



Winter ecology of moose on the Northern Yellowstone Winter Range
by Daniel Bruce Tyers

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of
Philosophy in Fish and Wildlife Biology
Montana State University
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Abstract:

Shiras moose (*Alces alces shirasi*) invaded the Northern Yellowstone Winter Range (NYWR) in the 1800's. Management of this species has been handicapped by limited population data and reliance on habitat use paradigms from other areas in North America. For example, although moose in most regions forage in recently disturbed forests with abundant deciduous shrubs, I did not find this to be true on the NYWR. I used multiple methods to determine population status, including aerial surveys, horseback surveys, road surveys, and ground counts in willow habitats. Moose were most easily seen when they foraged in willow (*Salix* spp.) stands in November-December and May-June. Attempts to count moose at other times resulted in marked under-sampling. Fires in 1988 removed mature forests at a landscape level resulting in a loss of preferred winter habitat and a sustained population reduction. I also investigated moose winter foraging activities among burned (1988), logged, forested, and forest edge environments. Logged areas and recent burns were rarely used, but forest interiors were important habitat. The edge effect did not benefit moose in winter. NYWR moose coped with winter by seeking concentrations of food to maximize feeding and minimize movement. They optimized foraging by using 2 taxa that grow in patches, willow and subalpine fir (*Abies lasiocarpa*). Moose fed in willow until snow forced them to nearby forested hillsides where they browsed subalpine fir <5 m in height. Subalpine fir, a shade tolerant tree, grows more rapidly under a forest canopy. It can reproduce through layering, creating an expanding patch of small trees around the parent. Patches are largest and most numerous in the oldest lodgepole pine (*Pinus contorta*) forests. Moose used other characteristics of lodgepole forests to reduce energy output by finding routes with less than average snow depth to reach subalpine fir patches. Moose also browsed gooseberry (*Ribes* spp.) and buffaloberry (*Shepherdia canadensis*), nutrient rich shrubs that are scattered and energetically expensive to obtain. Exclosure studies showed willow was suppressed before 1988, and fires and drought increased negative effects. Higher willow utilization rates in 1989 probably reflected a response by moose to a loss of winter habitat due to the 1988 fires, a foraging strategy that may have contributed to observed willow mortality. From 1989 to 1997, some willow showed signs of recovery. Replacement of older forests where moose foraged before 1988 could take several hundred years. Maintaining remaining populations should concentrate on minimizing loss of mature forests and adjacent willow and careful hunting management.

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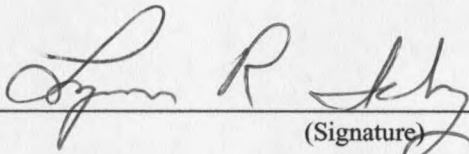
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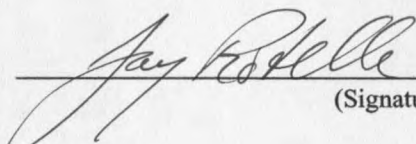
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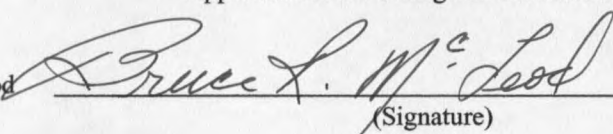
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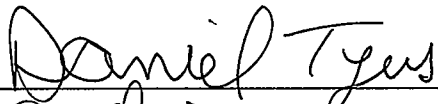

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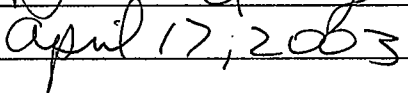
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ABSTRACT

Shiras moose (*Alces alces shirasi*) invaded the Northern Yellowstone Winter Range (NYWR) in the 1800's. Management of this species has been handicapped by limited population data and reliance on habitat use paradigms from other areas in North America. For example, although moose in most regions forage in recently disturbed forests with abundant deciduous shrubs, I did not find this to be true on the NYWR. I used multiple methods to determine population status, including aerial surveys, horseback surveys, road surveys, and ground counts in willow habitats. Moose were most easily seen when they foraged in willow (*Salix* spp.) stands in November–December and May–June. Attempts to count moose at other times resulted in marked under-sampling. Fires in 1988 removed mature forests at a landscape level resulting in a loss of preferred winter habitat and a sustained population reduction. I also investigated moose winter foraging activities among burned (1988), logged, forested, and forest edge environments. Logged areas and recent burns were rarely used, but forest interiors were important habitat. The edge effect did not benefit moose in winter. NYWR moose coped with winter by seeking concentrations of food to maximize feeding and minimize movement. They optimized foraging by using 2 taxa that grow in patches, willow and subalpine fir (*Abies lasiocarpa*). Moose fed in willow until snow forced them to nearby forested hillsides where they browsed subalpine fir <5 m in height. Subalpine fir, a shade tolerant tree, grows more rapidly under a forest canopy. It can reproduce through layering, creating an expanding patch of small trees around the parent. Patches are largest and most numerous in the oldest lodgepole pine (*Pinus contorta*) forests. Moose used other characteristics of lodgepole forests to reduce energy output by finding routes with less than average snow depth to reach subalpine fir patches. Moose also browsed gooseberry (*Ribes* spp.) and buffaloberry (*Shepherdia canadensis*), nutrient rich shrubs that are scattered and energetically expensive to obtain. Exclosure studies showed willow was suppressed before 1988, and fires and drought increased negative effects. Higher willow utilization rates in 1989 probably reflected a response by moose to a loss of winter habitat due to the 1988 fires, a foraging strategy that may have contributed to observed willow mortality. From 1989 to 1997, some willow showed signs of recovery. Replacement of older forests where moose foraged before 1988 could take several hundred years. Maintaining remaining populations should concentrate on minimizing loss of mature forests and adjacent willow and careful hunting management.

INTRODUCTION

Project Origin

This project was conducted at the request of the Northern Yellowstone Cooperative Wildlife Working Group (NYCWWG). The NYCWWG is comprised of 4 agencies with management or research responsibilities for the NYWR. They are Montana Fish, Wildlife, and Parks (MFWP), Yellowstone National Park (YNP), Gallatin National Forest (GNF), and Biological Resource Division/United States Geologic Survey.

In 1986, NYCWWG members expressed concern over the population status of Shiras moose on the NYWR. However, data were insufficient to assess population changes and reasons for changes. As a result, this study was initiated to address the winter ecology of moose along the northern boundary of YNP. Data collection began in September 1985 and concluded in October 2001.

Two unexpected events caused the project to be extended beyond its planned 4-year duration. One was a series of fires during the summer of 1988 that had major effects on vegetation at the landscape level. They interrupted data collection but also provided an opportunity to investigate the impact of large fires on moose. The second was the reintroduction of a new and potentially important predator, the wolf, to YNP in 1995. Neither of these events necessitated major changes in methodology but did, at the request of the agencies, extend population monitoring longer than was originally proposed.

Data collected were in response to information needs of the respective agencies, but ecological relationships between Shiras moose and habitat perturbations in the northern Rocky Mountains were also examined. I focused my ecological investigations on foraging theory. Many authors have discussed the concepts of foraging theory and have proposed various models to explain how animals perceive their environment (Stephens and Krebs 1986). However, the relationship between theory and practical wildlife management has not been well defined (Nudds 1982, Jenkins 1982, Morrison et al. 1998). Jenkins (1982) stated that combining foraging theory with empirical data on food selection might lead to valuable new insights about wildlife management problems. This project provided an opportunity to make such a linkage.

Management issues prompting this project involved direct and indirect effects on moose, i.e., predation and natural and human-induced habitat alterations. In this context, I explored theories of moose biogeography and current views of optimum foraging strategies. I derived explanations for the current status of the moose population on the NYWR and made predictions for its future by examining theory in light of management practices.

NYCWWG members provided a long list of issues and topics related to moose to be addressed through this study. Some were project specific, while others dealt with the natural history of this species. With the addition of a pre- and post-fire assessment, all were covered by 3 objectives:

1. Determine population size and trend while testing various monitoring techniques.
2. Determine movements and home range of radiocollared moose.
3. Determine winter diet and habitat and describe the ecological parameters of this habitat.

Background information

When this project was initiated, site-specific data were limited. The status of the NYWR moose population and past trends were unsubstantiated, and no food habits or habitat use studies had been conducted. Published studies of other moose populations provided background information for assessing the winter ecology of NYWR moose

Four subspecies of moose are recognized in North America. Differentiation is based primarily on skull characteristics (Coady 1982), but the systematics are not considered definitive (Bubenick 1997). Ranges of the subspecies are adjacent and nearly discrete. Moose are distributed from coast to coast across the continent and coincide with the distribution of boreal forests. *A.a. americana* occurs from Ontario eastward; *A.a. andersoni* occurs from Ontario to British Columbia; *A.a. gigas* occurs in Alaska, western Yukon, and northwest British Columbia; and *A.a. shirasi* occurs in the mountains of Wyoming, Idaho, Montana, southeastern British Columbia, southern Alberta, northeast Utah, and Colorado (Bubenik 1997).

Moose may have been comparatively rare in North America when Europeans first arrived. Explorers and trappers indicated they were still scarce throughout much of the Rocky Mountains as recently as the middle 1800's (Peterson 1955, Kelsall and Telfer 1974, Kay 1997). However, since about 1900 moose appear to have extended their range and/or become more numerous across the continent, including the intermountain west (Kelsall and Telfer 1974, Kay 1997, Bubenick 1997). Efforts to understand current moose population trends are confounded by the ambiguous origin of moose on this continent and by a poor understanding of recent biogeographical changes. Reasons for the earlier limited distribution of moose and range expansion in the past 100 years have implications for the management of moose on the NYWR.

There are several viable theories to explain the prehistoric invasion of moose into North America and the development of the 4 subspecies (Peterson 1955, Bubenik 1997). It is generally recognized that moose, or genetically similar ancestors, came from Eurasia across the Bering land bridge. However, the timing is uncertain. Successive immigrations probably took place periodically during the Pleistocene Epoch (1.8

million to 11,000 years B.P.). Moose-like animals may have arrived during the Illinoian ice age (240,000 to 128,000 years B.P.) (Kelsall and Telfer 1974, Coady 1982). Lankester and Samuel (1997) considered North American moose a relatively recent arrival from Asia (70,000 to 10,000 years B.P.). Peterson (1955) hypothesized that moose reached the tiaga before the development of the Wisconsin ice shield (20,000 years BP), and Bubenik (1997) believed they occupied the Great Lakes region about 10,000 years B.P.

Four refugia for moose were created by the distribution of ice and resulting ice-free areas during the Wisconsin glacial period. Glacial barriers and grasslands may have provided the isolation necessary for the development of the four subspecies identified today. Following the retreat of the glaciers and return of vegetation, moose dispersed from these refugia to further colonize what are now Canada and the U.S.

Bubenik (1997) proposed an alternative explanation. Two different subspecies of moose may have invaded North America, with 1 taking a more southern route across sea-ice during the mid-Wisconsin glacial period. The presence of 2 subspecies initially may have contributed to the eventual development of 4.

In the recent context, a number of hypotheses have been forwarded to account for the considerable expansion of moose in North America over the past century. These include: 1) a limited amount of time to colonize North America since the last glaciation; 2) climatic variation - the Little Ice Age and associated severe winter weather limited moose populations ca 1700-1800; 3) disease - moose numbers may have once been limited by disease, particularly the meningeal worm (*Parelaphostrongylus tenuis*); 4) modification of the original climax forests, which were generally poor moose habitat, by European settlement; 5) extermination of native carnivores allowing moose to extend their range and expand their populations (Kelsall and Telfer 1974); and 6) cessation of Native American hunting pressure - moose were extremely vulnerable to human predation which controlled moose numbers and distribution until recent times (Kay 1997).

Loope and Gruell (1973) proposed a seventh hypothesis specific to the Shiras moose and the GYA: low moose populations during the 19th century were the result of fires that maintained early successional vegetation. Subsequent population increases in this century in northwest Wyoming were possible because forests matured under a management policy of fire suppression. A primary factor in this, they believed, was an increase in subalpine fir, a shade tolerant species found in older forests. They further hypothesized that subalpine fir is the staple food item in the diets of moose in the area.

Peek (1974a) reviewed literature documenting range expansion in the 20th century of just the Shiras moose, the subspecies found in the GYA. He described important increases in territory, especially southward, and reported that all suitable habitats in southwestern Montana had been occupied by 1970. Kelsall and Telfer (1974) also found evidence of recent Shiras moose range expansion, in this case,

northward into British Columbia and Alberta. Coady (1982) considered the Shiras moose to be stable or slightly increasing across its range in 1982.

Some historical information on moose populations in the GYA is available. Houston (1982) reported that moose have not been found in archaeological sites in northwest Wyoming and south central Montana. He concluded that moose had not yet occupied northwest Wyoming in 1830 (Houston 1968) but had colonized the Yellowstone area by the 1870's; he believed they appeared on the NYWR around 1913 (Houston 1982). Shullery and Whittlesey (1992) reviewed the documentary record of wolves and related wildlife species in the Yellowstone Park area prior to 1882. Based on historical accounts, they concluded that moose were common in the southern part of the Park in 1882, and rare sightings were made near or on the NYWR around the same time.

Moose morphology and physiology and concomitant foraging strategies help explain moose biogeography. Habitat occupied by all 4 subspecies indicates that the moose is an animal of the boreal forests - coniferous forests that occur in a broad band across northern North America and Eurasia. Boreal forests also extend southward at higher elevations. The climate within this biome is characterized by cold winters and short, mild summers (Brewer 1994). Food and cover are apparently the primary factors limiting moose geographic distribution to the north (Kelsall and Telfer 1974) and climate to the south (Renecker and Hudson 1986a). An important determinant to the southern distribution of moose is high temperature (Karns 1997).

Moose foraging strategies have developed primarily in the context of forests where cold temperatures, snow conditions, and the presence or absence of forest canopies are important variables affecting winter survival. Coady (1982) stated that the distribution of moose is more closely related to the range of northern trees and shrubs than to any other factor. Renecker and Hudson (1992) reported that available forage biomass, forage quality, and ambient temperature influence activity and energy budgets for moose.

Moose are browsers - herbivores that eat primarily shrubs and trees (Peterson 1955, Renecker and Schwartz 1997). Specifically, they eat twigs and foliage high in cell-soluble sugars that ferment readily in the rumen. Ruminants with a large body size, like moose, require large quantities of food and are usually constrained by the time required to search for and process it. Processing is likely to be less important than locating adequate quantities of food. Because of their dietary requirements, the quantity of available forage determines moose density. Consequently, trade-offs between time-energy constraints and food acquisition influence foraging strategies (Peek et al. 1992, Renecker and Hudson 1992).

To satisfy the need for large amounts of winter food, they seek concentrations or patches of vegetative biomass in the environment where they can spend relatively long periods of time foraging. Renecker and

Hudson (1992) speculated that moose use forage resources that are densely clumped so that high feeding efficiency is possible. As examples, they list species from northern climates that tend to be concentrated on the landscape such as willow, aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). Van Ballenberghe and Peek (1971) described moose home ranges in northeastern Minnesota as a series of high use areas connected by travel routes. Cedarlund and Okarma (1988) hypothesized that moose home areas may be comprised of closely located feeding sites of a few hectares or less, each of which can be used for several days or weeks.

The large body size of moose is a favorable adaptation in boreal regions for coping with predators and periods of extreme cold and deep snow (Renecker and Hudson 1986a,b; 1989a,b). Its large body size minimizes heat loss through low surface area to volume ratios, but this same characteristic also makes them prone to heat stress and resultant higher energy expenditures through increased metabolism and heart and respiration rate (Renecker and Hudson 1992). Thermal cover is necessary to shelter moose from extreme cold in the winter, but habitat to buffer heat loading in both summer and winter is also necessary (Renecker and Hudson 1992). Ambient air temperatures above 23° F (-5 C) in winter and above 57° F (14 C) in summer can be stressful and cause moose to seek cooler areas. In a broad sense, thermal regulation requirements restrict range expansion of moose into more temperate climates.

Snow conditions also have an important influence over moose distribution and habitat-use patterns (Peek 1997). Factors which affect the ability of moose to access browse include snow density, hardness, and depth (Peek 1971, Schladweiler 1973, Peek 1986). The presence or absence of a forest canopy can have a significant effect on snow conditions. For example, moose often prefer open brush fields where browse is abundant for foraging, but they have also been known to seek coniferous forests when snow conditions impeded movements in open areas (Des Mueles 1964, Kelsall 1969, Telfer 1970, Peek et al. 1976, Rolley and Keith 1980, Thompson and Vukelich 1981). Travel in forests is often less energy demanding because tree branches ameliorate snow density, hardness, and depth through shading and intercepting falling snow.

Several studies have reported specific snow depth thresholds for moose. Although there is variation among the 4 subspecies, snow depths of 65-70 cm have commonly been reported to affect habitat use and movements of moose (Kelsall 1969, Thompson and Vukelich 1981, Pierce and Peek 1984). In Quebec, Des Mueles (1964) found that moose shifted to denser conifer types when snow depth reached 77 to 86 cm, and they did not use areas where the snow exceeded 107 to 122 cm, even when the snow was soft. Kelsall (1969) reported moose to be severely restricted by snow depths of 70 to 90 cm. Kelsall and Prescott (1971) found that when snow depths reached 97 cm in New Brunswick moose were confined to areas with high forest canopies.

Habitat patch size, shape, juxtaposition, interspersions, and amount of edge have impacts on moose (Peterson 1955, Schwartz and Franzmann 1989). Forests can be altered using the mechanisms of fire and logging to create patterns of timber and openings that benefit moose. Manipulations may involve many silvicultural practices, but common to all is edge, the interface between forest and forest opening (Franklin and Forman 1987, Thompson and Stewart 1997). Understanding the effect of edge on moose is critical to agencies mandated to provide forest products and manage for natural disturbances.

Various attempts have been made to characterize habitats currently occupied by moose in North America. Telfer (1984) placed moose habitat in 5 broad categories: boreal forests, mixed forest, large delta floodplains, tundra and subalpine shrub, and stream valleys. These may be further described as either permanent or transitory in nature (Geist 1971, Peek 1997). Permanent habitats are those that persist and do not succeed over time to a different pattern of vegetation. For example, alluvial habitats are dynamic in that flooding and streambed alteration produce a constantly changing system, but they are permanent in the sense that the same type of vegetation is present after a disturbance. In contrast, boreal forests are transitory. Fire can radically alter the successional stage and hence the vegetative composition; a mature forest can be changed to a shrub community. A forest that is vulnerable to a fire event will eventually replace the shrub community. The pattern is cyclic and each successional stage is transitory to the next.

Throughout much of their range, moose are most abundant in transitory habitats. Specifically, they are closely linked to early seral stages where shrub biomass is plentiful (Aldous and Krefting 1946, Hatter 1949, Dyrness 1973, Whittinger et al. 1977, Irwin and Peek 1979). In many areas, moose benefit from the removal of the forest canopy (Taber 1966, Krefting 1974, Kelsall and Telfer 1974, LeResche et al. 1974, Irwin 1975, Peek et al. 1976). Disturbances such as fire, logging (or other forms of mechanical manipulation), disease, or wind events can create favorable moose habitat by removing trees that compete for resources with shrubs. The use of conifer types instead of seral habitats was considered by Peek (1974a) to be indicative of marginal moose habitat in some areas but not in others. Coady (1982) stated that an intensified policy of fire suppression and a general decrease in disturbances in forests has greatly decreased the amount of early seral moose range in some regions and caused a corresponding reduction in moose numbers.

However, it is also known that moose winter habitat-use patterns can be highly variable among regions and years (Peek 1974a), which reflects adaptive responses to different environmental conditions. Peek (1974a) cautioned against making unequivocal generalizations about moose winter habitat selection and suggested that the amount of variability can make these descriptions misleading. He believes this

variability has special consequences to management because it is important to determine the forage species locally preferred by moose and then favor those species through management actions.

Peek (1974a,b) reported on the variability in the winter habitat used by moose in North America. He reviewed 41 different reports; 13 from the intermountain west, 6 from Alaska, and 22 from Canada, Minnesota, and Maine. His review highlighted the variation and commonality in the diet and successional stage used by moose. In addition, he identified 5 different types of winter habitat used specifically by the Shiras moose in the intermountain west, an area that includes the GYA:

1. Willow /conifer/ high gradient stream complex.
2. Floodplain or basin riparian community where willow is a dominant landscape feature.
3. Drainages where willow is sparse and of little importance to moose, conifer and aspen types are important and moose diets are more varied than in areas where willow is plentiful.
4. Arid juniper hills.
5. Intermediate sized willow stands associated with meandering streams. Moose are forced from these by snow conditions to adjacent forested slopes where subalpine fir stands support low-density moose populations in winter.

Studies in the GYA portion of the intermountain west report variability in moose habitat use consistent with Peek's (1974a) 5 categories. McDowell and Moy (1942) described moose habitat use in the Hellroaring/Slough Creek area north of YNP (Type 5) - a portion of the study area for this project. They noticed an early winter association of moose with the limited willow areas and then a move to adjacent conifer types, presumably in response to increasing snow depths. Harry (1957) and Houston (1968) documented winter use by moose of the extensive willow areas on the floodplains of Jackson Hole, Wyoming (Type 2). Stevens (1970) found Douglas fir (*Pseudotsuga menziesii*) and aspen communities to be the key winter range in the Gallatin Mountains (Type 3).

Although the Shiras moose is a relatively recent arrival to the GYA, available habitat is now thought to be occupied (Houston 1982, Kay 1997). However, future population trends are uncertain. Moose in the GYA are exposed to increasing levels of human activity and resulting habitat alterations. Riparian areas with deciduous vegetation are limited in size and distribution and are particularly vulnerable to human impacts. Moose have been exposed to landscape level perturbations in forest canopy (logging and the 1988 fires). Understanding the effect on moose of forest overstory removal through fire and other mechanisms is critical to addressing the management issues specified for this project. The wolf, a new and efficient predator, is also now present. The addition of wolves is a variable with unknown consequences. Some

have speculated that wolves will play a major role in regulating moose populations, and a decrease in moose numbers will result (Messier et al. 1995).

Project Organization

To explain the biogeography and ecology of the Yellowstone Shiras moose, I focused on the untested hypotheses of McDowell and Moy (1942), Loope and Gruell (1973), and Peek (1974a) that have been forwarded to account for range expansion of this subspecies in the GYA. Loope and Gruell (1973) proposed that moose populations in the GYA were low during the 19th century because fire maintained early successional vegetation and that population increases in this century occurred as forests matured under a management policy of fire suppression. This increased the abundance of subalpine fir, a shade tolerant tree common to mature coniferous forests and the main winter food item of moose in this area. McDowell and Moy (1942) and Peek (1974a) proposed that moose habitat along the northern border of YNP consisted of willow stands that are important to moose but spatially limited. Moose are forced from these by snow to adjacent forested slopes where subalpine fir stands support low-density moose populations in winter.

This dissertation is organized into 8 chapters in which I use multiple methods to describe moose abundance and ecology in the context of the 1988 Yellowstone fires. In Chapter 1, I repeated methods from earlier work to address long-term population changes in this century. I investigated the relationship of moose to mature forests using several population indices to track the response of moose numbers to the 1988 fires. I also determined the best conditions for observing moose to develop these indices. In Chapter 2, I used telemetry to evaluate the survival of radiocollared moose and changes in home range size after the 1988 fires. In Chapter 3, I identified additional aspects of moose habitat relationships, including diet, foraging patterns, and quality of browse. Seasonal and pre- and post-fire cover type use was determined in Chapter 4 by the locations of radiocollared moose, beds and pellet groups found while back-tracking moose, moose seen along roadways, and tracks on track-intercept transects. In Chapter 5, I addressed the effects of snow depth on moose habitat use. I also investigated (Chapter 6) the factors influencing the distribution of moose in coniferous forest. Because subalpine fir is important in explanations of moose ecology for both the GYA and NYWR, I addressed the role of this species in moose foraging strategies, especially as it relates to the successional stages of lodgepole forests. In Chapter 7, I addressed the impacts of clearcut logging on moose in lodgepole pine dominated landscapes. Specifically, I looked at the winter distribution of moose in relationship to recently disturbed forests, forest edges, and forest interiors. In Chapter 8, I described the relationship of moose to willow as a habitat determinant.

STUDY AREA

The study area was part of the GYA, a large, mountainous region of southwest Montana and northwest Wyoming (Figure 1). Bozeman, MT, bounds the GYA on the north, Jackson, WY, on the south, Cody, WY, on the east, and Ennis, MT, on the west. It includes YNP and Grand Teton National Parks and all or part of 6 National Forests.

