INTERACTIONS BETWEEN MOOSE, ELK AND BUFFALO
IN ELK ISLAND NATIONAL PARK, ALBERTA

by

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We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1960
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Department of Zoology

The University of British Columbia, Vancouver 8, Canada.

Date May 2nd 1960
ABSTRACT

A study of the interactions between moose (*Alces alces*), elk (*Cervus canadensis*) and buffalo (*Bison bison*) was carried out during the summer of 1959 in Elk Island National Park, Alberta. The interactions studied were the possibility of competition for food and habitat, transmission of disease and dominance relations.

A description of the Park is given. The distribution, habitat selection and food habits of each of the three species are discussed. The greatest interaction between these animals occurs through their effects on the range.

Data, collected over the past years, on the incidence of brucellosis and its effect on the reproductive rate and health of the animals are presented. The high incidence of brucellosis in buffalo indicates that they are the source of the organism infecting moose and elk.

Buffalo were found to be dominant over moose and elk. The effects of the existing dominance relations could not be evaluated.
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"This summer I continued my investigations as to which plants are consumed by cattle, which are ignored, and which are avoided; this work in my opinion, is of fundamental importance both for private owners of livestock and for animal husbandry as a whole."

Carolus Linnaeus, 1748
This study is concerned with the interactions of moose (*Alces alces*), elk (*Cervus canadensis*), and buffalo (*Bison bison*), on a woodland range in central Alberta. These three species, and deer, are potentially capable of using the same foods and same habitat. Interaction between them is, therefore, possible.

Although there have been many previous studies concerned with various problems of interspecific interactions between different species of wild ruminants, and between wild ruminants and domestic animals, few studies have considered more than one type of interaction. The present study combines the effects of several environmental factors. Interactions considering competition for food are numerous (Cowan, 1947; Julander, 1958; Mair, 1952; McMillan, 1953; Morris and Schwartz, 1957; Murie, 1951; Peterson, 1955; and many others). McHugh (1958) and Altman (1951, 1956) studied interspecific behavioral interactions of buffalo and elk respectively. Grzimek and Grzimek (1960) censused the plains animals of the Serengeti National Park, Tanganyika, and found each of the ten common herbivores concentrated in certain places and missing in other regions.

Studies of food habits, habitat selection and behavior have been conducted on a variety of birds and mammals. Lack (1944) cites several instances of potential ecological overlap in similar sympatric species, but in each case where they are occupying similar habitats, close observation reveals that they are really using separate portions of the environment. Lack suggests that overlap in food habits indicates a superabundance of food, and competition between the species is seldom involved.

In North America, prior to the extermination of the large plains animals by white man, seven native ruminants and the feral horse roamed the great plains. Elimination of elk and buffalo over much of their former range has precluded such studies of interaction as might have been carried out 100 years ago. Only in Yellowstone National Park, Wyoming, and Elk Island National Park, Alberta, do large
herds of the former dominant plains species co-exist in areas which they formerly occupied and under conditions similar to the primitive state. Even in these parks, the situation is somewhat artificial owing to selective stocking, predator control, selective harvesting and restriction of movements of the animals.

During the summer of 1959 (May to September) and during a brief period in December, 1959, the interactions of moose, elk and buffalo in Elk Island National Park were studied. A short visit was made in September to the National Bison Range, Montana, and to Yellowstone National Park, Wyoming.

To understand the implications of the data presented in this study, it is necessary to be familiar with the habitat in which the animals live. Following a description of the habitat, the results of determining distribution, habitat selection, food habits, diseases, predation and behavior of the animals are presented. Only after correlation of these factors are some suggestions warranted on how moose, elk and buffalo interact.

In the following pages, each of the factors will be considered in turn. The interspecific effects of each will be discussed and finally, the effects of all factors will be evaluated.

A. Historical Background

For ten thousand years, or more, buffalo, elk, pronghorn antelope, moose, and deer have lived together in the aspen parkland and sub-climax aspen forest of the coniferous biome of Alberta, Saskatchewan and Manitoba. Until the coming of white man to the Prairie Provinces, buffalo, elk and moose were numerous. Anthony Henday, the first white man to enter Alberta, records that his Indians killed eight elk, three buffalo and four moose on his first two days in "Alberta". Paul Kane, the artist, came to Edmonton 89 years later, in 1845. He records the numbers of buffalo as follows, "...three days it took us to reach Edmonton House, we saw nothing else but these
animals (buffalo) covering the plains as far as the eye could reach, and so numerous were they, that at times they impeded our progress..." By 1900 all buffalo were gone from the plains and parklands of Alberta. Settlers, which had been moving into the area since the early 1880's had also extirpated most of the elk and moose.

In March, 1906, five pioneers east of Edmonton, cognizant of the pending loss of these native ungulates approached the Minister of the Interior to have 16 square miles set aside as a deer park and game preserve. On August 4, 1909, Elk Island Game Preserve became Elk Island National Park.

This Park did not "just happen" to be located in an area that still had a few moose and elk. In contrast to the surrounding parkland where trees are limited to stream valleys and depressions, the Beaverhills have a forest of aspen, balm and birch, and a climax forest of white spruce. The heavy forest discouraged the early settlers from farming this rolling ground, and gave protection to the few elk and moose still present.

The Pablo—Allard herd of buffalo in Montana came up for sale in 1906, and the Dominion of Canada bought them to stock a new Park which was being created at Wainwright, Alberta. Because the Wainwright park was not completely fenced, 250 buffalo were released in the Elk Island Game preserve for temporary holding. In 1909, most of these buffalo were removed and transported to Wainwright. About 50 buffalo, mostly old bulls too wild to catch, remained in the park. Thus the present herd had its beginning from the enclosed moose and elk and the remaining 50 buffalo.

A purchase of 34 square miles immediately south of the initial 16 square mile block was made in 1922. The old south boundary fence was removed, providing the herds with nearly 50 square miles of range. In 1947, a 24 square mile area was bought from the Blackfoot Grazing Association. That area was fenced and crossfenced dividing it into three 8 square mile ranges. Most of the moose and elk were removed from the new area.
In the spring of 1951, 67 young buffalo cows and 10 young bulls were introduced into the two western ranges. In 1959, the eastern third was opened to the buffalo. The 24 square mile area was originally designed as an "Isolation Area" to protect the buffalo herd from extermination should an epizootic occur (e.g., foot and mouth disease). The part of the Park north of Highway 16, will be referred to as the "park" without a capital "p".

For many years the stocking level of the range has been very high. As many as 1,500 buffalo, possibly 1,200 to 1,500 elk and 600 or more moose have occupied the park (considered as 45 square miles of useful range) at one time. The effect these large herds on the range has been to change the composition and physiognomy of the plants. It is through these changes in floral structure that interspecific interactions are most effective.

The number of animals in the park during the summer of 1959 was estimated as 650 buffalo, 600 elk, and 300 moose. The population of the isolation area was considered to be approximately 450 buffalo, 40 elk, 100 moose and 150 deer.
DESCRIPTION OF THE PARK
A. Physical Features

1. Geology

During the Keewatin glaciation the ice sheet moved in a generally south-westerly direction, and in passing over the area, materials it had carried for a considerable distance were mixed with the materials from the underlying bedrock. The glacial drift was deposited as a mantle over the Park. The Beaverhills represent a terminal moraine located on a bedrock high. Material in this moraine is mainly of Edmonton formation origin (Allen).

2. Topography

Most of the park is hilly. The isolation area is gently rolling. Extremes in elevation are from 2,375 to 2,475 feet in the park and from 2,350 to 2,425 feet in the isolation area. The northern half of the park tends to be very hilly with numerous potholes and sloughs. The south-east quarter is level to gently rolling, and the south-west quarter is characterized by several large hills, and numerous morainic ridges running approximately in an east-west direction. The hills in the isolation area are confined to the south-west portion where again east-west morains occur. Although there is little altitudinal change, because of the latitude, the actual inclination of the ground has a great effect on the amount of heat and light received from the sun, and a difference in vegetation is noticeable on north and south slopes.

3. Soils

The soil over most of the area of Elk Island National Park is classed as Cooking Lake Loam which is an orthic grey wooded soil. The loam is relatively low in natural fertility. Most of the soluble plant food has been leached from the upper horizons and deposited in the B horizon. The soil has a high lime content, and is
not low in sulphur and magnesium as are many of the grey wooded soils. Salt content of the C horizon is relatively low. Detailed analysis of a very similar soil, the Breton Loam, indicates that there is no one essential element distinctly deficient, although phosphorous is in lower supply than are the others (Bowser and Erdman, 1947).

Areas of deep organic soil, many of them caused by gradual filling in of beaver ponds with vegetation, occur throughout the Park (about 15% of the total area).

4. Climate

The Park is in a region of typical continental climate of northern latitudes. It is characterized by a long, cold, dry winter and a growing season of about three months, during which the days are long, bright and moderately warm. The mean annual precipitation is about 18 inches, one-third falling in June. Owing to the prevailing low humidity during the day, the rate of loss of water from the soil and vegetation is high. However, very heavy dews fall every night during the summer.

Weather data are presented in Table I, as recorded at Edmonton, 30 miles west of the Park (Canada Year Book, 1957-58).

<table>
<thead>
<tr>
<th>Mean Temperature°F</th>
<th>Mean Frost-free Period</th>
<th>Precipitation</th>
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<tr>
<td>36.8</td>
<td>7.7</td>
<td>62.9</td>
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</table>

B. Vegetation

With the exception of the organic soil areas, all soils in the Park would naturally support either a forest of aspen and balm, or white spruce. (Latin and
vernacular names of all plants mentioned in text are listed in Appendix A).
The theoretical climatic climax vegetation of the grey-wooded soil is white spruce. However, prior to settlement of western Canada, grass and forest fires were a normal occurrence and seldom was a spruce forest maintained over a large area for a long time. Consequently, the area is a checkerboard of seral stages; each habitat type reflecting its past history. Demonstrating the regular occurrence of fires, a profile of a sphagnum bog in the north end of the park showed fourteen layers of charcoal in the first three feet of moss. Below this depth, the charcoal layers were indeterminable.

1. Description of habitat types.

Seven habitat types occur within the Park. These are: a. Lakes, b. Sloughs, c. Wet meadows, d. Bogs, e. Grass meadows, f. Grass-shrub meadows, g. Aspen-balm forests. A detailed description of each habitat type follows.

a. Lakes

The lakes present in the Park appear to be due to hollows in the superficial glacial deposits and not to excavation by glacial action. The largest and deepest lake, Astotin, has several small rocky islands devoid of glacial debris. Tawayik, Little Tawayik, and Flyingshot Lakes are very shallow and have gently sloping shores. The margins of these lakes have extensive sedge meadows in drier years. Oster and Adamson lakes are located in an area of morainic ridges and consequently have more sharply defined shorelines. All lakes have an abundance of submerged vegetation; however, much of it is in water too deep to be of use to moose. The other named lakes in the Park must be classed as temporary water bodies or sloughs.

b. Sloughs

There are six large, temporary water bodies in the isolation area and many small ones in the park. During the average summer there are over 200 small potholes in the park, many of them less than 50 feet in diameter.
Floating vegetation was not abundant in 1959. Emergent vegetation was lacking from many of the sloughs and confined to the periphery of others. Submerged aquatic plants common to most of the sloughs were *Ranunculus aquatilis*, *Ceratophyllum*, *Myriophyllum*, and some *Potamogetons*. *Typha*, *Scirpus*, *Sparganium* and *Eleocharis* were present on only a few ponds, mostly those in the north end of the park. Peripheral vegetation was primarily *Carex*, *Glyceria* and *Calamagrostis*. Forbs included *Galium*, *Petasites* and *Caltha*. The commonest shrubs on the margins of sloughs were willow (several species) and alder. Bog birch, paper birch and balm were present in a few areas. Alder was most common in the north end of the park and almost absent in the isolation area where willows were dominant.

c. Wet meadows

About one-quarter of the sloughs are the result of previous beaver activity. Several *Carex-Calamagrostis-Glyceria* meadows, one to five acres in size occur in chains, each separated from the adjacent one by the remnants of a beaver dam. Often the only open water in the meadow is a small pond a few yards across on the "upstream side" of the dam. The old beaver dams are easily recognized by their position and by the vegetation, either balm, willow or alder, growing on them. Other wet meadows, having similar floristic composition to the filled-in beaver ponds, have been produced by hydrosere development.

