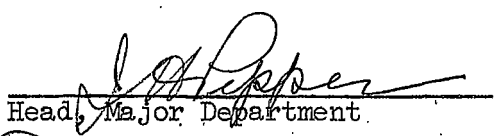

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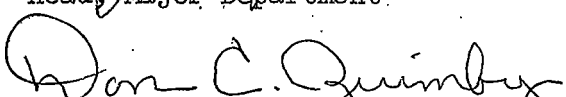

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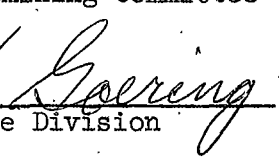
Ass't 

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ABSTRACT

A study was conducted from June through September 1963 and from May through November 1964 to obtain quantitative data on the distribution, population status, social habits, movements and habitat relationships of the relatively non-migratory elk of Jackson Hole Valley, Wyoming. The physiography of the area was described. The eight major plant communities, sagebrush-bunchgrass, coniferous forest, aspen, cottonwood-spruce, willow, bunchgrass-shrub, sedge-bluegrass and agricultural were described from measurements of 31 representative stands. A total of 42,237 elk observations was recorded during 302 observation trips. The locations of elk observed indicated resident population segments for the Refuge, Central Valley, Uhl Hill and Moran Meadows. Total population estimates were 1,162 in 1963 and 1,793 in 1964. Classifications of 1,302 elk in 1963 and 1,356 in 1964 indicated different sex and/or age structures for the Refuge and Central Valley segments. A disproportionate occurrence of yearling males and, to a lesser extent, yearling females apparently resulted from numbers of these animals from the herd that migrates from Jackson Hole in summer becoming a part of the resident herd. Proportions of adult males in 1964 did not reflect the high occurrence of yearling males in 1963. Five periods relative to elk social habits were recognized on the basis of grouping and association data: June 1-15, calving; June 16 - August 15, aggregation; August 16 - September 15, dispersal; September 16 - October 15, breeding; October 16-31, re-aggregation. Movements were analyzed from 1,240 relocations of 383 marked elk. The percentage of migratory elk that were associated with resident elk declined from a maximum in May to a minimum in early July indicating the period of movement for migratory elk. The movement patterns of resident elk were discussed from the records of representative animals. During early summer the yearling male group showed the most extensive movements. The movements of females with calves and yearling females increased in late summer while those of yearling males decreased. Average home ranges varied from 3.6 square miles for females with calves to 5.7 square miles for yearling males. Fall movements suggested that hunting may have been effective in restraining resident elk within or influencing movements to areas closed to hunting. Sagebrush-bunchgrass was the most important vegetation type used for feeding during all months of the study. Relatively high use of the bunchgrass-shrub type in May was related to the earlier development of green vegetation on south exposures. Food habits were studied from 24,240 instances of plant use at 172 feeding sites. Forbs averaged 50 percent, grasses and grass-like plants 29 percent and browse 21 percent of the diet for the May - October period. Forage-class use varied on the different vegetation types but important seasonal and in-season differences occurred only on the sagebrush-bunchgrass and bunchgrass-shrub types. Rumen analysis for September - October specimens supplemented the data from feeding site examinations.

INTRODUCTION

Numerous authors have discussed the migration patterns and summer distribution of the elk (Cervus canadensis nelsoni) which winter within the Jackson Hole Valley in northwestern Wyoming. Reports prior to 1963 generally emphasize the elk migration from the valley to summer ranges in mountains to the east and north, a part of which are in southern Yellowstone National Park (Preble, 1911, Graves and Nelson, 1918, Sheldon, 1927, Anderson, 1958 and others). Only a few references to elk summering within the valley are included in these reports. Cole (1963) tentatively established that a portion of the elk that wintered in Jackson Hole during 1961-62 was relatively non-migratory and summered on valley ranges within Grand Teton National Park and the National Elk Refuge. The segment of the population involved and other pertinent factors were not known.

This study was conducted from June through September 1963 and from May through November 1964 to obtain quantitative data on the distribution, population status, social habits, movements and habitat relationships of the elk that summer in Jackson Hole Valley.

PHYSIOGRAPHY OF STUDY AREA

Jackson Hole, an intermountain basin approximately three to 15 miles wide, extends 48 miles in a southwest direction along the east slopes of the Teton Mountain Range. The Pinyon Peaks, Mount Leidy Highlands and the Gros Ventre Range border the valley to the east.

Topographic features are varied but distinct. Flat glacial outwash plains increase in elevation from 6,200 feet in the southern part of the valley to 6,800 feet in the extreme northern portion. Rolling glacial moraines border the valley on the west. Potholes, formed by the melting of large blocks of ice within the glacial outwash, are prominent in the north-central portion of the valley. The outwash plains and moraines were formed during the Bull Lake and Pinedale glacial stages (Fryxell, 1930). Outwash alluvium consists of unconsolidated and poorly consolidated clay, silt, sand and gravel while the moraines are deposits of sand, gravel and boulders (Love, 1956). Isolated buttes near the north and south ends of the valley extend as high as 1,000 feet above the valley floor. The buttes, which protrude through the outwash plain, are of Tertiary origin and have fine textured, residual soils (Fryxell, 1930 and Love, 1956).

The Snake River, flowing in a southwest direction, drains the valley. The Buffalo Fork and Gros Ventre Rivers join the Snake River from the east in the north and central parts of the valley, respectively. Minor drainage courses are conspicuously absent from the outwash plain.

The study area included approximately 130 square miles of the valley

floor from the north end of the National Elk Refuge through Grand Teton National Park to the Moran Meadows (Figure 1).

Records maintained at Grand Teton National Park Headquarters at Moose from 1936 to 1964 show that about one-third of the average annual precipitation of 25.86 inches fell as rain from May through September. The northern portion of the valley was generally snow covered from November through March. Maximum accumulated snow depths varied from 33 to 70 inches. The mean annual temperature was 37.3° F with extremes of -44° F (February 1951 and January 1963) and 93° F (August 1961).

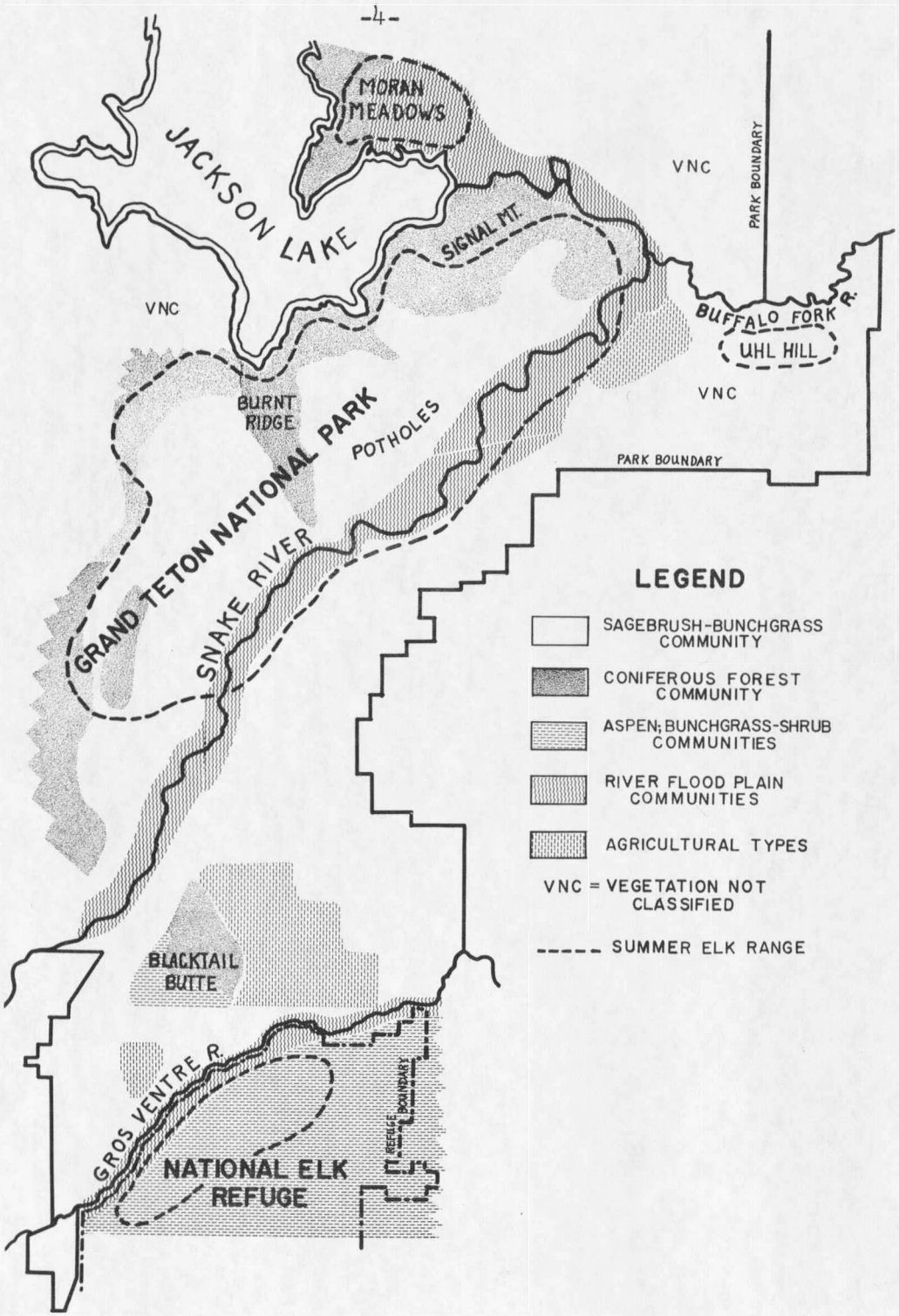

Figure 1. Map of the study area showing vegetation types and summer elk distribution.

VEGETATION OF STUDY AREA

The vegetation of the study area was sampled by measurements of 31 representative stands supplemented by general observations. Low shrub and herbaceous vegetation was measured by the canopy coverage method (Daubenmire, 1959). For each stand, the projected ground coverage for each taxon was estimated by coverage-classes in each of a series of 20 X 50 centimeter plots. The average canopy coverage per plot and the percent frequency were computed. Since measurements were made after July 15 many of the characteristic plants of the spring aspect were not fully represented within the plots. In the discussion of the tabular data that follows, important species of the spring aspect are mentioned regardless of their occurrence in the plots. Plant nomenclature follows Davis (1951).