Moose are found throughout the GYA, but concentrations correspond with locations of larger willow stands in Jackson Hole, WY (Houston 1968), the Thoroughfare Region of YNP (J. Mack, YNP, personal communication), Hebgen Lake, MT, Gallatin Canyon, MT (K. Alt, MFWP, personal communication), and the NYWR. There are no barriers to movement between moose populations. Moose in Yellowstone and Grand Teton National Parks are not subjected to hunting, while those outside the Parks are.

The study area included the NYWR, which involves parts of YNP and the southern 1/3 of the Gardiner Ranger District, GNF, and mixed private and state lands. When snow accumulates in the higher elevations, larger mammals migrate to the milder climate, lower elevations, and open grasslands of this range. The boundary of the NYWR is defined based on winter distribution of elk (*Cervus canadensis*) (Houston 1982). At the time of this study, elk were the dominant ungulate species (10,000 to 25,000), but mule deer (*Odocoileus hemionus*) (2,000 to 3,000), bighorn sheep (*Ovis canadensis*) (100 to 200), bison (*Bison bison*) (500 to 1,000), and pronghorn (*Antilocapra americana*) (100 to 300) also occupied the NYWR. The winter range of moose is not restricted to the NYWR, but it still serves to define the general focus of the study. Moose wintered throughout the study area in scattered areas of suitable habitat, most of which were at elevations above elk winter range.

There were five moose hunting districts in the Montana portion of the study area: Cooke City (HD 322), Slough Creek (HD 318), Buffalo Fork (HD 317), Hellroaring (HD 316), and Bear Creek (HD 328). When the project began in 1986, the combined quota was 55 of either sex. By 1996, this was reduced to a combined total of 15 antlered bulls, a 66% reduction.

I divided the study area into four study units based on hydrologic divides, political boundaries, or changes in habitat: Soda Butte (SB), Slough Creek (SC), Bear Creek (BC), and Yellowstone Park (YP) (Figure 1). Resource extraction had been an issue in 2 - BC and SB, but SC and YP were managed as wilderness. Travel regulations for the first 2 allowed for extensive motorized access, while the others, with the exception of a year-round road in the YP study unit, were accessed by primitive means.

The SC and SB study units had large, centrally located willow stands, however, willows were widely scattered in the other two study units. SB had few wintering ungulates other than moose, but a portion of the largest migratory elk herd in the world wintered in YP. The others had intermediate numbers of wintering ungulates.

The 1988 fires had a widely different effect on the study units. BC was not affected, but most moose winter range in SC burned, removing the forest canopy over a large area. About half of SB was affected. The burn pattern in YP was complex with mosaics of burned and unburned forests and burns of different intensity, as well as large expanses of completely burned and unburned forests.

Soda Butte Study Unit

SB involved portions of the GNF and YNP and was the high, eastern extent of the NYWR. It included the Cooke City basin as defined by Soda Butte Creek, Fisher Creek, Miller Creek, Sheep Creek, Woody Creek, and Republic Creek. I used Cooke Pass to represent the northeast edge of the study unit and Round Prairie, YNP, the southwest edge. Elevation ranged from 2,100 to 3,300 meters.

Most of the SB study unit was timbered with Engelmann spruce (*Picea engelmannii*), subalpine fir, and lodgepole pine. Extensive willow stands were located on the GNF between YNP and Cooke City. They also occurred at higher elevation along Soda Butte and Fisher Creeks. Forested mountainsides rose sharply from the valley floor. As with all study units, whitebark pine (*Pinus albicaulis*) was found at higher elevations. The open grasslands dominating the NYWR did not occur in this study unit.

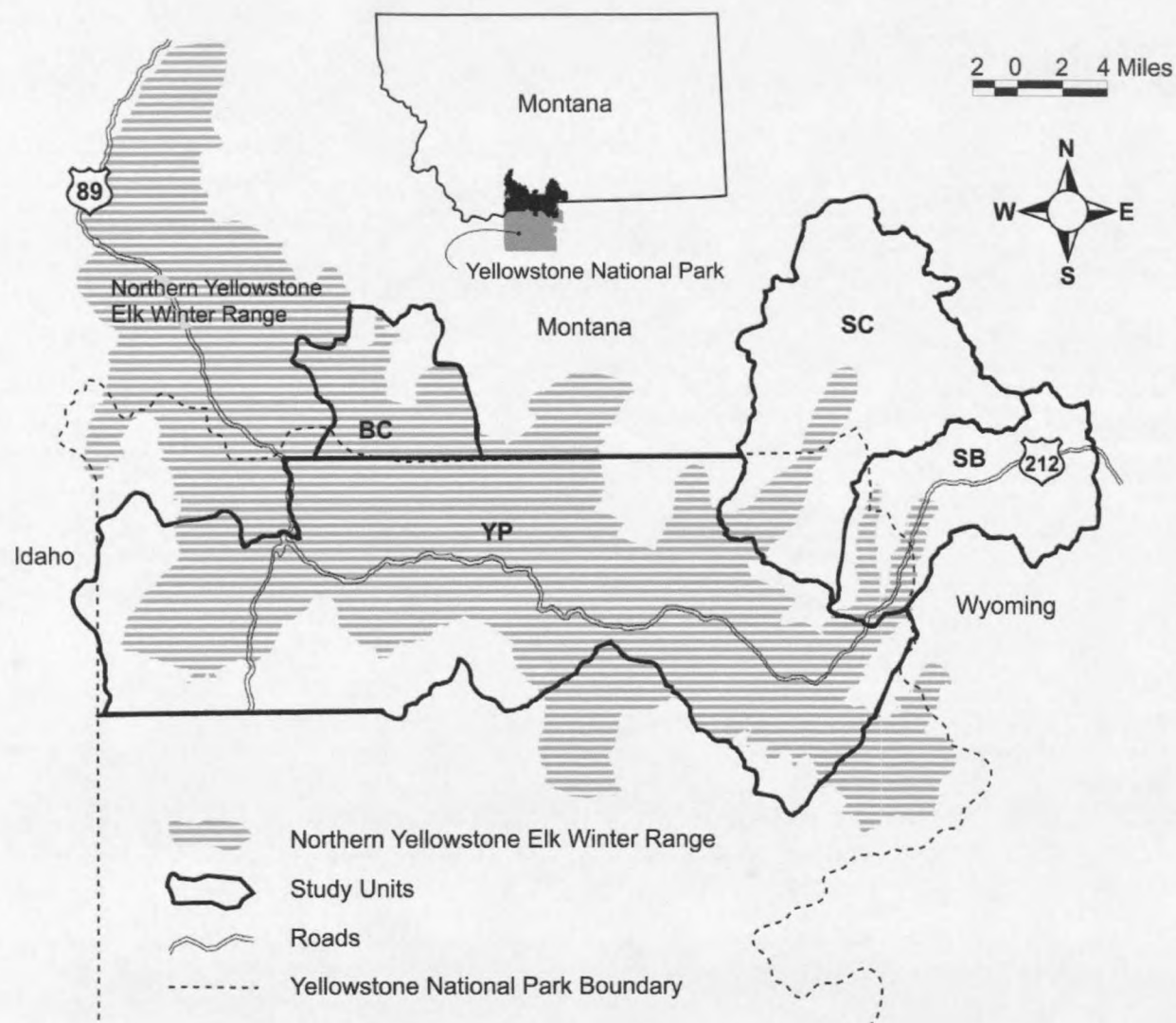


Figure 1. Study area, study units, and the Northern Yellowstone Winter Range boundary.

The SB study unit was moose summer and winter range and had 1 of the larger populations in this part of the GYA. Hunting quotas were 15 moose (10 antlered and 5 antlerless) in 1986 when the project began. This was reduced in 1996 to 5 antlered bulls.

A year-round road continued from YNP to the GNF where it linked the small communities of Silver Gate, Cooke City, and Cooke Pass. The non-wilderness portion was a patchwork of private and public land, while the non-wilderness public land (GNF) was managed for resource extraction with constraints. The YNP portion was managed to protect native animals and natural processes, i.e. no extractive activities or hunting.

The Cooke City Basin had been mined extensively since the late 1800's, but during recent decades mining activity had been limited to exploration or curtailed. Comprehensive mine reclamation was in progress in 2001. Timber harvesting was proposed but not accomplished before the 1988 fires. The northern half of the Basin burned in 1988; the southern half did not. Timber was removed to salvage burned trees during 1989 to 1995. Off-road vehicle and snowmobile enthusiasts used the non-wilderness portion outside of YNP, and an extensive network of roads provided access to old and new areas of mining activity.

Other ungulates included a few elk that began the winter in the Basin. Mountain goats (*Oreamnos americanus*) and bighorn sheep occupied open ridges year-round.

Slough Creek Study Unit

This unit included the upper drainage basin of Slough Creek from the Boulder Divide to Plateau Creek. Elevation ranged from 1,860 to 3,000 meters.

Most of the drainage was a wide, grassy valley with forested slopes rising sharply from the valley bottom. Frenchy's Meadow, about 5 km north of the YNP boundary, was a mosaic of grasslands, sloughs, alluvial out-wash, and willow stands. Above Frenchy's Meadow the drainage was less linear and more dendritic. Several large streams joined Slough Creek at Frenchy's Meadow. These tributaries and the upper reaches of Slough Creek were heavily forested with spruce-fir or lodgepole pine before the 1988 fires.

The hunting quota in Slough Creek in 1986 was 10 (5 antlered bulls and 5 antlerless), which was reduced in 1996 to 3 antlered bulls. Frenchy's Meadow and upper Slough Creek had historically been known as important moose range.

The GNF portion was in primitive area status before its inclusion in the Absoraka-Beartooth Wilderness in 1978. It had not been logged, but cattle grazing and irrigation associated with a homestead established around 1900 altered Frenchy's Meadow. The YNP portion was managed to perpetuate native animals and natural processes. Private land was limited to a guest ranch of <300 ha.

Elk were found in early winter as far north as Frenchy's Meadows but were seldom north of the GNF-YNP boundary by mid-winter. The broad valley of lower Slough Creek supported large elk herds through much of the winter. The SC study unit burned extensively in 1988. Moose winter range in some upper tributaries burned completely, while forests south of the GNF-YNP boundary burned in a mosaic pattern.

Bear Creek Study Unit

The BC study unit was entirely on the GNF. Bear Creek flows into the Yellowstone River near Gardiner, MT. This study unit was limited to the heavily forested upper end of the drainage between the elevations of 2,040 to 3,300 meters.

This unit was almost entirely forested until harvesting of lodgepole pine, Douglas fir (*Pseudotsuga menziesii*) and spruce began in the 1950's. Forests at the time of the study were a mixture of these species and non-marketable subalpine fir and whitebark pine. Douglas fir forests were the lowest in elevation, while whitebark pine forests were the highest. There were small, scattered stands of aspen and willow.

Bear Creek was summer and winter moose habitat. I did not find any records of previous attempts to survey this population. The hunting quota was 2 antlered bulls in 1986 when the project began and is the same today. Forest Service management designations allowed timber harvesting and encouraged dispersed recreation.

Surrounded by private land, the small community of Jardine was the center of an historical mining district. Hard rock mining began in the late 1800's and waned in the middle of the 20th century. Mineral Hill Mine was initiated about 1981 and remained active until 1996. As the Mineral Hill deposit was failing, a satellite mine was proposed for nearby Crevice Mountain where, until recently, mining activity associated with this claim was sporadic but chronic. The Crevice project was unsuccessful, and in 2001 mine reclamation was in progress across the entire mining district.

Clearcutting over the past 50 years was extensive in the middle third of the drainage, as was road building to accommodate timber removal. House log, post and pole, and firewood sales had also taken place, and a 2-million board-foot harvest was planned for 2002. The upper third of the drainage became

part of the Absaroka-Beartooth Wilderness in 1978 and was thereafter not a part of the GNF available timber base.

Sagebrush-grasslands dominated the lower reaches. This was not moose habitat but was part of the migration corridor and winter range of several other ungulate species. In the Gardiner Basin, including Bear Creek, there were 5,000 to 10,000 wintering elk, 2,000 mule deer, and 100 or more bighorn sheep, and 100-200 pronghorns. Ungulate herds encroached into the forested higher reaches where moose were found. The 1988 fires did not affect the Bear Creek drainage.

Yellowstone Park Study Unit

This study unit was entirely in YNP and was not defined by a hydrologic divide. It was delineated to roughly encompass the portion of the NYWR in YNP, but it also included higher adjacent elevations with moose habitat. The primary drainages were the Yellowstone, Lamar, and Gardner Rivers.

This unit was dominated by large valleys, basins, and rolling foothills of grasslands and sagebrush-grasslands. Forests included limber pine (*Pinus flexilis*), lodgepole pine, Douglas fir, spruce-fir, and whitebark pine types. The 1988 burn created a complex mosaic of burned and unburned forests and various levels of fire intensity. Willow stands, which included areas along Indian Creek, Blacktail Creek, and Glen Creek, were widely dispersed and uncommon but significant to wildlife.

Hunting did not occur in this unit. Moose population descriptions were limited to records of moose seen incidental to elk survey flights conducted between 1968 and 1978 (Barmore 1980, Houston 1982).

Management protected native animals and processes, i.e. resource extraction did not occur. A paved highway bisected the unit in an east-west orientation and another ran north-south along the west edge.

During winter, large herds of migratory ungulates occupied the unit. Elk were the most plentiful species, numbering from 10,000 to 25,000.

MOOSE POPULATION DESCRIPTION AND MONITORING
ON THE NORTHERN YELLOWSTONE WINTER RANGE

Introduction

Management of the NYWR has been a concern since the early 1900's and vegetation condition in the context of ungulate populations has been variously interpreted (Tyers 1981, Houston 1982, Despain et al. 1986, Kay 1990). This intense discussion has highlighted the need for accurate assessments of ungulate population dynamics and regulating factors to elucidate management options (Gasaway et al. 1986).

Van Ballenberghe and Ballard (1997) summarized population analysis as the numerical attributes of populations (numbers, sex and age ratios, and rates of increase) together with characteristics of the animals (age, sex, and life span) and properties of the environment (forage supplies, weather, and predator numbers) that determine these values. However, studying ungulate population dynamics is complex because it is difficult to determine population size and the interacting variables that produce population change (McCullough 1984, Saether 1987). A population at any given time and place reflects the composite effect of all limiting and regulating influences; rarely is it possible to measure the effect of any single factor or to rank its importance relative to other factors (Van Ballenberghe and Ballard 1997). Population analysis is further confounded for moose; they are the least social North American deer, often solitary, and frequently occupy habitats with poor observability (Schladweiler 1973, Houston 1974).

Moose population size is typically assessed in 3 ways- total area counts, sample estimates, and indices (Timmermann and Buss 1997). Timmermann and Buss (1997) advocated multiple information sources to assess population status. Because interpretation of population assessment information is possible only when trend-through time data are available, single surveys are rarely sufficient (Timmermann and Buss 1997). Caughley (1977) thought that the majority of animal population questions could be tackled with the help of indices of density; absolute estimates of density being unnecessary luxuries. Timmermann and Buss (1997) recommended strategic and carefully evaluated methods to assess a moose population because of the significant investment of time, energy, and expense that usually accompanies the effort. To guide managers in their attempts to evaluate methods for assessing the NYWR moose population, I combined aerial surveys with indices developed by observing moose in favorable habitats and along roads and backcountry trails.

I used multiple methods to investigate changes in moose numbers in response to major vegetation changes and to determine the efficacy of techniques for developing moose population monitoring indices. Some hypotheses were tested by more than 1 method. Null hypotheses included: 1) moose numbers have not changed on the NYWR historically, 2) optimum times to search for moose do not vary temporally (time of year and time of day), and 3) moose numbers are not affected by landscape level changes in amount and distribution of mature coniferous forests.

Methods

Historical Documents

I searched agency files and archives for statements on moose populations specific to the study area. I was especially interested in documents not considered by other authors that provided an historical context for population monitoring.

Horseback Transect Index

In 1947, 1948, and 1949 Montana Fish and Game Biologist Joe Gaab looked for moose each September in the Absaroka Primitive Area (now the Absaroka-Beartooth Wilderness) on about 177 km of trail. From 1985 to 2001 I repeated his route through Hellroaring, Buffalo Fork, and Slough Creek 34 times between July and late October to develop a moose population index.

Gaab rode primarily to look for moose. My crews conducted other tasks along the way, including trail maintenance, hunter compliance checks, and outfitter camp inspections. Party size varied during each day of searching, as did the number of days traveling the route. Party size ranged from 1 to 6. The days spent covering the transect ranged from 5 to 32. The trails were not traveled in any particular sequence. Searching for moose was restricted to daylight hours but was not otherwise standardized.

Gaab and I recorded the sex of the moose and distinguished between calves and adults. Sightings were reported as number of moose seen per day of searching.

Road Transect Index

The road from Gardiner to Cooke City is the only road in YNP maintained for wheeled vehicles year-round. It bisects the NYWR and covers 89 km. I used it as a transect for an index of moose distribution and abundance. I tested the hypotheses that there was no difference in the number of moose seen

seasonally or before and after the 1988 fires along the road. Data were collected between January 1987-December 1992 and January 1995-December 1997.

Each trip was considered 1 sample regardless of the direction of travel. No attempt was made to standardize time of day. I tried for a minimum sample of 4 transects per month, year-round. Occasionally, the trip was made to look for moose when additional samples were needed. Most of the time, the trip was made for other reasons. The road was divided into 5 sections based on similar vegetation and topography for analysis.

The first section, Gardiner to Mammoth (8.0 km), included the Gardner River canyon. Topography was broken and the surrounding vegetation was arid grasslands and dry sagebrush unaffected by the 1988 fires. Gardiner was the lowest point along the road (1,585 m).

The second section was from Mammoth to Tower Junction (29.1 km). Topography and vegetation were diverse. Vegetation included open grasslands and Douglas fir, but there were also mature spruce-fir forests, isolated stretches of stunted willow and aspen, and 1 small area of insect-killed Douglas fir. This section was heavily impacted in 1988 by the fires creating a mosaic burn pattern.

The third section extended from Tower Junction to Round Prairie (30.9 km). This stretch was mostly a broad open valley with expanses of grasslands and sagebrush along the Lamar River. Because most of this section was unforested, the 1988 fires did not cause much change in vegetative structure.

The fourth section was from Round Prairie to Warm Creek (13.2 km) through mature lodgepole pine. The 1988 fires did not reach this area.

The fifth section, Warm Creek to Cooke City (8.0 km), followed Soda Butte Creek through the largest willow stands along the transect. The rest of the vegetation was mature lodgepole pine and spruce-fir. The north side of the road burned in 1988. Cooke City was the highest point along the road (2,134 m).

I used a 0/1 measurement scale to analyze the probability of observing ≥ 1 moose. I treated each trip as an independent trial resulting in a set of 1,020 observations. Typically, each day resulted in 2 observations, although there were exceptions. I did not differentiate between east and west trips. I defined season as 6 2-month intervals with 1=November/December, 2=January/February sequentially to 6=September/October. Data were also analyzed by year with year 1=1987, year 2=1988 sequentially to year 6=1992. No data were collected during years 7 and 8 (1993 and 1994), years 9, 10, and 11 indicated 1995, 1996, 1997, respectively. The probability of sighting a moose was determined by season, all years combined, and by year.

To consolidate the analysis I built a logistic regression model in which the dependent variable is the 0/1 variable indicating whether or not at least 1 moose was sighted. Two independent variables, pre- versus

post-fire and season, were used to account for changes in probability of sighting a moose across time. The probability of at least 1 moose sighting on a trip was computed empirically to determine if the model adequately fit the data. To test if the pre- and post-fire differences were statistically significant and to control for location effects, individual sections were compared over time using a Z test ($P < 0.05$).

Willow Stand Over-flight Index

Based on Barmore's (1980) observations of moose distribution from 1968-1970 during NYWR aerial elk counts, I searched willow stands by fixed-wing aircraft to develop an index of seasonal moose abundance. I flew 2 of the largest willow stands in the study area twice a month year-round (1987-1990) to determine whether moose demonstrated a predictable temporal affinity for these locations. One willow survey area, Frenchy's Meadow, was in SC about 5 km north of YNP. The second was in SB between Silver Gate and Cooke City, MT. Three radiocollared moose in SC and 4 in SB (see Chapter 2) were available for use as a check on survey efficiency. All moose visible in the willow stands were counted and then radiocollared animals were located. Flights were done between first light and about 0900 hours.

For comparison, I considered 3 populations: 1) all moose- uncollared and radiocollared, 2) only radiocollared moose, and 3) the percent of radiocollared moose seen. Because the number of radiocollared moose varied over time as animals died, the third population estimate was based on the opportunity for observing a radiocollared moose. Observations were expressed as a percent of the instrumented population present in the 2 study units. I tested the hypothesis that there is no difference in the average number of moose seen per flight per year and per month over 4 years (1987-1990).

Daily Willow Stand Observations

I used ground observations to more precisely determine the time of year and time of day that moose were most easily observed in willow stands. From April 1996 through June 1997, daily observations were made of the main part of the willow stand between Silver Gate and Cooke City, SB. The number of moose present was recorded most days and every 1/2 hour from first light until dark. The time of day followed normal conventions for mountain standard and daylight savings time. To account for the disparity in number of daylight hours through the year and occasional gaps in data collection, data were standardized as number of moose seen per number of observation attempts. I tested the hypothesis that there was no difference in the average number of moose seen each month, week, and 1/2 hour period.

Census Flights

In addition to indices, I tried to determine moose numbers using aerial surveys. In an effort to increase the efficiency, preliminary data from the willow flight and road transect indices were examined. From these, I determined moose were most observable around December 1 and May 1. Survey flights were scheduled to coincide with these times.

Flights were organized using the methods of Gasaway et al. (1986). A combination of parallel transects approximately 0.4 km apart were established over flatter terrain in combination with curved routes to accommodate topographic contours. The study area was divided roughly in half along the Yellowstone River. Two fixed-wing aircraft were used for each flight with 1 covering the north half and 1 the south. Aircraft were flown about 97 to 113 kph at 61 to 152 m above the ground, depending on obstacles.

Eight survey flights were conducted between December 1988 and May 1992. During the first 2, an effort was made to follow transects. Success at adhering to methods varied among observers and each attempt. Deviations were made because of localized weather conditions, terrain features, and frustration by observers along unproductive sections. Some areas that seemed to have poor moose habitat or where dense forests limited visibility were searched with less intensity. Transects were not adhered to during the remaining 6 flights. Instead, they were searches by informed observers of the most reasonable locations to find moose. These corresponded to the major willow stands at Gardner's Hole, Blacktail Plateau, Hellroaring drainage, Buffalo Fork, Slough Creek, and Soda Butte Creek. Roughly the same area was searched each time.

Statistical Tests

Data collected during willow stand over-flights and daily willow stand counts were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met, ANOVA was used to test for differences among 3 or more independent, unmatched treatments ($P < 0.05$). To test assumptions, data were first examined for outliers. Levene's test addressed homogeneity and Shapiro-Wilks' W test assessed normality ($P < 0.05$). Questionable data were examined with histograms and scatterplots of means versus standard deviations. Data that did not meet the assumptions of ANOVA were tested using Kruskal-Wallis ANOVA by ranks, a test for multiple treatments involving nonparametric data. Because the F statistic is considered robust, the central limit theorem was evoked and ANOVA was used if data approximated a normal distribution and sample size was large ($n > 100$). The *post hoc* test, Newman-Keuls, was used to look for differences

among treatments when ANOVA demonstrated significance. Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance is being reported in the text, P values only appear in appendices. I used Spearman's rank correlation test to quantify the association among population index data.

Results

Historical Documents

McDowell and Moy (1942) reported that "old timers" regarded moose as a rarity in the Hellroaring to Slough Creek area north of YNP between 1907 and 1915. Rush (1942) considered moose fairly common by 1913 across the same area. He saw 6 moose at one time in Hellroaring and recalled seeing lone moose about 20 times. Stevenson (1920), U.S. Forest Service, believed there were 12 moose wintering in Hellroaring and 1 in Buffalo Fork in 1920. He stated that suitable habitat was available for more wintering moose than were present.

The Forest Service made more extensive winter patrols to deter poaching and monitor wildlife in Hellroaring, Buffalo Fork, and Slough Creek from 1921 to 1925. This occurred from December through April with rangers crisscrossing the backcountry on snowshoes looking for wildlife. Specifically, they sought out moose to determine population size. The survey area was not always consistent year to year. Efforts to find moose were facilitated by snow; moose movements and distribution were restricted by winter conditions and tracks helped locate animals. When animal tracks were encountered, they were often followed to verify species, number, and identify individuals. Crane (1922) counted 16 moose during the winter of 1921-1922. Uhlhorn (1923) estimated 25 moose for the winter of 1922-1923. I could not find records for 1923-1924. Johnson's (1925) report for 1924-1925 stated he could account for 65 moose. He thought they had accomplished a good count and added that the moose population was on the increase. He noted "an especially good calf crop".