The margins of some of the wet grass meadows have shore lines which show considerable erosion. Banks four feet high, or more, occur on the edge of some meadows which now have no open water throughout the year.

There are few meadows in the park which have extensive willow cover. The most common shrubs are gooseberry, bog birch and raspberry. *Triglochin*, *Potentilla palustris*, *Parnassia*, *Petasites* and other forbs are common on these meadows.

d. Bogs

About twenty black spruce-sphagnum bogs, more or less similar to the bog
forests of the Cordillaran area, occur in the Park. The bog forest is characterized by an association of black spruce 15 to 30 feet high, about seven feet apart, and growing on a wet bed of Sphagnum, Ledum and other bog plants. Carex, and often willow, growing in water, encircle each bog. Within this wet ring, Cladonia, Ledum and Vaccinium grow on mounds of Sphagnum. Other plants of the bogs are Ribes chamaemorus, Vaccinium oxycoccus, Eriophilum, Carex spp. and many others.

Although black spruce is the most common tree of the bogs, tamarack grows in association with it in the north end of the park. Both paper birch and scrub birch are present as shrubs in many of the bogs. No living paper birch trees are present, although trunks of dead trees still stand. Heavy browsing of this birch has prevented its maturation.

e. Grass meadows

Most of the grass meadows are the result of man's activity. In 1944, a series of small meadows along the road were created and sowed to tame grasses (probably Bromus and Poa). The exact extent of this "farming operation" could not be determined. Other meadows, created by early settlers are recognizable. Heavy browsing on these meadows has prevented regeneration of aspen trees. True prairie grasses are absent except on a small patch of "prairie?" in the south-east corner of the park where Koeleria can be found. That area is the only part of the park which might be considered to be a true grassland association. Even it, however, if protected from the effects of browsing would support a forest of aspen or spruce.

f. Grass-shrub meadow

There are two types of grass-shrub meadows. On the sandy soil, a hazel-rose shrub meadow occurs (see Appendix B, Transect 4). On the heavier soils, the shrub is mostly aspen and balm (see Appendix B, Transect 5). All meadows were covered with an aspen forest before the last fire. Their present condition is the result of browsing and grazing.
i. **Hazel-rose shrub meadow.**— On the sandy soils on the east side of the park, and in the regions west of Tawayik Lake, areas up to 300 acres are covered with hazel and rose, interrupted by grass meadows and aspen groves. These meadows provide a large part of the forage for moose and elk. All shrubs are kept browsed to a height of not more than four feet. Aspen, balm, willow and saskatoon have been largely eliminated from these areas by browsing and possibly by competition with hazel.

ii. **Aspen-balm shrub meadow.**— Associated with aspen, balm, birch, willow and snowberry shrubs, is a carpet of *Poa pratensis*, and *Trifolium repens*. The tree species are heavily browsed so that forest regeneration has been completely prevented in the past 50 years. Browsing, heavy enough to kill aspen and balm trees, has permitted some of the grass meadows, particularly those in the grass meadow-aspen grove association to persist. The introduced meadow plants (*Poa* and *Trifolium*) are more resistant to heavy grazing than the native *Calamagrostis*, *Agropyron* and *Bromus*. Consequently, as an area became denuded of its native vegetation, the introduced species were able to become established.

**g. Aspen-balm forests**

Fires started by lightning, by Indians and by white man have altered the floristic composition to some extent almost everywhere in the Prairie Provinces. The great expanse of aspen forest in Canada owes its presence to the effect of forest fires in preventing the spread of spruce. After a fire, aspen and balm are able to regenerate quickly from the underground parts of the burnt trees. This results in aspen forests being an even age stand. Spruce, on the other hand, is killed completely by severe fire and requires dispersion of seed to increase its range. Spread of spruce is, consequently, very slow.

Aspen is found in the Park in two situations: as groves in the grass meadow – aspen grove association, and as an aspen forest. Most of the aspen forest
in the Park originated as the primary succession following a fire. Some areas, possibly parts of the meadow-grove association, developed from a shrub meadow which had been released from the effects of heavy browsing.

Measurements of trees show that aspen in the park grow in 70 years to a height of 60 to 75 feet and attain a diameter of not more than 18 inches. The great majority of the trees never reach this size. The trees are shade intolerant and thus require considerable thinning before new growth can take place. Table II shows the rate of thinning of aspen stands as determined by the approximate numbers of trees in stands of different ages (Moss, 1932).

<table>
<thead>
<tr>
<th>Trees in Years</th>
<th>Number of Trees per 100 Square Meters</th>
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<tr>
<td>5</td>
<td>500</td>
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<tr>
<td>10</td>
<td>250</td>
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<td>15</td>
<td>175</td>
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<td>20</td>
<td>80</td>
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<td>70</td>
<td>10</td>
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<tr>
<td>110</td>
<td>3</td>
</tr>
<tr>
<td>120</td>
<td>0</td>
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In addition to the competition between the trees, thinning of the stand is hastened by the polypore, *Fomes igniarius* which attacks nearly all aspen over 50 years of age. The beetle *Saperda* sp. infects most trees about the same time and compliments the effects of *Fomes*.

The second most abundant tree, balm, is present in association with aspen nearly everywhere in the Park. Balm grows slightly faster than aspen on wetter sites, lives a few years longer, and is less subject to heart rot by *Fomes* (Moss, 1932).
Like aspen, it is shade intolerant. The number of balm present in relation to the number of aspen varies from practically none to 50% or more in some of the wetter areas.

Paper birch has greater tolerance to wet and acid conditions than either aspen or balm and consequently is found in wetter areas and occasionally on spruce bogs. Birch is more tolerant of shade than either balm or aspen. Outside the Park, birch trees are found scattered under a canopy of aspen and balm. In the park, only a few clumps of old trees occur. Although much birch is present in some areas of the park, it usually occurs only as a very heavily hedged shrub.

The oldest trees in the park occur in the north end around the area which was swept by fire in 1946. The trees in this area are about 70 to 85 years old, indicating that they followed a fire about 1880. Aspen and balm, about 50 to 60 years old, and most of the spruce are in the north-east side of the park. A fire occurred in 1900, or thereabouts, which cleared most of the trees from the remainder of the Park. Regeneration was somehow retarded in areas south of the original game preserve boundary. The presence of the younger trees in the southern portion of the park and most of the isolation area may be the result of more recent burning by settlers. The age of the trees of most of the southern portion of the park and the isolation area is 25 to 40 years. A few spots exist where the trees are 50 to 60 years old, but most of these trees show some fire scars. There are many areas where balm and aspen, three to five feet high, are over 15 years old. This indicates prolonged heavy browsing.

Within the aspen forest, small clearings exist. Vegetation of the forest floor varies considerably from one site to another. The composition of the under-story is correlated with the age and density of the dominant trees. There appears to be no correlation between form and composition of the aspen forest and soil types; therefore, it would appear that the different aspects of the forests are a reflection
of their individual histories. A similar conclusion was reached by Ellison and Houston (1958), "There is no indication that inherent soil differences are great enough or consistent enough to account for the marked differences that generally exist in the ground vegetation." and "... the tendency suggests that the cause of the type boundaries are historical rather than environmental...."

The aspen forest can be divided into five types.

i. Grass meadow— aspen grove association. — Heavy browsing by moose and elk, 15 to 25 years ago, killed most of the aspen and balm in the area west of the Tawayik lakes. On the southern slopes, a cover of grass or hazel shrub is established. On northern slopes and in wetter areas, aspen groves occur. In a few places, aspen is spreading from these clumps of trees onto the grassland meadow.

ii. Open aspen. — The habitats, with well spaced, old trees, have a lower stratum composed of varying amounts of shrubs. Some aspen, balm and birch are present, but more common are raspberry, rose, hazel and snowberry. The dominant understory vegetation is Calamagrostis grass (see Appendix C, Photograph 9).

iii. Semi-open aspen. — Under the "semi-open" aspen forest (trees 25 to 50 years old) the understory is composed of either sarsaparilla (Aralia) and snowberry or a mixture of hazel, rose, gooseberry and raspberry. Grass is absent under the more dense canopies, but in the stands approaching the "open" aspen type Calamagrostis becomes prevalent. Lacking in the understory of all aspen forests in the park is red-osier dogwood, listed by Bird (1930) as one of the two most outstanding subdominants of the shrub substratum in aspen forests. Well-browsed dogwood is present in the isolation area. Saskatoon, chokecherry and Viburnum are likewise fairly common in the isolation area but largely absent in the park. The reason for the difference in plant composition between the park and isolation area, is the high preference moose, elk and deer have for these plants and the low tolerance of the plants to heavy browsing. Hazel is maintained at a height of less than three feet
throughout the park. In the isolation area, hazel over five feet high is not uncommon. Other shrubs, less palatable, are not browsed to such a constant level. The height of rose, gooseberry and buffalo-berry in the park varies between two and six feet. With the exception of rose, these plants are eaten very little. Photograph 7 in Appendix C represents this habitat type.

iv. Dense aspen.— The dense aspen forest has an understory composed of almost 100% sarsaparilla. Other lesser vegetation in this habitat, as in the semi-open habitat, consists of snowberry, strawberry, wintergreen, bunchberry, violets and many other forbs. The trees are 15 to 35 years old and are closely spaced.

v. Aspen-balm forest outside the park.— Outside the park, and in the isolation area, the shrub strata is well developed, and the forb understory is greatly reduced. Sarsaparilla was found to be nowhere as abundant outside the park as it was in the dense aspen forest in the south-east quarter of the park. Birch, willow, saskatoon, hazel, red-osier dogwood and other shrubs are common in the areas free from heavy browsing.

2. Percentage occurrence of habitat types.

The percentage each habitat type represented in the park was determined from air photographs. The proportions were determined by examining, under a stereoscopic, a series of east-west transect lines spaced at one-half mile intervals over the whole park. Permanent water bodies and larger sloughs were excluded from the transects. The percentage habitat occurrence as shown in Figure 1, illustrates the dominance of the aspen forest habitats (nearly 70%). Wet meadows and grass meadows, which are interspersed in the aspen forests account for 14.5% and 9% of the area of the park. The isolation area was not included because it is nearly 100% aspen forest.
3. Distribution of habitat types.

The distribution of the habitat types is shown on the map (Figure 2). The limits of these regions of vegetation types were determined by examination of air photographs taken in 1948. Corrections for recent changes in vegetation were made where possible.

4. Analysis of Range.

Seven permanent range plots were established so that a quantitative description of vegetation in key areas could be made. These plots also serve as the beginning of a long term range trend study. Plots were located in the following habitat types: 1. and 2. Grass meadow; 3. 4. and 5. Grass - shrub meadow; 7. Burn in mature aspen forest; 9. Semi-open aspen association.

Range transect 8 was located in an aspen forest in the isolation area, but was not established as a permanent transect. A map showing location of the transects and a summary of the transect data are presented in Appendix B. The raw data and all photographs of range are on file in the offices of the Canadian Wildlife Service, Edmonton.

a. Location of transects

Transect locations were selected on the basis of being representative of the major habitat types existing in the park, or in places considered to be key areas. Four permanently located 100 foot transect lines were arranged at each range plot.