In stands where tall shrubs and/or trees were present the center of each canopy coverage plot served as the focus of a random-pair determination (Cottam and Curtis, 1949). The shortest distance between woody plants (greater than three feet tall) occurring on opposite sides of the plot was determined to establish pairs. The number of individuals less than three feet tall for each taxon was recorded for the three foot strip on each side of a wire stretched between each pair. The number of individuals per acre was computed for each species.

The distribution of plant communities (Figure 1) appeared to be influenced by the geologic substrate and/or the physiographic site. Outwash plain, glacial moraine, river flood plain and butte substrates

were present.

Sagebrush - Bunchgrass Community

This community (Figure 2) occurred extensively on outwash plains, river terraces and flood plains. It had limited distribution in open parks of forested areas and on south slopes of glacial moraines.

The dominant species associated with Artemisia tridentata on benches and terraces of the outwash plain were Agropyron spicatum, Festuca idahoensis, Koeleria cristata, and Eriogonum spp. (Table I). On extensive areas south of Burnt Ridge (Figure 1) Artemisia arbuscula equaled Artemisia tridentata in importance and Koeleria cristata became the dominant grass. Selaginella densa attained maximum abundance and formed extensive ground cover on sites east of Signal Mountain. Conspicuous forbs of the spring and early summer aspect included Antennaria spp., Balsamorhiza sagittata, Dodecatheon pauciflorum, Ranunculus glaberrimus, Senecio integerrimus and Viola nutallii. Dessication of the vegetation was evident after mid-July but Arenaria congesta, Erigeron spp., Eriogonum spp. and Lupinus leucophyllus remained in flower through early August.

On the south slopes of potholes, Antennaria spp. increased in importance with a decrease in aerial coverage by grasses.

Artemisia tridentata, Purshia tridentata and Agropyron spicatum dominated river banks and south slopes of moraines with Bromus marginatus also being important on the latter sites. Characteristic forbs were Arabis spp., Hackelia spp., Balsamorhiza sagittata and Lomatium spp. Amelanchier alnifolia occurred as scattered colonies and Berberis repens

Figure 2. Sagebrush-bunchgrass Community in foreground with Coniferous Forest and Aspen Communities (Moraine Substrate) in Background.

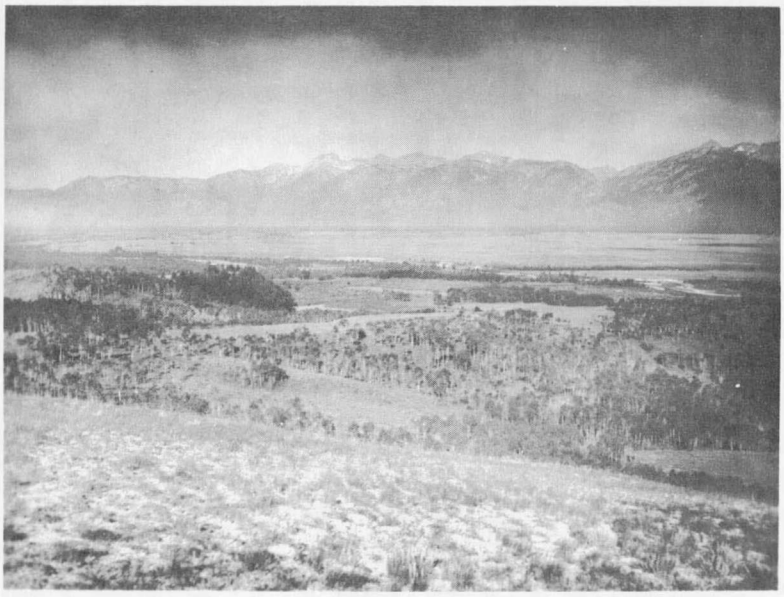

Figure 3. Aspen Community (Butte Substrate) Interspersed with Bunchgrass-shrub Community (Bunchgrass Phase).

TABLE I. AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF PLANT TAXA ON NINE REPRESENTATIVE STANDS OF THE SAGEBRUSH - BUNCHGRASS COMMUNITY

	Benches and Terraces				Pothole south slope	River bank	Moraine south slope	Forest ecotone	Forest park
	I	II	III	IV	V	VI	VII	VIII	IX
Number of plots	40	40	30	40	25	25	25	40	20
TAXA:									
Artemisia arbuscula[1]	-	-	-	10/70	-	-	-	-	-
Artemisia tridentata	21/70[2]	24/67	30/73	10/43	12/52	21/52	19/68	9/33	31/50
Purshia tridentata	-	-	-	-	-	31/56	14/32	-	-
Agropyron spicatum	8/55	15/77	2/13	2/38	6/92	36/84	16/60	-	-
Bromus marginatus	-	-	-	-	-	-	19/68	-	4/45
Carex spp.	1/5	5/67	-	3/8	3/20	-	-	5/25	14/30
Festuca idahoensis	7/30	17/100	13/83	1/18	+/4	-	-	-	-
Koeleria cristata	12/93	4/70	7/80	20/98	2/20	-	-	18/87	-
Antennaria spp.	1/8	12/92	10/56	6/33	20/88	-	-	+/5[3]	-
Balsamorhiza sagittata	11/45	-	2/30	+/3	+/4	11/28	2/12	-	10/20
Collinsia parviflora	7/90	-	-	2/28	1/20	-	-	5/80	16/70
Eriogonum spp.	18/90	13/77	21/80	28/95	1/16	2/8	5/24	37/90	26/80
Helianthella uniflora	-	-	-	-	-	-	1/36	-	34/65
Lupinus leucophyllus	7/55	+/5	2/27	1/30	-	-	2/20	16/45	-
Polygonum douglasii	6/85	-	-	2/73	-	+/16	5/40	10/80	10/85
Selagenella densa	-	32/88	-	-	6/52	-	-	-	-
Bare ground	29/83	9/85	32/90	34/92	53/100	25/68	25/64	26/100	25/100
Rock	2/13	-	-	+/10	15/84	7/24	1/16	1/13	1/5
Litter	33/97	21/100	29/90	41/100	19/100	64/100	66/100	44/98	58/100
Mosses and lichens	4/43	3/72	5/40	6/70	6/60	-	-	2/35	4/10

1/ Taxa with ten percent or more canopy coverage in at least one stand were included. Others appear in Table XVIII of the Appendix.

2/ The figure preceeding each / is average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

3/ +/ indicates occurrence in the plots with a covering value less than 0.5 percent.

was common.

Broad ecotones with coniferous forests were characterized by scattered Pinus contorta with Koeleria cristata the dominant grass. The aerial coverage of Artemisia tridentata was reduced while Eriogonum spp., Lupinus leucophyllus and Polygonum douglasii were more abundant than on open sites. Helianthella uniflora was conspicuous on rocky areas.

Parks within the coniferous forest community were dominated by Helianthella uniflora and Eriogonum spp. in association with Artemisia tridentata. Melica spectabilis and Carex spp. provided additional ground cover. Important forbs included Balsamorhiza sagittata, Collinsia parviflora and Polygonum douglasii.

Coniferous Forest Community

Extensive areas of moraines and the north slopes of buttes were occupied by coniferous forests (Figure 2). Small stands also occurred on the north slopes of potholes and river banks. Three forest types were recognized by the relative abundance of different conifer species (Table II).

Abies lasiocarpa Type: This type was limited in distribution to moraines of the valley floor. Stands were dominated by Abies lasiocarpa with scattered Picea engelmanni and Pinus contorta. The understory was characterized by a shrub stratum of Lonicera utahensis and Vaccinium membranaceum with a field layer dominated by Carex spp. and Calamagrostis rubescens. The abundance of young age-class Abies lasiocarpa indicated that this community was perpetuating itself.

Pinus contorta Type: This was the most extensive of the coniferous

TABLE II. NUMBER OF INDIVIDUALS PER ACRE FOR TREE SPECIES AND AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF SUBORDINATE VASCULAR SPECIES ON FOUR REPRESENTATIVE STANDS OF THE CONIFEROUS FOREST COMMUNITY

	Abies lasiocarpa	Pinus contorta		Pseudotsuga menziesii
	I	II	III	IV
		Old	Mature	
No. plots and/or pairs	25	25	25	25
TREES:				
Abies lasiocarpa	1050(63)[1]	710(96)	51(50)	-
Picea engelmanni	105(33)	-	-	-
Pinus contorta	158(38)	871(24)	782(6)	-
Pinus flexilis	-	32(50)	8(100)	-
Pseudotsuga menziesii	-	-	-	1830(0)
SUBORDINATE VASCULAR sp.[2]				
Carex spp.	14/36[3]	19/24	20/52	-
Calamagrostis rubescens	17/32	39/88	57/92	36/92
Lonicera utahensis	14/32	-	-	-
Pachystima myrsinites	5/44	4/28	-	14/76
Spirea betulifolia	+/20[4]	1/4	9/68	25/80
Vaccineum membranaceum	26/60	1/4	4/20	-
Vaccineum scoparium	9/20	43/76	16/40	-
Lupinus parviflorus	-	+/4	23/76	-
Soil	-	1/4	-	16/60
Rock	1/12	-	+/8	-
Litter	82/100	71/100	94/100	62/100
Mosses and lichens	9/56	21/60	18/52	25/76
Fallen timber	9/16	6/8	2/20	-

1/ Number in parentheses is the percent less than three feet tall.

2/ Taxa with less than 10 percent canopy coverage in each of the stands were excluded and appear in Table XVIII of the Appendix.

3/ The figure preceeding each / is the average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

4/ +/ indicates occurrence in the plots with a coverage value less than 0.5 percent.

forest community types. Recognition was afforded by the dominant overstory of Pinus contorta. A shrub stratum was conspicuously absent from most areas but Shepherdia canadensis was abundant on local sites. Dominant plants of the field layer included Carex spp., Calamagrostis rubescens and Vaccineum scoparium. Arnica spp. and Lupinus parviflora were common forbs. Low densities of young Pinus contorta in mature stands and an abundance of young Abies lasiocarpa in older stands suggested that this type would be replaced by the Abies lasiocarpa Type.