Forest Service reports (USDA 1936, McDowell and Moy 1942) from the mid- to late 1930's expressed concern over the long-term status of willow stands and the moose population that used them. Willow stands were considered to be showing signs of deterioration attributed to drought and over-browsing. Willow was described as progressively in worse shape with decreasing elevation and increased accessibility to elk and moose. Moose population estimates from surveys conducted between November 1935 and

March 1936 were 54 in Hellroaring, 80 in Buffalo Fork and 60 in Slough Creek. Over-winter utilization of willow was approximated at 90%, and 75% of willow in moose winter range was described as recently dead. Moose were reportedly browsing on Douglas fir, lodgepole pine, alder (*Alnus* spp), willow, aspen, "balsam" fir, and spruce.

McDowell and Moy (1942), Montana Wildlife Restoration Division, conducted a summer survey of moose in the Hellroaring to Slough Creek area north of YNP in 1942. From June through October they looked for moose, covering 341 miles (549 km) on foot, and 1,341 miles (2,158 km) on horseback. Detailed descriptions of each moose seen were made, including location, sex, age, antler characteristics, coloration, and any other distinguishing features. Based on these records, they state that their count of 194 moose did not include duplications. Any sightings that were questionable were removed from the data. They suggested that moose had expanded their range into the area from YNP and numbers were increasing. In addition, they called for a controlled harvest to prevent further damage to willow, which was described as extensive with more than 50% of plants severely damaged in some areas, although high elevation willow stands above ungulate winter range showed no browsing effects or senescence.

The 1945 Montana State Legislature passed Substitute Bill No. 41 which authorized the State Fish and Game Commission to "remove and dispose of moose increasing in numbers and damaging property by the limited license method". Harvesting only bull moose was recommended (Montana Fish and Game 1945). Quotas and harvest numbers for the first seasons vary among department documents, in part, because of an inconclusive hunter success reporting system. I used reports with later dates (McDowell 1946, Couey 1947). During the first season (1945), hunters filled 35 of 40 permits across a hunting area that included Hellroaring, Buffalo Fork, Slough Creek, and Cooke City (McDowell 1946). In 1946, 20 of 30 permits were filled and, at the request of local hunters and guides concerned about declining moose numbers, the 1947 quotas were further reduced (Couey 1947).

In September 1943, Robert Cooney, Montana Wildlife Restoration Division, spent 9 days riding Buffalo Fork, Hellroaring, and Slough Creek to record moose sightings, with the primary goal of continuing an index of moose in upper Buffalo Meadows initiated the previous year (McDowell and Moy 1942). He counted 31 moose along the upper meadow, an increase of 9 from 1942. He also found 8 individual moose in Hellroaring Meadows and 7 in Frenchy's Meadow, Slough Creek (Cooney et al. 1943). The survey was not done in 1944. McDowell returned in 1945 to monitor the new hunting season, but he was not successful at repeating the upper Buffalo Meadows survey (McDowell and Smart 1945b). However, a Forest Service employee reported 18 moose on the survey route. McDowell estimated that 30% of the moose migrated out of Hellroaring to the Slough Creek area between 1942 and 1945 due to a

decrease in available forage (willow). He reported impressive willow growth in exclosures established in 1942 and a 25% reduction from over-browsing in nearby unprotected willow.

In 1942, 1944, and 1945, Montana Wildlife Restoration Division employees conducted December or January moose surveys in Slough Creek (Parsell and McDowell 1942, McDowell and Page 1944, McDowell and Smart 1945a). They reported hundreds of elk south of the YNP boundary and small groups throughout the upper drainage in moose winter range. They found about 10 to 15 moose utilizing willow stands in and around Frenchy's meadow and expressed surprise at the large numbers also occupying the adjacent heavily forested mountainsides. On the 1945 survey, the Silver Tip Ranch caretaker reported counting 34 moose in Frenchy's meadow earlier in the year. On all trips, they found moose and elk browsing willow with availability of willow stands strongly influenced by snow conditions. An estimated 90% of current willow growth had been utilized in December 1942, browsing that Parsell and McDowell (1942) attributed to both elk and moose. They also reported moose foraging occasionally on alder, Engelmann spruce, and the tips of lodgepole pine. Use of (sub)alpine fir was described as potentially extensive. They repeated what all winter survey reports to date had indicated- moose "yarding" behavior was not observed. They expressed frustration at their inability to accurately assess moose numbers in the drainage and recommended a definitive survey.

For many years Tony Bliss was co-owner of the Silver Tip Ranch, a small private inholding in Slough Creek a few miles from the large willow stand in Frenchy's Meadow. He summarized his observations of moose population trends (Kehrberg 1964): "1926 to 1935 - lots of tall willow and few moose, elk and moose fed hay by Yellowstone Park in lower Slough Creek; 1935 to 1945 - more moose, still lots of willow, feeding ended about 1936; 1941 to 1945 - away at war; 1955 to 1962 - fewer and fewer moose and extensive loss of tall willow".

In 1947, 1948, and 1949 Montana Biologist Joe Gaab conducted horseback surveys for moose and established an index of moose abundance (Gaab 1948, 1949, 1950). He traveled about 110 miles (177 km) of trail during September to count moose, using the same trails each year. He recorded 106, 71, and 30 independent moose sightings, respectively. In his opinion, the moose population was in a decline, which he attributed, in part, to a continued deterioration of willow stands (Gaab 1948, 1949, 1950). When I interviewed him in 2000, he stated that, during the first years of quota hunting, hunters shot "many more" moose than permits allowed, although 50 years later he could recall anecdotes but not actual numbers, nor could he find his field notes (J. Gaab, retired MFWP, personal communication)

A 1964 wildlife management plan for the Gardiner Ranger District, GNF, was the first such document I could find for this jurisdiction (Kehrberg 1964). In the Hellroaring - Slough Creek area, 1 management

priority was to address the "moose problem", i.e. declining populations and deteriorating willow communities. A parenthetical addition stated "...and what happened to all the beaver?" In 1964, Jim Peek submitted a proposal to the Montana Wildlife Restoration Division to study moose population dynamics and habitat for the Hellroaring to Slough Creek area, but it was not initiated (Peek 1964).

I did not find records of hunting quotas from 1948 to 1962, but in 1963 they were as follows:

Hellroaring - 10 either sex; Buffalo Fork - 10 either sex; Slough Creek - 10 either sex; Cooke City - 15 either sex (total of 45). When the project began in 1986, the combined quota was 55 of either sex (including Bear Creek). Changes were made subsequent to the 1988 fires and quotas in 1990 were as follows: Hellroaring - 5 antlered, 5 antlerless; Buffalo Fork - 3 antlered, 4 antlerless; Slough Creek - 5 antlered, 5 antlerless; Cooke City - 10 antlered, 5 antlerless (total of 42) (T. Lemke, MFWP, personal communication). Substantive changes were made to hunting quotas in 1991 in response to population declines observed during this study: Hellroaring - 3 antlered, 2 antlerless; Buffalo Fork - 2 antlered, 2 antlerless; Slough Creek - 3 antlered, 2 antlerless; Cooke City - 5 antlered, 2 antlerless (total of 21). Numbers were further reduced in 1996: Hellroaring - 3 antlered; Buffalo Fork - 2 antlered; Slough Creek - 3 antlered; Cooke City - 5 antlered (total of 13) (T. Lemke, MFWP, personal communication). The quota in Bear Creek, an area unaffected by the 1988 fires, has remained at 2 antlered moose post-fire.

Horseback Transect Index

From 1985 to 2001 I repeated Gaab's (1948, 1949, 1950) 177 km transect in the Absaroka-Beartooth Wilderness 34 times to develop an index of moose abundance (Table 1, Figure 2). The number of moose observed and the number of moose seen per observer day declined between 1947 and 2001. The years 1988 and 1989 were exceptions. More moose were seen in these years than those immediately following and preceding. The number of moose seen on surveys varied as follows: 30-106 during the 1940's, 12-20 during the 1980's pre-fire, and 0-20 between 1990 and 2001. Forty-nine and 40 moose were seen in 1988 and 1989, respectively. The average number of moose seen per observer day varied from 2.63 during the 1940's, to 1.15 in the early 1980's, and 0.34 post-fire (Figure 2). In 1988 and 1989 an average of 3.42 moose were seen per observer day.

Road Transect Index

The probability of seeing at least one moose while traveling the Gardiner to Cooke City road ($n = 1,020$) was 26.2% during the 9 years data were collected. The probability varied among years. It was highest in 1989 ($n = 84$, 48.8%) and decreased in subsequent years (Figure 3).

Table 1. Moose Horseback Index 1947-1949, 1985-1992, and 1995-2001; dates of searches, number of moose observed, and age and sex of moose seen.

Year	Dates	Observed	Bulls	Cows	Calves	Unknown
1947	9/5-10/3	106	30	38	4	27
1948	9/4-9/29	71	16	29	8	18
1949	9/8-9/27	30	7	17	0	6
1985	9/11-9/20	12	4	5	3	
1986	9/11-9/17	13	2	9	2	
1987	9/12-9/19	20	10	7	3	
1988	9/19-10/5	49	15	32	12	
1989	9/4-10/1	40	12	25	3	
1990	9/8-10,13-20	12	2	6	4	
1991	9/8-9/18	18	8	8	2	
1992A	9/2-9/14	11	3	5	3	
1992B	9/14-9/22	20	4	9	7	
1995A	8/22-9/4	0	0	0	0	
1995B	9/10-9/20	0	0	0	0	
1995C	10/3-10/24	5	2	3	0	
1996A	9/3-9/7	5	0	4	1	
1996B	9/13-9/18	0	0	0	0	
1996C	9/24-10/2	0	0	0	0	
1997A	7/24-8/25	6	0	6	0	
1997B	9/5-9/11	2	0	2	0	
1997C	9/12-9/17	6	3	3	0	
1997D	9/17-10/7	7	3	4	0	
1998A	8/17-9/9	7	0	5	2	
1998B	9/13-9/22	10	2	6	2	
1998C	9/28-10/7	4	1	3	0	
1998D	10/15-10/24	1	1	0	0	
1999A	8/2-9/8	1	1	0	0	
1999B	9/13-11/11	6	5	1	0	
2000A	7/10-7/28	0	0	0	0	
2000B	8/7-8/30	0	0	0	0	
2000C	9/11-9/29	0	0	0	0	
2000D	10/9-10/20	5	1	3	1	
2001A	7/16-8/10	1	0	1	0	
2001B	8/13-8/24	0	0	0	0	
2001C	8/27-9/7	2	0	1	1	
2001D	9/9-9/21	8	6	1	1	
2001E	9/24-10/19	2	1	1	0	

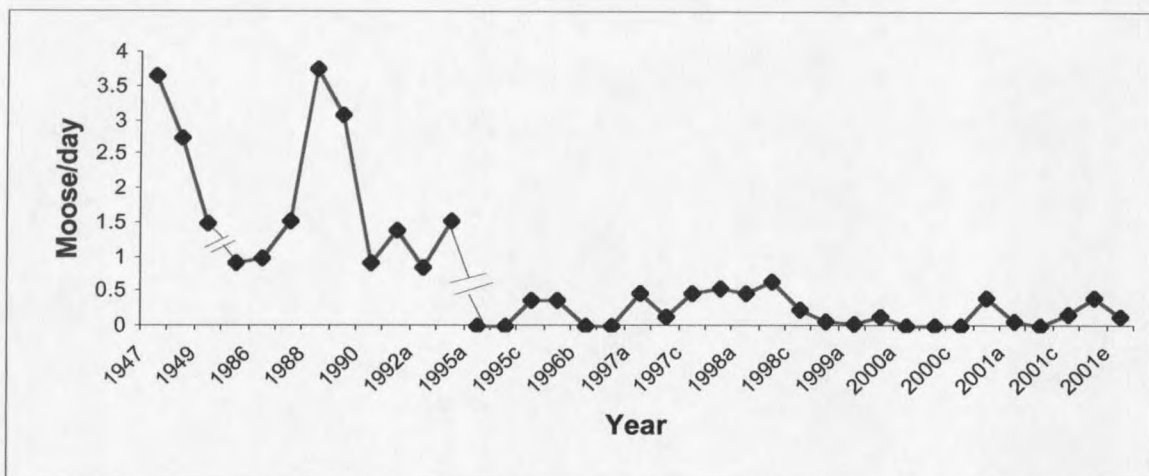


Figure 2. Moose Horseback Index 1947-1949, 1985-1992, and 1995-2001; moose seen per day of searching.

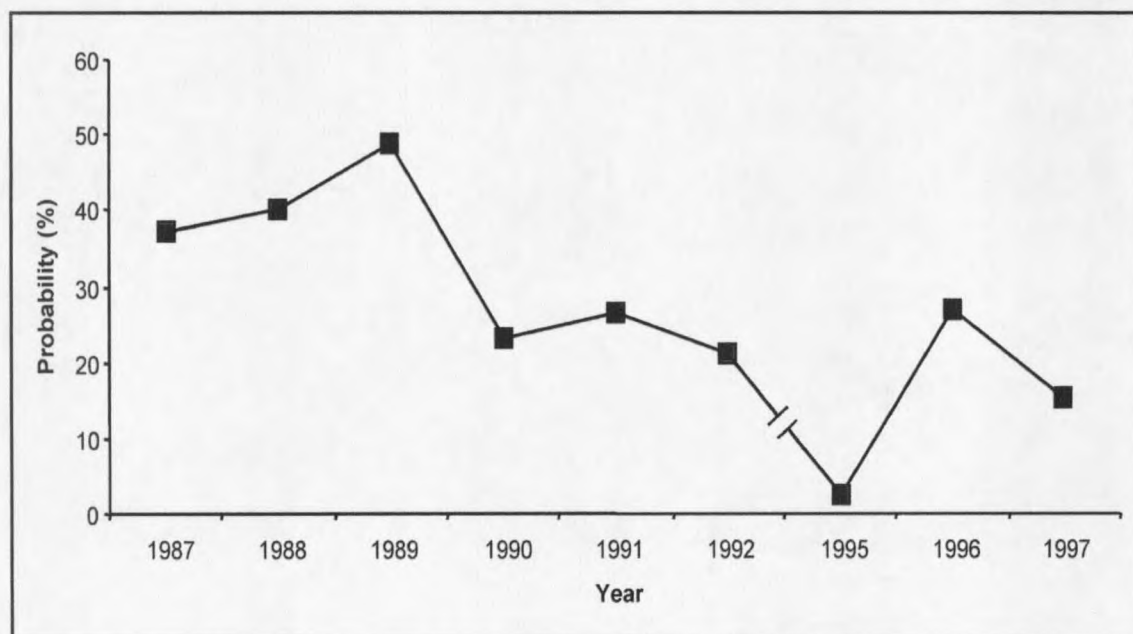


Figure 3. Probability of seeing at least 1 moose while traveling the road from Gardiner, MT to Cooke City, MT (89 km) for each of the years 1987-1992 and 1995-1997.

The probability of seeing at least one moose per trip also varied seasonally with the maximum sightings during May/June ($n = 220$, 50.45%) and November/December ($n = 99$, 40.4%) (Figure 4). When I compared annual means of moose seen on road transects with mean moose per day on horseback surveys, the correlation was positive ($r_s = 0.76$, $P = 0.017$, $n = 9$).



Figure 4. Probability of seeing at least one moose while traveling the road from Gardiner, MT to Cooke City, MT (89 km) by 2 month period for the years 1987-1992 and 1995-1997.

Sighting rates also varied by road section before ($n = 113$) and after ($n = 907$) the 1988 fires (Figure 5). No moose were seen in section 1 (Gardiner to Mammoth). In section 2 (Mammoth to Roosevelt Junction), the rate was 15% before the fires compared to 4% after the fires. In section 3 (Roosevelt Junction to Round

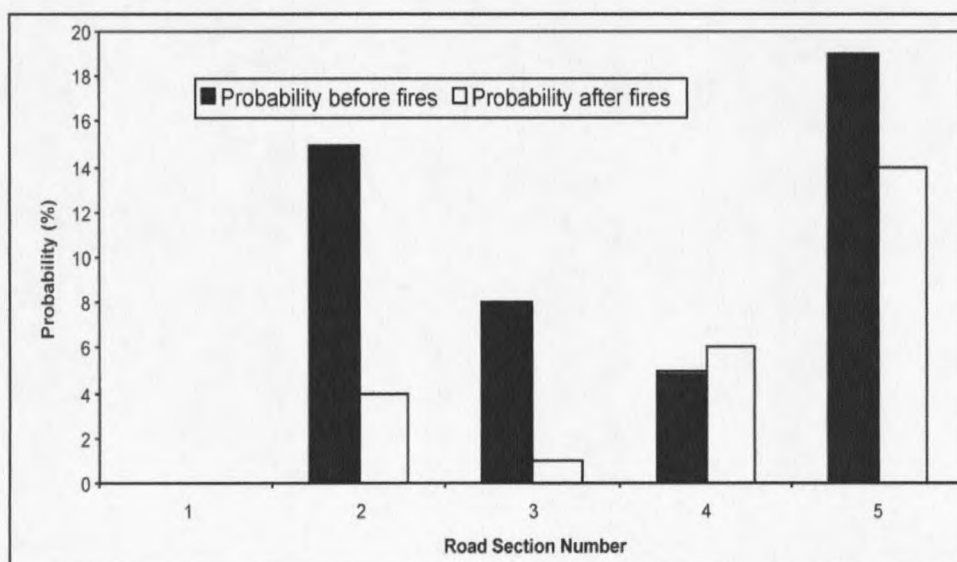


Figure 5. Probability of seeing at least 1 moose while traveling the 5 sections of road between Gardiner, MT, and Cooke City, MT, (177 km) before and after the 1988 fires for the years 1987-1992 and 1995-1997.

Prairie), the sighting rate was 8% pre-fire compared to 1% post-fire. In section 4 (Round Prairie to Warm Creek), the comparison was 5% versus 6% and section 5 (Warm Creek to Cooke City) was 19% versus 14%.

There was a statistically significant decline in moose sightings after the 1988 fires with a lag effect of about a year. The decline varied by road section, with sections 2 ($P = 0.044$) and 3 ($P = 0.004$) experiencing the most severe decreases. Section 4 did not experience a detectable decrease ($P = 0.954$) whereas section 5 had a statistically insignificant decrease ($P = 0.148$).

My analysis indicated that the pre-/post-fire difference did not vary by monthly period (Table 2). The relatively close agreement between the logistic regression model and empirical probabilities indicates the model adequately fits the data. Comparisons of individual sections over time indicated that moose using areas adjacent to roads declined in numbers rather than changing distribution.

Table 2. Probability of at least one moose sighting per trip along the road between Gardiner and Cooke City, Montana, in each 2-month period computed empirically and from a logistic regression model.

Monthly period	Model pre-fire	Model post-fire	Empirical pre-fire	Empirical post-fire
Nov/Dec	0.546	0.385	0.33	0.42
Jan/Feb	0.301	0.183	0.38	0.16
Mar/Apr	0.394	0.252	0.44	0.24
May/June	0.647	0.487	0.67	0.48
July/August	0.193	0.111	0.07	0.12
Sept/Oct	0.115	0.071	0.13	0.07

Willow Stand Over-flight Index

I completed 78 aerial searches of willow stands in SC and 73 in SB between June 1987 and December 1990. The average number of moose seen per flight did not vary significantly among the years 1987, 1988, 1989, and 1990 ($H = 1.95$, $P = 0.582$). The highest average number seen per flight was in 1988 (4.9), followed by 1989 (3.1). Results were the same for 1987 and 1990 (1.9). The difference in average number of moose seen per month over 4 years was significant ($H = 18.89$, $P = 0.026$) (Figure 6). The highest average number seen per flight was in November (9.3), followed by December (8.6), and May (7.6). The correlation between annual averages of moose seen aerially in willow stands and the mean number of moose observed per day in the same years on horseback surveys approached significance ($r_s = 0.95$, $P = 0.051$, $n = 4$).

The average number of radiocollared moose seen per flight did not vary significantly among years ($H = 5.81$, $P = 0.121$), and data were similar to the trend for all moose. The highest average number seen per flight was in 1988 (2.0), followed by 1989 (1.7), 1990 (0.8), and 1987 (0.0). Differences in the average

number of collared moose seen per month approximated significance ($H = 16.21$, $P = 0.06$). The highest average number per flight was seen in November (4.0), followed by December (3.7), and May (3.8) (Figure 6).

The percent of radiocollared moose available for observation (i.e. alive, in the drainage, and with operational radiocollar) seen per flight was not significantly different among years ($H = 5.26$, $P = 0.15$). Monthly means varied from 0 (1987) to 11.5% (1988). Although I was unable to detect significant differences in the percent of collared moose observed by month ($H = 13.41$, $P = 0.15$), the highest percent seen was in May (18.0%), followed by December (13.8%), and November (13.1%) (Figure 6).

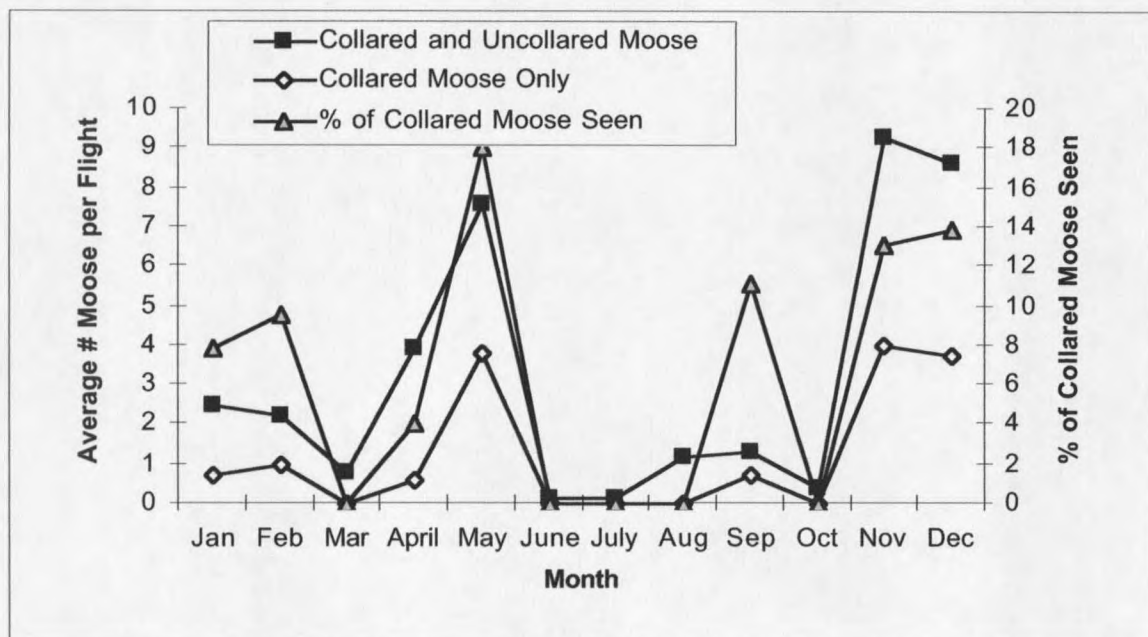


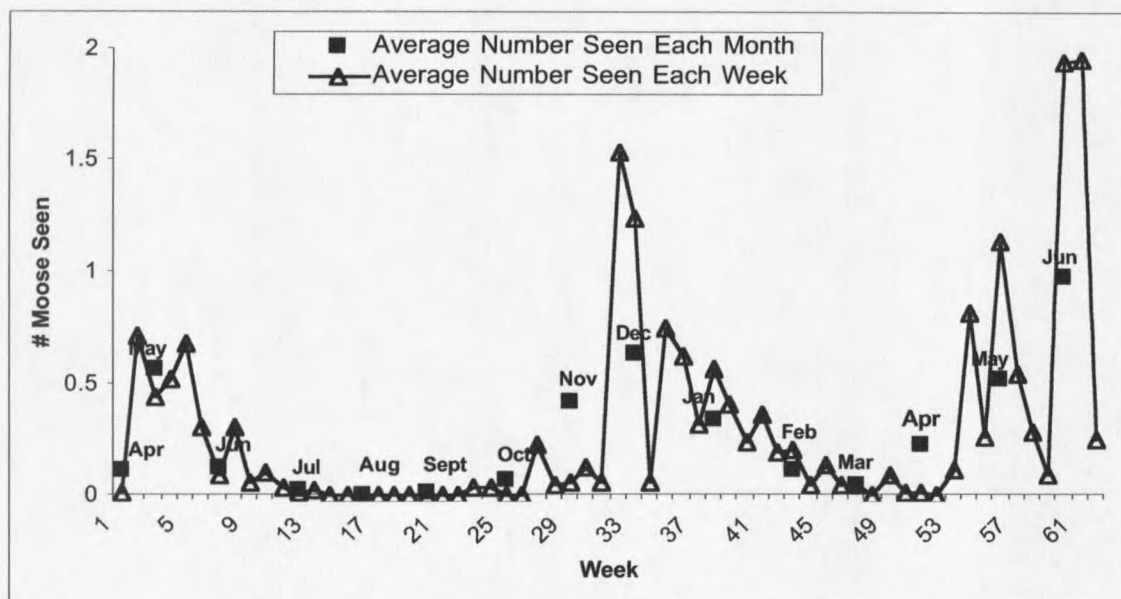
Figure 6. Observations of moose during flights over SB and SC willow stands 1987-1990. Monthly averages for number of moose per flight, average number of collared moose per flight, and % of collared moose seen.