Location of the transect lines in a cluster as shown in Figure 3, provides a measure of variation with a sampling site, more information per man-hour, and makes for easier relocation (Parker, 1954). The arrangement of the transects within the cluster was designed so as to sample as large an area as possible while remaining in a uniform habitat type. The distance between the center of the transect cluster and the "near" end of the transect line was designed to minimize the
HABITAT TYPES

Figure 1. Percentage occurrence in the park of habitat types as determined by 91 miles of line transects on air photographs. Permanent water bodies and isolation area are not included.
Figure 2. Distribution of Habitat Types
Figure 2. Layout of transect lines within range plots.
importance of the location of the hub stake but not oversampling the center of
the plot.

b. Analysis of the grassland vegetation

A transect line was run between the pairs of stakes, and at each foot
interval, the vegetation (root crown only) occurring within a three-quarter inch
circle directly below the foot mark, was recorded. The three-quarter inch circle
has all the advantages of both the "point" and the "area" method of determining
the sub-sample. The "point" has the disadvantages of being a point, theoretically
determinable, but in practice it must be an area. The size of the area of the
"point" makes considerable difference in the results obtained (Greig-Smith, 1957;
p. 6). The "area" sub-sample has the disadvantages of requiring subjective
interpretation as to percent of area occupied by each plant species. The 3/4 inch
"point" seldom contains more than one species, and when it does, the percent can
be estimated very quickly. In practice, if two species are present, each is credited
with 1/2 the area. Using the 3/4 inch circle has been found to be faster and less
subjective than the "area" sub-unit, more accurate, more informative, and faster
than the "point" sub-unit (Parker, 1954).

Permanent location of transect lines permits absolute comparisons of range
conditions from one year to the next.

c. Analysis of browse vegetation

The method outlined above is not suitable for sampling heavy woodland,
or browse habitat. Browse was sampled by counting the browse plants in 3 by 100 foot
plots adjacent to transect lines, and segregating the plants into species and
height classes. Notes were made on the vigor and extent of browsing on the plants.
Species present in the site, but not included in the transect were noted, and their
significance, if any, was recorded.
C. Classification of Ruminants in the Park

The common North American vernacular for the ruminants discussed in this study will be used. These names are: elk (*Cervus canadensis manitobensis* Millias, *C. c. nelsoni* Bailey); mule deer (*Odocoileus hemionus hemionus* Rafinesque); white-tailed deer (*O. virginianus dacotensis* Goldman and Kellogg); moose (*Alces alces andersoni* Peterson); and buffalo (*Bison bison bison* (L.)).
METHODS AND DATA
A. Distribution of the Animals

Three methods were used to determine the distribution of the animals in the park and their habitat selection throughout the year.

1. Winter distribution (Figure 5) and population estimates were made by aerial census in February, 1960, by Mr. D.R. Flook.

2. Summer distribution (Figure 4) was determined from direct observation during the summer of 1959 (May to September).

3. Late fall and winter distribution was determined by a defecation-site census conducted during the first two weeks of May, 1959.

The "defecation-site" census was used to determine distribution and habitat selection during the winter. An explanation of the method and discussion of the limitations of the information is necessary.

The new vegetation appears about the end of May. Before that time, the ground is quite bare and the winter's accumulation of dung is visible. Transects, 600 feet long and 12 feet wide were placed approximately at the center of every other quarter section. Location of the center of the transect was made from air photographs. Only dung, lying on top of the leaves and last summer's grass, was counted. The criterion for a pellet group was at least 10 pellets in a square foot, or for buffalo, a winter "chip" more than six inches in diameter. Where it was obvious that several chips belonged to one defecation, they were counted as one.

Proportions of total use made by moose, elk and buffalo on a single habitat type during the winter could not be determined exactly by defecation-site transects because several factors, for which valid correction cannot be made, alter the number of defecation sites of each species in a habitat. These factors are the defecation behavior of the species (e.g. do the animals defecate by their bed or on their feeding ground?) and frequency of defecation on a winter diet. Thus it is possible to make only a rough correlation between different species and habitat use.
The elk counts tend to be too low. Much of the time the elk are running when they defecate. The buffalo counts tend to be high because the period of accumulation is longer than for moose or elk. The grass on which the buffalo defecates reaches maturity by mid August and the buffalo dung changes from the loose summer dung to the more compact winter dung shortly after the grass cures. The time when the moose and elk pellets become hard coincides closely with the loss of green herbage, which is the same time the leaves fall. Moose and elk pellets look like "winter pellets" from then until green leaves appear about the middle of May. The time for which the defecation site distribution data for moose and elk is valid was set as October 1, 1958, to May 15, 1959, or about seven and one-half months.

The winter distribution of moose as determined by pellet group transect analysis is very similar to that shown by the distribution of moose in the aerial survey flown in February, 1960, (Figure 5). This correlation is a reflection of one sedentary habit of the moose.

No areas of concentration of elk were indicated by the pellet group transect analysis. The distribution of elk shown by the aerial survey (Figure 5) is a reflection of the position of elk only at the time of the survey. Herds of 20 to 150 elk are common during the winter. These herds move from one part of the park to another, apparently at random, utilizing suitable habitat as it occurs. Distribution of elk as indicated by pellet group locations (Figure 6) gives a much better picture of the winters use of the range. There is very little seasonal change in the distribution of elk. The apparent lack of use of range in the portion of the park north and west of Tawayik Lake may not be significant, but only a product of the sampling techniques.
Figure 4. Summer concentration areas of moose, elk and buffalo during the summer, determined by observations during the summer.
Figure 5. Winter concentration areas of moose and elk determined by an aerial survey during February, 1960. Seventy percent of the total population occurs within the delimited areas.
Figure 6. Winter concentration areas of elk as determined by pellet group transects.
B. Habitat Selection by the Animals

An attempt was made to cover all parts of the park evenly during the summer. The habitat type and location of each animal observed during the summer was recorded. Direct observation, and inferences gained by close examination of the habitat for signs of use by each species are summarized in the following Figures (see Figures 7, 8 and 9). Habitat selection during the winter is based on an analysis of the location of pellet groups and buffalo chips. Although the method has certain biases, it is the best reference to habitat selection which could be made by indirect methods. A description of the habitat selection, and the reason for each species selecting given habitat types is outlined in the following paragraphs.

1. Moose

a. Summer habitat selection

Habitat selection by moose, based on observations of animals coincides with the distribution of their preferred foods. This is to be expected since the moose are most visible when they are standing feeding.

Presence of moose in a given habitat is a direct response to available food. Moose on the wet meadows were eating willows, those on the shrub meadows and most other places were eating primarily aspen and balm. Lack of moose in open aspen habitat is to be expected since there is very little browse available. The few preferred browse plants which do occur have been browsed heavily by elk.

During the summer, 35% of the moose groups (one or more animals) seen were on, or near, wet meadows. Aspen-balm and hazel shrub meadows were the second most common habitats selected by moose and nearly 20% of all groups seen were in this habitat. Selection of other habitat types was about equal. With the exception of the open aspen areas, in which moose were never seen, the remaining 45% of the direct observations indicated that moose were preferring equally the six other habitat types.
A summary of habitat selection based on the summer's observations is presented in Figure 7a.

b. Winter habitat selection

Rumen analysis indicate that moose feed on hazel during most of the winter and this means that they are in the semi-open aspen habitat and on the hazel shrub meadows. Observations made during December, 1959, agree with the information yielded by the rumen analysis.

Habitat selection of moose as determined by defecation-site transects (Figure 7b) shows a heavy use of shrub meadows, semi-open aspen and the grass meadow-aspen grove habitats. The location of moose as determined by the aerial census in February, 1960, show a distribution similar to that determined from the defecation-site transect, and coincides with the suitable browse habitat.

2. Elk

a. Summer habitat selection

The elk show the least amount of specificity in habitat preferences. They were seen equally frequent on all habitat types except the spruce bog (Figure 8a). The use made of each habitat type was not, however, the same. Generally, the elk bed down in the wooded areas and during late spring and early summer they feed on the sedge meadows, and later, on the grass and shrub meadows. The amount of "use" elk (or other species) makes of a particular habitat may be calculated by dividing the per cent of the total area that a given habitat is represented in the park by the proportion of times elk were seen in that habitat. Such calculations clearly indicate that elk were not randomly distributed. The "use" elk make of the shrub meadow habitat is twice that of the sedge meadow and aspen forest combined.

Use of sedge meadows drops very sharply during June. During the calving period in early June, cow elk and young calves are seldom seen on the open meadows but can be encountered frequently in the forest. During late summer elk return to
Figure 7a. Summer habitat selection by moose. Determined by observations during May, June, July and August, 1959.
Figure 7b. Winter habitat selection by moose. Determined by defecation site transects.
the grass and sedge meadows.

b. **Winter habitat selection**

Pellet group locations, summarized in Figure 8b, indicate that during the winter elk have a strong preference for the grass meadow habitats and a lesser preference for the shrub meadows. It is significant that only 15% of the pellet groups were found in the semi-open aspen habitat which covers nearly 60% of the park, whereas during the summer, semi-open aspen was the preferred habitat. The low use of the aspen forest during the winter corresponds to the high proportion of meadow grasses eaten during the winter as revealed by rumen analysis. The winter "use" factor for grass meadow, shrub meadow and aspen grove habitat types was 0.225 as compared to 0.08 for sedge meadow and 0.04 for aspen forests.

3. **Buffalo**

a. **Summer habitat selection**

The buffalo show a very decided preference for grassland meadows. On all habitats the buffalo were using, only the grass areas were used for feeding. Buffalo use forested areas only in travelling from one grass meadow to another. They do not go to the forests for shade even on the hottest days. In the park, the only buffalo feeding on the sedge meadows are the small bull herds. In the isolation area, the only available buffalo food is on the sedge meadows and the buffalo must, therefore feed on these meadows. Use of emergent aquatic plants, mostly sedges, by buffalo in the isolation area was observed several times. Habitat selection by buffalo during the summer as shown by Figure 9a, indicates a slightly biased emphasis on the grass meadows. The most extensive system of grass meadows are those along the road, and consequently, if buffalo were on them they were seen every time the road was travelled. Probably a more accurate representation of habitat selection would show a higher use of the grassy areas of shrub meadows and the grass meadow–aspen grove association.
Figure 8a. Summer habitat selection by elk. Determined by observations during May, June, July and August, 1959.
Figure 8b. Winter habitat selection by elk. Determined by defecation site transects.
Figure 9a. Summer habitat selection by buffalo. Determined by observations during May, June, July and August, 1959.
Figure 9b. Winter habitat selection by buffalo. Determined by defecation site transects.
b. **Winter habitat selection**

Winter habitat preference of the cows, yearlings and most of the other age classes is not known since the herds are on the feedlot shortly after the first snow falls. The habitat selection of the solitary bulls appears to be very similar both summer and winter.

The only segregation of buffalo chips that could be made with any constancy was whether or not they were deposited on last summers grass or earlier. Therefore Figure 9b, representing the habitat selection of buffalo based on chip counts, should be referred to as late summer, fall and early spring distribution. On this basis, the habitat selection of buffalo based on defecation sites is not significantly different from the summer's observations. The high number of occurrences of chips on the meadow-grove habitat may be due to sampling error. The transect data probably represents a truer picture of summer distribution than that recorded by direct observation in the summer.

Less than 10% of all buffalo chips were found in aspen forest habitats. Sedge meadows accounted for 8% of the defecation sites. Seven per cent of the defecations occurred on the shrub meadow, but all these were on the interdigitating grassy areas of the shrub meadow. It is evident that over 80% of all were on upland meadows during the fall and winter. The small percentage on the sedge meadow probably represents the solitary-bull component of the herds.

**C. Food Habits of the Animals**

Observation of animals feeding during the summer were made through eight power binoculars and a 20 power telescope. The limitations of such observations in determining food preferences and diet are as follows: a. tall plants are seen more easily than lower vegetation; b. long-stemmed plants which are pulled up when eaten (e.g. vetch) are more easily seen; c. browse and large forbs are easier
to identify from a distance than grasses and small forbs; d. animals feeding in open areas are more easily observed than animals in the forest, although the latter are easier to approach.