Pseudotsuga menziesii Type: Dense stands of Pseudotsuga menziesii of all age classes were typical on north slopes of Blacktail Butte. Scattered groves also occurred on south slopes and ridgetops of moraines. Calamagrostis rubescens, Pachystima myrsinites and Spirea betulifolia dominated the understory. The stands appeared to be a topo-edaphic climax on most sites but many of the stands on moraines were being replaced by Abies lasiocarpa.

Aspen Community

Groves of this community occurred on moraines (Figure 2) and on north slopes as well as snowbank areas of buttes (Figure 3). Open stands of Populus tremuloides were characteristic (Table III).

Stand I represents groves occurring on buttes. The understory was dominated by Calamagrostis rubescens and Poa spp. Rosa woodsii, the characteristic shrub, was associated with a shrub stratum of Prunus virginiana, and Amelanchier alnifolia with Symphoricarpus sp. on some sites. Lupinus parviflorus was the only abundant forb.

TABLE III. NUMBER OF INDIVIDUALS PER ACRE FOR TREE SPECIES AND AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF SUBORDINATE VASCULAR SPECIES ON TWO REPRESENTATIVE STANDS FOR EACH OF THE ASPEN AND THE COTTONWOOD-SPRUCE COMMUNITIES

	Aspen		Cottonwood	Spruce
	I	II	III	IV
Site or type	Butte	Moraine	Populus angustifolia	Picea pungens
No. plots and/or pairs	25	25	25	25
TREES:				
Picea pungens	-	-	-	419
Populus angustifolia	-	-	318	-
Populus tremuloides	427	552	-	-
SUBORDINATE VASCULAR SPECIES:[1]				
Rosa woodsii	18/68[2]	-	1/4	6/20
Agropyron spp.	-	29/72	+/4[3]	+/8
Bromus marginatus	-	25/76	-	-
Calamagrostis rubescens	61/76	4/4	-	37/52
Elymus glauca	12/40	12/36	-	-
Poa spp.	49/84	+/16	34/84	13/16
Achillea millefolium	1/24	12/52	-	2/16
Aster spp.	2/16	4/40	3/36	17/52
Lupinus parviflorus	24/76	9/44	-	-
Medicago lupina	-	-	19/48	-
Solidago sp.	-	10/40	-	-
Taraxacum officinale	1/24	34/92	+/12	5/40
Soil	-	1/8	13/40	1/16
Rock	-	4/4	11/56	-
Litter	98/100	96/100	74/100	93/100
Mosses and lichens	-	1/12	-	3/36

1/ Taxa with less than 10 percent canopy coverage in each of the stands were excluded and appear in Table XVIII of the Appendix.

2/ The figure preceeding each / is average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

3/ +/ indicates occurrence in the plots with a coverage value with less than 0.5 percent.

For groves occurring on moraines Agropyron spp., Bromus marginatus and Taraxacum officinale were dominant associes of the understory. Common forbs included Achillea millefolium, Aster spp., Solidago spp. and Lupinus parviflora. A shrub stratum of Prunus virginiana occurred in some stands. An abundance of young conifer species in many stands suggested that the community was seral on these sites.

Cottonwood-Spruce Community

Extensive areas of the flood plain along the Snake and Gros Ventre Rivers were occupied by this community (Figure 4). Pure stands of Populus angustifolia and Picea pungens occurred (Table III) and intergradations between the two were common. Picea pungens appeared to replace Populus angustifolia on stabilized sites while the latter species may replace itself for a relatively long period of time on sites subject to periodic flooding.

Stand III represented a relatively unstable site with Populus angustifolia occurring as the monotypic dominant. On these gravelly locations Poa spp. and Medicago lupina were the important species in the ground stratum. On more stable sites Trifolium spp. and Aster spp. became more abundant while Shepherdia canadensis and Eleagnus angustifolia formed a conspicuous shrub stratum in many stands.

Calamagrostis rubescens dominated the field layer of monotypic stands of Picea pungens. Other common species included Poa spp., Aster spp. and Shepherdia canadensis.

Figure 4. Cottonwood-Spruce Community.

Figure 5. Bunchgrass-shrub Community.

Bunchgrass-Shrub Community

This community (Figure 5) occurred on south, east and west exposures as well as ridgetops of buttes in the southern portion of the study area. A bunchgrass and a shrub phase were recognized (Table IV).

The bunchgrass phase occurred on south to west slopes and was dominated by scattered clumps of Agropyron spicatum, Oryzopsis hymenoides and Stipa comata interspersed with Gutierrezia sarothrae. Poa spp. replaced Oryzopsis hymenoides and Stipa comata on west slopes and ridgetops and Astragalus miser was abundant on west slopes. Bare ground was conspicuous on these sites.

The shrub phase occurred on southeast exposures. The dominant shrubs were Amelanchier alnifolia, Artemisia tridentata and Purshia tridentata. Agropyron spicatum, Festuca idahoensis and Poa spp. were the important grasses. Common forbs included Commandra pallida, Erigeron spp., Geranium viscossissimum and Lupinus leucophyllus.

Swales were characterized by Artemisia tripartita and Symphoricarpus spp. Calamagrostis rubescens, Festuca idahoensis, Koeleria cristata and Poa spp. formed a closed canopy of grasses. Lupinus leucophyllus was the most important forb and Erigeron spp. and Geranium viscossissimum were common.

Willow Community

Willow communities (Figure 6) occurred commonly as small to extensive stands on gravel bars and moist flats of the river flood plain (Table V).

Gravel bars were dominated by Agrostis alba and Muhlenbergia spp. in

TABLE IV. AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF PLANT TAXA ON SIX REPRESENTATIVE STANDS OF THE BUNCHGRASS-SHRUB COMMUNITY

	Bunchgrass Phase				Shrub Phase	
	I	II	III	IV	V	VI
Exposure	South		West	Ridge-top	Swale	South-east
No. of plots	27	34	25	30	25	25
BROWSE:						
Amelanchier alnifolia	-	-	-	-	-	754[1]
Artemisia tridentata[2]	-	-	-	1/10[3]	-	22/64
Artemisia tripartita	-	-	-	-	10/64	-
Gutierrezia sarothrae	15/70	6/29	23/92	9/70	4/12	-
Purshia tridentata	-	-	-	-	-	17/36
Symphoricarpus sp.	-	-	-	-	12/16	7/36
GRASSES:						
Agropyron spicatum	6/33	16/88	29/92	7/40	1/4	30/68
Agropyron trachycaulum	5/33	1/3	-	+/6[4]	12/56	6/32
Calamagrostis rubescens	-	-	-	-	25/40	4/8
Festuca idahoensis	-	-	-	+/3	46/72	13/32
Koeleria cristata	-	2/26	1/8	+/16	24/56	9/32
Oryzopsis hymenoides	14/59	4/29	-	-	-	-
Poa spp.	3/19	2/35	18/88	23/90	38/72	14/32
Stipa comata	11/59	11/73	-	-	9/32	6/28
FORBS:						
Astragalus miser	-	-	10/80	-	3/16	1/8
Lupinus leucophyllus	-	-	-	-	30/88	7/32
Phlox spp.	6/33	1/18	6/84	11/80	-	-
Soil	76/100	70/100	49/100	56/100	9/40	7/40
Rock	2/15	4/38	1/4	-	-	2/4
Litter	1/37	-	5/100	+/13	85/100	88/100

1/ Number per acre.

2/ Taxa with less than 10 percent canopy coverage in each of the stands were excluded and appear in Table XVIII of the Appendix.

3/ The figure preceeding each / is the average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

4/ +/ indicates occurrence in the plots with a coverage value less than 0.5 percent.

Figure 6. Willow Community on Snake River Flood Plain

Figure 7. Bluegrass Meadow within the Willow Community.

TABLE V. NUMBER OF TALL SHRUBS PER ACRE AND AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF SUBORDINATE VASCULAR TAXA ON THREE REPRESENTATIVE STANDS OF THE WILLOW COMMUNITY AND TWO REPRESENTATIVE STANDS OF SEDGE-BLUEGRASS COMMUNITY

	Willow			Sedge-Bluegrass	
	I	II	III	IV	V
Site	Gravel	Dry	Wet	Mesic	Wet
No. plots and/or pairs	25	25	25	25	40
TALL SHRUBS:					
Salix geyeriana	-	144	516	-	-
Salix pseudocordata	-	114	2711	-	-
SHORT SHRUBS: 1/					
Populus angustifolia	9/52 2/	-	-	-	-
Potentilla fruticosa	-	23/52	5/28	-	7/32
Salix spp.	23/52	-	-	-	-
Salix wolfii	-	28/40	9/20	-	-
GRASSES AND GRASS-LIKE:					
Agrostis alba	20/68	-	5/24	-	-
Carex spp.	6/28	45/58	81/96	+/3 3/	64/100
Deschampsia caespitosa	2/4	-	3/20	-	43/80
Juncus spp.	6/12	6/20	29/60	-	43/96
Muhlenbergia spp.	18/52	4/8	1/8	-	28/64
Phleum pratense	-	-	1/4	10/50	3/24
Poa spp.	-	19/24	9/20	75/100	4/16
FORBS:					
Aster spp.	1/20	10/52	7/44	3/43	-
Equisetum vareigatum	16/32	-	-	-	-
Frageria sp.	-	11/64	3/28	-	+/8
Taraxacum officinale	-	17/52	+/4	58/100	2/20
Trifolium spp.	4/32	2/20	5/32	70/98	-
Soil	69/100	8/16	-	1/15	1/8
Litter	23/84	80/92	73/88	42/100	93/100
Mosses and lichens	2/32	16/36	27/64	1/13	10/28
Water	-	-	14/20	-	-

1/ Taxa with less than 10 percent canopy coverage in each of the stands were excluded and appear in Table XVIII of the Appendix.

2/ The figure preceeding each / is the average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

3/ +/ indicates occurrence in the plots with a coverage value less than 0.5 percent.

association with Salix spp. and Populus angustifolia. Trifolium spp. and Equisetum variegatum were common and Meliotus spp. occurred on some sites. Exposed sand and gravel were conspicuous.

Dry willow flats were characterized by scattered clumps of Salix geyeriana and Salix pseudocordata. Potentilla fruticosa, Salix wolfii and Carex spp. dominated the field layer. Common forbs included Aster spp., Fragaria sp. and Taraxacum officinale.

Wet meadows were characterized by a greater density of Salix pseudocordata while Salix geyeriana was reduced in relative abundance. Carex spp. and Juncus spp. dominated the field layer and low shrubs as well as forbs were less abundant than on dry sites.