Daily Willow Stand Observations

I used ground observations to validate results from willow stand over-flights and to establish the best time of day to observe moose. Daily records of moose were made for 15 months at a willow stand in the SB study unit. The mean number of moose seen in willow per 1/2 hour of daylight varied significantly among months ($F = 10.76$, $P < 0.001$). The highest average number seen per 1/2 hour was in June 1997 (0.9), followed by December 1996 (0.6), and May 1996 (0.6) (Figure 7).

Average number of moose seen per 1/2 hour also varied significantly by week for the 64 weeks that data were collected ($F = 10.44$, $P < 0.001$). Again, there were 2 peaks - early winter and late winter/early

spring. The late winter/early spring peak occurred later in 1997 than 1996 (Figure 7). Opportunities to see moose were greatest during early summer (June 1-7, 1997 -1.9, and also June 8-14, 1997 -1.9) and early winter (November 24-30, 1996 -1.5, and December 1-7, 1996- 1.2). *Post hoc* tests revealed that most of the difference among means came from the high numbers from the highest 4 averages (Appendix A, Table 50).



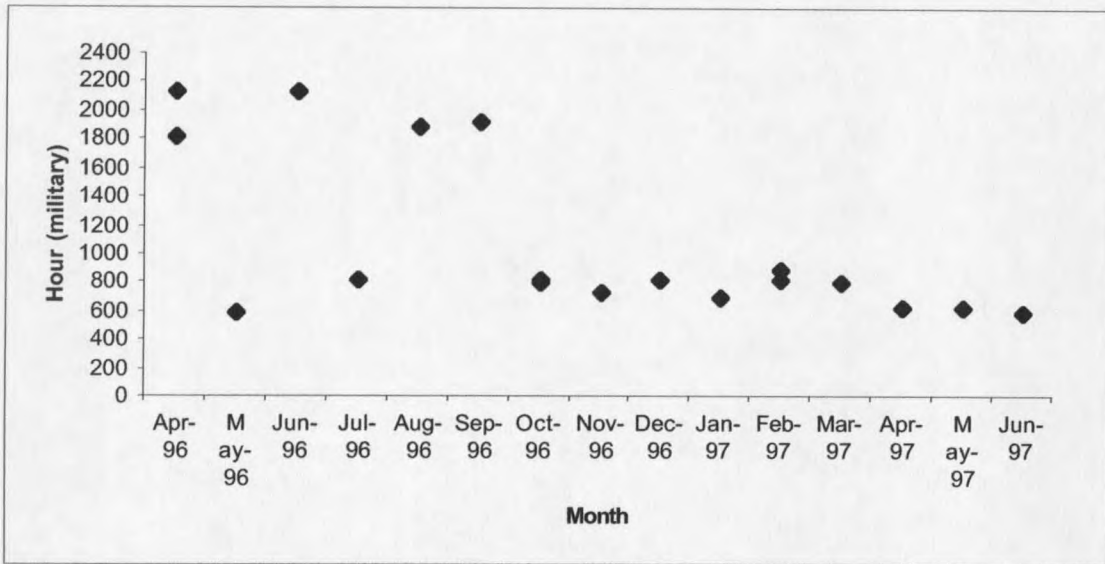


Figure 8. Ground observations of moose made daily every 1/2 hour during daylight hours at a SB willow stand, April 1996-June 1997. Highest average number of moose seen per 1/2 hour each month. Months with 2 values indicate ties. Hour of the day follows standard conventions for mountain standard and daylight savings time.

Census Flights

The number of moose found on survey flights decreased post-fire. The highest number seen was 59 in November 1989, and numbers declined by 78% in subsequent flights to a low of 13 in May 1992 (Figure 9)

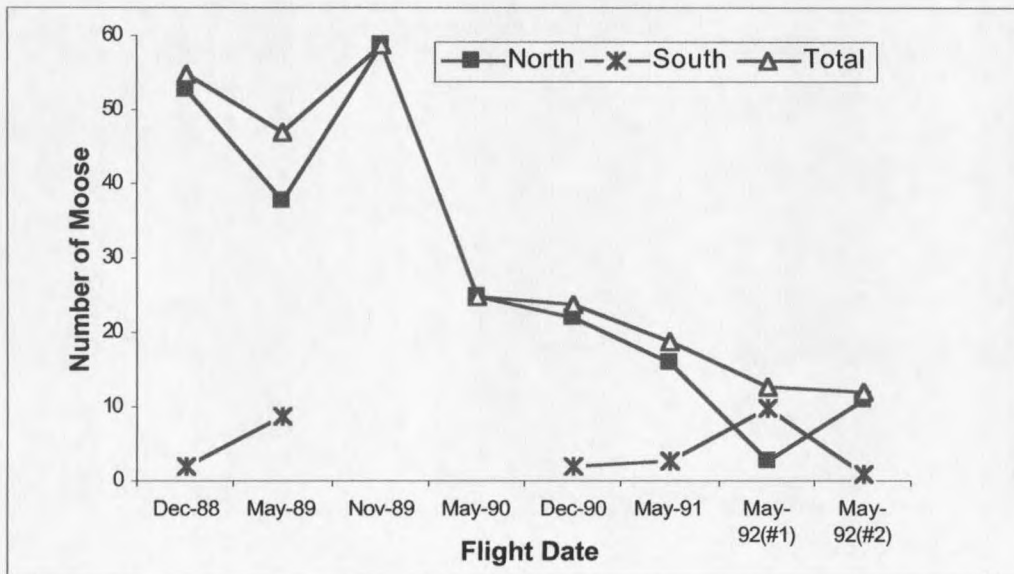


Figure 9. Number of moose seen during flights of the NYWR and only north and south of the Yellowstone River from December 1988-May 1992.

(Appendix B, Table 51 and 52). Moose numbers from survey flights were not closely correlated with the results of the horseback transect index in the same years ($r_s = 0.6$, $P = 0.4$, $n = 4$).

Discussion

Population History

Long-term studies in North America support the idea that moose populations consistently erupt, crash, and then stabilize at various densities depending on prevailing ecological conditions (Van Ballenberghe and Ballard 1997). Geist (1971, 1974) attributed this pattern to a basic response by moose populations to changes in habitat quality. In his opinion, over the species' evolutionary history, moose have typically occupied limited areas of permanent habitat in low densities. When fire has created transient habitat, they have rapidly colonized these areas and reached comparatively high densities. For example, at Isle Royale, moose colonized about 1910, erupted to high densities in the absence of predators, and then crashed by the early 1930's (Mech 1966). A second eruption followed a wildfire in 1936 that increased available browse. As wolves were colonizing the island about 1948, a second moose population decline had begun in response to over-utilization of their food supply. Since then, the moose population has fluctuated with predation and competition for high-quality forage (Messier 1991).

Trends were similar on the northern Kenai Peninsula in Alaska (Schwartz and Franzmann 1989, Loranger et al. 1991). Moose were rare before the late 1800's but increased beginning about 1885 following several human-caused fires. Over-browsing was noted in 1913 followed by a sharp population decline in the mid- 1920's and late 1930's. Another fire in 1947 created optimum habitat for moose and another population increase that continued until 1969. As plant succession advanced and habitat quality declined in the area burned in 1947, winter moose density dropped substantially beginning in the early 1970's.

Peek et al. (1976) reviewed historical trends of moose numbers in northwest Minnesota between 1885 and 1972. Moose were scarce in the mid 1800's but became common about the time caribou disappeared in 1890. The population increased until 1933, declined until about 1950, and then increased again in response to a hunting ban and favorable habitat created by logging.

Moose on the NYWR followed a similar pattern of colonization and subsequent population changes in response to habitat quality. However, population determinants appear to be different in this environment

than described for other important moose ranges. NYWR moose did not invade large, recently burned areas as described by Geist (1971, 1974).

Moose probably invaded the NYWR in the late 1800's. They encountered an environment in transition with the influence of European settlement. Human predation was initially important and then curtailed. Forest succession was altered with attempts to suppress fires. Moose immigration was followed by expansion into all suitable habitats by the middle of the 20th century. The population was subsequently stable or possibly declining. Quota hunting reintroduced human predation and likely facilitated the decline. The 1988 Yellowstone fires affected moose habitat at a landscape level. My data indicated that these fires were a major negative influence on moose. All methods gave some evidence of a post-fire population decrease. In areas where fire effects were severe, the reduction in numbers was substantial.

State and Federal agencies kept various records of moose numbers north of the GNF-YNP boundary from 1907 to 1949. Although these records were based on surveys of highly variable intensity and unsophisticated techniques, they have some validity. They documented increasing moose numbers and reported deteriorating willow condition. Declines in willow were attributed to drought and over-browsing by elk and moose. Indications of a decreasing moose population were noted in the mid 1900's, about the time efforts to record moose numbers ended. The establishment of quota hunting during the same period was, in part, a response to concern over willow status.

Optimal Population Monitoring

Moose in the study area evidently will not reach distribution or densities that lend themselves to efficient population estimation. I tested several different methods for monitoring trends. All methods detected a decline associated with the 1988 fires, but all had limitations for application to post-fire population monitoring.

Several long-term indices I developed successfully detected moose population trends before and after the 1988 fires and had similar findings. A horseback transect index showed a general decline in moose abundance from 1947 to 2001, with a major decline following the 1988 fires. Consistently lower counts did not occur until 1995 and probably reflected the lag time before effects of the 1988 fires were expressed in lower moose survival and recruitment. Higher numbers of moose seen in 1988 and 1989 were exceptions to the downward trend. During these years, moose were likely more observable because the 1988 fires removed dense forest cover over large areas. In addition, moose sought unburned streamside willow for feeding during the early post-fire years. Trails used as transects often followed riparian

corridors where moose were concentrated and visible. This spike in the data immediately following the fires reveals that, although useful for trend data, the horseback transect index probably underrepresented actual moose numbers prior to 1988.

An index of moose seen along the Gardiner to Cooke City road corroborated the horseback index and demonstrated a post-fire decline in abundance specific to areas affected by the 1988 fires. The decrease was most pronounced on the sections where forests were most impacted by fire (Mammoth to Round Prairie), while the unburned forested section (Round Prairie to Warm Creek) showed a statistically insignificant increase and a partially burned forested stretch (Warm Creek to Cooke City) showed a statistically insignificant decrease. It is possible moose simply relocated after the fire instead of experiencing an overall population decline. However, no section had a significant increase over time, which suggests an overall decrease. The probability of seeing a moose on the road transect was highest in 1989. As with the horseback transect index, moose were probably more visible with the forest cover removed by fire. The road transect index may be more sensitive than the horseback transect index - the post-fire decline was apparent as early as 1990. It is also possible the moose south of the Yellowstone River along the road were more severely impacted than those north of the River in the area of the trail transects.

Time of year can affect sightability of moose (Lynch 1975, Crete et al. 1986, Gasaway et al. 1986, Bisset and Remple 1991). February and March are considered the most difficult months to find moose because they are more likely to be in dense cover (LeResche and Rausch 1974, Novak and Gardner 1975, Novak 1981). Sightability in November and December may be higher because moose form larger groups and have stronger preferences for vegetation with low, open canopies. This has been found in Alaska (Peek et al. 1974, Gasaway et al. 1986), Minnesota (Mytton and Keith 1981, Peek et al. 1974), Michigan (Peterson and Page 1993), Alberta (Lynch 1975), and Ontario (Bisset and Remple 1991). However, 34 consecutive years of aerial surveys in Saskatchewan were successfully conducted in January and February (Stewart and Gauthier 1988).

Barmore (1980) also found seasonal variation in moose sightability during attempts to count NYWR moose incidental to elk distribution flights between 1968 and 1970. He concluded that moose were difficult to observe in this environment. Although there are many hectares of open grassland and sagebrush where they could have been seen, they were not commonly found there. In addition, they were hard to find in forested areas. Most moose Barmore (1980) saw were associated with willow, and he was most successful at finding them in these plant communities in May, early June, and December. I had similar results from an index of moose abundance developed from systematic over-flights of 2 important willow

stands. Radiocollared and uncollared moose were significantly easier to observe in early winter (November and December) and May. Insignificant differences in the average number of moose seen among years (1987-1990) indicates that this method was probably not continued long enough to detect moose population declines after the 1988 fires. Developing an index of moose abundance using radiocollared animals observed in willow stands was hampered by a limited sample size. However, this method does have some potential for following moose population trends. Although the number of radiocollared moose observed was not positively correlated with the results of the horseback transect index, when radiocollared as well as uncollared moose were considered, the correlation approached significance.

A similar temporal distribution of moose was observed during intense ground sampling at one of the willow stands, thus validating the willow over-flight index. The highest average number of moose seen during daily 1/2- hour observations in the SB willow stand occurred in June, followed by December and May. Specifically, the highest weekly averages were in late November- early December and late May-early June.

Time of day also affects visibility of moose (LeResche and Rausch 1974). Timmermann (1974) suggested from 1000 to 1400 as the optimal time for moose aerial surveys in Ontario. Peterson and Page (1993) preferred just after sunrise for moose surveys in Minnesota. Although there were monthly variations, on average, I found that early morning (0600- 0930) and late evening (2030-2130) were the best times of the day to see moose in the SB willow stand.

Total counts of moose are preferred over indices for population assessments (Timmermann and Buss 1997). Aerial surveys of moose have been persistently attempted on several continents with mixed results (Novak 1981). Inherent problems are well documented, but counting moose on winter range from aircraft is still considered the most practical method for estimating moose numbers over large areas in North America (Gasaway et al. 1986, Gasaway and Dubois 1987, Timmermann and Buss 1997). However, many variables affect accuracy and precision and are hard to correct (Timmermann and Buss 1997). LeResche and Rausch (1974) and Stevens (1974) concluded that aerial counts do not provide valid estimates. Mantle (1972) thought results of moose surveys from aircraft were conservative. In a comparison of aerial counts and ground searches, Edwards (1954) reported that 78% of moose were seen from the air. In verifying results of a fixed-wing survey by using a helicopter, Evens et al. (1966) found that the fixed-wing crew saw 94% of moose. Gasaway et al. (1978) discovered that 91% of radiocollared moose were found during intensive searches from the air.

My efforts to count NYWR moose using fixed-wing aircraft did not produce complete survey data or repeated standardized methods as described by Gasaway et al. (1986). In addition, moose numbers from

survey flights were not closely correlated with other moose population trend data, such as the results of the horseback transect index. However, flight data were useful to show general population trends. A decline after the 1988 fires was apparent by 1990. Numbers have also decreased since earlier YNP surveys (Barmore 1980, Houston 1982).

From 1968 to 1978 Houston (1982) and Barmore (1980) collected data on moose abundance incidental to elk survey flights in designated elk count units, including a portion of my search area (Appendix B, Table 51 and 52). With the exception of upper Slough Creek (located north of the river), they only surveyed south of the Yellowstone River. My search area included their elk count units plus the remainder of the watershed at higher elevation north of the Yellowstone River. They reported the highest yearly moose count among all elk survey flights, and I reported the results of each moose survey flight. In upper Slough Creek, their high counts averaged 13 moose per flight with a high of 27 and a low of 3, while I found an average of 10.3 with a high of 28 and a low of 0. In the southern portion of the study area (roughly YP study unit), their high counts averaged 38.6 moose per flight with a high of 73 and low of 23, while I found an average of 4.5 with a high of 9 and a low of 1(excluding 2 good months for moose searching, November 1989 and May 1990, when coverage was not complete).

Unless well planned, efforts to sample moose in this environment are not effective. Although survey flights did not prove to be a good investment on the NYWR, the value of this and other methods was markedly improved by timing. These data confirmed what has been found on other moose ranges- moose were seasonally most observable during November-December. In this study area, May and June were also favorable months for finding moose. This phenomenon was tied to annual patterns of habitat use involving moose foraging in willow stands as opposed to the adjacent dense coniferous forests (see Chapters 3, 4, and 8). Because moose appear to be temporally and spatially predictable during these seasons, monitoring moose in key willow stands has potential for developing a long-term index of moose abundance. In addition, because the willow stands in the study area are uncommon, < 40 hectares each, and have discrete boundaries, search areas would be small. Time of day was also critical, with moose most likely to be seen in early morning and late evening.

Because of the limited efficacy of fixed-wing surveys in this environment, total NYWR moose numbers will may never be known without intense searching with helicopters and probably not then. Given low moose densities and low visibility, indices such as trail counts, road section counts, and counts in selected habitats and sites were a cost effective and reasonably reliable mechanism for determining trend because they were done in combination. For example, using a suite of indices provided a description of moose abundance from colonization in the late 1880's to the present, including a downward trend since

about 1950 and a significant decline after the 1988 fires. Managers should continue to monitor the NYWR moose population by implementing a combination of long-term indices similar to those described here, especially since the gray wolf (*Canis lupis*) has recently (1995) been reintroduced in the GYA. Even combinations of indices, however, are unlikely to produce rigorous data on moose population trends on the NYWR.

CHAPTER 2

MOOSE HOME RANGE CHARACTERISTICS AND SURVIVAL
ON THE NORTHERN YELLOWSTONE WINTER RANGEIntroduction

I used standard conventions to investigate the ecological significance of NYWR moose home range selection and the survival of radiocollared animals using those ranges. Included were calculations of home range size, average distance between radio location points, and proportions of available habitat. I also identified areas where moose concentrated activities (core areas) and assessed the relationship between the associated habitat features and moose foraging habits. This provided insights into the winter ecology of Shiras moose in an environment with highly variable topography and distribution of vegetation types. In the past 50 years, variability in the NYWR environment has also included significant changes in vegetation (Yellowstone fires-1988, localized timber harvesting- 1940-1995) and changes in the numbers and types of potential predators (GNF quota hunting initiated in 1945, grizzly bear population protection initiated in 1975, wolf reintroduction initiated in 1995).

Moose movements and distribution in space and time are indicators of the ecological constraints they face. Therefore, to successfully manage a moose population it is necessary to characterize the space occupied by individual animals and their movements within that space. The primary area occupied by an animal is its home range, which is defined as a familiar area that provides opportunities to feed, rest, escape predators, and pursue all other activities necessary to sustain life (Pianka 1994, Hundertmark 1997). Similarly, home range size and location are influenced by food supply, density of conspecifics, predators, and landforms (Pianka 1994, Morrison et al. 1998). Moose tend to exhibit a strong fidelity or philopatry to their home range and return to the same seasonal range or remain in the same home range for years (Bailey and Franzmann 1983).

Knowledge of moose home range and movements has developed only recently. Early descriptions of home range (Seton 1927, Murie 1934) were highly speculative and based on localized observations of recognizable individuals (Hundertmark 1997). Collection of reliable information on individual animals was enhanced dramatically with the advent of chemical immobilization and radiotelemetry, and now movements and survival can be tracked through time (White and Garrott 1990, Hundertmark 1997, Morrison et al. 1998). Computer models can assess associations among radio location data (Worton 1989,

White and Garrott 1990, Kie et al. 1994, Hundertmark 1997, Morrison et al. 1998), and Geographic Information System technology (Bernhardson 1992) allows quantification of habitat features to clarify the ecological significance of home ranges. Several algorithms have been devised for estimating home range size, each designed to estimate different aspects of spatial use. They include: the overall area circumscribed by movement of an animal in a given time period (measured or estimated by use of minimum or maximum convex polygon); the geographic areas of concentrated occurrence of an animal (harmonic mean) and the general area most used by an animal (95% confidence ellipse) (Kie et al. 1994, Hundertmark 1997, Morrison et al. 1998).

Home range can be described using size, animal movements within the range, resident survivorship, and habitat characteristics. The interrelationship of these factors can provide insights into the ecological significance of home range selection (Hundertmark 1997, Peek 1997, Van Ballenberghe and Ballard 1997). Home range size is often compared among geographic areas and populations and has been used as a relative statement of habitat quality (Peterson 1955, McNab 1963, LeResche et al. 1974, Hundertmark 1997). Mean distance between successive radio locations can also be a statement of the ecological aspects of range use (Addison et al. 1980, Hauge and Keith 1981). The distances moved by a moose over a given time period may be directly related to available forage biomass and, therefore, habitat quality (Lynch and Morgantini 1984, Miquelle et al. 1992). In addition, sources of individual moose mortality may reveal attributes of home ranges. Predation (Ballard and Van Ballenberghe 1997), hunting pressure (Van Ballenberghe and Ballard 1997), and forage availability (Peek 1997) vary among moose home ranges and affect each animal's chances for survival. Home ranges may be described and compared using relative proportions of vegetative stands (cover types), and the age and distribution of those stands (Neu et al. 1974, Peek 1997, Thompson and Stewart 1997).

Although regional variation in North American moose home range size, movements, and survivorship, as well as the vegetative characteristics of home range, have been investigated, less effort has gone into explaining their ecological significance (Pianka 1994, Hundertmark 1997, Morrison et al. 1998). Habitat selection is an optimization process involving many factors, and home range is an expression of the process (Pianka 1994, Morrison et al. 1998). Characteristics of home range vary among and within populations and likely influence individual fitness. The size and characteristics of a home range may determine what strategies individuals adopt for survival (Leptich and Gilbert 1989, Peek 1997, Ballard and Van Ballenberghe 1997). Implicit in the definition of home range is the assumption that the area provides an animal with the resources necessary to sustain life (e.g. food, water, and shelter), an assumption that may or

may not hold. Animals probably try to establish a home range with a size appropriate for ensuring survival through critical biological periods (Lindstedt et al. 1986). However, environmental changes, such as the 1988 Yellowstone fires, Gallatin Forest timber harvesting, and the 1995 GYA wolf reintroduction, may significantly affect the spatial and temporal distribution of moose and their chances for survival.

The ultimate factor determining home range size may be energetics (McNab 1963, Pianka 1994). McNab (1963) postulated that animals living in relatively poor quality habitat have larger home ranges than conspecifics living in more productive areas. However, this hypothesis is not easily tested because of many confounding factors including sex and age of the animal, season, weather, and distribution of suitable habitat. For example, because moose habitat is a matrix of different habitat types, home range size would be determined, in part, by juxtaposition of those types and the interspersions of unsuitable habitat, which is difficult to quantify (Ballard et al. 1991, Hundertmark 1997). Although numerous studies have reported correlations between body size and home range size, none have confirmed McNab's (1963) hypothesis that energetics is the ultimate factor that determines home range size (Hundertmark 1997). However, there is evidence for moose that the distance moved by an animal over a given period of time - which can be related to home range size - is directly associated with the amount of available forage biomass (Lynch and Morantini 1984, Miquelle et al. 1992). I quantified NYWR moose home range parameters to address these concepts in the context of several theories forwarded to explain the ecological significance of moose habitat use in this environment.

Moose are browsers - herbivores that eat primarily shrubs and trees (Peterson 1955, Renecker and Schwartz 1997). Ruminants with a large body size, like moose, require large quantities of food and are usually constrained by the time required to search for and process it. Processing is likely to be less important than locating adequate quantities of forage (Peek et al. 1992). Because of their dietary requirements, the quantity of available forage determines moose density. Consequently, trade-offs between time or energy constraints and food acquisition influence foraging strategies (Renecker and Hudson 1992).

Many North American studies have compared seasonal advantages of forest successional stages and cover type combinations for moose. In these investigations, North American moose have consistently been associated with early successional communities growing on burned or logged sites (Peterson 1955, Taber 1966, Krefting 1974, Kelsall and Telfer 1974, LeResche et al. 1974, Irwin 1975, Peek et al. 1976, Peek 1997). Studies indicate that moose habitat is enhanced post-disturbance by a temporary increase in available woody browse species generated by the removal of trees that compete for resources with shrubs (Spencer and Hakala 1964, Dryness 1973, Kelsall et al. 1977, Whittinger et al. 1977, Parker and Morton 1978, Irwin and Peek 1979, Oldemeyer and Regelin 1987, Thompson and Stewart 1997). Natural and

human-induced disturbances that create early successional stage forests are often considered necessary to replenish moose habitat across the continent (Thompson and Stewart 1997).