The place the animals feed and the way they feed make a great deal of difference to the accuracy and amount of observations made. Buffalo graze much closer to the ground than do the elk. Buffalo tend to eat all grasses and soft forbs in a patch; elk are selective in their diet and wander as they eat. Moose strip and nip willow, aspen and balm of their leaves and terminal buds during the summer; elk nip only the ends of the branches.

Direct observations were made on the plants to determine utilization. The important limitations in this method are listed as follows: (a) browsing on shrubs by stripping leaves is easier to spot than nipping; (b) removal of twigs from heavily hedged shrubs is very difficult to evaluate; (c) grazing on immature stages of grass is more difficult to evaluate than grazing on mature grass; (d) removal of only the main stem of grass without eating leaves cannot be detected with accuracy; (e) grazing on rhizomatous species such as clover and strawberry is almost impossible to detect by direct observation of vegetation.

The time spent feeding on a particular plant or in a particular site does not necessarily bear a direct relation to the amount of food consumed (Dzubin, 1951; Smith and Hubbard, 1954). Feeding minute counts, although producing data that looks "quantitative" actually means very little.

Winter food habits were determined by examination of rumen contents collected from animals killed during the herd reduction slaughter in November and December, 1959.

The food habits of moose, elk and buffalo cannot be determined accurately by any one method. Only by considering observations of animals, examination of
individual plants and the range, and rumen analysis, can a reasonable impression of the animal's diets be achieved.

1. Moose

a. **Summer food habits**

During the summer months all age classes of moose fed on leaves of aspen, balm and willows. Paper birch was eaten, but birch browse has been severely reduced due to heavy browsing in the past. Alder was abundant, especially in the north end of the park, but it was not eaten. Other shrubby plants, such as rose, gooseberry, raspberry, buffaloberry and snowberry were used slightly. Hazel provides not more than 25% of the summer food, but comprises about 65% of the winter diet. Three plants, saskatoon, red-osier dogwood and chokecherry are highly preferred browse species but have been nearly eliminated from the park by heavy browsing. The approximate composition of the moose's diet during the year is shown in Figure 10. Comparative values for elk and buffalo are presented in Figure 11.

Aquatic plants were used very little during the summer. The number of flies and mosquitoes was abnormally low. Possibly the moose were not driven by the insects to seek the protection of the water. Park wardens report that during the fly season in some years, moose can be seen nearly every day feeding in the potholes and lakes.

b. **Winter food habits**

The results of analysis of samples from 15 moose rumens clearly indicates that during December, the bulk (65%) of their diet is hazel (Figure 10). Aspen and balm were represented in 60% of the rumens analysed, but responsible for only 25% of the total rumen contents analysed. It is significant that willow, which represent the larger part of the moose's diet in the spring and early summer, is eaten only very little (less than 5%) in the winter. The diet during the whole winter is not known but it can be assumed that as long as the hazel lasts moose will
continue to eat it.

The cause of the changes in food habits and/or habitat selection during the year may be a function of the palatability and availability of the browse species. Once the leaves are out, the moose turn away from the willow and begin feeding on aspen and balm. When the moose switch from hazel to willow is not known.

All trees and shrubs in the park drop their leaves about the same time in the fall. Aspen and balm are by this time severely browsed; willows are scarcely touched. Hazel, a soft browse, which has been growing without much browsing all summer, now receives the attention of the moose and becomes the major food item of the moose until it is browsed down to the point where it is no longer easily available. By late winter, willow is the only browse which has not been fully utilized, whereas aspen, balm and hazel are severely hedged (see Appendix C, Photograph 6).

The heavy hedging of the palatable browse causes them to produce a large number of new shoots every year. The forage production of the park is thus very high, and this is reflected in the high carrying capacity of the range, high reproductive rate and the fat condition of the moose.

In the isolation area the browse is much more plentiful than in the park. However, the willows are more heavily browsed. This may be the result of the lack of hazel in the understory of the aspen forest and the non-availability of aspen and balm.

2. Elk

a. Summer food habits

During the first two weeks in May food was scarce. The elk were feeding on whatever green food they could find. Observations suggest that elk were spending much more time feeding during May because 85% of all elk seen in May were
Figure 10. Diet of moose in Elk Island National Park based on spring and summer observations and analysis of contents from rumens of animals killed in December.
Figure 11. Diets of moose, elk and buffalo in Elk Island National Park based on observations of animals and plants during the summer.
Figure 12. Diet of moose, elk and buffalo during December as determined by analysis of rumen contents.
feeding. In August only 50% of the elk herds seen were feeding. Most of the elk during May were in sedge meadows feeding on Carex shoots. Four elk were even seen feeding on sedge in two feet of water. As the grass on the periphery of the sloughs started to grow, the elk left the sedge in favor of the green grass. By the end of May, much green vegetation was available and elk were seldom seen on the Carex-Calamagrostis meadows.

With the onset of calving, about the first week in June, cow elk retreated to the aspen cover. Adult bull elk became very inconspicuous. Most of the bulls observed during June and July were yearlings and two year olds which remained with the cow herds.

Food during most of the summer was varied. Vetch and peavine, when they became available about the end of May, were selected ahead of all other plants and represented at least 25% of the elk's diet. Feeding on browse consisted mostly of idly nipping rose, snowberry and buffaloberry while searching for the legumes. Vetch and peavine must be considered the preferred food species and probably the most important food items during June. As the grass and upland meadow forbs became abundant during the latter part of June, an increasing number of elk was observed in the grass-shrub meadow and grass meadow-aspen grove habitats. Summer food habits of elk are summarized in Figure 11.

Poa, the most common grass on the meadows, undoubtedly was the most important grass in the elk's diet, representing about 15% of the total food eaten. Agropyron, Bromus and Calamagrostis were used more by elk than by buffalo, but they were of minor importance in the elk's diet. Although 10 to 15% of the park has a cover of Calamagrostis under an open aspen forest, there was very little use of the grass or the associated shrubs, gooseberry and raspberry.

The preferred forbs, second to vetch and peavine, were white clover and strawberry. Sarsaparilla, although very abundant in the aspen forest, was not eaten at all. Other forbs were taken in small amounts. Forbs made up 40 to 60% of the
diet during the summer.

From the observations made during the summer, it appeared that the common browse in the diet of the elk was rose. Buffaloberry, hazel, aspen, balm, snowberry, paper birch, saskatoon, raspberry, willow and gooseberry were of secondary importance. Browse makes up 25% of the elk's summer diet once the browse plants are in full leaf. One third of the browse diet is rose.

b. Winter food habits

Analysis of samples from 29 elk rumens showed the composition of winter food to be 30% browse, 15% forbs, 35% grass and 20% leaves of aspen and balm. The browse was predominantly aspen and balm with lesser amounts of willow, birch, saskatoon, raspberry, buffaloberry and hazel. Identified forbs were thistle, dandelion, blueberry, strawberry, clover, goldenrod and moss. Most of the forbs were represented only by leaf skeletons and a few stems. Mushrooms were found in three rumens. A summary of winter food habits, based on rumen analysis, are presented in Figure 12.

3. Buffalo

a. Summer food habits

Buffalo have the most rigid habitat requirements of the three species concerned in this study. All feeding of buffalo, except that of some older bulls, occurs on the upland grass meadows. During the summer, almost all feeding buffalo were seen on grassland meadows, or closely cropped areas of wet meadows. The principle vegetation of the upland meadows is introduced bluegrass and white clover, also occurring are a variety of native plants such as strawberry, yarrow, bunchberry, anemone and miscellaneous other grasses and sedges. All grasses and smaller forbs appear to be utilized. Yarrow, goldenrod, and similar tall, hardstemmed plants are not eaten. Snowberry, which is the most common browse on the grassland
range is eaten by elk but not by buffalo. Grasses growing in the protection of snowberry, gooseberry and other shrubs are not eaten by buffalo. Figure 11 shows the summer food habits of buffalo and the corresponding data for elk and moose.

The buffalo typically feeds very close to the ground. As it feeds, it generally clears off an area one to two feet square before making a step. All plants are removed to within one to three inches of the soil. Buffalo feed very carefully around all small shrubs and tall forbs, never making any attempt to feed on them.

The only times buffalo were observed utilizing browse was when they were walking through the aspen-balm forests. Occasionally hazel, or other browse, was nipped. The leaves were dropped from the mouth more often than they were swallowed. The more solitary bull buffalo, although they feed most of the time on the meadows, are often found at the edges of meadows and sloughs. At times they even wade into the water and feed on emergent sedges.

In the isolation area, all buffalo seen were either on the roads, or fence lines, or on the sedge meadows of the larger sloughs. There are practically no grass meadows in the isolation area, so nearly 100% of the food must come from the sedge meadows.

b. Winter food habits

Over 90% of the winter diet of the free ranging buffalo in the park and isolation area is composed of grass-like plants. The greater majority of the food is sedge. Although not all small scraps of grass were examined in the six rumens analysed, very little Poa was found. All food that could be identified was Carex sp., but it is known from observation that the bulls do feed on the grass meadows to some extent during the winter. From the rumens analysed, it appears that less than 10% of the winter diet of bull buffalo is browse, forbs and leaves. The lack of leaves, forbs and Poa in the buffalo rumens, and the presence of these foods in
the elk rumens indicate that the buffalo are feeding in different habitat types than the elk.

The majority of the buffalo are on the feed lot during the whole winter. The buffalo are baited into the feed lot with feedlines as soon as the first snow falls. During the winter, the buffalo have very little effect on the sedge and grass meadows. The winter food habits of the buffalo are summarized in Figure 12.

D. Disease

Disease and parasites can be a significant factor in controlling the population of a herd. Conversely the population density may be one of the most important factors in determining the incidence of infection of a disease or parasite. A high incidence of a disease in one species may serve as a source of infection for the other species. This will be shown to be the case in Elk Island National Park.

1. Brucellosis

Investigation of the prevalence of brucellosis in the Park started in 1946–47, but it was not until 1957 that significant data had been collected. Corner and Connell (1957) found 42% of the buffalo infected, and reported a "large number of abortions" in the buffalo feeding grounds. Elk had a 13% incidence of brucellosis. The only reactors among moose were two sick animals; 124 healthy animals tested were negative. Data collected in 1958–9 have been added to that published by Corner and Connell and are presented in Table III.
Table III. Incidence of Brucellosis in Moose, Elk and Buffalo Killed During the Herd Reduction in Elk Island National Park (December, 1956 to December, 1959).

<table>
<thead>
<tr>
<th></th>
<th>Number Tested</th>
<th>Number Positive</th>
<th>Number Suspect</th>
<th>Number Negative</th>
<th>% Reactors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buffalo</td>
<td>753</td>
<td>253</td>
<td>91</td>
<td>164</td>
<td>45.5</td>
</tr>
<tr>
<td>Elk</td>
<td>653</td>
<td>40</td>
<td>22</td>
<td>585</td>
<td>9.5</td>
</tr>
<tr>
<td>Moose</td>
<td>264</td>
<td>5</td>
<td>—</td>
<td>259</td>
<td>1.9</td>
</tr>
</tbody>
</table>

a. Effects of brucellosis on moose

*Brucella abortus* is apparently fatal to moose. Two of the five reactors found in Elk Island National Park were shot because they were obviously ill. Symptoms of advanced brucellosis infection in moose are described by Corner and Connell (1958).

b. Effects of brucellosis on elk

The impossibility of getting a sufficiently accurate estimate of the birth rate of elk to compare with the pregnancy rate found in the cows during the herd reduction slaughter, precludes determining the effects of a 10% incidence of brucellosis on the reproductive rate.

c. Effects of brucellosis on buffalo

The high incidence of *Brucella abortus* in buffalo is attributed to their grazing habit providing a greater possibility of their picking up the organism, and to their confinement to the feed lots during the winter. The first investigations of the rate of conception and calving was conducted by Corner during 1955-6. Pregnant and lactating buffalo were infected to the same degree as the barren cows. This situation is similar to that found in chronically infected herds of domestic cattle (Corner and Connell, 1958). Table IV is a summary of the data presented in Table II of Corner and Connell.
Table IV. Calving and Conception Rates in the Elk Island National Park Buffalo Herd, 1951 to 1956.