Sedge-Bluegrass Community

This community occurred as small to extensive meadows (Figure 7) on the river flood plains and had limited distribution in moist depressions on the outwash plain and moraine substrates.

Poa spp., Trifolium spp. and Taraxacum officinale dominated the mesic sites (Table V) while Carex spp., Deschampsia caespitosa, Juncus spp. and Muhlenbergia spp. dominated the wet areas. Forbs were unimportant on wet sites. Intergradations between the two types were common.

Agricultural Communities

Pasturelands and hayfields were present on areas east of Blacktail Butte and north of Spread Creek. An abandoned field occurred south of Blacktail Butte.

Composition of these communities was variable (Table VI). Bromus

TABLE VI. AVERAGE PERCENT CANOPY COVERAGE AND PERCENT FREQUENCY OF PLANT TAXA ON THREE AGRICULTURAL COMMUNITIES

	Pastureland	Hayfield	Abandoned Field
Number of plots	40	25	25
GRASSES:[1]			
Agropyron spp.	10/18[2]	-	5/16
Bromus inermis	17/20	78/100	32/60
Phleum pratense	37/78	-	2/12
Poa spp.	67/78	21/64	75/92
FORBS:			
Medicago sativa	-	29/72	33/80
Taraxacum officinale	22/78	1/8	-
Trifolium spp.	9/33	-	+/8[3]
Soil	-	16/88	22/92
Litter	98/100	81/100	68/100

1/ Taxa with less than 10 percent canopy coverage in each of the stands were excluded and appear in Table XVIII of the Appendix.

2/ The figure preceeding each / is the average percent canopy coverage for all plots of the stand and the figure following is the percent frequency within the plots.

3/ +/ indicates occurrence in the plots with a coverage value less than 0.5 percent.

inermis, *Phleum pratense* and *Poa* spp. were the important grasses. *Medicago sativa* and *Taraxacum officinale* were the common forbs.

POPULATION STATUS

Distribution

A total of 42,237 observations of elk was recorded during 302 early morning and late evening periods from June 6 - September 26, 1963, and from May 15 - October 31, 1964, while systematically covering routes through the study area by vehicle. Locations of elk were recorded to the nearest one-fourth mile from a gridded one inch scale map. Vegetation types utilized by elk were determined. Sex and age classifications and the identifcation of marked elk were aided by the use of a 15 to 60 X spotting scope.

Resident elk were considered to be those represented by 21,281 observations from July 15 to September 15, 1963 and 1964 (see Movements). The locations indicated population segments for the Refuge, Central Valley, Uhl Hill and Moran Meadows (Figure 1).

The present distribution is more extensive than that reported by Sheldon (1927) and Jepson and Anderson (1951). These authors did not report elk summering south of the forested areas near Spalding Bay and Signal Mountain (Figure 1). Substantial numbers of elk summering in the central portion of the Central Valley area were reported for 1958 (McClaren, 1964). Murie (1943) reported an elk population of "several hundred" for the summer of 1943 on the north end of the National Elk Refuge.

Population Size

Estimates of the population for the different herd segments were

derived from direct counts, ratios of marked to unmarked elk observed and calculations from sex and age ratios.

Maximum unduplicated counts from the ground for the female-calf-yearling male components of the Refuge, Central Valley and Moran Meadow segments were obtained between August 1 and 20, 1963 and 1964. That for Uhl Hill was obtained October 1, 1964 (Table VII). The female-calf-yearling male component was also computed in 1964 for the Refuge and Central Valley segments using the Lincoln Index. There were 38 marked elk in the Refuge segment and 96 marked elk in the Central Valley segment as determined by intensive observations between July 16 and September 15 (see section on Movements).

The adult male component of the Refuge and Central Valley segments was computed from maximum estimates of the female component (direct count or calculated) and adult male/female ratios. September 1 - 15 classifications of 564 elk in 1963 and 615 elk in 1964 gave maximum numbers of adult males per 100 females (see section on Social Habits).

Maximum estimates for total elk are presented in Table VII. Data for 1962 were obtained from an August 13 aerial flight (Cole, 1963) on which the writer served as an observer.

Differences of total population estimates for 1962 as compared to 1963 and 1964 probably reflect techniques. The low estimate for 1962 was provided by aerial flight following an established transect line which only sampled the population. The northern portion of the study area was covered about one hour after sunrise. Field observations indicated

TABLE VII. MAXIMUM COUNTS AND/OR CALCULATED SIZE FOR VARIOUS COMPONENTS OF THE RESIDENT ELK OF JACKSON HOLE, WYOMING, 1962, 1963 and 1964

Herd Segment	Female-calf-yearling male component			Calculated adult male component		Maximum estimate for total elk		
	Maximum count		Calculated					
	1963	1964	1964	1963	1964	1962	1963	1964
Refuge	365	346	288	21	6	242	386	352
Central Valley	643	557	1,129	80	194	295	723	1,323
Uhl Hill	*[1]	75	*	*	*	*	*	75
Moran Meadows	53	43	*	*	*	56	53	43
Totals	1,061	1,021	1,417	101	200	593	1,162	1,793

1/ No data.

that elk usually moved from open habitat types to forest types within one hour after sunrise.

The difference between the 1963 and 1964 population estimates resulted from the use of Lincoln Index figures for the Central Valley segment in 1964. The use of forested areas by a portion of this herd segment was not conducive to total counts but their occasional appearances in edge areas allowed the identification of marked individuals.

The 1964 total estimate of 1,793 elk summering within the valley represents 23 percent of the 1963-64 classified Refuge winter count of 7,916 (Yorgason, 1964).

Sex and/or Age Structure

A total of 5,883 elk was classified as to sex and/or age from June 7 - September 26, 1963, and 9,393 elk from May 15 - October 31, 1964. Female, calf, yearling male and adult male classes were recognized. Unduplicated classifications of 738 elk on August 9, 14 and 15 in 1963 and 741 elk on August 4, 5 and 6 in 1964 provided the largest sample of females, calves and yearling males in the Refuge and Central Valley segments. Cumulative classifications from September 1-15 both years sampled the maximum numbers of adult males (see section on Population Size). Numbers of calves, yearling males and adult males per 100 females were computed. Sex and/or age structures were calculated from these ratios for the Refuge and Central Valley segments (Table VIII).

The two herd segments had different sex and/or age structures. Numbers of yearling males per 100 females were higher and numbers of calves as well

TABLE VIII. SEX AND/OR AGE STRUCTURE OF THE RESIDENT VALLEY ELK HERD AS DETERMINED FROM MID-AUGUST CLASSIFICATIONS FOR FEMALES, CALVES AND YEARLING MALES AND SEPTEMBER CLASSIFICATIONS FOR ADULT MALES 1963 AND 1964.

Herd Segments	Year	Numbers per 100 females			Percentages			
							Males	
		Calves	Yearling males	Adult males	Females	Calves	Yearling	Adult
Refuge	1963	21	50	10	55	12	28	5
	1964	22	44	3	59	13	26	2
Central Valley	1963	35	34	21	53	18	18	11
	1964	38	29	29	51	19	15	15

as adult males per 100 females were lower in the Refuge than in the Central Valley segment.

Yearling males occurred in greater proportions in both herd segments in 1964 than would have been expected from the proportion of calves in 1963 summering herds. About ten yearling males per 100 females were expected in the Refuge segment in 1964 as recruitment from 21 calves per 100 females in 1963 and about 15 per 100 females in the Central Valley segment from 35 calves per 100 females in 1963. The disproportionate occurrence of yearling males in valley herds apparently resulted from substantial numbers of these animals from the migratory herd not migrating to mountain areas thus becoming a part of the resident valley herds. This was illustrated by male No. 113 which was observed in mountain areas with migratory elk as a calf and in valley areas as a yearling. The difference between the expected and actual proportions of yearling males was less in the Central Valley than in the Refuge segment suggesting that the tendency to remain in valley areas decreased northward from the winter range.

Yearling males also occurred in greater proportions in both summer resident herd segments than would have been expected from proportions of calves reported in 1962-63 and 1963-64 winter Refuge classifications by Yorgason (1964). If yearling males were evenly distributed among summer herds eight per 100 females were expected in 1963; 15 per 100 females in 1964 in the valley residents. The difference between the expected and actual values for the two years suggests that the numbers of yearling males remaining in valley areas as residents may vary between years.

Calf per 100 female values in the Central Valley summer herd were comparable to those obtained from Refuge classifications during the winters of 1963-64 and 1964-65 (Yorgason, 1964 and 1965). Lower numbers of calves per 100 females in the Refuge summer herd as compared to the following winter classifications may have resulted from a disproportionate occurrence of yearling females in the herd and/or the tendency for poor condition adult females not to migrate from the winter range.

Yearling females were expected to occur in a ratio of nine per 100 older females in 1963 from the 1962-63 winter classification of 18 calves per 100 females. Examination of the mandibular dentition of 60 female elk killed during the early 1963 hunting season (September 10 - October 15) on the north end of the Refuge indicated 24 yearling females per 100 older females. Sixteen yearling females occurred per 100 older females in the Central Valley segment (Cole, 1964). These data show that yearling females occurred in greater than expected proportions in valley summer herds but to a lesser extent than yearling males. Female No. 110 showed residency in mountain areas as a calf and in the valley as a yearling. Yearling females showed the same tendency as yearling males to decrease in proportions northward from the winter range.

Disproportionate numbers of yearling females may not remain in valley areas every year. Yearling females occurred in a ratio of 19 per 100 older females in 1964 in Central Valley mandible samples (Cole, 1965). This value was close to the 18 yearling females per 100 older females expected from 35 calves per 100 females in the Central Valley segment in

1963 (Table VIII).

Based on preceding winter classifications adult males were expected to occur in a ratio of 24 per 100 females in 1963 and 26 per 100 females in 1964 if they were evenly distributed among summer herd segments. Lower than expected numbers occurred in the Refuge segment both years. Proportions of adult males in 1964 did not reflect the high occurrence of yearling males in either herd segment during 1963. Adult males were expected to occur in ratios of 60 and 65 per 100 females in the Refuge and Central Valley segments, respectively (from 1963 yearling male plus adult male per 100 female values). Disproportionate hunter harvests of male elk (Cole, 1964) account for only a portion of the difference between expected and actual values. The remaining difference suggests that yearling males were more observable than adults or that as adults they migrated from valley areas with the migratory herd.