North American moose are also occasionally associated with habitats where fire is infrequent. High-density moose populations can exist where fire is either not a major factor or is detrimental to habitat availability (Peek 1997). For example, in central Idaho, moose inhabit areas of densely forested steep terrain with limited riparian vegetation that burn infrequently (Peek et al. 1987). These forests have double canopies - a sub canopy of available coniferous browse beneath an overstory of >150 year-old mixed conifers. The double canopy provides accessible food and ameliorates snow conditions.

In contrast with what has been commonly reported about moose habitat use in North America, Loope and Gruell (1973) hypothesized that low moose populations in the 19th century in the GYA were because fire maintained early successional vegetation. Subsequent population increases in this century in northwest Wyoming were because forests matured under a management policy of fire suppression. A primary factor in this, they believed, is an increase in subalpine fir, a shade tolerant species found in older forests. They further hypothesized that subalpine fir is the staple food item in the diets of moose in the area. Similarly, McDowell and Moy (1942) and Peek (1974a) proposed that moose habitat along the northern border of YNP (the study area for this project) consisted of willow stands that are important to moose but spatially limited. Moose are forced from these by snow to adjacent forested slopes where subalpine fir stands support low-density moose populations in winter.

Pre-fire vegetation mapping in YNP by Romme and Despain (1989) supports these hypothesis. They noted that coniferous forests characterized by patches in different stages of post-fire development dominated the landscape. They also reported that in 1988, >300 year-old lodgepole pine forests were more prevalent than at any time in the past 3 centuries. The quantity of these old forests, which are considerably more flammable than earlier successional stages, in combination with extreme weather conditions, resulted in the 1988 fires.

Using home range parameters, I investigated whether NYWR moose are, like most North American populations, associated with early successional vegetation or were anomalous and relied on limited willow stands in association with double-canopy climax coniferous forests as proposed by Loope and Gruell (1973), McDowell and Moy (1942) and Peek (1974a). Environmental variability among 4 study units, especially landscape-level changes created by the 1988 fires, allowed me to test the hypothesis that there are no differences in moose home range parameters among study units with varying proportions of mature and recently disturbed forests.

The SC and YP study units were substantially affected by the 1988 fires, SB was moderately affected, and BC did not burn. Pre-fire timber harvesting occurred in BC and post-fire salvage logging of burned forests occurred in SB. Moose quota hunting was a factor in 3 of 4 study units (BC, SC, and SB) but not in YP. Other predators (grizzly bears and wolves) were common throughout the study area. Moose habitat was generally characterized by small but well-defined willow stands along drainages with adjacent forested slopes (see chapters 3 and 4).

Methods

Animal Capture and Radio Locations

In 1987-88, 14 moose were immobilized using dart-delivered drugs (Succostrin n=3; M99 n=1; Carfentil n=4, and Telazol n=6) and fitted with radio-transmitters with 14-hour mortality indicators (166-167 mHz, Telonics, Mesa, AZ). Moose capture was opportunistic, but I was able to deploy 3 or 4 radiocollars in each of 4 study units for a fairly even distribution. Radiocollared moose were located 1-2 times per month year-round from fixed-wing aircraft and, in winter, an additional 1-3 times per month from the ground using trucks, snowmachines, or skis during January 1987 through February 1991. I attempted to separate locations by at least 5 days to maximize independence of locations. All locations were made during daylight hours.

Home Range Analysis

I investigated differences in home range size of radiocollared moose among study units with different habitat characteristics and changes in home range size before and after alterations in vegetation caused by the 1988 fires. Hypotheses included: 1) there is no difference in moose home range size among study units with different habitat characteristics; and 2) moose home range sizes are not affected by landscape level changes in amount and distribution of mature coniferous forests.

Home range sizes were calculated with the adaptive kernel method (Worton 1989, Kie et al. 1994, Hundertmark 1997) using point percentage contours, 95% of points, grid cell size of 50x50, and optimum bandwidth default. Home range size was calculated in hectares and converted to square kilometers, and the average distance between points was calculated in meters. A minimum of 30 data points per winter was used to calculate home range. I combined annual data and analyzed home range size differences among study units. Data were inadequate to compare pre- and post-fire differences in moose home ranges among

study units. Instead, I pooled limited data for moose from fire-affected areas for which pre- and post-fire radio locations were sufficient.

I also used the adaptive kernel method with the 100%, 95% and 75% point percentage contours to determine the presence or absence of winter "core areas", areas of concentrated activity where moose proportionally spent a greater amount of time (Mohr and Stumpf 1966, Worton 1989, Kie et al. 1994, Hundertmark 1997). Hundertmark (1997) defined core areas as one or more areas within the home range where a disproportionately high percentage of observations occurred, indicating that the habitat in these areas is important in satisfying the animals' needs. Model point percentage contours that included >75% of radio locations were considered a core area. I transposed these areas onto cover type maps to determine the dominant (>50%) vegetation within the contour. The cover type maps were a preexisting data base prepared for federal lands in the GYA by the Departments of Interior and Agriculture (Mattson and Despain 1985). It characterizes forested areas by dominant tree species and successional stage. Descriptions of shrub lands and grasslands are based on dominant vegetation. Discrete vegetation patterns were mapped to a 5-acre (2.02-ha) resolution. When point percentage contours formed 2 activity centers, I selected the visual center of each and measured the distance between them using GIS. This allowed me to compare the average distance between moose core areas among study units.

In addition, I used the cover type maps and GIS to calculate the percent of each cover type in each of the 4 study units. With GIS, I calculated the area burned in 1988 and the amount of habitats most used by NYWR wintering moose (see chapters 3 and 4), including willow and mature conifer forests.

Survival of Radiocollared Moose

I examined differences in survival of moose in study units with and without hunting and with different levels of 1988 fire impacts. I transposed home range areas onto vegetation base maps to assess fire effects. All radiocollared moose legally killed by hunters were reported by MFWP and examined to determine age and condition. All radiocollared animals that died from other causes during the study were located as soon as feasible and examined to determine cause of death. Starvation was assigned as the cause of death to carcasses that showed no evidence of predation, bullet wounds, fire-related injuries, or obvious disease symptoms and had femur bone marrow visually classified as "red and jellylike" (Cheatum 1949). Predation was determined by carcass disposition, and predator teeth marks, tracks, scats, and hair samples. The status of radiocollared animals was monitored with telemetry equipment from June 1987 to February 1991 and by sightings in traditionally utilized locations from March 1991 to October 2001.

Statistical Tests

Data were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met, ANOVA, Kruskal-Wallis ANOVA by ranks, and Newman-Keuls *post hoc* test were used to test for differences among data ($P < 0.05$) (see Chapter 1). Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance are reported in the text, P-values only appear in appendices.

When 2 unpaired groups were compared, a Student's t-test for independent samples was used if assumptions of normality were met ($P < 0.05$). Histograms were used to examine distribution of the data. If Levene's test was statistically insignificant, then the hypothesis of homogeneous variances was accepted. When 2 paired groups were compared, an unpaired t-test was used if assumptions of normality were met ($P < 0.05$). If Levene's test was statistically significant, then the hypothesis of homogeneous variances was rejected. Nongaussian populations were tested using Mann-Whitney U.

Results

Home Range Size

Of the 12 moose that were located sufficient times, 7 cow moose had a slightly larger average annual home range size (64.0 km^2) than 5 bulls (62.0 km^2), although the difference was not significant ($t = 0.0624$, $P = 0.951$, $df = 10$). The average distance between radio locations for cows and bulls was also similar (1,787 m and 1,842 m, respectively) and implies nonsignificance ($t = -0.180$, $P = 0.916$, $df = 10$). With home range size similar between sexes, it was appropriate to pool the 2 populations to compare home range data among study units.

Home range size differed markedly among the study units. Moose in the YP and SC study units averaged about 3 times the home range size of moose in the SB and BC study units. Three SB cows and 1 bull had the smallest average home range size (27.0 km^2), followed by 1 BC cow and 2 bulls (30.0 km^2), 1 SC cow and 2 bulls (108.0 km^2), and 2 YP cows and 1 bull (113.0 km^2) (Table 3). Differences in average annual moose home range size among study units were significant ($F = 42.2929$, $P < 0.001$). The *post hoc* test revealed the source of the difference to be between the SB and BC home range averages and the SC and YP averages. Differences were not significant between the SB and BC averages or between the SC and YP averages (Appendix C, Table 53).

Moose radio locations in BC had the smallest average distance between them (1,103 m), followed by SB (1,245 m), SC (2,595 m), and YP (2,745 m.). The differences were significant ($H = 8.5449$ and $P = 0.036$)

Average annual pre-fire home range size for 2 SB and 1 YP moose was 25.0 km² compared to 34.0 km² post-fire, a significant increase ($Z = 2.201$, $P = 0.003$, $df = 4$). The average distance between radio location points pre- and post-fire (1,624 m and 2,152 m, respectively) was also greater, but the difference was not significant ($t = -0.5615$, $P = 0.604$, $df = 4$).

Table 3. Study unit location and sex of 14 radiocollared moose. Adaptive Kernel estimations of average home range size in square kilometers and average distance in meters between radio location data using 95% of points, 1987-1991. Data were insufficient for moose indicated by 'a' (<30 locations available). Date radiocollar was deployed, last radio location, and date of death, January 1987 to October 2001.

Study Unit	Sex	Home Range Size in km ² -95%	Average distance between points (m)	Date Collared	Last Radio Location	Date of Death
BC	Bull	10.0	1,001.0	1/5/88	9/17/89	9/89
	Bull	42.0	1,229.0	3/9/87	9/26/91	9/91
	Cow	39.0	1,080.0	3/20/87	2/5/91	Alive 10/01
SB	Bull	17.0	990.0	12/10/88	9/15/89	9/89
	Cow	24.0	1,411.0	12/2/87	9/26/90	9/90
	Cow	34.0	1,269.0	3/3/87	2/5/91	5/96
	Cow	36.0	1,310.0	1/8/88	2/5/91	4/99
SC	Bull	119.0	2,870.0	5/5/88	2/5/91	Unknown
	Bull(a)			5/5/88	4/12/89	4/89
	Cow	97.0	2,320.0	5/5/88	9/26/91	9/91
YP	Cow(a)			4/18/88	2/22/89	2/89
	Cow	123.0	3,118.0	4/29/87	2/22/89	2/89
	Cow	104.0	3,024.0	1/15/87	2/5/91	4/00
	Cow	114.0	2,093.0	4/4/88	2/5/91	5/00

Home Range Configuration

Of the 9 moose that were located sufficient times pre- and post-fire to analyze radio locations for winter home range configuration, 6 displayed home range as 2 disconnected areas around concentrations of data points (core areas) at either the 100% or 95% point percentage contour and 1 at the 75%. In all cases, 1 home range core area corresponded to a willow stand and the other to a higher elevation mountainside with mature conifer forests. The post-fire home range configuration for 1 SC moose did not show distinct core areas. Instead, use was centered around a willow stand and an immediately adjacent unburned conifer stand in a much larger matrix of severely burned forest. A BC moose, that also did not show a home range

configuration of core areas, wintered in small patches of willow scattered throughout a mature conifer forest. The average post-fire distance between activity centers for 2 YP moose (15 km) was 15 times the average distance between activity centers for 3 SB moose (1 km), 10 times the distance (1.5 km) for 1 BC moose, and >2 times the distance (6.5 km) for 1 SC moose. The remaining 5 moose were not located sufficient times post-fire to conduct this analysis, but pre-fire winter data revealed the same relationship of 2 distinct core areas, 1 centered around a willow stand and the other a mountainside mature conifer stand.

Habitat Changes

Before the 1988 Yellowstone fires, the BC study unit had the highest percentage of recently disturbed forests (4.8%) (Table 4). While early successional stage forests in BC were created by timber harvest, in YP (2.9%), SC (0.7%), and SB (0.3%) fires in the past 100 years were the source of the disturbance. Before the 1988 fires, the proportion of mature conifer forests (>100-years-old) was about equal among the study units (57-61%), as was the proportion of mature lodgepole pine forests (18-25%), an important winter cover type for NYWR moose (see Chapters 3 and 4).

Table 4. Percent of conifer cover types in 4 study units pre- and post-1988 Yellowstone fires. The youngest forests are 0-100, mid-age are 100-300, and the oldest forests are >300 years old (Mattson and Despain 1985).

	SC		YP		SB		BC	
	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-
Oldest conifer forests	53.0	27.0	42.0	31.0	48.0	43.0	30.0	30.0
Mid-age & oldest forests	61.0	33.0	60.0	43.0	57.0	51.0	58.0	58.0
Oldest lodgepole pine	16.0	6.0	6.0	2.0	11.0	9.0	6.0	6.0
Mid-age & oldest lodgepole	23.0	9.0	25.0	14.0	18.0	16.0	23.0	23.0
Youngest conifer forests	0.7	28.0	2.9	17.0	0.3	6.0	4.8	4.8

Effects from the 1988 Yellowstone fires were greatest in the SC and YP study units where 35% and 30% of the area burned, respectively, while only 8% of SB burned and BC was not affected (Figure 10).

The same pattern of proportional habitat alteration was evident when only conifer cover types were considered (Figure 11). Conversion of mature forests to an early successional stage by fire was greatest in the SC and YP study units.

Willow comprised <1% of each study unit but was most abundant in SC (0.68%) followed by SB (0.22%), YP (0.18%), and BC (0.08%). About 53% of willow burned in the YP study unit, 18% in SC, and 9% in SB.

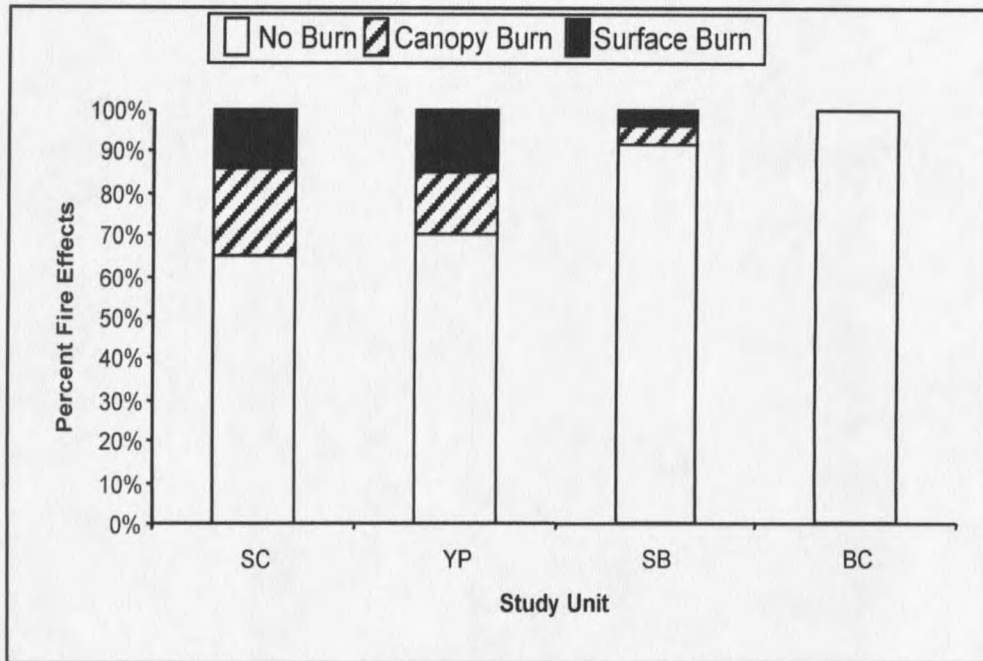


Figure 10. Percent of 4 study units affected by the 1988 Yellowstone fires.

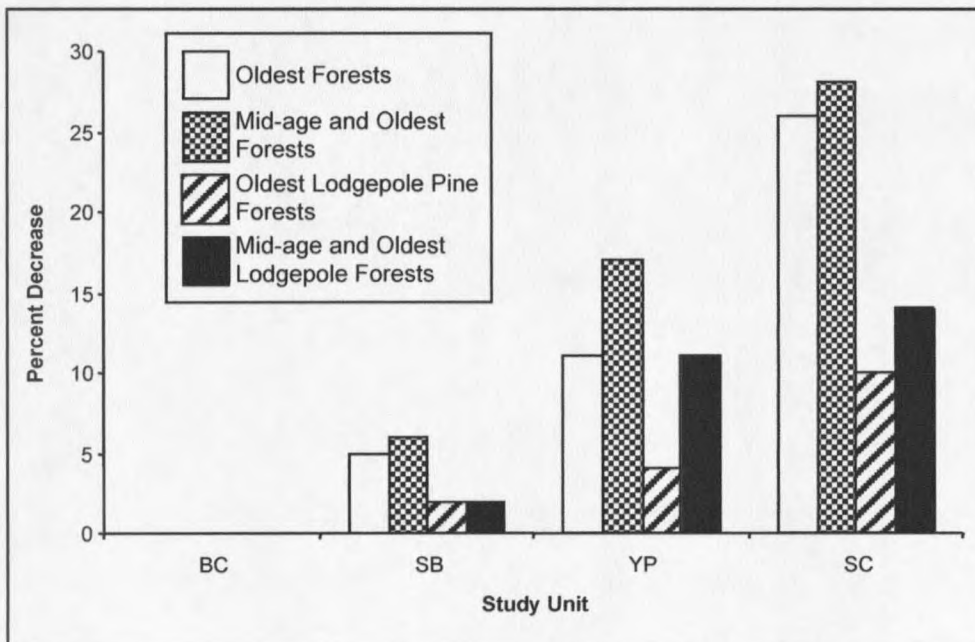


Figure 11. Percent decrease in conifer forests in 4 study units due to the 1988 Yellowstone fires. Mid-age forests are 100-300 and the oldest forests are >300 years old (Mattson and Despain 1985).

Survival of Radiocollared Moose

The fate of 12 of 14 radiocollared moose was determined (Figure 12). Between 1987 and 2001, 3 of 14 radiocollared moose starved the winter following the 1988 Yellowstone fires, 5 were killed by hunters by 1991, 1 died of senescence in 1996, 1 was probably killed by predators in 1999, another met the same outcome in 2000, 1 died by drowning in 2000 (exacerbated by an injury), and the status of the remaining 2 is currently unknown, although 1 is presumed dead because it has not been seen on traditional winter ranges (Table 3). One was alive when the project ended in October 2001. Death of 8 animals while radiocollars were being monitored, and interruption of the 1988 fires limited collection of radio location data.

The 1988 fires had a substantial affect on the survival of radiocollared moose. Most (>75%) of the home range area for 4 radiocollared animals burned (2 in YP and 2 in SC study units). As mentioned, 3 of the 4 starved in 1989. The fourth utilized an unburned willow stand (<100 ha) and an immediately adjacent unburned conifer stand (<120 ha) in a very large matrix of burned forest until shot by hunters in 1991. These animals survived an average of 21.8 months after capture and 10.6 months after the 1988 fires. By contrast, 8 radiocollared moose in home ranges with little or no fire affects (2 in YP, 4 in SB, 3 in BC study units) survived an average of 94.6 months post-capture and 83.2 months after the fire.

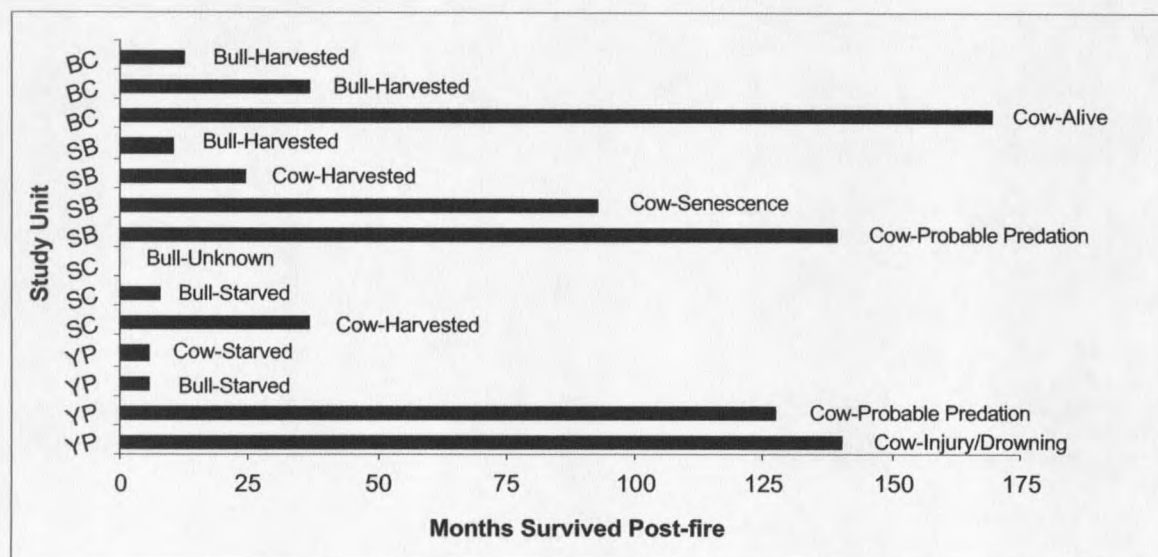


Figure 12. The fate of 14 radiocollared moose in 4 study units and the number of months each survived after the 1988 Yellowstone fires.

Discussion

Although a limited sample size of radiocollared animals hampered home range studies, I found that, unlike most North American populations, NYWR moose were not associated with early successional stage forests. By assessing a series of home range parameters, I concluded that the previously untested hypothesis forwarded by Loope and Gruell (1973), McDowell and Moy (1942), and Peek (1974a) was accurate - NYWR moose habitat consists of small willow stands and nearby mature conifer forests, each used a portion of the winter. Moose that proportionally had the largest amount of these cover types available with the shortest distance between them, presumably had the most energetically favorable winter home range habitat. By all measures, post-fire moose habitat in the study units most affected by the 1988 fires (YP and SC) was of poorer quality. Consequently, moose with home ranges in these areas had a decreased chance of survival.

Willow is a minor component of the study area, comprising <1% of any of the 4 study units, but it appears to be a relatively important habitat feature to NYWR moose. Home range configurations showed that a proportionally high number of radio locations were in these areas, willow stands served as 1 of 2 core areas for winter moose activity. The other cores were mature conifer stands, often on nearby mountainsides. The post-fire distance between the willow and mature conifer core areas was >8 times more for YP and SC moose as opposed to the same measurement for SB and BC moose.

The 1988 Yellowstone fires reduced mature conifer forests. Before the fires, <5% of any of the 4 study units was an early successional stage conifer forest and from 57% to 61% was mid-age and older forests. Reductions in mid-age and older forests from fire damage were greatest in SC (decrease by 28%) and YP (decrease by 17%), while declines were much less in SB (6%) and BC was not affected.

Home Range Size

I found important differences among NYWR moose home range characteristics that could not be attributed exclusively to gender-specific habitat requirements. They included variation in home range sizes and average distances between radio locations. Because of habitat needs associated with mating for bulls and calf rearing for cows, bull and cow moose may have different home range sizes. When differences in home range size are attributed to sex, male moose occupy the larger areas (Ballard et al. 1991, Hundertmark 1997). However, as with NYWR moose, a gender related disparity in home range size is not always present (Phillips et al. 1973, Taylor and Ballard 1979, Hauge and Keith 1981).

McNab (1963) hypothesized that home range size is determined by energetics, i.e. moose living in more productive habitats use smaller home ranges. However, the analysis of home range characteristics in relation to habitat productivity is difficult because of the nature of the variables involved as well as other confounding factors. Where habitats are markedly dissimilar, a link between home range size differences and habitat quality may be more apparent. For example, Leptich and Gilbert (1989) reported that moose home range sizes in Maine varied from 2 to 60 km², with much of the variation explained by distribution of high quality aquatic feeding sites. Ritchie (1978) thought that the relatively large moose home ranges he observed in Idaho in comparison with nearby locations were attributable to relatively unproductive lodgepole pine habitat.

I could not use NYWR moose home range parameters to test McNab's hypothesis. However, I compared home range size and average distance between radio location points among substantially different environments. Differences in moose habitat among the study units were important, and the 1988 Yellowstone fires added greatly to the variability. Home ranges in SB and BC were smaller and included more mature coniferous forests interspersed with patches of willow, a more energetically advantageous environment for NYWR moose. Average distance between radio location points was also smaller for moose in these study units. SC and YP moose home ranges were larger and were dominated by early post-fire forests and unforested habitats where moose probably expended more energy to sustain life. Similarly, a small sample of NYWR moose from several study units had smaller home ranges and traveled less within them before the fires as opposed to post-fire.