<table>
<thead>
<tr>
<th></th>
<th>1951</th>
<th>1955</th>
<th>1956</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number mature cows killed</td>
<td>246</td>
<td>244</td>
<td>227</td>
</tr>
<tr>
<td>Percentage pregnant</td>
<td>85</td>
<td>67</td>
<td>89</td>
</tr>
<tr>
<td>Percentage mature cows raising calves (i.e. lactating cows)</td>
<td>77</td>
<td>32</td>
<td>13</td>
</tr>
</tbody>
</table>

By comparison, in the brucellosis-free herd at the National Bison Range, Montant, about 85% of the mature cows are pregnant each year. Abortions must be few, because the percentage of cows having calves equals the pregnancy rate found during the herd reduction slaughter (Henry, pers. comm.). It is evident that the reproductive rate of buffalo in Elk Island National Park is seriously depressed by the high incidence of brucellosis in the herd.

2. Tuberculosis

There has been no evidence in recent years of tuberculosis in the animals of Elk Island National Park.

3. Parasites

Assessment of the parasite load of the animals in the park is not complete enough to determine whether any parasites are having a significant effect on the health of the animals. During the past several years, only three or four bull buffalo have been shot because they were infected with lungworm (Dictyocaulus sp.). Holmes (in litt., 1960) examined 11 buffalo and 5 elk for parasites and did not find any animals having a seriously heavy infection.

There has been no record of warble grubs (Hypoderma sp.) in the animals in recent years. During the summer (1959) the animals were observed being bothered by flies on only two occasions. Horse flies (Tabanidae) were probably the cause of the annoyance.
E. Predators

There are no effective predators in the park. Only 25 coyote were counted during an aerial survey in February, 1960. During December and January the coyotes probably live on the viscera of moose and elk shot in the Park, but grouse, rabbits and mice are no doubt their main food source. A few calves and fawns may be taken in the spring, but the loss cannot be very high. Black bear and wolves have been reported in the vicinity of the Park, but the reports could not be satisfactorily confirmed.

F. Mortality Due to Other Causes

Very few recent skeletal remains can be found in the Park so it must be assumed that by far the highest mortality factor is the herd reduction slaughter. During the past four years, 10 to 40% of the population has been removed each year. Starvation is thought to have accounted for the death of 60 or more buffalo on the feed lots during the winter of 1947-8. Similar losses occurred other years but records are not complete.

Accidents are responsible for loss of some animals. Drowning, after breaking through the ice of the lakes, is known to have caused the death of 15 buffalo and at least one elk in the past 10 years.

G. Behavior

1. Dominance relations

Domination of one species by another, or of one age class by another, may affect the habitat selection and food habits of the animals. The frequency of such interactions depends on the frequency of contact between the animals. The total effect of these interactions is very difficult to assess, but the presence of a "peck order" between species was evident. Three examples of observations made during the summer which indicate that there is a real social hierarchy
between buffalo, elk and moose are given below.

a. **Buffalo dominant over elk**

July 30. A herd of 180 buffalo had been at the "soap-hole" in the south-east corner of the park for three hours. They had begun to move northward when a herd of 10 elk entered the meadow from the south. Two bull elk came to the soap-hole to drink and lick or eat the saline soil. About one minute after the elk arrived at the soap-hole, two buffalo calves ran down to the soap-hole; the elk retreated to the edge of the forest, then slowly started back to the soap-hole. Almost as if the elk and buffalo calves were playing a game, the calves would leave the soap-hole, the elk would approach and then retreat as the buffalo calves came towards them again. They maintained this play for nearly 10 minutes, advancing and retreating six times in all. Finally the elk retreated and remained by the edge of a nearby slough until the buffalo left the vicinity twenty minutes later.

b. **Buffalo dominant over moose**

Three bull buffalo were feeding on a grass meadow about 100 yards from an artificial salt lick. A cow moose had been at the salt lick for 15 minutes when one of the buffalo walked over to the salt. The bull approached to within 40 feet of the moose, stopped and slowly swung his head from side to side (the usual buffalo threat display). The cow moose retreated. The buffalo walked to the salt blocks and began licking salt. The moose remained about 50 feet away for five minutes, then started to walk slowly up to the bull buffalo. The buffalo looked up, threatened, and the moose retreated. This was repeated twice more, ending in final retreat of the moose.

c. **Elk dominant over moose**

Elk and moose were seen together 14 times during the summer. Generally neither paid much attention to the other. On two occasions the actions of elk showed its dominating effect on the moose.
On June 18, a cow elk chased a cow moose from an artificial salt lick. On July 29, a bull moose had been feeding on an aspen-balm shrub meadow for 30 minutes or more when three cow elk walked onto the meadow. The moose looked at them for a moment, then trotted off. The elk remained and fed for nearly one hour.

No observations were made which were contrary to the above observations. The hierarchy of dominance appears to be buffalo dominant over moose and elk. Although the observations above concerning elk and moose suggest dominance. The relation between them is nearly neutral. From the observations made, elk seem to be more tolerant of moose than moose were of elk. This dominance order is in agreement with that of Altmann (1952), McHugh (1958) and Brown and Simon (1947) (cited in Peterson, 1955)). McHugh records instances of buffalo finding elk calves and chasing them or trampling them; buffalo herds chasing elk herds; buffalo chasing a moose calf and killing it; and elk displaying dominance by charges, by swinging antlers or by striking with the forelegs. Such actions indicate that dominance is an active aggression. However, much of the social interaction between species is of a passive nature where no treat or aggression takes place. Avoidance of the dominant is the only indication of interaction.

2. Herding Behavior

It is well known that the buffalo, a plains animal is strongly gregarious. The gregariousness of the elk depends on the type of habitat and the season of the year. The elk is the only North American ruminant regularly found in dense forests in herds. The moose is a non-gregarious animal. During the summer the largest herd of moose observed was a group of three 2 year olds which are known to be triplets.

During the summer buffalo are in mixed herds. Mature bulls remain in small groups until the latter part of July when they begin joining the mixed groups. The decrease in numbers of large bull groups corresponds to the increase in numbers of bulls in the mixed herds. The number of lone bulls and pairs changes very little
during the summer. The result of the bulls joining the mixed herds is to decrease the territory occupied by buffalo. The greater use made of grass meadows by elk in late summer may be a reflection of the extra unoccupied territory.

Similarly, the effective territory occupied per moose in the park is greater than the effective territory occupied per elk, or buffalo. The significance of this is not known.
DISCUSSION
Summarizing the facts presented thus far, indicate that although there is a very high population of moose, elk and buffalo in the Park, there is very little overlap in the distribution, habitat selection and food habits of the animals. Moose are concentrated in a belt across the center of the park. The elk, although they use some of the same foods as moose, seldom occur in the region where moose congregate. Neither do the elk frequent the range used by buffalo. The overlap in food habits of elk and buffalo are consequently minimized by a spacial separation of the herds.

It appears that each species is occupying a different niche in the Park, and, therefore, direct "competition" is of little importance. Nevertheless, the interactions between them can be very real and can have significant, long-lasting effects. The greatest effect the animals have on each other is through their effects on the range.

A. Effects of the Animals on the Range

1. Browsing

For the past 30 years, heavy browsing of aspen, balm and birch by moose during the summer has prevented regeneration of deciduous forests. By the end of each summer all aspen and balm saplings have been stripped of their available leaves, and the terminal bud removed preventing further upward growth. The areas in the park protected from the effects of browsing show aspen, balm and willow growing at a normal rate and assuming their natural form. Elsewhere in the park, large shrub meadows are present. The shrubs are predominantly hazel and rose on sandy soils, and aspen, balm and willow on the clay soils.

Upon close examination of the shrub meadows, evidence of fire could be found. Charred aspen or balm, and roots of birch formed the major evidence. In 1946, a fire in the north end of the park cleared 40 acres. Similar fires have occurred at frequent intervals. "Old-timers" say that much of the area was burned over about 1900.
The exact date, cause and extent of fires in the Beaverhills could not be determined except by inference from the age of aspen and balm trees. The fact that there are still many areas of shrub meadow which have not been able to attain an aspen–balm forest, indicates that a high population of browsers must have been present for many years.

Warden Roberts says that in 1943, the condition of browse was much worse than now. Willows were eaten down and broken over in many areas. Aspen and balm regeneration was in a more critical condition than in 1959. Warden Henderson remarked that in 1947, trees and brush in the south-west corner of the park were so tangled with dead branches that it was difficult to ride a horse through the area. The area now supports a grass meadow–aspen grove association.

Comparison of air photographs taken in 1948 with the park in 1959 indicate that some areas of shrub meadow are now tall saplings. Examination of trees in such areas show the age of the trees above three feet to be about 15 to 18 years. The age of the trees near ground level was indeterminable, but in some cases as many as 30 rings could be counted.

The killing of aspen, balm and birch by browsing permits an increase in available forage for buffalo and elk. Without the protection the grazing land receives by the browsing of the moose, the carrying capacity of the range for buffalo and to a lesser degree, elk, would be considerably reduced.

Heavy utilization of hazel appears to have little effect in reducing its abundance in the park. On the contrary, browsing causes an increase in hazel. Because it can withstand heavy browsing better than the other shrub plants it is more successful in competition with them. If hazel is absent in an area, moose are not attracted to the area to the same degree. Consequently, the amount of browsing on aspen, balm and willow is reduced.

Heaviest browsing on aspen and balm occurs in areas adjacent to large willow
covered sloughs and spruce bogs in the center of the park. Degree of browsing of willow during mid-summer was very light in comparison to the extremely heavy use adjacent aspen and balm received. The moose were using the willow areas for bedding grounds and the shrub areas for feeding.

2. Grazing

The grassland ranges of the park, many of them the result of cultivation, have a plant composition largely of introduced flora. They are probably as productive as any grassland range in the region, natural or cultivated. Kentucky bluegrass and white clover are considered to be excellent forage and able to withstand extremely heavy use. Sampson (1952) says that Kentucky bluegrass "endures close grazing better than most species and does best when kept closely grazed."

Very few unpalatable forbs are present. Yarrow, the commonest, may be considered to be an indicator of heavy grazing, but nowhere on the grass range is it very abundant.

The damaging effect of the buffalo and elk on the soil is very slight. Some compaction of soil occurs on heavily used areas and trails, but the grass and clover seem to be able to grow even on the main trails across the meadow. The greatest disturbing factor of the soil is that of the bull buffalo in creating wallowing areas. Each meadow is pockmarked with one to a dozen or more areas of bare soil about eight to ten feet in diameter. Generally, the wallows are not on hillsides, so the possibility of them initiating erosion is slight. Only on sandy soil in shrub meadow areas on the east side of the park is there any evidence of recent erosion. In that region, a few erosion gullies can be found. Generally, throughout the park, hillsides are well covered with vegetation and no terracing is evident.

The increased productivity of the range, produced by feces of the animals, partially offsets any damaging effects caused by compaction, erosion or wallows.

3. Combined effects of browsing and grazing

The degree of browsing on the range will determine the amount of available
grass. Complete removal of the suppressive effects of moose and elk on the browse
would rapidly decrease the grazing area to nearly nil. Heavy browsing, to the point
where all shrubs were killed, would increase the available grazing area by about 100%.

Clearly, the carrying capacity and physiognomy of the range can be determined
by manipulation of the numbers of animals in the park. Continued fire suppression
will, however, result in only one habitat type - the white spruce climax. The trend
towards a climax white spruce forest will persist in spite of any stocking level imposed
on the range.