SOCIAL HABITS

Grouping Habits

Observations of 558 single and 2,193 groups of elk were recorded during 1963 and 1964. Numbers of elk observed per observation trip, percentages of elk observed as single individuals, frequency of occurrence of different size groups for elk observed in groups and average group sizes are shown by periods in Table IX.

Observations prior to June 1, 1964, included elk migrating to northern mountain areas (see section on Movements). Subsequent data are considered as relating to summer valley herds. The average number of elk per group observed was lowest in early June, increased to a maximum by late July - early August, declined to a low value in late September - early October and showed an increase for the latter part of October. The frequency of occurrence of the smallest and largest groups as well as the percentages of elk observed as singles in general reflect the trend shown by the average group sizes (Table IX).

The percentage of elk observed as single individuals was less and the number of groups of 2-10 were fewer in 1963 than in 1964. Average group sizes and percentages of groups with 51 or more elk were greater in 1963 than in 1964. After June 15 numbers of elk observed per observation trip were less in 1964 than in 1963. This was apparently related to group sizes, since summer populations as indicated by maximum counts were approximately the same for both years (see section on Population Size).

TABLE IX. NUMBER OF ELK OBSERVED PER OBSERVATION TRIP, PERCENTAGES OF ELK OBSERVED AS SINGLE INDIVIDUALS, AND FREQUENCY OF OCCURRENCE OF DIFFERENT SIZE GROUPS, AVERAGE GROUP SIZES OBSERVED IN 1963 AND 1964

Dates	Total elk observed		No. obs. per trip		Single elk (Percent of total obs.)		Elk Groups: Frequency of occurrence 2 - 10		11 - 25		26 - 50		51 plus		Average size	
	1963	1964	1963	1964	1963	1964	1963	1964	1963	1964	1963	1964	1963	1964	1963	1964
5/15-17	-[1]	2,724	-	389	-	0.4	-	68	-	19	-	7	-	7	-	21
6/1 -15	976	3,205	75	160	5.3	2.7	78	71	15	20	6	7	2	2	7	10
6/16-7/15	5,799	4,188	157	127	1.3	2.2	66	75	17	15	6	5	11	5	20	14
7/16-8/15	5,554	5,428	163	139	0.3	0.7	45	57	19	18	11	9	25	16	42	25
8/15-9/15	3,773	3,978	114	111	0.5	1.2	47	65	23	18	11	8	20	8	32	19
9/16-10/15	-	2,697	131	96	-	2.8	-	77	-	14	-	6	-	2	-	11
10/16-11/1	-	2,488	-	226	-	0.6	-	62	-	17	-	7	-	14	-	30

1/ No data.

Association Habits

A total of 461 elk observed as single individuals was classified as to sex and/or age and 1,561 elk groups were classified as to their sex and/or age composition in 1963 and 1964 (Table X).

The proportion of females among the single elk observed progressively declined from a maximum in early June to a minimum for the late September - early October period. Increases from minimum to maximum percentages occurred over the same period for single yearling and adult males.

The decline from early June to late July - early August in the proportion of female-calf associations among observed groups coincided with an increase in female-calf-yearling male associations. Decreases in female-calf-yearling male associations after August 15 coincided with an increase in female-calf-yearling male-adult male associations.

The combined data from Tables IX and X supplemented with field observations suggested that five periods relative to elk social habits occurred from June through October. Calf tagging records indicated that June 1 - 15 represented the period of calving activity. Johnson (1951) reported that calving generally occurred from May 15 to June 15 with peak about June 1. Relatively large numbers of single females and small groups of females with or without calves were characteristic.

June 16 - August 15 was a period of aggregation. Single females, small female-calf groups and female-yearling male groups appeared to aggregate into associations reaching maximum group sizes in late July - early August. Groups of adult males were conspicuous.

August 16 - September 15 was a period of dispersal. Decreased group

TABLE X. THE SEX AND/OR AGE CLASS OF ELK OBSERVED AS SINGLE INDIVIDUALS OR IN GROUPS EXPRESSED AS PERCENTAGES. DATA FOR 1963 AND 1964 ARE COMBINED

	Percentages					
	6/1-15	6/16-7/15	7/16-8/15	8/16-9/15	9/16-10/15	10/15+
Singles						
Females	85	68	63	36	32	
Calves	3	0	4	4	0	
Yearling males	4	11	9	16	21	
Adult Males	8	21	24	43	47	
Total Elk Classified	118	145	46	67	85	
Group Associations						
Fe-(Ca) 1/	43	26	19	20	22	26
YM's 1/	*2/	3	1	3	6	4
AM's 1/	5	10	8	9	5	7
Fe-(Ca)-YM	23	28	39	29	17	18
Fe-(Ca)-(YM)-AM's	29	31	29	39	48	44
AM's-YM's	*	2	2	*	*	2
Total Groups Classified	290	407	259	302	247	57

1/ Parenthesis indicate with or without this class present; Fe=females; Ca=calves; YM=Yearling males; AM=Adult males.

2/ Less than 0.5 percent.

sizes coincided with increased attachment of adult males to associations of females, calves and yearling males. Yearling males and adult males were observed more frequently as single individuals.

Maximum breeding activity occurred between September 16 and October 15 although the first "display" by an adult male was recorded on August 21 and the first formation of a harem group was recorded on September 2. Small harem associations, characterized by the presence of a single adult male, and the frequent occurrence of single yearling males as well as single adult males were characteristic. Sixty-eight percent of the groups with which adult males were associated were harem groups. The attending male was characterized by the antlers of a two-year-old in 21 percent of the harem groups.

October 16 - 31 was a period of re-aggregation. Associations differed only slightly from the previous period but large groupings became common.

Altmann (1952, 1956 and 1960) has previously reported on the behavioral patterns of elk in the Jackson Hole area. Her results generally agree with those reported here.

MOVEMENTS

Each of 183 elk in 1963 and 779 in 1964 was individually marked on the Refuge winter range (Yorgason, 1964). Markers were a numbered plastic ear tag (Perma-Tag Co.) or a colored plastic symbol marker (Johnson, 1951). Each of 19 newborn calves was marked with both the Perma-Tag and symbol marker in Central Valley calving areas from May 29 - June 14, 1963. Three were marked from May 21 - June 21, 1964.

One-hundred-eighty-seven relocations of 37 marked elk were recorded from June 7 - September 26, 1963, and 1,053 of 346 from May 6 - November 30, 1964. Additional relocations were obtained from hunter kills of 49 marked elk between September 10 and November 30, 1964.

Spring Migration

One-hundred-one marked elk, each of which was relocated in the valley at least once between July 16 and September 15, 1964, were considered to be residents of Central Valley areas. One-hundred-thirty-five marked elk, each of which was relocated prior to July 15 but not after that date, were considered to be migrating through the Central Valley area.

The first significant movements (500 or more elk) northward from the Refuge winter range were observed on May 14, 1964 (Cole, 1965). The relative percentages of marked migratory and resident elk observed within the Central Valley herd segment varied between May 6 and July 15 (Table XI). Maximum percentages of marked migratory elk were associated with marked resident elk of valley areas from May 6 - 31. Average observations of 367 elk per observation trip during this period, as compared to values

TABLE XI. RELATIVE PERCENTAGES OF MARKED MIGRATORY AND RESIDENT ELK PRESENT ON AREAS NORTH OF THE REFUGE BETWEEN MAY 6 AND JULY 15, 1964

Dates	Number Marked Elk Observed	Percent Migratory Elk	Percent Resident Elk
May 6-15	13	77	23
May 16-31	102	78	22
June 1-15	113	56	44
June 16-30	67	42	58
July 1-15	49	18	82

less than 160 after June 1 substantiated that this was the period of peak migration.

Relative percentages of migrating elk among marked elk observed progressively declined after June 1 to a minimum value during the July 1 - 15 period. Calf tagging and relocation records show that a portion of the migratory elk present after June 1 were females with newborn calves. Only eight of 22 calves marked on the study area during 1963 and 1964 were relocated as summer residents of the valley. Calf No. 118 was last observed within the valley on July 10, 1964, and was subsequently relocated in southern Yellowstone National Park on July 20.

Relocations of elk tagged as calves on the winter range showed that at least some migratory yearling males and females remained on valley areas until about mid-July. Migratory adult males apparently moved through the valley during the main migration in May.

Summer Movements and Home Range

The movements and home ranges of elk summering within the valley were analyzed from 461 relocations of 59 marked animals, each relocated five or more times. The relocations of each elk were plotted to the nearest one-fourth mile on a gridded map and distances between relocations were determined to 0.1 mile. The greatest distance between two relocations five or more days apart was determined for individuals. These were averaged for each sex and/or age class to provide an estimate of maximum distances traveled (Table XII). Mean distances between consecutive relocations for each individual were computed. These were then averaged for the individuals of each sex and/or age class to provide a measure of the magnitude of movement within home range.

Considerable variation occurred among individuals but differences in movements were indicated for different groups. For the May 6 - July 15 period movements of yearling males were the most extensive of all groups while those of calves and yearling females were relatively restricted. Movements of calves, which reflected the movements of females with calves, increased for the July 16 - September 15 period as did those of yearling females while those of yearling males became more restricted than during the previous period. The movements of the adult female group, which doubtless included a high percentage of barren females, (see section on Sex and Age Structure) remained relatively stable.

Movement patterns of marked adult females and calves indicated three separate female-calf groups within the Central Valley prior to the breeding

TABLE XII. MEAN MAXIMUM DISTANCES BETWEEN OBSERVATIONS AND MEAN DISTANCES BETWEEN CONSECUTIVE OBSERVATIONS FOR THE INDIVIDUALS OF EACH SEX AND/OR AGE GROUP BY PERIODS FOR 1963 AND 1964.

Sex and/or age group	Sample size	No. of Relocation	Mean maximum distances between observations (mi.)			Consecutive distances between observations (mi.)	
			5/7-7/15	7/16-9/15	Summer	5/6-7/15	7/16-9/15
Calves	5	42	2.1(0.6-2.3)	2.8(1.8-4.2)	3.6(2.3-5.7)	1.6(1.4-1.9)	1.6(1.2-2.0)
Yr. females	11	82	2.5(0.7-5.2)	3.4(1.1-7.7)	5.4(1.2-13.1)	1.4(0.3-2.7)	2.3(0.6-4.8)
Yr. males	21	161	4.0(1.5-7.6)	3.1(0.5-6.0)	5.4(1.9-11.7)	2.3(0.6-4.8)	1.7(0.3-3.1)
Ad. females	21	170	3.7(1.0-6.8)	3.5(1.0-6.7)	4.4(1.9-6.8)	2.0(0.7-5.8)	1.9(0.6-3.5)
Ad. males	1	9	*1/	*	4.2	*	*

1/ Insufficient data.

season (Figure 8). The presence and location of these appeared to be an important factor influencing the movements of yearling elk.