Moose average annual home ranges size and quality varies widely in North America and comparisons may be misleading because of temporal sampling differences among studies (Hundertmark 1997). The largest home ranges and potentially most energetically expensive to occupy have been reported in Alaska - 218 km² on the Seward Peninsula (Grauvogel 1984) and 290 km² in the Nelchina Basin (Ballard et al. 1991). Average annual home range sizes of 28.4 km² along the Stikine River (Doerr 1983) and 51.7 km² on the Kenai Peninsula (Bangs et al. 1985) in Alaska and 97 km² in northeast Alberta (Hauge and Keith 1981) are more representative. Phillips et al. (1973) reported one of the smallest average home range sizes, 3.6 km² in northwest Minnesota.

The average annual home range size of 70 km² for 12 NYWR moose was not anomalous. Based on an intra-continental comparison, 4 SB moose and 3 BC moose occupied good quality habitat as expressed by small annual average home range sizes (28 and 30 km² respectively), while 2 SC and 3 YP moose had large average annual home ranges (108 km² and 114 km² respectively) and, therefore, traveled greater distances to meet life requirements than moose in many North American populations.

Survival of Radiocollared Moose

Home range use was altered for NYWR moose living in areas affected by a 300-year, landscape-level fire that occurred in 1988 (Romme and Despain 1989). Home range locations in areas affected by the 1988 fires proved fatal for 3 moose. Their home ranges were in the areas most affected by fire, and they starved the first winter post-fire, while moose with mature unburned forests available lived longer and met other fates.

NYWR moose were exposed annually to varying risks inherent to their respective home range locations. NYWR moose outside YNP and in unburned areas had higher quality home ranges as indicated by size but faced the risk of being killed by hunters. Five of the 9 moose within Montana hunting districts were harvested. Of the remaining 4, 3 were cows that benefited from a change to bulls only hunting in 1996.

Wolves, grizzly bears, and black bears are the principal predators of moose (Ballard 1991, Ballard and Van Ballenberghe 1997). Predation is a major cause of mortality of moose calves (Ballard et al. 1991), but impacts to adults can also be substantial (Van Ballenberghe 1987, Ballard et al. 1990). None of the study area radiocollared moose were known predator kills before wolf reintroduction in 1995, although the fate of 1 was undetermined. There were insufficient radiocollared moose alive after wolf reintroduction to test the effects of multiple predators on NYWR moose.

Of the 6 moose available to wolves as prey after 1995, 1 died of senescence, 1 was found dead with inconclusive wolf and bear sign nearby, 1 was probably killed by a grizzly bear, 1 was injured and drowned, the fate of 1 was unknown, and 1 was alive when the project ended in October 2001. Evidence indicates that the 2 moose with predator sign at the carcasses were killed by grizzly bears. Both were in the SB study unit near Cooke City, MT, an area with a high grizzly bear density (K. Frey, MFWP, personal communication). This is commensurate with findings from other North American studies where grizzly bears were shown to be significant predators of adult moose (Ballard 1992).

Ecological Implications

The ecological implications of the factors that determine moose population size are not fully known, especially in naturally regulated ecosystems. Hundertmark (1997) believed that obtaining the necessary data to understand these processes would require a combination of case history studies, long term population monitoring, and large-scale experiments replicated in different geographic areas. However, identifying the determinants of the most energetically advantageous habitat and the factors that influence moose numbers is a complex problem. A given population reflects the composite effect of all limiting and

regulating influences, as such, it is unlikely that the effect of any single factor can be measured or its importance ranked (Hundertmark 1997).

Houston (1968) characterized limiting factors for a Wyoming moose population as a complex interaction of many variables. Numerous other studies have confirmed this and have identified specific determinants including habitat quality, availability of food resources, nutrition, weather, hunting, disease, predation, forage quality, and snow accumulations, although the proportional affect of each factor is rarely, if ever, determined (Peek et al. 1976, Peterson 1977, Fuller and Keith 1980, Messier and Crete 1984, Franzmann and Schwartz 1985, Ballard et al. 1991, Messier 1991, Gasaway et al. 1992).

It is known that major oscillations in moose numbers often involve substantial and comparatively abrupt changes in habitat quantity and quality. Evidence from long-term studies in North America demonstrates that moose populations typically erupt, crash and then stabilize at various densities depending on prevailing conditions (Mech 1966, Peek et al. 1976). These population increases are often tied to changes in the abundance of an important habitat component, such as post-disturbance increases in shrub fields over a few years or decades. In addition, more rarely and through very different mechanisms, an increase over several centuries in mature, double canopy forests may also result in moose population increases (Peek et al. 1987).

Where moose numbers are linked to the availability of post-disturbance shrub fields, maintenance or manipulation of habitat and populations is comparatively straightforward (Thompson and Stewart 1997). However, management of moose populations dependent upon mature forests is problematic because climax forests are vulnerable to stochastic events. Planned disturbances such as timber harvesting can be controlled, but fires are inevitable in older boreal forests. In environments where moose are associated with older forests, moose numbers may cycle over much longer periods of time and be much harder for managers to favorably influence than where moose are associated with early seral stages.

The 1988 Yellowstone fires provided an opportunity to address factors affecting NYWR moose numbers. Although not a substitute for the types of investigations called for by Hundertmark (1997), if addressed in combination, home range parameters, resident survivorship, and characterizations of habitat components can provide comparative measures of several important population limiting factor - habitat quality and quantity. Using these measures, I identified the presence of willow stands in combination with mature conifer forests as one of the important factors influencing NYWR moose numbers. Therefore, because NYWR moose appear to be dependent upon mature forests, managers will have few options for habitat improvement or manipulation in a post-fire environment. With numbers of NYWR moose reduced

after the 1988 fires because of diminished habitat, other population regulating factors may now be increasing important. In particular, managers should carefully monitor moose numbers to assess the effects of continued quota hunting and a new predator, the gray wolf.

CHAPTER 3

MOOSE DIET AND FORAGING PATTERNS
ON THE NORTHERN YELLOWSTONE WINTER RANGEIntroduction

Winter survival for moose involves a complex series of foraging decisions designed to optimize food consumption, conserve energy, and minimize risk. As large-bodied browsers, moose must find an abundant supply of low quality woody twigs to satisfy their winter food requirements (Peterson 1955, Telfer 1978, Coady 1982, Telfer 1984, Peek et al. 1992, Renecker and Schwartz 1997). Within this constraint, moose diet composition is likely to vary spatially and temporally. Renecker and Schwartz (1997) reviewed North America studies and found that moose used 221 different plant species and/or genera. Although moose repeatedly eat large quantities of a few plentiful species, they also opportunistically utilize new plants and search for uncommon high quality plants or plant parts. Renecker and Schwartz (1997) concluded that plant quality and quantity addressed many differences in seasonal and regional moose food preferences; they also encouraged investigation of other diet determinants.

NYWR moose food habits have not been investigated, but others have speculated on foraging patterns. Loope and Gruell (1973) postulated that GYA moose are primarily associated with late successional stage lodgepole pine stands during winter where they browse on subalpine fir, a shade-tolerant tree that may be more abundant in mature forests. They also theorized that GYA moose numbers increased through most of the 20th century in the absence of landscape-level disturbances. Similarly, McDowell and Moy (1942) and Peek (1974a) proposed that NYWR moose utilize permanent streamside willow stands until forced by snow accumulations to dense conifer forests on adjacent mountainsides. Both descriptions are anomalous for North America where early seral stages usually support the highest winter moose densities. In these post-disturbance landscapes, shrub fields provide biomass concentrations of deciduous woody browse and efficient foraging opportunities (Peterson 1955, Geist 1971, 1974, Telfer 1978, Coady 1982, Telfer 1984). The 1988 Yellowstone fires provided an environment to compare foraging patterns between NYWR moose and boreal forest populations associated with recently burned and logged habitat.

I examined spatial and temporal differences in NYWR moose diet and foraging patterns among winter periods, diverse habitats, and areas with variable fire effects. Following the 1988 Yellowstone fires, I looked for a diet shift from unburned to burned plant materials, potentially an expression of deteriorated habitat conditions (Ellis et al. 1976). Moose diet and foraging patterns are likely to be influenced by forest

structure and age, so I investigated diet distribution among cover types to clarify these relationships (Parker and Morton 1978). Relative abundance and size of forage species can influence use, so I assessed use in relation to proportionate availability (Risenhoover 1987, Saether 1990). I also compared the efficiency of moose seeking food in different environments (Risenhoover 1987, Vivas and Saether 1987). Because browsing intensity on subalpine fir, a major winter food source in the Yellowstone ecosystem, may be an indication of moose habitat quality, I examined how winter severity influenced patterns of browsing on this species and how size of individual trees influenced intensity of use (Saether 1990). Quality of subalpine fir and other winter food resources was determined through chemical analysis (Schwartz and Renecker 1997).

Methods

Fourteen radiocollared moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were available for browse studies. Fresh tracks from a minimum of 2 radiocollared and 2 uncollared moose were located monthly during the winter (November - April) in each study unit from 1986 to 1990. These animals were back-tracked through snow to collect data on diet and browsing activity (Litvaitis 1994). I did not follow moose because I did not want the animals to respond to my presence. Browsed stems and twigs were counted along the route. Each truncated twig was considered one "bite" (Cole 1959). I recorded the number of stems removed per plant and the plant species. I tried to get a minimum sample size of 500 bites for each tracking effort. The cover types along the route were described and bites were recorded by cover type. I summarized cover types where browsing occurred into 20 cover categories (Table 5) (Mattson and Despain 1985).

Moose behavior and typical snow conditions allowed for use of the "bite method" to determine browsing activity and diet. Attempts to find fresh tracks were successful because the snow pack was consistent, and deep and fresh snow was common. In addition, track patterns were relatively simple because moose were usually solitary. New bites were easy to distinguish because tracks of the moose led to the browsed plant and the color of the cambium was light green. Weathering turned cambium to yellow or tan in a short time.

Data were divided into subsets for analysis. Unless otherwise noted, the divisions were: early winter= November-December, mid-winter= January-February, late winter= March-April, all winter= November-April, pre-fire= November 1986-June 1988, post-fire= July 1988-April 1990, and all winters= 1986-1990.

I used the Mattson and Despain (1985) cover type key for describing vegetation patterns, a system specific to the GYA and the accepted standard for vegetation mapping by the Departments of Interior and

Table 5. Cover categories (Mattson and Despain 1985) where moose were back-tracked to record browsed twigs.

Cover categories	Description
Willow	Includes tall (>1.5 m) and low (<1.5 m) willow.
Young conifer/willow	Lodgepole pine 0-100 years post-disturbance and tall and low willow.
Mid-age conifer/willow	Pole-size spruce-fir and lodgepole pine 100-300 years post-disturbance with tall and low willow.
Oldest conifer/willow	Mature spruce-fir or lodgepole pine 300 years + post-disturbance and tall or low willow.
Young Douglas fir	0-100 years post-disturbance.
Mid-age Douglas fir	100-300 years post-disturbance.
Oldest Douglas fir	300+ years post-disturbance; also includes oldest Douglas fir in a matrix of grasslands or sagebrush/grasslands.
Young lodgepole pine	0-100 years post-disturbance; also includes lodgepole pine in a matrix of moist to dry grasslands and sagebrush.
Mid-age lodgepole pine	100-300 years post-disturbance; also includes lodgepole pine in a matrix of moist to dry grasslands and sagebrush.
Oldest lodgepole pine	300+ years post-disturbance; also includes lodgepole pine in a matrix of moist to dry grasslands.
Young spruce-fir	Pole-size and smaller.
Mid-age spruce-fir	Pole-size to mature; also includes spruce-fir in a matrix of moist grasslands.
Oldest spruce-fir	Mature spruce-fir; also includes spruce-fir in a matrix of wet to moist grasslands.
Young whitebark pine	0-100 years post-disturbance
Mid-age whitebark pine	100-300 years post-disturbance.
Oldest whitebark pine	Mature whitebark pine, often mixed with other conifer species including lodgepole pine and spruce-fir.
Aspen/conifer	Mature stands of aspen, also includes conifer encroachment.
Sagebrush	Moist to dry sagebrush grasslands.
Meadow	Moist to dry meadows and grasslands.
Other	Streambeds, talus, shrub dominated avalanche chute, urban areas, and roads.

Agriculture. It characterizes forested areas by dominant tree species and successional stage. Descriptions for shrub lands and grasslands are based on dominant vegetation. Mattson and Despain called discrete vegetation patterns "cover types". Where I lumped several similar cover types, I called the result "cover categories".

Browse Use Variation

Bite data were compared among several spatial and temporal scales including: early winter, mid-winter, late winter, pre-fire, post-fire, and by study unit. I considered the hypothesis that there is no difference in the diet of moose among winter periods, between pre- and post-fire, and among study units. I summarized use of burned plant materials by winter period and study unit. I considered the hypothesis that there is no difference in the use of browse material burned in 1988 among winter periods or among study units.

Use of Browse in Relationship to Abundance

To determine if moose use potential browse in proportions equal to, less than, or greater than availability I back-tracked animals to find areas where feeding was most intense. At these sites, I used 3 3-m radius circular plots located using random numbers to characterize available trees. In each plot, the species and height of each tree were recorded. I tested the hypothesis that the use of 5 tree species (subalpine fir, lodgepole pine, spruce, Douglas fir, and whitebark pine) as browse in young, mid-age, and the oldest successional stages of lodgepole pine, Douglas fir, and spruce-subalpine fir (spruce-fir) forests did not differ from availability.

Variation in Browse Use in Cover Categories and Among Successional Stages

I compared bite data collected while back-tracking moose to address the hypothesis that there is no difference in the diet of moose among 20 cover categories (Table 5) and by pre- and post-fire periods and among study units. I also analyzed bite data among the early (0-100 years), mid- (100-300 years), and late (300+ years) successional stages of 3 coniferous forest types (spruce-fir, Douglas fir, and lodgepole pine). I addressed the hypothesis that there is no difference in the diet of moose in forests of different ages.

Variation in Browsing Rate by Cover Category

After the 1988 fires, I compared winter foraging efficiency among cover types using the number of browsed stems per meter traveled as an index of efficiency. The index was created by measuring the distances within each cover type from the first to the last recorded browsed stem encountered during a tracking session and dividing the number of bites counted by the linear distance measured. I determined the distance traveled by laying a flexible tape along the route taken by the moose. Records of browsed stems were kept from where the tracks were first found until the moose entered another cover type or 500 browsed stems had been located. The average was determined for 20 cover categories (Table 5) for the early, mid-, late, and total winter periods. The average number of bites taken per meter in 6 burned cover types was also calculated. I tested the hypothesis that there was no difference in the average number of browsed stems per meter traveled among cover categories, winter periods, and among unburned and burned cover types.

Variation in Browsing on Subalpine Fir

I compared browsing intensity on subalpine fir by study unit, winter period, and pre- and post-fire using bite data collected while back-tracking moose. I tested the hypothesis that there was no difference in the average number of bites taken per subalpine fir among study units, pre- and post-fire, and winter period. Availability of different sized subalpine fir may change over the winter as snow depth changes. I determined frequency of browsing on individual subalpine fir size classes. Size classes were in 50 cm increments from 50 to 500. This was done for the all, early, mid-, and late winter periods. I addressed the hypothesis that there is no difference in the intensity of browsing on different size classes of subalpine fir during different winter periods.

Nutritional Analysis of Browse Species

I analyzed changes in nutritional content of browse species among winter periods post-fire to investigate reasons for variability in moose diet. Current year's growth was collected from the 5 most common browse species in the diet of moose determined while back-tracking. Included were subalpine fir, willow, lodgepole pine, gooseberry, and buffaloberry. Samples from about 50 plants of each were collected monthly, November-April, 1998-1999. All samples were collected in the BC study unit but at a wide variety of sites in moose winter range. No attempt was made to determine species of willow or gooseberry, or to collect the same proportion of each species each month. Samples for November and December and

January and February were pooled for analysis. Samples for the critical months of March and April were analyzed separately. The Montana State University Agricultural Experiment Station Analytical Laboratory conducted the nutrient analysis. Analysis included elemental (calcium, potassium, magnesium, sodium, and phosphorus in parts per million) and proximate analysis (ash, crude fiber, crude protein, ether extract, total moisture as percent received and dry weight basis). I followed Kubota's (1974) description of calcium, potassium, magnesium, sodium, and phosphorus as macronutrients. Calculations of total digestible nutrients were not possible because of a lack of digestion coefficients for these materials.

Statistical Tests

Data were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met, ANOVA, Kruskal-Wallis ANOVA by ranks, Newman-Keuls *post hoc* test, Student's t-test, and Mann-Whitney U were used to test for differences among and between data ($P < 0.05$) (see Chapters 1 and 2). In addition, I used the Spearman's rank correlation test to quantify associations between nonparametric bivariate populations.

Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance are reported in the text, P values only appear in appendices.

Analysis of habitat selection is a common aspect of wildlife science and various methods were available. I reviewed several documents to determine appropriate tests and the best way to organize the data (White and Garrott 1990, Alldredge and Ratti 1986, Alldredge and Ratti 1992). A method associated with Chi-square goodness of fit test as described by Neu et al. (1974) best matched these data. Differences in use patterns were tested using Chi-square in conjunction with Bonferonni Z-statistic when data on use and availability were recorded. Results appear in the Appendices. To ensure that Chi-square tests were robust, I limited the number of cover categories representing what was available in the environment to 10. In addition, no more than 20% of the categories reflected 5% or less of the actual use data.

Results

Diet Composition Variation

Back-tracking moose through the snow revealed a NYWR moose diet dominated by conifers and deciduous shrubs both pre- and post-fire (Appendix D, Table 54). Subalpine fir, willow, lodgepole pine,

gooseberry, and buffaloberry accounted for almost 85% of browsing. Of the 8 conifer species utilized, only subalpine fir, lodgepole pine, and Douglas fir contributed >1% to any seasonal diet. Burned material from 4 conifer species was browsed post-fire, but only burned lodgepole pine was used to any extent. Browsing also occurred on plants in 19 genera of deciduous shrubs or trees. Seven forb genera were represented in the diet. Graminoids, principally *Carex* spp., were grazed, as were various annual composites. Composites (*Compositae*) were difficult to identify in winter condition and so were not distinguished by genus.

Diet, expressed as a percent of browsed stems, varied among winter periods (Figure 13) (Appendix E, Table 55). Willow and subalpine fir were important forage plants all winter, but proportional use changed as winter progressed. In early winter ($n=36,383$), willow was the primary food for NYWR moose, but in mid- ($n=56,208$) and late winter ($n=51,748$), use decreased by 50% and browsing of subalpine fir more than doubled. Use of lodgepole pine and buffaloberry also increased as winter progressed. Use of gooseberry decreased after the early winter period, and by mid-winter it was only a minor item in the diet.

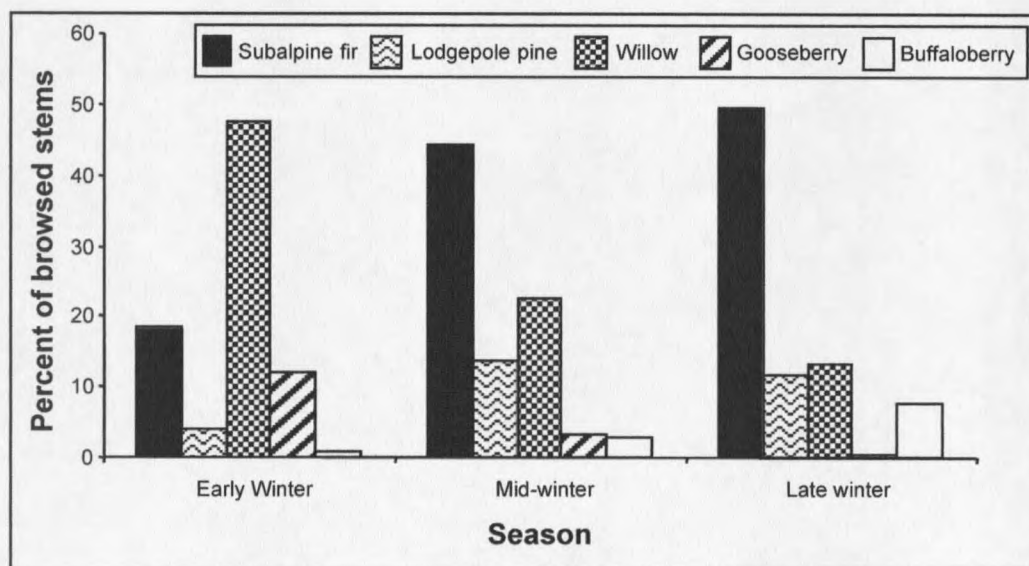


Figure 13. Plant species that comprised $\geq 5\%$ during any winter period of the total number of stems browsed by moose observed for the early (November-December), mid- (January-February), or late (March-April) winter periods over 4 years (1986-1990).

Use of browse species also varied before and after the 1988 fires by winter period (Table 6) (Appendix F, Table 56). In early winter before the 1988 fires, annual composites, Labrador tea (*Ledum glandulosum*), willow, gooseberry, and subalpine fir were used about equally. After the fires, most of the early winter diet was willow, subalpine fir, and gooseberry. Shifts in diet also occurred pre- and post-fire during the mid-

winter period. Use of subalpine fir and lodgepole pine increased post-fire, while use of willow decreased. In late winter, subalpine fir was the most important browse species both before and after the fires, but use increased post-fire. Willow and buffaloberry were also important during late winter pre-fire, but post-fire use declined by >50% for each. Lodgepole pine comprised about 1% of the pre-fire diet, but contributed about 20% post-fire and was the second most important late winter food.

Table 6. Percent of moose diet represented by plant species comprising ≥ 5 percent of browsed stems during any period recorded before (1986-1988) and after (1988-1990) the 1988 fires and the early (November-December), mid- (January-February), and late (March-April) winter periods. Numbers of bites used to calculate percent are given in parentheses.

Species	Early winter %		Mid-winter %		Late winter %	
	Pre-fire (2,628)	Post-fire (34,195)	Pre-fire (18,263)	Post-fire (34,195)	Pre-fire (23,535)	Post-fire (28,213)
Subalpine fir	11.7	19.0	30.6	50.9	44.2	53.8
Lodgepole pine	0.0	4.6	2.5	19.3	1.3	20.5
Willow	19.5	49.8	45.0	11.5	18.8	8.5
Gooseberry	14.2	11.9	8.6	0.8	1.3	0.0
Alder	1.6	0.3	2.0	3.6	5.7	1.2
Buffaloberry	0.5	1.0	4.9	1.6	14.1	2.2
Labrador tea	22.8	0.8	0.0	0.0	0.1	0.0
Annual composites	24.3	3.0	2.7	0.0	0.1	0.0

Subalpine fir and willow were the most important browse species pre- and post-fire in all study units, but proportional use of these and other species changed after 1988 in the 3 study units affected by fire (Table 7) (Appendix G, Table 57). In the pre-fire SB study unit, willow and subalpine fir were used equally, but after the fire subalpine fir was a more important browse species. Lodgepole pine was a minor food item pre-fire, but post-fire it was 10 times more prevalent in the diet. In the YP study unit post-fire, use of subalpine fir and willow decreased while use of lodgepole pine and Douglas fir more than tripled. The greatest diet changes occurred in the SC study unit. Use of subalpine fir was about 3 times greater prior to the fires. After the fires, willow use increased and lodgepole pine was 5 times more prevalent in the diet. The only use of burned plant material I found was post-fire browsing of burned lodgepole pine, subalpine fir, and Douglas fir in the SC study unit. BC study unit did not burn in 1988 and changes in diet pre- and post-fire were minor.

Table 7. Percent of moose diet represented by plant species comprising ≥ 5 percent of browsed stems during any period recorded before (1986-1988) and after (1988-1990) the 1988 fires in the SB, YP, SC, and BC study units. Numbers of bites used to calculate percent appear in parentheses.