4. Effects of other herbivores on the range

a. Deer

White-tailed and mule deer are present in the region around Elk Island
National Park, but in the park they are seldom seen. Although the deer are able to
enter and leave the Park at will, they are largely absent from the park. The aerial
survey flown in February, 1960, indicated that there were 100 deer in the isolation
area and six on the overbrowsed range of the park. In contrast, 213 elk were counted
in the park and only eight in the isolation area.

Deer cannot compete with elk when food is limiting. Elk browse higher,
paw more effectively, move through deeper drifts and range further than deer. In
addition they are less specific in their food habits and will eat more dry grass than
deer (Cliff, 1939).

The presence of a heavily browsed range, and/or the presence of elk appear
to be the major factors in preventing white-tailed deer from becoming established in
the park.

White-tailed deer were unknown in the Park as late as 1951. A steady
increase in numbers has been observed since then. During the summer, only white-tailed
deer were seen. Since 1900 there has been a steady northward movement of the white-
tailed deer on the prairies (Soper, 1951) with a corresponding decrease in the numbers
of mule deer. Whether the change in distribution is a cause and effect relation, or a different reaction to a common cause (e.g. increase in amount of land cleared, or temperature change) has not been determined.

b. Rodents

The varying hare (Lepus americanus) was not present in the park except around the periphery and in areas from which the large herbivores had been excluded. More hares could be seen in the isolation area in one day than were seen in the park all summer. However, even in the isolation area they were not sufficiently numerous to have an appreciable effect on the vegetation. The numbers of hares may vary considerably, but there is no record of a dense population ever having been present.

There are several species of mice present in the Park, but generally they have little effect on the vegetation. During the winter, Microtus runways were present on the meadows around Tawayik Lake. Elsewhere grazing had been so heavy that there was little suitable habitat.

Ground squirrels and gophers were present in the park, and mounds could be found in a few areas. Their effect on the vegetation was small.

Beaver (Castor canadensis) were re-introduced rather recently. In the past they have had a great effect in creating sedge meadows, but now the park is in such condition that beaver can have very little effect except around the margins of the lakes.

Muskrats (Ondatra zibethica), porcupines (Erithizon dorsatum), and marmots (Marmota monax) are not present in sufficient numbers to have significant affect on the range.

c. Other factors affecting the range

Apart from the effects of Fomes and Saperda on aspen, the only other non-mammalian factor which must be considered are the Chrysomelid beetles which defoliated large areas of willow in the isolation area during July, 1959. Aspen and balm were infected only lightly.
B. Effects of Range Conditions on Food Habits of the Animals

Heavy browsing maintains much of the aspen, balm and birch at a height where maximum forage is available. Consequently, there are more of these foods in the diet of elk and moose than would occur if browsing was light enough to permit tree growth. The heavy grazing the grassland receives probably forces elk and buffalo to make more use of the sedge meadow than would occur if grass were plentiful.

It is very difficult to correlate accurately the food preferences of animals in Elk Island National Park with food preferences of similar animals elsewhere. First, the combination of dominant herbivores is unique. Only in Yellowstone Park is the situation even closely comparable. Second, the variety of available food plants is characteristic of only a similar habitat. No other study is known to the author which discusses the food habits of moose or elk living together in an aspen forest with a significant understory of hazel, rose, buffaloberry, gooseberry, raspberry and sarsaparilla.

Buffalo, on the other hand, have less variation in food preferences, and everywhere they are found to be eaters of grasses or grasslike plants. Fuller, (1957) and Soper (1941), record the food of buffalo in Wood Buffalo National Park as being predominantly sedge. Grass in Wood Buffalo National Park is very scarce and the buffalo have little choice. In the National Bison Range, Montana, buffalo eat primarily grass with the addition of some forbs (Henry, pers. comm.). In Alaska, sedge sloughs furnish the bulk of the winter food. Summer food is practically all *Calamagrostis canadensis* and *C. purpurascens*. Only wolf-willow is browsed to any extent. (Hogben, in litt., 1959). The U.S. Fish and Wildlife Service (1955) reports that on southern ranges, *Buchloe* and *Bouteloua* spp. are the most "acceptable" foods. On northern ranges, *Agropyron*, *Poa*, and *Festuca* spp. are eaten in addition to *Buchloe* and *Bouteloua*. They say that the shorter grasses appear to be preferred to the taller and coarser species.
The food habits of elk at different seasons are given in various studies as being nearly 100 per cent grass or sedge (Murie, 1951) to nearly all browse (Baldwin and Patton, 1938). In other studies, various proportions of browse, grasses and sedges are listed as the common or preferred foods of elk (Murie, 1951; deWio, 1938; Gaffney, 1941; Cowan, 1947; Morris and Schwartz, 1957; Anderson, 1958). Clearly, they are very adaptable in food habits and are able to live in a wide variety of habitats and eat many types of food. It may be profitable to study elk in several areas and relate food habits with food available. Possibly a direct relation exists between the percentage of each palatable forage species present and the importance of the species in the diet of elk. Coupled with the labile nature of the elk's food habits is its non-specificity in habitat selection. The elk's ability to use a wide variety of foods and habitats permits it to compete with many of the other ungulates.

C. Effects of the Animals on Each Other

1. Food

The principle interactions between the animals occur through their effects on the range. Any action which changes the amount of browse available will directly affect the moose by changing the amount or nature of its food. Similarly any action which affects the grass and sedge meadows will directly affect the buffalo. The flexible nature of the elk in food and habitat choice suggests that reduction in either available browse or grass, would affect the elk's diet but probably would not affect its health or reproductive rate.

The consequence of unrestricted increase in numbers of moose, elk and buffalo in Elk Island National Park would be that food would become limiting. Then the elk would have the best chance of survival. If grazing ranges became depleted first, the buffalo would starve. The elk and moose could feed on browse. When browse became short, the elk could live on what was left of the grassland, but moose would
starve. This sequence of events is not unrealistic. In several instances elk
have increased at the expense of deer, moose, pronghorn antelope, and bighorn sheep,
e.g. Mayr, 1952, and Murie, 1951, p. 296-300.

2. Social Interactions

The dominance exhibited by one species over another was not sufficient to
be considered a significant factor in affecting the survival of either species. If
food was in short supply the dominant species would have the best chance of survival.
In fact, it has been noticed by the wardens that, if elk are enclosed in the winter
feed lot with the buffalo they soon become very thin. They will not feed until after
the buffalo have finished feeding and left the feeding area.

In the feed lot, the buffalo display a social hierarchy, which, if food is
short, can affect certain members of the herd. The bulls, cows and calves have little
trouble in getting sufficient food. The long-yearlings, two and three year olds
have lost the protection of their mothers which they enjoyed during their first winter,
and are not yet large enough to assert themselves. Thus, it is this group of sub-
adult buffalo which comes through the winter in the poorest condition if food is
scarce. During winters when large losses of animals occurred because of starvation
it was the group of sub-adults which suffered the heaviest mortality (Warden Henderson,
pers. comm.).

3. Brucellosis

Nearly half the buffalo population is infected with brucellosis, but only
10% of the elk have contacted the disease. Obviously, the buffalo must come in
contact with the disease organism more often than elk or moose, or must be considerably
more susceptible to infection, or must have a greater ability to survive when infected.
The last two suggestions have not been shown to be so. Since the disease organism
is transmitted by ingestion, interspecific transfer of the disease must occur by
contact with infected milk, placenta, newborn or aborted calf, – or with contaminated
food. The likelihood of elk or moose coming in contact with any of the above sources
during the six months the buffalo are on the feed lot is very remote. However, uninfected buffalo have an excellent chance of encountering viable bacteria. Since most abortions occur while the buffalo are on the feed lot, this area is likely to be the most heavily contaminated area of the Park.

The only chance elk and moose have for contacting the brucellosis organism is on the open range during the summer. Because of the high incidence of Brucellosis in buffalo and the similarity in habitat selection of elk and buffalo, the chance of elk contacting brucellosis from buffalo is greater than its chance of contacting it from another elk or a moose. Similarly, moose must achieve most of their infections by contact with vegetation contaminated by buffalo. Possibly moose and elk are more resistant to infection. However, in view of the information available there is no need to postulate a difference in susceptibility to explain the variation in incidence between species. Differences in the probability of contacting the organism are sufficient to explain the differences in incidence between the three species.

D. Influence of Environment on Habitat Selection and Distribution of the Animals and the Carrying Capacity of the Range

1. Climate

Snow is probably the only climatic factor which can directly limit the distribution of moose, elk and buffalo. Low winter temperatures do not affect the healthy, well-fed animal. Other climatic factors produce their effects on the distribution through changes in vegetation and availability of water.

The amount of precipitation will severely affect the availability of food. Seldom is rainfall insufficient to produce adequate forage on upland meadows, but after a series of wet years the large sedge meadows become flooded. The present high carrying capacity of the buffalo range in the isolation area is due to a series of relatively dry years. A few wet years would have drastic results on the buffalo
population unless artificial feeding was conducted on a year-round basis.

2. Water

Because of the very heavy dew which occurs every night, the animals seldom find it necessary to go to watering holes. Although several thousands of animal-hours of observations were made, drinking animals were observed on only four occasions. No watering places were found which were used frequently by moose and elk. Buffalo frequent a few areas which look like watering holes, but they were never observed drinking at these places.

Wide distribution of water and the heavy dews indicate that available water has little affect in restricting the distribution of the animals. On the contrary, it probably permits as even a use of the range areas as could be attained by any method.

3. Food

Food habits and habitat selection of moose, elk and buffalo in Elk Island National Park are in accordance with the hypothesis "Sympatric species or strains either occupy different habitats within the same territory, or exploit the habitat in different ways..." (Dobzhansky and Pavan, 1950).

Under present range conditions there is very little overlap in food habits, either in summer or winter, between moose, elk and buffalo. As can be seen from Figures 4, 5 and 6, distribution of the three species overlaps very little. Differences in habitat preference indicate that even where distribution overlaps, the animals are not occupying the same niche.

E. Anatomical Reasons for Habitat Selection

Structural modifications permit the buffalo to utilize the grassland range better than the forest. The buffalo has short legs and carries its head low. Conversely, moose with their long legs and long neck are able to reach higher than
a buffalo but are unable to graze short grass ranges. The large nose on the moose is an advantage in browsing, but a hindrance to close grazing. Allee et al. (1949, p. 241) noted similar anatomical differences between the black rhinoceros which feeds on browse and the grazing white-rhinoceros.

Elk and deer are less specialized and are able to use all types of food. The distribution of moose and buffalo in North America prior to the presence of white-man was limited by the distribution of particular forms of food, e.g. browse and grass-like plants respectively. Elk use a wider variety of plant forms for food than do moose or buffalo and has a correspondingly wider geographical distribution.
SUMMARY
1. The soil, climate and vegetation of Elk Island National Park indicate that with continued fire suppression the Park will eventually support a climax forest of white spruce. The rate of formation of a spruce forest is dependent only on the rate of dispersal of spruce and the complete absence of fire. It is not affected by heavy grazing or browsing.

2. All grasslands in the Park are the result of cultivation or heavy browsing preventing establishment of an aspen-balm forest.

3. The stocking level of the range is heavier than the range would support under pristine conditions: a. buffalo have to be fed during the winter; b. browsing is heavy enough to nearly eliminate three common shrubs, viz. saskatoon, dogwood, and chokecherry; c. regeneration of an aspen-balm forest is prevented by heavy browsing.