The relatively extensive wandering of yearling males prior to mid-July was related in at least some instances to associating with two or more female-calf groups as illustrated by yearling male No. 642 (Figure 8). After about July 15 most individuals had developed an association with one specific female-calf group and movements became restricted to the areas occupied by that group. Data are limited but yearling male movements during the breeding season appeared to become more extensive and generally erratic. Leopold et al. (1951) and Cole (1956) have reported the wandering tendencies of yearling male mule deer and antelope, respectively.

Restricted movements of yearling females in early summer appeared to be related to their association with particular female-calf groups while the more extensive movements for late summer were related to movements to other groups (Figure 9).

The location of a calf at the time of marking was not necessarily included in the subsequent summer range (Figure 10). More extensive movements of calves after mid-July was probably related to the aggregation of small female-calf groups into larger assocations (see section on Association Habits) which moved over greater areas.

Prior to late August the movements of most adult males were independent from those of the female-calf yearling male herd component. Their movement patterns in general were reflected in the numbers observed.

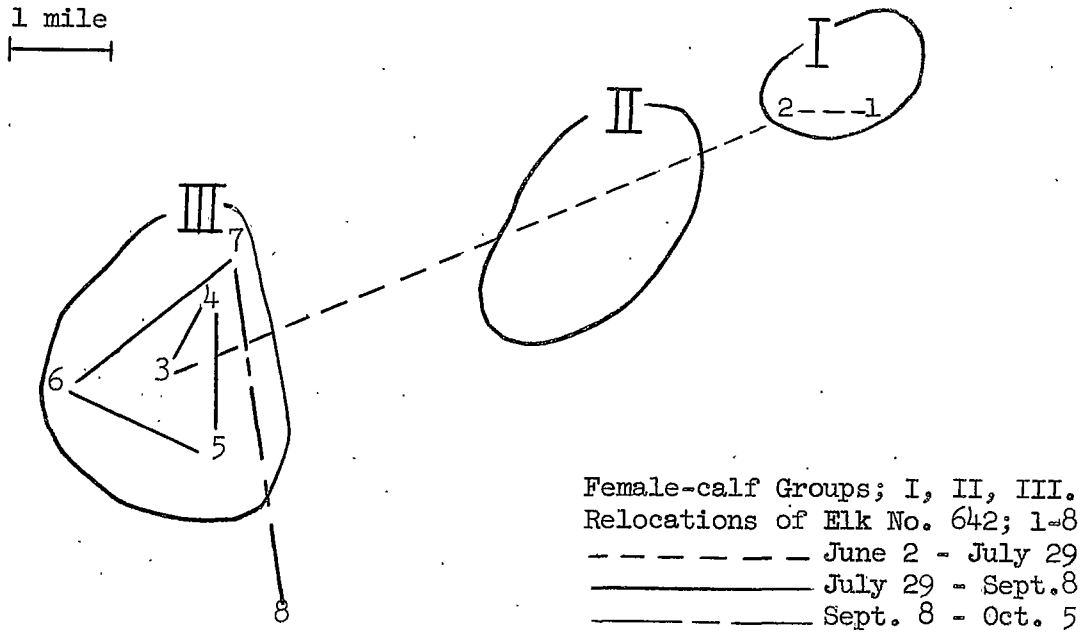

Figure 8. Movements of Yearling Male Elk No. 642 with Respect to Three Female-calf Groups of the Central Valley.

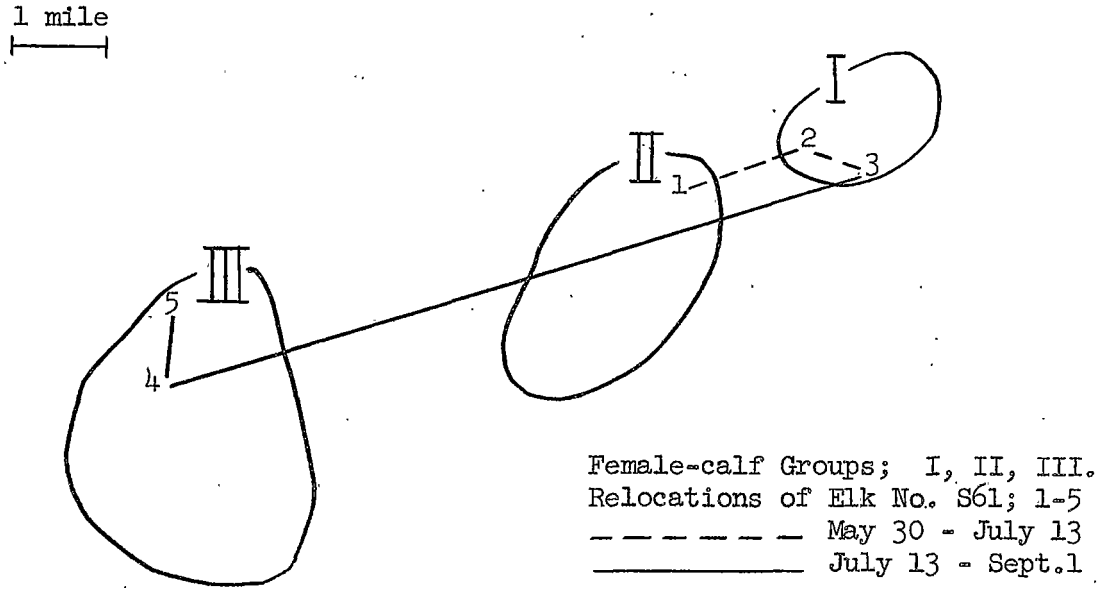

Figure 9. Movements of Yearling Female Elk No. S61 with Respect to Three Female-calf Groups of the Central Valley.

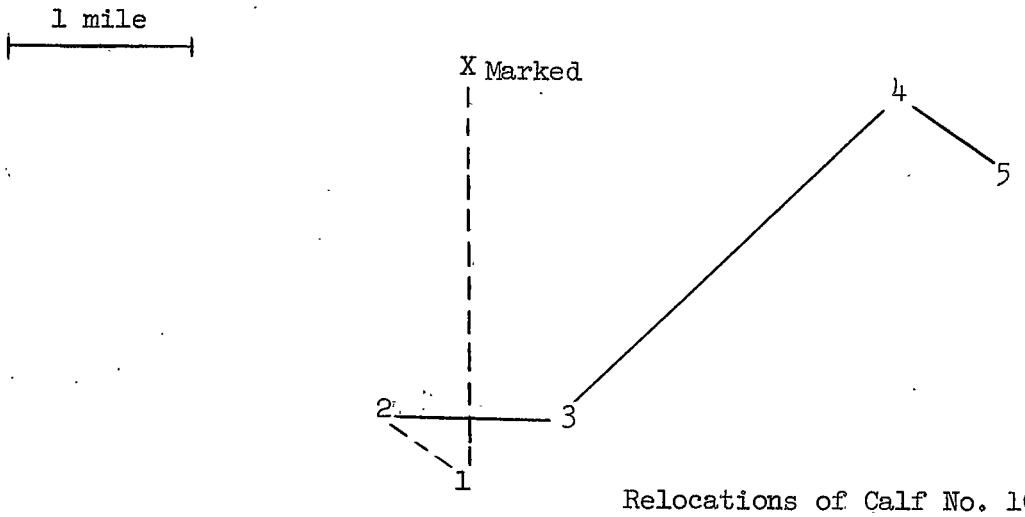

Figure 10. Movements of Calf No. 107.

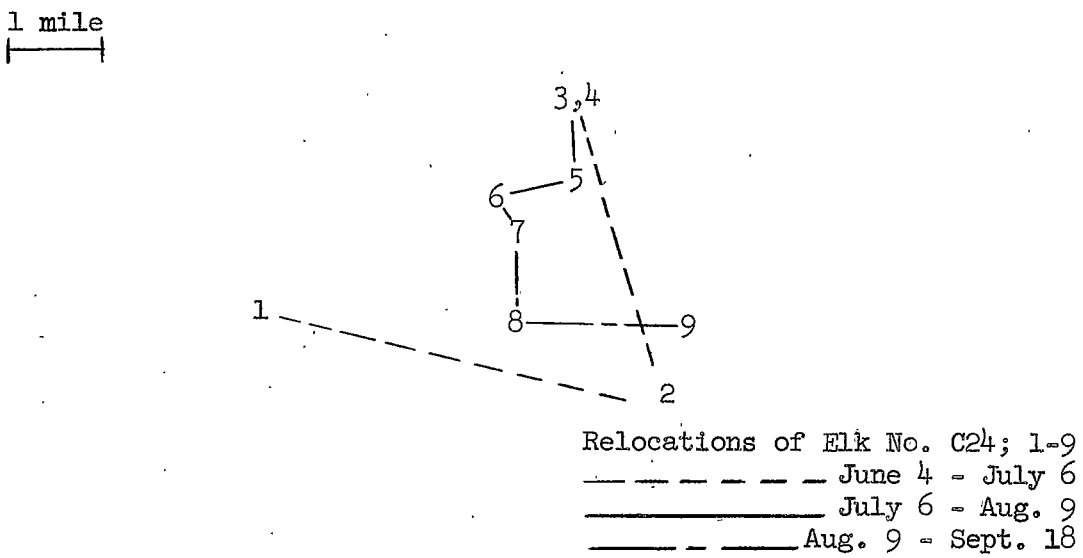

Figure 11. Movements of Adult Male No. C24.

TABLE XIII. AVERAGE HOME RANGE AREAS AND FREQUENCY WITHIN THREE-MILE-CLASS INTERVALS FOR SEX AND/OR AGE GROUPS 1963 AND 1964. SAMPLE SIZE IN TABLE XII.