Species	SB %		YP %		SC %		BC %	
	Pre (16,311)	Post (25,618)	Pre (5,663)	Post (23,219)	Pre (5,257)	Post (25,016)	Pre (17,381)	Post (26,294)
Subalpine fir	28.4	46.8	45.5	36.1	56.6	16.8	51.5	54.6
Lodgepole pine	0.5	10.9	4.2	13.6	7.9	34.8	0.1	0.0
Douglas fir	6.2	0.8	0.7	6.6	0.0	0.3	0.4	0.0
Willow	28.6	30.6	24.7	12.3	21.5	33.9	23.2	25.0
Gooseberry	2.7	2.9	10.4	4.9	3.3	0.0	8.1	7.3
Maple	5.1	0.1	4.6	4.5	0.0	0.0	0.1	0.0
Alder	0.8	1.6	0.1	0.0	6.8	2.5	4.5	3.5
Ninebark	0.1	0.0	5.0	2.4	0.0	0.0	0.0	0.0
Buffaloberry	16.3	2.9	0.4	1.4	1.9	0.0	4.4	4.6
Annual composites	5.7	0.9	0.1	1.0	0.1	0.0	2.8	0.6

Use of burned plant material, potentially an expression of impoverished habitat conditions, varied among winter periods and study units (Table 8). Post-fire, 1.8% of all recorded browsed twigs were burned. In early winter among all study units, no browsing was found on burned plant material. However, browsing increased to 1.8% by mid-winter and to 4% in late winter. The highest percentage of browsing on burned vegetation occurred in SC, 7.0%. No burned vegetation was browsed in early winter in SC, but 6.6% of the browsed twigs were on burned plants in mid-winter and 19.0% in late winter. No browsing on

Table 8. Percent of twigs browsed by moose on burned and unburned plants reported for all burned study units (excludes BC), each study unit, and the all (1988-1990), early (November-December), mid- (January-February), and late (March-April) winter periods post-fire.

Study unit	Winter period	Sample size	Burned twigs -%	Unburned twigs-%
Combined	Early	34,195	0.0	100.0
	Mid-	37,945	1.8	98.2
	Late	28,213	4.0	96.0
SC	All	25,016	7.0	93.0
	Early	9,014	0.0	100.0
	Mid-	10,393	6.6	93.4
SB	Late	5,609	19.0	81.0
	All	41,956	0.0	100.0
	Early	11,270	0.0	100.0
YP	Mid-	17,322	0.0	100.0
	Late	13,364	0.0	100.0
	All	23,219	0.3	99.7
	Early	6,809	0.0	100.0
	Mid-	9,768	0.0	100.0
	Late	6,642	1.0	99.0

burned vegetation was documented in SB and only a small amount (0.3%) in YP. All use of burned material in YP occurred in late winter.

Use of Browse in Relationship to Abundance

Tests for differences in the proportion of trees browsed versus trees available for browsing showed that in all ages of lodgepole pine, Douglas fir, and spruce-fir forests, subalpine fir was browsed in proportions greater than availability. Lodgepole pine and spruce were browsed in proportions less than availability in all ages and types of forests. Douglas fir was also used in proportions less than availability except in mid-age Douglas fir forests where it was used in proportions greater than availability, and in old spruce-fir forests where it was used in proportion to availability. Whitebark pine was not found in the young and mid-age Douglas fir forests. It was used in proportion to availability in the old spruce-fir forests and less than availability in the other types and ages of forests (Appendix H, Tables 58-65).

Variation in Browsing Among Cover Categories

In the early winter period, 71% of browsed stems were found in willow and spruce-fir cover categories (43% and 28%, respectively) (Table 9) (Appendix I, Table 66). As winter progressed, use in these areas decreased by more than 5-fold to 13%, whereas an opposite pattern of use occurred in the mature lodgepole pine and Douglas fir forests with use increasing from 13% in early winter to 65% in late winter.

Table 9. Cover categories with $\geq 4\%$ of browsed stems in any period over four winters (1986-1990) in the early (November-December), mid- (January-February), and late (March-April) winter periods. Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Numbers of browsed stems used to calculate percent appear in parentheses.

Cover category	Early winter (%) (36,823)	Mid-winter (%) (56,246)	Late winter (%) (51,782)
Willow	30.8	12.4	2.9
Young conifer/willow	3.9	4.5	6.4
Oldest conifer/willow	7.9	6.6	3.7
Oldest Douglas fir	0.0	4.7	17.2
Young lodgepole	4.3	4.3	2.5
Mid-age lodgepole	3.3	16.2	24.6
Oldest lodgepole	9.7	31.0	25.0
Oldest spruce-fir	28.4	13.4	7.7
Sagebrush	4.7	0.7	0.0

There were also differences in the distribution of browsed stems before and after the fires (Table 10) (Appendix J, Table 67). Early winter browsing shifted from mature coniferous forests to areas with willow after the fires. The mid- and late winter post-fire trend was reversed. Post-fire use was less in willow areas, while the number of browsed stems found in the mature coniferous forests increased. Use in mature spruce-fir forests was an exception in that post-fire use declined.

Table 10. Cover categories with $\geq 4\%$ of twigs browsed by moose during any period as expressed by a percentage of the total for the early (November-December), mid- (January-February), and late (March-April) winter periods before and after the 1988 fires (1986-1990). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Numbers of browsed stems used to calculate percent appear in parentheses.

Species	Early winter %		Mid winter %		Late winter %	
	pre-fire (2,628)	post-fire (34,195)	pre-fire (18,263)	post-fire (37,983)	pre-fire (23,569)	post-fire (28,213)
Willow	7.5	32.6	21.0	8.3	4.8	1.2
Young conifer/willow	8.6	3.5	4.1	4.7	10.3	3.2
Mid-age conifer/willow	3.5	1.9	4.6	0.0	0.0	1.9
Oldest conifer/willow	0.0	8.5	18.8	0.7	3.4	3.9
Oldest Douglas fir	0.0	0.0	0.0	6.9	18.8	16.0
Young lodgepole	0.0	4.7	0.3	6.2	0.0	4.6
Mid-age lodgepole	20.6	1.9	4.3	21.9	21.7	27.0
Oldest lodgepole	9.4	9.7	29.3	31.9	18.2	30.8
Oldest spruce-fir	50.4	26.7	16.1	12.2	12.6	3.7
Sagebrush	0.0	5.1	0.0	1.0	0.0	0.0

Browsing activity varied pre- and post-fire among cover categories in the study units (Table 11) (Appendix K, Table 68). Most SB browsing activity before the fire was in the oldest Douglas fir and lodgepole pine. However, significant amounts of the oldest Douglas fir burned in 1988, and post-fire use shifted from these areas to the less affected oldest lodgepole pine. Similarly in YP, most browsing activity before the fire was in the oldest lodgepole pine, oldest spruce-fir, and willow. Extensive fires removed winter range of mature lodgepole pine and spruce-fir, and post-fire browsing activity shifted to unburned mid-age lodgepole pine. Willow use also declined post-fire in YP. Two radiocollared moose that utilized the Blacktail Creek willow stand starved in 1989 with the loss of adjacent forested winter range (see Chapter 2). No moose were subsequently observed using the former home ranges of these animals. The oldest lodgepole stands in SC also burned in 1988, and browsing activity shifted from these areas to the willow stands in Frenchy's Meadow and adjacent young lodgepole stands. BC did not burn and no shift in cover types use was observed, browsing activity was divided between mid-age lodgepole pine, oldest lodgepole, and oldest spruce-fir both pre- and post-fire.

Table 11. Cover categories with $\geq 4\%$ of twigs browsed by moose during any period as expressed by a percentage of the total for the SB, YP, SC, and BC study units before (1986-1988) and after (1988-1990) the 1988 fires. Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Numbers of browsed stems used to calculate percent appear in parentheses.

Cover category	SB%		YP%		SC%		BC%	
	pre-fire (16,365)	post-fire (25,646)	pre-fire (5,663)	post-fire (23,219)	pre-fire (5,257)	post-fire (25,016)	pre-fire (17,381)	post-fire (26,294)
Willow	17.3	16.7	25.9	11.7	8.1	21.4	5.3	6.2
Young conifer/willow	0.0	1.3	0.0	0.0	4.3	10.6	8.9	9.4
Mid-age conifer/willow	1.8	2.5	0.0	0.0	5.4	2.2	0.4	0.8
Oldest conifer/willow	9.0	9.5	0.0	0.0	3.1	0.6	13.2	9.7
Young Douglas fir	0.5	0.0	7.1	5.5	0.0	0.0	0.0	0.0
Mid-age Douglas fir	0.0	0.0	0.0	6.6	0.0	0.0	0.5	0.1
Oldest Douglas fir	21.6	9.9	9.9	8.5	0.0	2.1	4.4	5.5
Young lodgepole	0.0	2.0	0.0	2.5	1.1	10.6	1.1	3.5
Mid-age lodgepole	5.8	6.6	0.0	18.7	9.5	20.6	20.5	23.8
Oldest lodgepole	19.2	30.2	30.4	18.2	49.9	20.9	28.0	21.3
Oldest spruce-fir	13.2	17.9	26.8	13.6	18.7	6.1	17.0	18.5
Sagebrush	0.0	0.0	0.0	3.9	0.0	4.9	0.0	0.0

Browsed plant species varied among cover categories (Table 12), but willow and subalpine fir were the most common. In cover categories where willow was dominant or co-dominant with young to mature conifers, willow received the most browsing of any available woody plant. Subalpine fir was the preferred browse species in all categories that included mid-age and older conifers, regardless of dominant tree species.

The preferred browse species varied by stand age in the Douglas fir type. In young stands most browsed stems were ninebark (*Physocarpus malvaceus*), while in mid-age Douglas fir, most were gooseberry, and in the oldest stands, most were subalpine fir. There were also differences among successional stages of lodgepole pine. In young stands, most browsed stems were lodgepole pine, while in mid-age and the oldest lodgepole pine, the preponderance of browsing occurred on subalpine fir. The sample size was too small to make a statement for the young spruce-fir cover category, but in mid-age and the oldest spruce-fir, most browsed stems were also subalpine fir. Too few bites were recorded in young and mid-age whitebark pine cover categories for valid estimates, but in the oldest whitebark pine, most browsed stems were from subalpine firs.

Moose browsed more intensively in the late successional stage of 3 types of coniferous forests (Table 13). About 10 times more browsing was recorded in the oldest than the youngest forests and about 2.5 times more in the oldest forests than the mid-successional stage forests.

Table 12. Five plant species with the most recorded twigs browsed by moose during the winter (1986-1990) in each cover category expressed as a percent of the total twigs browsed in that category. Young = 0-100, mid-=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Only cover categories in which >100 bites were recorded are included. Scientific names are give in Appendix D, Table 54.

Cover category size (n)	Sample	Species 1	%	Species 2	%	Species 3	%	Species 4	%	Species 5	%
Willow	19,810	Willow	97.4	Cinquefoil	1.5	Gooseberry	0.6	Subalpine fir	0.2	Others	0.1
Young conifer/willow	7,317	Willow	74.1	Lodgepole	18.9	Subalpine fir	4.7	Buffaloberry	1.7	Others	0.1
Mid-age conifer/willow	2,131	Willow	90.5	Lodgepole	4.7	Buffaloberry	3.2	Subalpine fir	1.0	Honeysuckle	0.5
Old conifer/willow	8,491	Willow	83.9	Gooseberry	9.2	Subalpine fir	3.0	Alder	1.4	Lodgepole	1.2
Young Douglas fir	1,758	Ninebark	36.6	Douglas fir	25.3	Maple	20.0	Buffaloberry	4.8	Lodgepole	3.6
Mid-age Douglas fir	1,569	Gooseberry	24.9	Douglas fir	24.8	Snowberry	10.3	Maple	9.6	Composites	9.1
Oldest Douglas fir	12,069	Subalpine fir	57.9	Douglas fir	12.9	Buffaloberry	9.2	Maple	8.2	Honeysuckle	4.2
Young lodgepole pine	5,322	Lodgepole	61.7	Subalpine fir	20.0	Alder	4.9	Willow	4.7	Burn lodgepole	3.8
Mid-age lodgepole pine	23,039	Subalpine fir	48.8	Lodgepole	28.0	Buffaloberry	9.3	Alder	2.9	Burn lodgepole	1.9
Old lodgepole pine	34,217	Subalpine fir	75.8	Lodgepole	10.9	Buffaloberry	4.4	Alder	1.6	Honeysuckle	1.4
Mid-age spruce-fir	1,316	Subalpine fir	54.3	Cinquefoil	10.3	Buffaloberry	10.0	Labrador tea	7.3	Gooseberry	5.5
Old spruce-fir	22,016	Subalpine fir	45.4	Gooseberry	20.8	Alder	8.3	Composites	7.9	Buffaloberry	5.1
Old whitebark pine	1,391	Subalpine fir	71.9	Buffaloberry	24.7						
Aspen/conifer	894	Aspen	46.8	Cottonwood	27.0	Willow	24.8	Ninebark	0.9	Gooseberry	0.6
Sagebrush	2,115	Willow	59.6	Lupine	25.0	Cinquefoil	10.9	Dwarf birch	3.0	Lodgepole	0.5
Other	1,029	Sumac	82.1	Willow	11.6	Elderberry	5.9	Serviceberry	0.4		

Table 13. Distribution of browsed twigs among the early, mid-, and late successional stages of 3 types of coniferous forests. Data are reported as a percent of the total browsed twigs found in each type of forest. Data are also summarized as a percent of the total browsed twigs counted in each successional stage for the 3 forest types combined. Browsed twigs were recorded while back-tracking radiocollared and uncollared moose during the winter in 1986-1990.

Forest type	Early successional		Mid-successional		Late successional	
	%	Sample size	%	Sample size	%	Sample size
Spruce-fir	0.0	n=0	5.6	n=1,316	94.7	n=22,016
Douglas fir	11.8	n=1,758	10.6	n=1,569	77.6	n=11,543
Lodgepole pine	8.5	n=5,322	37.0	n=23,039	54.5	n=33,975
Total of 3 forest types	7.0	n=7,080	25.8	n=25,924	67.2	n=67,534

Variation in Browsing Rate in Cover Categories

Comparisons of twigs browsed per meter traveled in different cover categories after the 1988 fires, different periods of the winter, and burned and unburned areas showed that in each time period, the greatest number of twigs browsed per meter traveled were in cover categories that included willow (Table 14).

Table 14. Average number of twigs browsed by moose per meter traveled in different cover categories during the first 2 winters (1988-89, 1989-90) post-fire and the early (November-December), mid- (January-February), and late (March-April) periods of those winters. Young = 0-100, mid-=100-300, and old-est=300+ years post-disturbance (Mattson and Despain 1985).

	All	Early	Mid-	Late	Burned areas
Willow	4.0	4.3	3.4	3.2	
Young conifer/willow	5.1	12.1	4.0	4.4	
Mid-age conifer/willow	11.6	9.5		15.8	0.1
Oldest conifer/willow	4.7	5.7	1.8	4.2	
Young Douglas fir	1.2		1.6	0.7	
Mid-age Douglas fir	0.3	0.1	1.6	0.6	
Oldest Douglas fir	2.0		1.7	2.4	0.6
Young lodgepole pine	1.6	1.6	1.9	1.5	1.1
Mid-age lodgepole pine	1.6	0.3	2.4	1.5	1.0
Oldest lodgepole pine	2.5	1.8	2.8	2.4	1.3
Young spruce-fir					
Mid-age spruce-fir	0.5	0.5			
Oldest spruce-fir	1.6	1.9	1.2	0.7	0.1
Young whitebark pine					
Mid-age whitebark pine					
Oldest whitebark pine	5.5			5.5	
Conifer aspen	5.4	4.2	7.3		
Sagebrush	0.9	1.1	1.6		
Grass/forb meadow	0.1		0.1		
Other	0.7		0.7	0.8	

Post-fire, the 5 cover categories with the highest number of twigs browsed per meter traveled were mid-age conifer/willow, the oldest whitebark, aspen and cottonwood, young conifer/willow, and the oldest conifer/willow. In early winter, they were young conifer/willow, mid-age conifer/willow, the oldest conifer/willow, willow, and aspen/cottonwood. Mid-winter they were aspen/cottonwood, young conifer/willow, willow, the oldest lodgepole, and mid-age lodgepole. Late winter, mid-age conifer/willow, the oldest whitebark, young conifer/willow, and willow had the highest number of browsed twigs recorded per meter traveled.

The average number of twigs browsed per meter traveled post-fire in all unburned cover categories was: all winter- 2.9, early winter- 3.6, mid-winter-2.3, late winter- 3.3. The average number of twigs browsed per meter traveled was 0.7 in burned areas. Differences were not significant between early, mid-, and late winter periods ($H = 0.23$, $P = 0.891$). However, the difference in twigs browsed per meter traveled was significant between unburned and burned areas ($Z = 21.67$, $P = 0.03$).

Variation in Use of Subalpine Fir

In all winter periods, nearly 100% of the browsed subalpine fir trees were <5 m tall and almost 1/2 were <1 m tall (Table 15). More trees <1 m were browsed in early winter than in mid-winter or late winter. Over all years and sites, the greatest frequency of browsing was on the 50-99 cm size class (32.7%). However, in early winter, the most frequently browsed size class was 0-49 cm.

Table 15. Frequency of browsing on subalpine fir by size class. Data are reported for all winters (1986-1990), early (November-December), mid- (January-February), and late (March-April) winter periods.

Size class	Early winter % of browsed n=664	Early winter % of total	Mid-winter % of browsed n=1,302	Mid-winter % of total	Late winter % of browsed n=1,595	Late winter % of total	All winter % of browsed n=3,561	All winter % of total
0-49	40.8	40.8	12.5	12.5	10.2	10.2	16.5	16.5
50-99	39.0	79.8	30.3	42.8	32.7	42.9	32.7	49.2
100-149	11.9	91.7	23.2	66.0	23.9	66.8	21.5	70.7
150-199	5.6	97.3	16.5	82.5	15.3	82.1	14.1	84.8
200-249	1.2	98.5	7.5	90.0	8.2	90.3	6.8	91.6
250-299	1.0	99.5	4.5	94.5	4.2	94.5	3.7	95.3
300-349	0.2	99.7	3.3	97.8	2.9	97.4	2.6	97.9
350-399	0.1	99.8	1.5	99.3	1.9	99.3	1.4	99.3
400-499	0.1	99.9	0.7	100.0	0.5	99.8	0.5	99.8
450-500	0.0	99.9	0.1	100.1	0.1	99.9	0.1	99.9

The difference in number of twigs browsed per subalpine fir tree was significantly different pre- and post-fire for each study unit except YP (Table 16). It was also significantly different when data for all study units were combined and when data for all study units except BC (which did not burn) were combined. In each study unit and when the data were combined, the post-fire average was higher than the pre-fire average.

Table 16. Average number of twigs browsed per subalpine fir by radiocollared and uncollared moose backtracked through the snow. Data are reported as the number of browsed twigs/browsed trees for the pre- (1986-1988) and post-fire (1988-1990) periods in all study units combined and each study unit. Data from Bear Creek, which did not burn, were excluded from one test. T and P values of tests are given in the table.

	Pre-fire	Post-fire	T	P<
All (w/o BC)	10,218/1,206 = 8.5	124,982/1,899 = 13.2	-10.2	0.001
All (w/ BC)	16,302/1,947 = 8.4	41,399/3,309 = 12.7	-12.05	0.001
BC	6,084/741 = 8.2	1,410/16,417 = 11.6	-6.69	0.001
YP	2,579/220 = 11.7	8,381/693 = 12.1	-0.36	0.723
SB	4,664/661 = 7.1	111,990/956 = 12.5	-9.75	0.001
SC	2,975/325 = 9.2	4,611/250 = 18.4	-8.19	0.001

The average number of twigs browsed per subalpine fir tree was significantly different between winter periods ($F = 64.7$, $P < 0.001$). The highest average was during mid-winter (24,993 twigs/1,969 trees=12.7) and the lowest during early winter (6,793 twigs/936 trees=7.3). The average in late winter was 11.0 (25,915 twigs/2,351 trees). *Post hoc* tests revealed that the early winter average was significantly different from the mid- and late winter averages (Appendix L, Table 69).

The average number of twigs browsed per subalpine fir tree was significantly different between study units before and after the fire (Table 17). Pre-fire, the highest average was in YP and the lowest in SB. *Post hoc* tests revealed that the high average in YP was significantly different from each of the other averages and the low average in SB was also different from the average found in SC (Appendix L, Table 70). Post-fire, the highest average was in SC, the unit that burned the most extensively. The lowest was in BC where no burning occurred. *Post hoc* testing revealed that only the high average in SC was different from the other averages (Appendix L, Table 71).

Table 17. Average number of twigs browsed per subalpine fir by radiocollared and uncollared moose backtracked through the snow. Data are reported as the number of browsed twigs/browsed trees for the pre- (1986-1988) and post-fire (1988-1990) periods in each study unit. F and P values of tests are given in the table.

	BC	YP	SB	SC	F	P<
Pre-	6,084/741 = 8.2	2,579/220 = 11.7	4,664/661 = 7.1	2,975/325 = 9.2	11.2	0.001
Post-	16,417/1,410 = 11.6	8,381/693 = 12.1	11,990/956 = 12.5	4,611/250 = 18.4	21.04	0.001

Nutritional Analysis of Browse Species

Nutritional analysis of 5 plant species used extensively by moose showed that gooseberry, with the highest winter averages of calcium, magnesium, sodium, and phosphorus, was the best overall source of macronutrients (Kubota 1974) (Figures 14-18) (Appendix M, Tables 72-76). Levels were comparatively high throughout the winter. Only subalpine fir had more potassium on average. Subalpine fir was the next best macronutrient source, although it had the lowest average dry matter weight of sodium. Willow, buffaloberry, and lodgepole pine had the lowest macronutrient levels. Variation in dry weight quantity of macronutrients was not correlated with seasonal differences in moose use of willow ($r_s = 0.5$, $P = 0.667$), subalpine fir ($r_s = 0.5$, $P = 0.667$), lodgepole pine ($r_s = -0.5$, $P = 0.667$), gooseberry ($r_s = 1.0$, $P = 1.0$) or buffaloberry ($r_s = 1.0$, $P = 1.0$).