4. The principle interactions between the animals are through their effects on the range.
   
i. Moose have the greatest effect in determining the physiognomy of the range. During the summer, browsing on aspen, balm and birch prevents a deciduous forest from becoming established on the grass-shrub meadows. Prevention of reforestation provides more grassland range for elk and buffalo.
   
   ii. The habits of the elk permit them to utilize either forest or meadow habitats. During the summer, elk were concentrated in the aspen forest and areas of aspen grove. The effects of elk during the summer on browse plants is very slight. During the winter, as grass ranges become depleted, elk turn more to browsing. Browsing by elk compliments the effects of moose. Heavy use by elk of sedge meadows during early spring prepare these meadows for buffalo. The flexibility of the elk's habits would permit it to survive at the expense of deer, moose, and buffalo if food were in critically short supply.
   
   iii. Buffalo prefer to feed on short grass and sedge plants rather than on
tall coarse grasses and sedges. They assist the elk in consuming all available forage on grass meadows each year. Use of sedge meadows by elk and buffalo is a response to the shortage of suitable grass.

5. The condition of the range in the park, produced by the combined effects of moose, elk and buffalo, makes it unsuitable habitat for deer and hares.

6. Brucellosis has a depressant effect on the reproductive rate of buffalo. Buffalo serve as a reservoir host of *Brucella* and are probably responsible for the occurrence of brucellosis in elk and moose.

7. Interspecific dominance was not shown to be a significant factor in determining the habits and survival of the animals under existing conditions.
LITERATURE CITED

Allan, J.A. Geology. Alberta Research Council Report No. 34.


LIST OF PLANTS OF ELK ISLAND NATIONAL PARK

For proper interpretation of the data presented in the sections on Park vegetation, food habits of the animals and analysis of the range (Appendix B), a list of nearly all vascular plants commonly found in the Park has been included. Thus, the total range of foods available to the animals can be learned and the reasons for the animals not eating many of the foods eaten elsewhere are soon evident. For example, the Park is far outside the distribution of fir, the common winter food of deer, elk and moose in many areas. Buffalo grass and gamma grass, once the mainstay of buffalo on the prairies, are now uncommon everywhere. However, they probably never did occur in the Park. The list of plants also provides a quick reference to the names of plants referred to only by their common names in the main body of this paper. Conversely, for one not familiar with scientific plant names, it provides an index to the common names of plants which have been mentioned only by their latin names.
List of Plants of Elk Island National Park*

<table>
<thead>
<tr>
<th>Pinaceae (Pine Family)</th>
<th>Typhaceae (Cattail Family)</th>
<th>Sparganaceae (Bur-reed Family)</th>
<th>Najadaceae (Pondweed Family)</th>
<th>Juncaginaceae (Arrow-grass Family)</th>
<th>Gramineae (Grass Family)</th>
<th>Cyperaceae (Sedge Family)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larix laricina</td>
<td>Typha latifolia</td>
<td>Sparganium eurycarpum</td>
<td>Potamogeton pusillus</td>
<td>Triglochin maritima</td>
<td>Agropyron subsecundum</td>
<td>Carex aenea</td>
</tr>
<tr>
<td>Picea glauca</td>
<td></td>
<td></td>
<td>Potamogeton richardsonii</td>
<td></td>
<td>Agropyron trachycaulum</td>
<td>Carex antheroides</td>
</tr>
<tr>
<td>Picea mariana</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Agrostis scabra</td>
<td>Carex aquatilis</td>
</tr>
<tr>
<td>Pinus sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Beckmannia syzigachne</td>
<td>Carex bebbii</td>
</tr>
<tr>
<td>Tamarack</td>
<td></td>
<td>Broad fruited bur-reed</td>
<td></td>
<td></td>
<td>Bromus ciliatus</td>
<td>Carex canaescens</td>
</tr>
<tr>
<td>White spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Bromus inermis</td>
<td>Carex crawfordii</td>
</tr>
<tr>
<td>Black spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Calamagrostis canadensis</td>
<td>Carex interior</td>
</tr>
<tr>
<td>Pine (one specimen, dead)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Danthonia spicata</td>
<td></td>
</tr>
<tr>
<td>* All specimens collected by the author and identified by Dr. E.H. Moss and staff at Department of Biology and Botany, University of British Columbia.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Plant Family</td>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>---------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| **Carex** | Carex rostrata  
  Carex sp.  
  Eleocharis palustris  
  Eriophorum angustifolium  
  Eriophorum sp.  
  Scirpus microcarpus |
| **Lemnaceae (Duckweed Family)** | Lemna minor |
| **Juncaceae (Rush Family)** | Juncus balticus |
| **Liliaceae (Lily Family)** | Disporum trachycarpum  
  Lilium philadelphicum var. andinum  
  Maianthemum canadense  
  Smilacina stellata  
  Smilacina trifolia |
| **Orchidaceae (Orchid Family)** | Corallorhiza striata  
  Habenaria hyperborea |
| **Salicaceae (Willow Family)** | Populus balsamifera  
  Populus tremuloides  
  Salix bebbiana  
  Salix commutata  
  Salix discolor  
  Salix drummondiana  
  Salix maccalliana  
  Salix melanopsis  
  Salix myrtillifolia  
  Salix pedicellaris var. hypoglaucus  
  Salix pyrifolia |
| **Betulaceae (Birch Family)** | Alnus tenuifolia  
  Alnus crispa ?  
  Betula papyifera var. subcordata  
  Betula pumila var. glandulifera |
| **Corylaceae (Hazel Family)** | Corylus cornuta |
| **Urticaceae (Nettle Family)** | Urtica gracilis |
| **Polygonaceae (Buckwheat Family)** | Polygonum achoreum  
  Polygonum amphibium var. stipulaceum |
Chenopodiaceae (Goosefoot Family)
- *Axyris amaranthoides*
- *Monolepis nuttalliana*

Caryophyllaceae (Pink Family)
- *Arenaria lateriflora*
- *Stellaria longifolia*

Ceratophyllaceae (Hornwort Family)
- *Ceratophyllum demersum*

Ranunculaceae (Crowfoot Family)
- *Actaea rubra*
- *Anemone multifida*
- *Caltha palustris*
- *Ranunculus aquatilis var. capillaceus*
- *Ranunculus gmelini*
- *Ranunculus sceleratus*

Cruciferae (Mustard Family)
- *Descurainia sophia*
- *Draba nemorosa*
- *Lepidium densiflorum*

Saxifragaceae (Saxifrage Family)
- *Chrysosplenium iowense*
- *Parnassia palustris*
- *Ribes lacustre*
- *Ribes oxyacanthoides*
- *Ribes triste*

Rosaceae (Rose Family)
- *Agrimonia striata*
- *Amelanchier alnifolia*
- *Fragaria virginiana var. glauca*
- *Geum aleppicum var. strictum*
- *Potentilla gracilis var. rigida*
- *Potentilla norvegica*
- *Potentilla palustris*
- *Potentilla pensylvanica*
- *Potentilla platensis*
- *Prunus pensylvanica*
- *Prunus virginiana var. melanocarpa*
- *Rosa acicularis*
- *Rubus acaulis*
- *Rubus chamaemorus*
- *Rubus pubescens*
- *Rubus strigosus*

Leguminosae (Pea Family)
- *Lathyrus ochroleucus*
- *Lathyrus venosus*

Russian pigweed
Spear-leaved goosefoot
Blunt-leaved sandwort
Long-leaved stitchwort
Hornwort
Red baneberry
Cut-leaved anemone
Marsh marigold
Small yellow water-crowfoot
Cursed crowfoot
Flixweed
Wood whitlow grass
Common peppergrass
Golden saxifrage
Northern grass of Parnassus
Bristly black current
Wild gooseberry
Wild red current
Agrimony
Saskatoon berry
Smooth wild strawberry
Yellow avens
Graceful cinquefoil
Rough cinquefoil
Marsh cinquefoil
Prairie cinquefoil
Pin cherry
Choke cherry
Prickly rose
Dwarf raspberry
Cloud berry
Running raspberry = Dewberry
Wild Red Raspberry
Cream-coloured vetchling
Wild pea-vine
Trifolium pratense
Trifolium repens
Vicia americana

Balsaminaceae (Touch-me-not Family)
Impatiens capensis = biflora

Violaceae (Violet Family)
Viola glabella
Viola rugulosa

Elaeagnaceae (Oleaster Family)
Elaeagnus commutata
Shepherdia canadensis

Onagraceae (Evening Primrose Family)
Epilobium angustifolium

Haloragidaceae (Water-milfoil Family)
Myriophyllum exalbescens

Araliaceae (Ginseng Family)
Aralia nudicaulis

Umbelliferae (Parsley Family)
Heracleum lanatum
Sanicula marilandica

Cornaceae (Dogwood Family)
Cornus canadensis
Cornus stolonifera

Pyrolaceae (Wintergreen Family)
Pyrola asarifolia
Pyrola secunda

Ericaceae (Heath Family)
Ledum groenlandicum
Vaccinium microcarpos ?
Vaccinium myrtilloides =
Vaccinium oxycoccos
Vaccinium vitus-idaea

Primulaceae (Primrose Family)
Androsace septentrionalis var. puberulent
Lysimachia ciliata

Gentianaceae (Gentian Family)
Menyanthes trifoliata

Boraginaceae (Borage Family)
Mertensia paniculata

Red clover
White clover
American vetch

Spotted touch-me-not

Western Canadian violet

Silver willow = wolf willow
Canadian buffalo berry

Fireweed

Spiked water milfoil

Wild sarsaparilla

Cow parsnip
Snake root

Bunchberry
Red Osier dogwood

Common pink winter-green
One-sided wintergreen

Laborador tea
Small bog cranberry
V. canadense - Blueberry
Swamp cranberry
Bog cranberry

Fairy candelabra
Fringed loosestrife

Buck-bean

Tall lungwort
Labiatae (Mint Family)
- Agastache foeniculum
- Mentha arvensis var. villosa

Scrophulariaceae (Figwort Family)
- Castilleja rhexifolia
- Orthocarpus luteus

Plantaginaceae (Plantain Family)
- Plantago major

Rubiaceae (Madder Family)
- Galium boreale
- Galium labroducticum
- Galium trifidum
- Galium triflorum

Caprifoliaceae (Honeysuckle Family)
- Linnaea borealis var. americana
- Lonicera dioica var. glaucescens
- Lonicera involucrata
- Symphoricarpus albus var. pauciflorus
- Symphoricarpus occidentalis
- Viburnum edule

Campanulaceae (Bluebell Family)
- Campanula rotundifolia

Compositae (Composite Family)
- Achillea millefolium ssp. lanulosa
- Achillea sibirica
- Antennaria neglecta
- Antennaria parviflora
- Arnica cordifolia
- Artemisia frigida
- Artemisia ludoviciana var. gnaphalodes
- Aster ciliolatus
- Aster conspicuus
- Aster modestus
- Aster pannus
- Aster puniceus
- Bidens cernua
- Chrysanthemum leucanthemum
- Cirsiurn arvense
- Cirsiurn undulatum
- Crepis tectorum
- Eriogonum philadelphicum
- Hieracium umbellatum
- Matricaria matricarioides
- Petasites sagittatus
- Senecio congestus var. palustris

Giant hyssop
Wild mint
Common Indian paint-brush
Owl clover
Common plantain
Northern bedstraw
Laborador bedstraw
Small bedstraw
Sweet-scented bedstraw
Twin-flower
Twining honeysuckle
Involucrate honeysuckle
Few-flowered snowberry
Western snowberry
Lowbush cranberry = Mooseberry
Bluebell
Woolly yarrow
Many-flowered yarrow
A. campestris - Pussytoes = Everlasting
Small leaved everlasting
Heart-leaved arnica
Pasture sage
Prairie sage
Showy aster
Purple stemmed aster
Nodding beggar-ticks
Ox-eye daisy
Canada thistle
Wavy-leaved thistle
Annual hawks beard
Philadelphia fleabane
Narrow-leaved hawks weed
Pineapple weed
Arrow-leaved coltsfoot
Marsh ragwort
Senecio pauperculus
Solidago decumbens var. oreophila
Solidago lepida var. elongata ?
Solidago pruinosa
Sonchus aspen
Sonchus uliginosus
Taraxacum officinale

Balsam groundsel
Mountain goldenrod
Graceful goldenrod
Canadian goldenrod
Annual sow thistle
Perennial sow thistle
Dandelion
APPENDIX B

SUMMARY OF RANGE ANALYSIS

In the following summaries of transect analysis a general description of the habitat is given. The per cent of "hits" on each class of plant (grass, forb or shrub), segregated into an arbitrarily determined classification of palatability, are listed in a table. The percentage plant cover indicates the number of points which hit vegetation other than moss. The percentage composition of the plants listed in the final paragraph of each transect summary is based on the number of hits on each species in relation to total plant cover.