Sex and/ age group	Average home range ($mi.^2$)	Percentages by square mile-class			
		0.0-3.0	3.1-6.0	6.1-9.0	9.0 plus
Calves	3.6 (1.0-10.1)	60	20	0	20
Yr. female	3.8 (1.0-8.8)	55	27	29	9
Yr. male	5.7 (1.3-15.5)	25	35	25	15
Ad. female	4.8 (1.0-12.8)	37	32	26	5
Ad. male	4.8		100		

Relatively extensive movements prior to early July and after mid-August (Figure 11) coincided with maximum numbers observed. Restricted movements between these dates coincided with minimum observations. The use of forest habitat types during this period also affected observability.

The area of summer home range (May 6 - September 15) was determined for individual elk by connecting peripheral observations and estimating in square miles the enclosed area (Table XIII). Average home range sizes show the same trend as the mean maximum distances between relocations for the summer period (Table XII), for all but the yearling female group.

Fall Movements and Related Effects of Hunting on Movements

Sixty-two marked elk, each of which was observed in the valley after September 15, 1964, but not between July 16 and September 15 were considered to be migrating southward from mountain summer ranges.

Forty-four marked elk that were observed after September 15 were summer residents of Central Valley and Refuge herd segments (see section on Spring Migration). Additional relocations of marked elk were obtained from 19 resident and 30 migratory elk killed during the 1964 hunting season.

Most resident and migratory elk traversed areas where hunting was permitted and areas where it was not permitted while moving to the Refuge winter range. That portion of the study area west of the Snake River was closed to hunting while on valley areas to the east hunting was allowed by special permit (Figure 1). The northern portion of the National Elk Refuge was open from September 10 - October 15, 1964, and areas within Grand Teton National Park were open from October 1 - November 30.

Marked elk observed on areas open or closed to hunting were classified as migratory or resident (Table XIV). The proportion of migratory elk among marked elk observed on both open and closed areas increased from a minimum during the September 16 - October 15 period to a maximum between October 16 and 31. After October 16 the proportion of migratory elk exceeded that of resident elk among marked elk observed.

The proportion of residents among marked elk observed on closed areas was greater than the proportion of residents among marked elk observed on open areas while the reverse was true for migratory elk. This possibly suggests that resident elk sought the sanctuary of closed areas or that hunting may have been effective in restraining their movement to the winter range. The first major movement of migratory elk through the study

TABLE XIV. PERCENTAGE OF TOTAL MARKED ELK OBSERVED FOR MIGRATORY AND RESIDENT ANIMALS RELOCATED ON AREAS OPEN OR CLOSED TO HUNTING 1964.

	Sept. 16-31		Oct. 1-15		Oct. 16-31		Nov. 1-15	
	Open	Closed	Open	Closed	Open	Closed	Open	Closed
Migratory elk	18	7	46	36	92	63	64	50
Resident elk	82	93	54	64	8	37	36	50
Total observed	11	14	26	14	50	19	11	36

area on October 20 and 21 effected a southward drift of resident elk within the Central Valley segment. Five marked elk commonly observed in the northern portion of Central Valley in summer were each observed in the southern part after October 20 but never in the open area. It was necessary for resident elk to cross the open area to reach the Refuge winter range but relatively few were observed or killed on this area in late October. Only three of 24 marked elk identified on the Refuge winter range on October 29 were resident elk. The second major movement of migratory elk was in November. It apparently stimulated substantial numbers of resident elk to move across the open area. Thirty-six percent of the marked elk killed or observed on the open area were residents as compared to eight percent during the previous period.

Hunting appeared to be an important factor in effecting elk movements from the Refuge area (open to hunting September 10 - October 15) to closed areas. The records of 12 marked elk indicated residency in the Refuge prior to the hunting season but during the hunting season each of them was observed in adjacent closed areas within Grand Teton National Park. Ten

moved two to five miles northward to Blacktail Butte and the remaining two, both yearling males, moved 14 miles to the Central Valley area.

HABITAT RELATIONSHIPS

Use of Vegetation Types

Percentages of total elk observed that were on the different vegetation types indicated relative use during monthly periods (Table XV). Feeding was the characteristic activity for undisturbed animals.

Use of sagebrush-bunchgrass was greatest in October but this type was used more heavily than any other type during all months of observations for 1963 and 1964. Greater use in 1964 than in 1963 was coincident with increased use of aspen and decreased use of willow and sedge-bluegrass types. This appeared to be related to unexplained distributional differences between years. An individually marked elk was observed along the Snake River in 1963 and in upland areas in 1964.

Use of the bunchgrass-shrub type was second highest for all types in May. This was probably related to the earlier development of green vegetation on south and west exposures, particularly grasses, which developed two to four weeks earlier than on other exposures. Use declined in late May as elk shifted to other sites and types on which green vegetation appeared as they became snow-free.

Use of other types varied from minor to moderate and the combined use of all was directly related to the intensity of use of sagebrush-bunchgrass. Increased use of agricultural types near the southern portion of the study area after mid-August was probably related to the presence of Medicago sativa which retained succulence into September. Records of eight marked elk suggested that elk of the Refuge segment

TABLE XV. PERCENTAGES OF ELK OBSERVED ON THE DIFFERENT PLANT COMMUNITIES BY MONTHLY PERIODS 1963 AND 1964

	May	June		July		August		September		October
Plant Community	1964	1963	1964	1963	1964	1963	1964	1963	1964	1964
Sagebrush-Bunchgrass	64	48	60	57	62	47	66	28	53	83
Sedge-Bluegrass	1	20	12	10	12	12	7	22	7	7
Willow	*[1]	13	6	10	2	15	3	4	5	1
Aspen	3	2	10	5	11	1	11	12	7	2
Cottonwood-Spruce	*	3	*	1	4	2	1	12	7	1
Coniferous Forest	1	7	9	9	3	5	7	4	7	2
Agricultural	*	5	1	2	*	5	4	9	6	4
Bunchgrass-Shrub	31	2	2	6	6	13	1	8	8	*
Total elk observed[2]	2724	3232	5248	6010	5107	4806	4715	3502	2814	4079

1/ Less than 0.5 percent.

2/ Includes repeated observations of same individuals.

were mainly involved but in 1963 two marked elk of the Central Valley segment, eight miles to the north, were observed using hayfields after August 15.

The difficulty of observing elk within forest types indicated that the tabular data do not reflect actual use levels. Forest types adjacent to feeding areas were important for bedding and resting. The lower numbers of elk observed per observation trip after August 15 (Table IX) probably reflect increased use of forest types (Brazda, 1953; Cole, 1963; Kirsch, 1962; Stevens, 1964 and others) as well as reduced group sizes (see section on Grouping Habits). Increased use of cottonwood-spruce, a relatively open type, was recorded during September.

Food Habits

Elk food habits were studied primarily by examining feeding sites and recording instances of use for individual plant taxa (Cole, 1956). Use of a rooted stem for single-stemmed grasses and forbs, an entire aggregation of stems for bunchgrass and a single leader for woody plants were each considered as one instance of use. The aggregate percentage method (Martin, et al. 1946) was used in computing percentages. The percent of the total plant use for each taxon on each site was determined. Percentages for different sites of each vegetation type were then aggregated and averaged for each taxon to determine the percentage use in relation to all plants used on the different vegetation types.

A total of 24,420 instances of plant use was recorded at 172 feeding sites from May through October 1963 and 1964 (Table XVI). Considering all

TABLE XVI. ELK FOOD HABITS AS DETERMINED FROM 24,450 INSTANCES OF PLANT USE AT 172 FEEDING SITES MAY - OCTOBER 1963 AND 1964

Taxa used[1]	Vegetation Type: Sagebrush-bunchgrass	Sedge-bluegrass	Willow	Aspen	Cottonwood-spruce	Coniferous Forests	Agricultural	Bunchgrass-shrub
Total instances of use	10,290	3,767	1,750	3,737	1,010	1,138	1,166	1,592
Number of sites exam.	87	22	9	22	4	11	6	11
Agropyron spicatum	2/17[2]	--	--	1/9	Tr/25[3]	--	--	35/82
Agropyron spp.	Tr/10	1/9	--	7/68	2/50	--	--	1/18
Bromus innermis	Tr/1	8/32	5/22	--	--	--	28/50	--
Bromus marginatus	1/11	--	--	9/64	Tr/25	--	--	--
Festuca idahoensis	3/16	Tr/5	Tr/11	Tr/9	--	--	--	Tr/9
Oryzopsis hymenoides	Tr/1	--	--	--	--	--	--	--
Poa spp.	4/24	47/100	6/67	2/36	1/75	6/18	7/50	13/64
Carex spp.	2/36	4/36	2/44	6/64	1/75	3/27	--	1/18
TOTAL GRASSES & GRASSLIKE	17/51	63/100	13/67	29/86	7/100	10/54	35/50	57/82
Agoseris glauca	5/34	2/5	Tr/22	6/55	1/25	1/9	2/17	--
Aster spp.	6/32	5/64	2/67	11/17	19/100	4/36	2/33	1/18
Balsamorhiza sagittata	7/29	--	--	1/5	--	5/9	--	Tr/9
Campanula rotundifolia	1/9	--	--	7/55	--	--	--	--
Castilleja spp.	Tr/6	--	--	--	--	--	--	8/18
Commandra pallida	1/8	--	--	--	--	--	--	14/27
Epilobium angustifolium	--	--	--	--	--	3/9	--	--
Erigeron spp.	1/20	--	Tr/22	2/14	3/25	--	--	1/9
Eriogonum spp.	4/45	--	Tr/11	1/36	Tr/25	--	--	2/9
Geranium viscossissimum	1/7	--	--	3/59	--	Tr/9	--	--

TABLE XVI. (Continued)

Taxa used	Vegetation Type: Sagebrush-bunchgrass	Sedge-bluegrass	Willow	Aspen	Cottonwood-spruce	Coniferous Forests	Agri-cultural	Bunchgrass-shrub
Helianthella uniflora	6/17	--	--	1/9	--	1/9	--	9/9
Hieracium spp.	3/11	--	--	1/18	--	Tr/9	--	--
Lupinus leucophyllus	35/69	--	--	--	--	--	5/33	--
Lupinus parviflora	--	--	--	2/59	--	3/18	--	--
Medicago sativa	--	--	--	--	12/25	--	44/50	--
Meliotus offininale	--	--	4/11	--	19/50	--	1/33	--
Phlox caespitosa	Tr/1	--	--	--	--	--	--	5/36
Taraxacum officinale	Tr/12	7/77	1/22	7/64	3/75	8/18	2/50	Tr/9
Trifolium spp.	Tr/1	19/73	4/56	1/14	12/50	--	8/50	--
Equisetum spp.	Tr/1	3/18	1/22	--	Tr/25	--	1/33	--
TOTAL FORBS	83/100	37/100	17/78	54/95	73/100	30/64	65/100	43/100
Amelanchier alnifolia	Tr/1	--	--	1/9	--	9/9	--	--
Ceanothus velutinus	--	--	--	--	--	11/18	--	--
Pachystima myrsinites	--	--	--	--	--	5/18	--	--
Populus tremuloides	Tr/1	Tr/5	2/11	8/23	--	--	--	--
Prunus virginiana	--	--	--	3/9	--	--	--	--
Rosa woodsii	--	--	2/33	3/18	Tr/25	--	--	--
Salix spp.	--	--	66/10	--	2/25	--	--	--
Shepherdia canadensis	--	--	--	--	15/50	6/27	--	--
Symphoricarpus spp.	--	--	--	2/18	--	13/27	--	--
Spirea betulifolia	--	--	--	--	--	6/36	--	--

TABLE XVI. (Continued)

Taxa used	Vegetation Type							
	Sagebrush-bunchgrass	Sedge-bluegrass	Willow	Aspen	Cottonwood-spruce	Coniferous Forests	Agri-cultural	Bunchgrass-shrub
Vaccineum membranaceum	--	--	--	--	--	10/27	--	--
TOTAL BROWSE	Tr/5	Tr/55	70/100	17/50	20/75	60/82	--	Tr/18

1/ Taxa not constituting three percent in at least one vegetation type are not listed in the table but were incorporated into total figures for each forage class.