For the purposes of this summary, "palatable species" is used to mean a plant which is commonly eaten by one of the ruminants. Conversely, "unpalatable species" refers to a plant which the animals seldom eat or avoid eating.

Palatable grasses include Poa, Agropyron, Bromus, Agrostis, Koeleria, and most Carex species. Unpalatable grasses are Calamagrostis, Phalaris, Hordeum, Glyceria and the tall rank Carex species. Of the common forbs, all are palatable except Aralia, Solidago, Artemisia, Antennaria and Sonchus. Palatable browse species are aspen, balm, birch, willow, cherry dogwood, saskatoon, hazel, rose and Viburnum. The major unpalatable species are gooseberry, raspberry, buffaloberry, snowberry and alder.

Figure 13 shows the location of the range transects and following it (Figure 14) is a sample of the form used to record the range analysis data.
SUMMARY OF RANGE ANALYSIS

Transect 1. Tawayik Lake Meadow.

This meadow is a natural grass–forb meadow at the north end of Tawayik Lake. The presence of charred logs on the meadow indicate that this meadow, like many of the others, is a stage in a fire succession. There are very few shrubs, and those present are very heavily browsed. See Photograph 3.

Soil

The meadow has a heavy hydromorphic soil. Nearby areas have sandy or gravelly soils.

Vegetation

Table V. Summary of Data From Transect 1.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>45%</td>
</tr>
<tr>
<td>Forbs</td>
<td>29%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>tr.</td>
</tr>
<tr>
<td></td>
<td>2%</td>
</tr>
<tr>
<td></td>
<td>tr.</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>77%</td>
</tr>
</tbody>
</table>

Of the total palatable forage, 40% was *Poa pratensis*, and 29% was *Trifolium repens*. Other species present in amounts greater than 1% were: *Agropyron subsecundum*, 7%; *Agropyron trachycaulum*, 4%; *Agrostis*, 1%; *Taraxacum*, 3%; *Fragaria*, 4% and *Achillea*, 1%.

Transect 2. Soap-hole Meadow.

This meadow, located in the south east corner of the park, is possibly the only true parkland meadow in the Park. This is suggested by the absence of any indication of fire and the presence of at least one characteristically prairie
grass (Koeleria sp.). The range is less productive than the artificial grasslands located elsewhere in the park. See Photograph 2.

Soil

The soil has a five inch layer of black soil with a thick mat of grass roots. Below this, there is a very sticky, wet clay horizon with a lime layer at 21 inches. (The lime layer of grey-wooded soils is generally at 36 to 40 inches).

Vegetation

Table VI. Summary of Data From Transect 2.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>47%</td>
</tr>
<tr>
<td>Forbs</td>
<td>4%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>tr.</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>70%</td>
</tr>
</tbody>
</table>

Of the total forage, 18.5% was Poa pratensis, 36% was Koeleria and only 2% was Trifolium. Other species present in lesser amounts were: Agrostis, 8%; Agropyron sp., 1%; Poa nervosa, 2%; Potentilla, 5%; Achillea, 4%; Fragaria, 2% and Antennaria, 1%.


This meadow represents one of the cultivated grass meadows along the main road through the park. Appearance and species composition appear similar to the other meadows along the road. Considerable Symphoricarpos has established in spite of the heavy browsing and grazing the meadow receives. Growth of aspen, balm and willow present on the meadow is completely controlled by browsing. See Photograph 4.
Soil

Black soil extended to a depth of three to five inches; below this, a silty clay layer.

Vegetation

Table VII. Summary of Data From Transect 3.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>60%</td>
</tr>
<tr>
<td>Forbs</td>
<td>17%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>1%</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>78%</td>
</tr>
<tr>
<td>Shrub intersect</td>
<td>71 feet</td>
</tr>
</tbody>
</table>

Of the total vegetation 57% was Poa pratensis; Trifolium accounted for 13%. Other plants were: Agropyron, 6%; Taraxacum, 4%; Phleum, 2% and Carex sp., 2%.


Hazel and balm shrub are the dominant plants of this meadow. Grass occurs only in small patches interspersed in the thick shrub cover. This meadow on the east side of the park, and similar ones, one west of Tawayik Lake and one southwest of Astotin Lake, are all of the same general appearance. All are the result of a suppressed fire succession. The age of surrounding trees indicates that the fire burned the area about 1900.

Soil

Black soil two inches; sandy clay below.
Vegetation

Table VIII. Summary of Data From Transect 4.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>18%</td>
</tr>
<tr>
<td>Forbs</td>
<td>20%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>tr.</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>48%</td>
</tr>
</tbody>
</table>

Shrub intersect: 210 feet

The meadow was composed of 30% Poa, 17% Fragaria, and 15% Trifolium. Several other species were present in amount of 3% or less. The dominant browse plants were predominantly hazel, but with significant amounts of willow, balm, aspen, snowberry and birch. All but a few shrubs were less than three feet high.

Transect 5. Grass-shrub meadow.

Transect 5 is located about one mile east of the north end of Tawayik Lake. Aspen and balm are the dominant shrubs. Hazel, which was most abundant on Transect 4, is represented by only one plant in the transects on this meadow. Age of aspen trees and shrubs varies from eight to twenty years. The height of all shrubs is less than six feet.

Soil

The meadow has a black soil two inches deep, a leached A horizon of ten inches and a B horizon of brownish clay with some sand.
Table IX. Summary of Data From Transect 5.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>29%</td>
</tr>
<tr>
<td>Forbs</td>
<td>25%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>0</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>58%</td>
</tr>
</tbody>
</table>

The vegetation of the meadow was composed of 35% Poa, 20% Trifolium, 11% Agropyron, and 9% Fragaria. Many other plant species were present in lesser amounts. Solidago sp. was abundant on the meadow. In the browse transects (1,200 square feet) there were the following number of shrub plants: 96 aspen, 80 balm, 52 rose, 58 willow, 39 buffalo berry, 33 snowberry, 26 birch, 19 raspberry, and 22 hazel. Lesser numbers of gooseberry, saskatoon and chokecherry were present. Photograph 5 represents a typical portion of this meadow.

Transect 7. 1946 Burn.

This transect is located in a burned over stand of mature aspen. In 1946, fire killed all live trees on about 40 acres in the north end of the park. No regeneration of aspen or balm has taken place. Tree trunks which are still standing can be pushed over easily. The ground is covered with a tangle of rotting logs and a heavy cover of grass. (See Photograph 10).

Soil

The soil has considerable sand and gravel.
Vegetation

Table X. Summary of Data From Transect 7.

<table>
<thead>
<tr>
<th></th>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>7%</td>
<td>11%</td>
</tr>
<tr>
<td>Forbs</td>
<td>13%</td>
<td>3%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>1%</td>
<td>2%</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>37%</td>
<td></td>
</tr>
</tbody>
</table>

Phalaris and Calamagrostis accounted for 27% of the vegetation. Other species were: Agropyron, 8%; Poa, 4%; Fragaria, 20%; Rubus, 10%; and several other species present in amounts less than 4%.

Eighteen per cent of the total transect points were rotting logs. Raspberry, rose, snowberry and hazel were the most abundant shrubs. All shrubs were less than four feet high.

Transect 8. Isolation area - Aspen forest.

This transect differs from the others in that no permanent transect lines were located. The shrub vegetation was analysed in the usual way, i.e., by four rectangular plots 3 feet by 100 feet. All shrubs, trees and tall forbs occurring within the plots were divided into height classes and counted.

The forest is composed of aspen and balm, 35 to 40 years old, with an understory three to ten feet high. In the 1,200 square feet (approximately 1/30 acres) there was the following number of tree, shrub and forb plants: Solidago, 200; rose, 108; raspberry, 88; saskatoon, 84; willow, 75; snowberry, 54; hazel, 51; Aralia, 45; aspen, 33; balm, 18 and cherry, 13. The willows and saskatoon were the tallest shrubs. They averaged three to six feet high.

The general form of the forest is represented by Photograph 8.
Transect 9. Semi-open aspen forest.

This transect is located about two miles south of the north boundary of the park and 1.25 miles from the east boundary. The forest is typical of most of the area designated on Map 2 as semi-open aspen. Aspen and balm trees are 38 to 50 years old, 50 to 60 feet high and four to nine inches in diameter.

Soil

The soil is a very sandy loam to a depth of at least eight feet.

Vegetation

Table XI. Summary of Data From Transect 9.

<table>
<thead>
<tr>
<th>Palatable species</th>
<th>Unpalatable species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasses</td>
<td>1%</td>
</tr>
<tr>
<td>Forbs</td>
<td>6%</td>
</tr>
<tr>
<td>Shrubs</td>
<td>2%</td>
</tr>
<tr>
<td>Total plant cover</td>
<td>17%</td>
</tr>
</tbody>
</table>

Most of the grass present in the transects was *Calamagrostis*. Rose and hazel were present in the shrub understory in equal amount. Raspberry was the third most abundant browse species. Nearly all browse plants were less than four feet.

Photograph 7 represents the semi-open aspen habitat.
Figure 13. Locations of range transects established in 1959.
**Record of Permanent Line Transect**

<table>
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<th>Park</th>
<th>Cluster No.</th>
<th>Date measured</th>
<th>Observer</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
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<th>Transect No.</th>
<th></th>
<th>Transect No.</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hits</td>
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</tbody>
</table>

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td>Bare Soil</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Erosion Pavement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moss</td>
<td></td>
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**Forage density index**
- Ground cover index
- Overstory
- Understory
- Annuals

*Figure 14. Sample of form used to record range transect data.*
### Plant Vigour Measurements

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<td><strong>Av. Max.</strong></td>
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**Pellet Group Counts**

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Photograph 1. Large slough by road near north end of Elk Island National Park, June 23, 1959. Typical slough, sedge meadow with willow, birch and gooseberry shrub on periphery.

Photograph 3. Grass-forb meadow north end of Tawayik Lake, August 14, 1959. This is the natural meadow type for the Beaverhills. Note the large number of forbs, (mostly Yarrow), and the presence of *Agropyron*. See summary of Transect 1.

Photograph 4. Grass meadow formed by cultivation in 1944, August 14, 1959. This grass meadow consists largely of *Poa* and white clover. Aspen, balm, willow, saskatoon and other shrubs are present but cannot mature because of heavy browsing. See summary of Transect 3.
Photograph 5. Aspen-balm shrub meadow, August 25, 1959. This is a thick stand of aspen and balm on a grass meadow. All browse is maintained within reach of moose and elk. See summary of Transect 5.

Photograph 6. Aspen-balm shrub meadow, May 5, 1959. This meadow is similar to the one in photograph 5. Note heavily browsed condition of aspen and extreme close cropping of grass. Also note the presence of grass stems where protected by the shrubs. Similar close grazing is found on all grass meadows in early May.
Photograph 7. Semi-open aspen habitat, August 17, 1959. Note thick understory of hazel and sarsaparilla. Height of all browse, except rose, is less than three feet. Very little grass is present. See summary of Transect 9.

Photograph 9. Open aspen stand with understory of *Calamagrostis* grass. West of Tawayik Lake, May 6, 1959. Note heavy browsing of shrubs in foreground and lack of use of grass.

Photograph 11. Open aspen stand after burn in 1946, August 29, 1959. Calamagrostis, Bromus and Agropyron grasses present show very little evidence of grazing. All browse species are suppressed. See summary of Transect 7.