2/ Average percent use of all plant use per site / Percent of sites within that type in which taxa was used.

3/ Tr indicates less than 0.5 percent use of that taxa within that type.

vegetation types for the entire period forbs average 50 percent, grasses and grass-like plants 29 percent and browse 21 percent of the diet. The importance of most forage species was restricted to one or two vegetation types but Poa spp., Aster spp., Taraxacum officinale and Trifolium spp. received relatively widespread use. Use of browse was substantially greater than that reported for the same seasons of the year by Cole (1963 and 1964), Kirsch (1962), Morris and Schwartz (1957), Murie (1951), Stevens (1964) and others. Schwartz (1943) and Young and Robbinette (1939) indicated that browse was an important summer forage on habitat types where it was available.

Differences occurred in the relative percentage of use of forage-classes on the different vegetation types. Grasses and grass-like plants constituted the most important forage class on the sedge-bluegrass and bunchgrass-shrub types. The percent use of browse exceeded that of other forage-classes only in willow and coniferous forests. For the remaining vegetation types use of forbs was greater than that for either grass or browse.

Important seasonal differences in the use of forage-classes and of individual taxa occurred on only two vegetation types. On the sagebrush-bunchgrass type grasses and grass-like taxa constituted 54 percent (15 sites) of the spring (May) diet as compared to six percent (63 sites) for the summer period (June - August). Early May use was confined to southern exposures where Agropyron spicatum was the important forage. Utilization of Festuca idahoensis increased as flat areas became snow-free in late

May. Forbs constituted the important forage-class in summer. A variety was taken during June but from July 1 - August 31 use of Lupinus leucophyllus amounted to 65 percent of all forb use. Use of grasses and grass-like plants increased to 29 percent (9 sites) of the fall diet (September and October) as the use of forbs decreased. Utilization of Festuca idahoensis constituted 35 percent of the grass use.

A switch from grasses in spring to forbs in summer also occurred on the bunchgrass-shrub type where grasses and grass-like species comprised 81 percent (7 sites) of the spring diet as compared to 13 percent (4 sites) for the summer period. Agropyron spicatum and Poa spp. amounted to 58 and 27 percent, respectively, of the grasses used during spring.

Significant differences occurred in forage-use on different sites for the aspen and agricultural types. In aspen stands of the moraine substrate use was restricted to grasses and forbs while utilization of browse constituted 75 percent of total plant use in groves on the butte substrate. After August 15 an apparent preference for the leaves and terminal buds of Populus tremuloides resulted in heavy use in many reproducing stands. Bromus inermis was important on pasturelands while Medicago sativa was preferred on other sites of the agricultural type.

Rumen analyses: Analyses of rumen samples from 18 hunter-killed elk (11 in 1963 and 7 in 1964) supplemented September and October feeding site data. Following the procedure of Cole (1956) the volume of recognizable items in a one-quart sample was determined and expressed as

a percentage of the total volume. Percentages of individual items for all samples in 1963 were then aggregated and averaged (Table XVII). The difficulty of species identification in 1963 prompted the use of the point-frame method (Chamrad and Box, 1964) for 1964 samples. Fifty cubic centimeters of rumen material was evenly distributed in a laboratory tray and 100 pin-drops were made at equal intervals from a point-frame containing ten pins. The forage-class of each "hit" was recorded and these were totaled to determine percentages. Aggregate percentages were used in final analyses (Table XVII).

Grasses and grass-like plants constituted the major portion of the rumen contents both years. Data from feeding sites aggregated for all vegetation types for the same period showed that grasses and grass-like plants comprixed 41 percent of the diet. The location of elk kills and observations of many prior to being killed suggests that the rumen data best represents the combined use of the willow, aspen, bunchgrass-shrub and sedge-bluegrass vegetation types.

TABLE XVII. SEPTEMBER-OCTOBER ELK FOOD HABITS AS DETERMINED FROM THE ANALYSIS OF 18 RUMEN SAMPLES COLLECTED DURING 1963 AND 1964

Items identified[1]	Aggregate percentages	
	1963 (11 rumens)	1964 (7 rumens)
Avena fatua	2	R[2]
Unidentified grasses and grass-like	65	74
TOTAL GRASSES AND GRASS-LIKE	67	74
Lupinus spp.	4	R
Medicago sativa	2	R
Meliotus officinale	1	-
Trifolium spp.	1	R
Unidentified forbs	9	15
TOTAL FORBS	17	15
Pachystima myrsinites	6	-
Populus tremuloides	2	-
Rosa spp.	1	-
Salix spp.	2	R
Shepherdia canadensis	1	-
Unidentified browse	3	11
TOTAL BROWSE	15	11
Fungi	1	-

1/ Taxa with an aggregate percentage of less than 0.5 percent are not listed.

2/ R indicates that the taxon was recognized as abundant in at least one sample.

APPENDIX

TABLE XVIII. TAXA WITH LESS THAN 10 PERCENT CANOPY COVERAGE IN EACH STAND OF THE EIGHT VEGETATION TYPES (TABLES I - VI OF TEXT).

Taxa	Sagebrush-bunchgrass	Coniferous forest	Aspen	Cottonwood-Spruce	Bunchgrass-shrub	Willow	Sedge-bluegrass	Agric.
GRASSES:								
Agropyron spp.				X	X		X	
Agrostis spp.			X					
Bromus nodosum						X		
Bromus tectorum	X							
Bromus intermis			X	X				
Calamagrostis rubescens						X	X	
Danthonia unispicata	X							
Deschampsia caespitosa						X		
Hordeum jubatum	X						X	
Melica spectabilis	X		X					
Oryzopsis hymemoides				X				
Phleum pratense			X			X		
Poa spp.	X							
Sitanion hystrix	X							
Stipa spp.	X		X			X		
FORBS:								
Achillea millefolium	X							
Agoseris glauca	X		X			X		
Allum sp.				X				
Androsacae sp.							X	
Antennaria spp.				X	X	X		
Arabis spp.	X						X	
Arenaria conjesta	X							
Arnica spp.		X						
Artemisia frigida	X							

TABLE XVIII (continued)

Taxa	Sagebrush-bunchgrass	Coniferous forest	Aspen	Cottonwood-Spruce	Bunchgrass-shrub	Willow	Sedge-bluegrass	Agric.
Aster spp.	X		X					
Astragalus decumbens				X				
Astragalus spp.	X					X		
Campanula rotundifolia								
Chrysopsis villosa				X				
Cirsium arvense			X	X		X		
Collomia linearis	X		X					
Commandra pallida	X				X			
Castilleja spp.	X							
Delphinium spp.	X							
Dodecatheon spp.	X							
Erigeron spp.	X				X		X	
Eriogonum spp.					X			
Erysimum sp.								
Eriophyllum lanatum	X							
Frageria spp.			X				X	
Galium boreale			X	X			X	
Geranium viscosissimum			X		X			
Gilia aggregata	X							
Glycyrrhiza lepidota				X				
Helianthella uniflora					X			
Hieracium spp.		X						
Hackelia spp.	X							
Lianthus septentrionalis	X							
Lithospermum ruderale	X							

TABLE XVIII (Continued)

Taxa	Sagebrush-bunchgrass	Coniferous forest	Aspen	Cottonwood-Spruce	Bunchgrass-shrub	Willow	Sedge-bluegrass	Agric.
Lomatium spp.	X		X					
Meliotus officinale				X				
Medicago sativa				X				
Mentha spp.	X							
Microseris nutans	X							
Nemophila breviflora	X							
Pedicularis sp.						X		
Perideridia gairdneri	X							
Penstemon spp.	X							
Phlox spp.					X			
Phacelia spp.	X							
Polygonum douglasii			X					
Potentilla spp.			X				X	
Pyrola sp.		X						
Rumex spp.	X							
Sedum stenopetalum	X			X				
Senecio spp.	X							
Swertia capitatum			X					
Smilacina stellata						X		
Solidago spp.			X			X		
Trifolium longipes				X				
Trifolium spp.			X	X				X
Thalictrum		X	X					
Tragopogon spp.	X		X					
Vicia americana	X							

TABLE XVIII (Continued)

Taxa	Sagebrush-bunchgrass	Coniferous forest	Aspen	Cottonwood-Spruce	Bunchgrass-shrub	Willow	Sedge-bluegrass	Agric.
Viola spp.	X		X			X		
Zygadenus paniculatus	X							
BROWSE:								
Amelanchier alnifolia	X							
Arctostaphylos uva-ursi						X		
Berberis repens	X			X				
Eleagnus	X							
Gutérrizia sarothrae	X							
Purshia tridentata	X							
Ribes setosum				X				
Rosa spp.	X			X				
Spirea betulifolia				X				
Symphoricarpus spp.	X		X					
Vaccineum spp.			X					

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[illegible]	Robin Wise 581-8906 1449 Fox.
[illegible]	[redacted]
	[redacted]