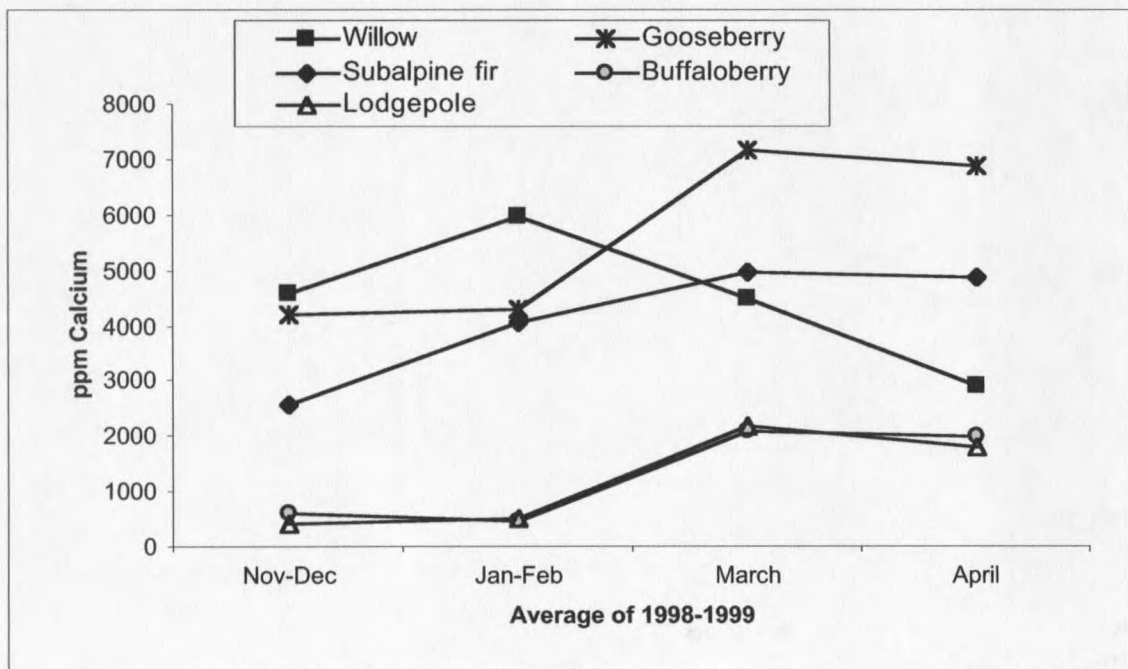


Figure 14. Dry weight quantity (ppm) of calcium in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

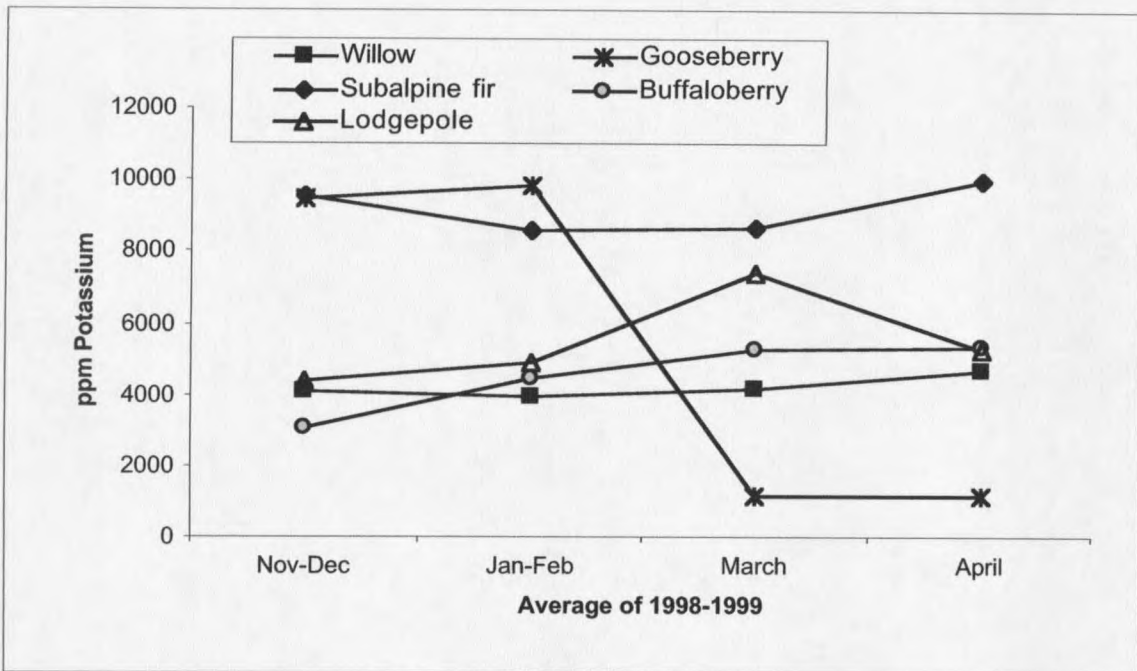


Figure 15. Dry weight quantity (ppm) of potassium in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

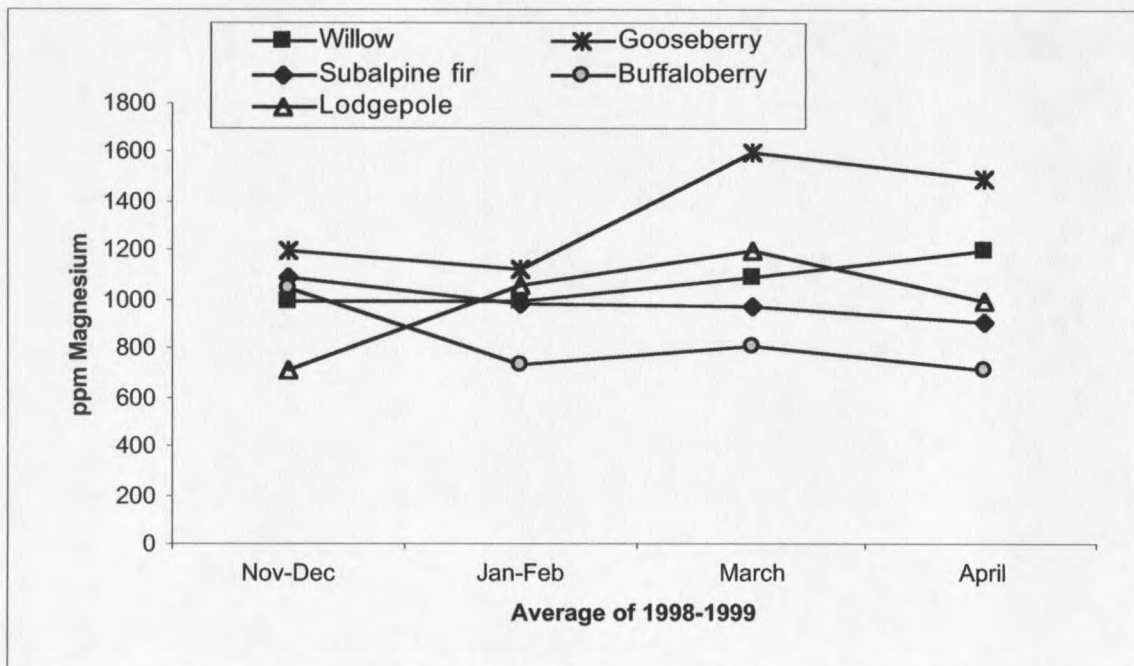


Figure 16. Dry weight quantity (ppm) of magnesium in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

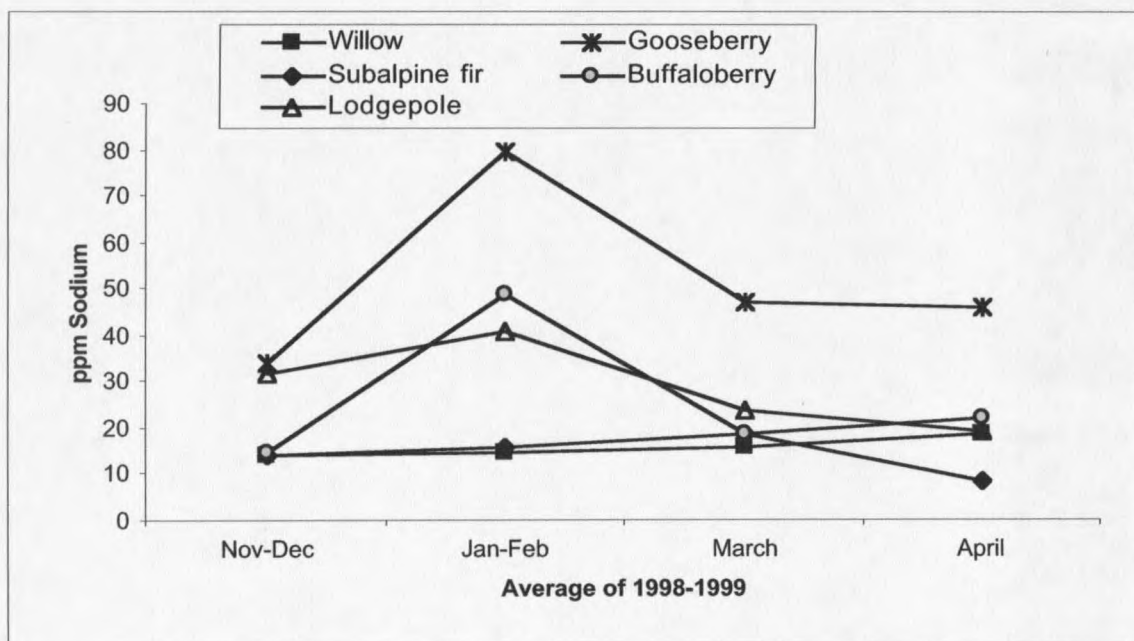


Figure 17. Dry weight quantity (ppm) of sodium in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

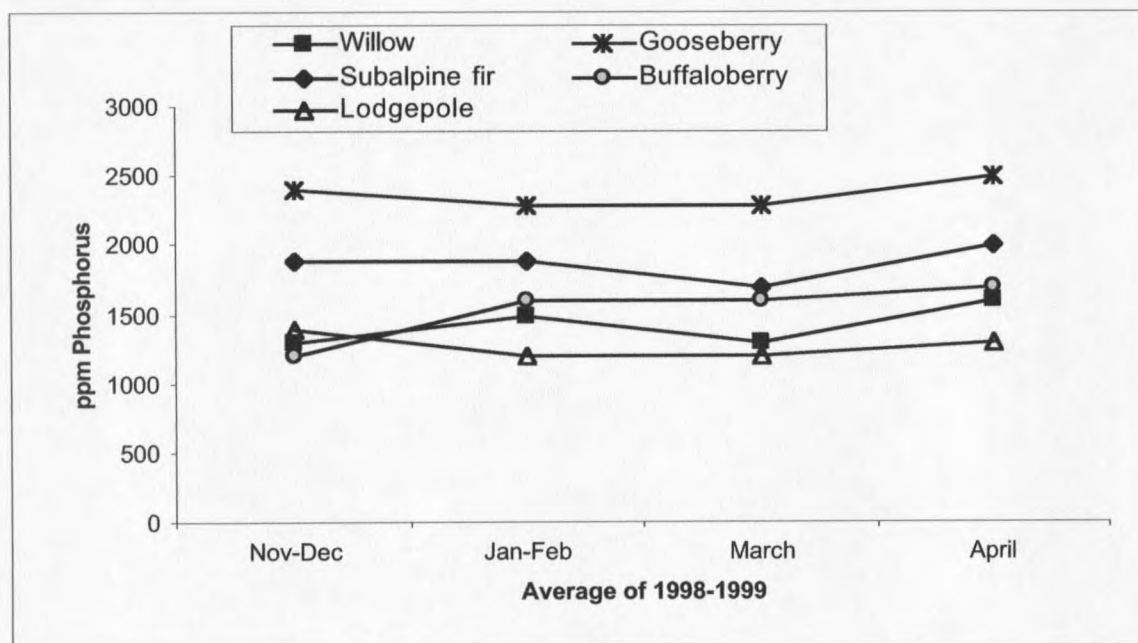


Figure 18. Dry weight quantity (ppm) of phosphorus in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

Gooseberry and subalpine fir had the highest and next highest percent dry weight of ash on average and during each winter period, respectively (Figure 19). Next in ranked order were willow, buffaloberry, and subalpine fir.

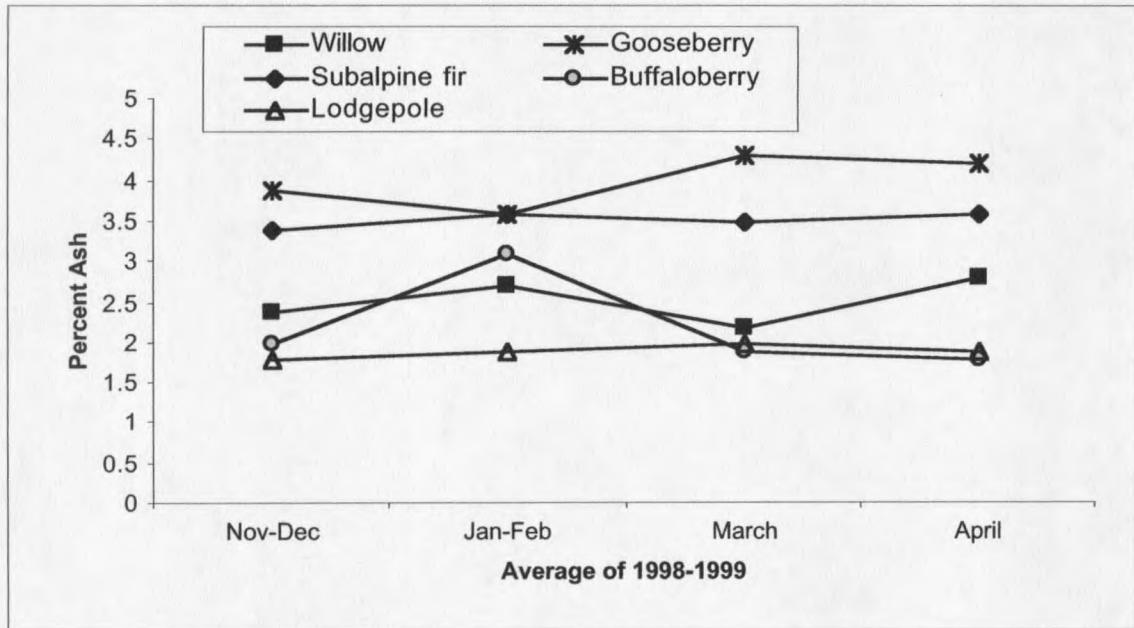


Figure 19. Dry weight quantity (%) of ash in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

Gooseberry also had the highest percent dry weight of crude fiber (Figure 20). This was true on average and for each winter period except November-December where willow had the highest. Willow had the highest percent in the later part of the winter and on average. Lodgepole pine, buffaloberry, and subalpine fir ranked next.

Buffaloberry had the lowest percent dry weight of crude protein in November and December but the highest in January-February, March, and April, and on average (Figure 21). During these periods, it consistently had about twice as much or more than the other species. Lodgepole pine had the highest percent in November and December, second highest in January-February, April, and on average. Gooseberry, subalpine fir, and willow were similar in average percent of crude protein. Variation in dry weight quantity of crude protein was not correlated with seasonal differences in moose use of willow ($r_s = -0.866$, $P = 0.333$), subalpine fir ($r_s = -0.866$, $P = 0.333$), lodgepole pine ($r_s = -1.0$, $P = 1.0$), gooseberry ($r_s = -0.5$, $P = 0.666$) or buffaloberry ($r_s = 1.0$, $P = 1.0$).

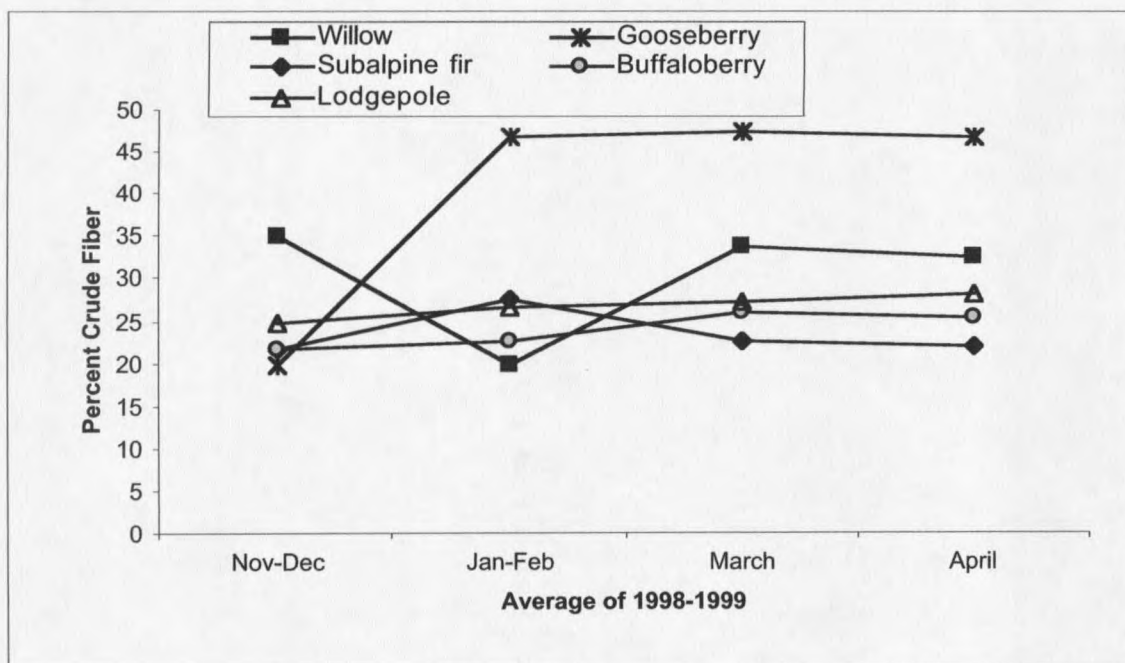


Figure 20. Dry weight quantity (%) of crude fiber in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

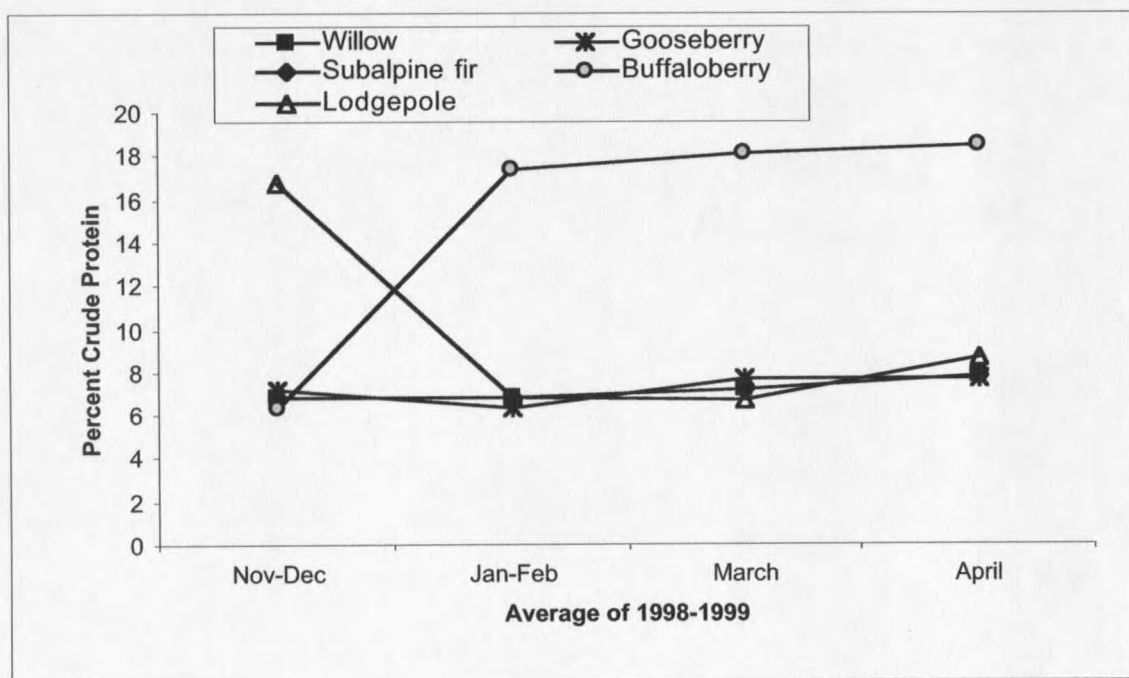


Figure 21. Dry weight quantity (%) of crude protein in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

Subalpine fir had the highest percent dry weight of ether extract on average and for each winter period except April (Figure 22). Lodgepole pine ranked second on average and had the highest percent in April. This was followed by willow and buffaloberry. Gooseberry had comparatively very little. Variation in dry weight quantity of ether extract was not correlated with seasonal differences in moose use of willow ($r_s = 1.0$, $P = 1.0$), subalpine fir ($r_s = -0.5$, $P = 0.666$), lodgepole pine ($r_s = 1.0$, $P = 0.10$), gooseberry ($r_s = -0.5$, $P = 0.666$), or buffaloberry ($r_s = -1.0$, $P = 1.0$).

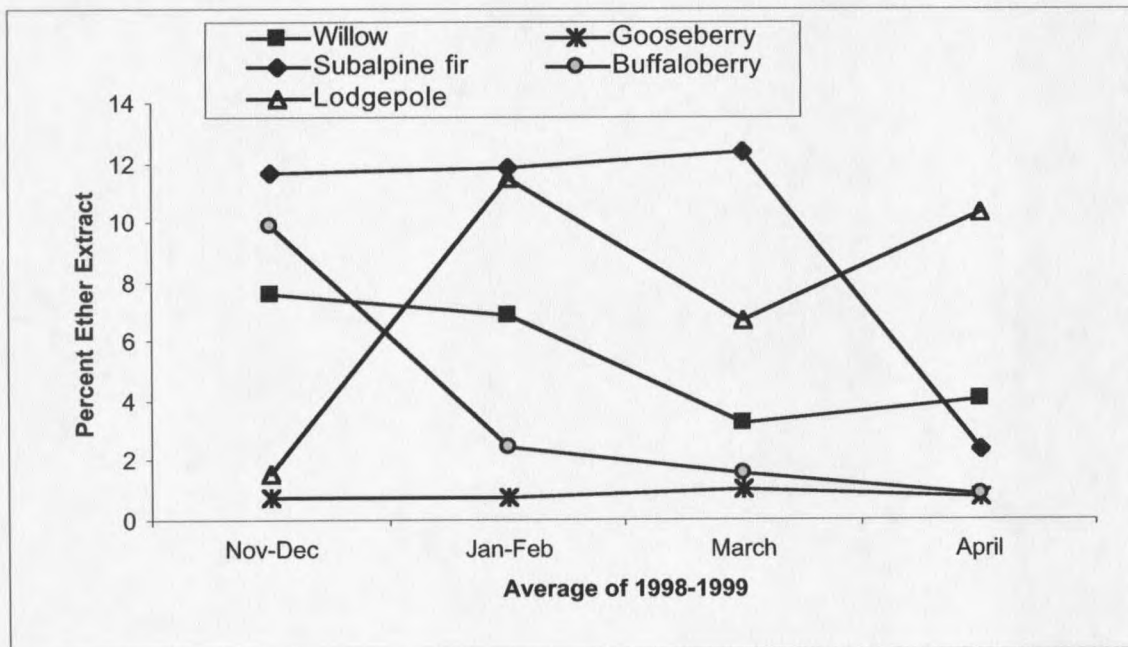


Figure 22. Dry weight quantity (%) of ether extract in 5 moose browse species summarized for 4 winter periods, 1998-99; Bear Creek Study Unit.

Discussion

Limitations of each ruminant species and its feeding strategy are determined by tradeoffs between the time available to carry out daily activities, the energy cost of these activities, and the constraints of eating food, such as ruminoreticulum capacity (Renecker and Hudson 1986a, 1992). Moose possess a unique set of ecological and physiological adaptations for balancing their energy budgets and exploiting forage resources in the harsh conditions of northern circumpolar latitudes (Telfer 1984). The larger body size of moose allows them to reduce the risk of predation, deal with cold weather, and travel long distances rapidly in difficult terrain (Telfer and Kelsall 1984). However, to compensate, moose must obtain quantities of

digestible food in patches that permit high rates of intake (Saether 1990, Saether and Anderson 1990). Moose could not survive only on sparse high-quality food because too much time would be spent in searching rather than harvesting. Thus the operating niche of moose is defined in terms of forage and nutrient distribution (Regelin et al. 1985, Renecker and Schwartz 1997).

Assessing seasonal diet composition changes for moose is difficult because not only must the food items be identified, but their amount, availability, current nutritional value, and risk of acquisition should also be determined (Schwartz and Renecker 1997). To meet winter food needs, NYWR moose used season-specific foraging patterns in response to some combination of these determinants. Well-developed pre-fire methods for finding food were interrupted by the 1988 fires that significantly altered habitat and required new foraging strategies.

The 5 principal browse species used by NYWR moose occur in the diets of other North American moose (Renecker and Schwartz 1997), but the combination and relative proportions of plant species may be unique to this area. Subalpine fir, the principal food for NYWR moose (especially during mid- and late winter), has not been widely reported in other food habits studies, but it is browsed by moose in British Columbia (Eastman and Ritcey 1987), Alberta (Cowan et al. 1950), northwest Wyoming (Harry 1957, Houston 1968), and southwest Montana (Knowlton 1960, Smith 1962, Dorn 1970, Stevens 1970). Willow is a preferred moose food and is used whenever and wherever it is available (Renecker and Schwartz 1997), including the subalpine and subarctic regions of Alaska (Risenhoover 1989) and throughout the montane regions of North America (Peek 1974a and b). Lodgepole pine has been reported in the diet of moose in British Columbia (Eastman and Ritcey 1987), Washington (Poelker 1972), southwest Montana (Smith 1962), and central Canada (Barrett 1972, Risenhoover 1987). Documentation of winter buffaloberry use is limited to Manitoba (Trottier et al. 1983) and Alberta (Renecker 1987, Cairns 1976), although McDowell and Moy (1942) observed summer use in the study area. Browsing on various species of gooseberry is reported for Manitoba (Trottier et al. 1983), Alberta (Renecker 1987), southwest Montana (Knowlton 1960, Stevens 1970), northwest Wyoming (Houston 1968), and Alaska (Hosley 1949).

Moose density is often positively associated with food abundance, which varies with seral age of forests (Schwartz and Franzmann 1989). Biomass of desirable forage species and moose numbers usually increases within several years after a disturbance and then declines (Parker and Morton 1978, Eastman and Ritcey 1987). However, NYWR moose showed a more consistent association with mature coniferous forests than with early seral communities. Almost 10 times more browsing occurred in late as opposed to early forest successional stages.

As McDowell and Moy (1942) and Peek (1974a) theorized, NYWR moose begin winter in streamside willow stands before a mid-winter shift to adjacent mature forests. In the early winter, NYWR moose consumed quantities of willow in widely scattered but concentrated areas where it was dominant or a co-dominant with young to mature conifers. They also sought nutrient-rich gooseberry in mature spruce-fir forests and subalpine fir in this and other old conifer types. As winter progressed, subalpine fir became the dominant food while use of willow decreased, use of lodgepole pine and buffaloberry increased, and gooseberry became only a minor food item. Increased use of lodgepole pine probably reflected more difficult late winter foraging conditions and the need for moose to make up for diet shortfalls. With its high winter-long content of the macronutrients calcium, magnesium, sodium, and phosphorous, gooseberry is probably nutritionally valuable to moose during all winter periods. However, it is low growing and unavailable under snow after early winter (see Chapter 5). Buffaloberry, comparatively unused in early winter, probably increased in importance because of its high late-winter crude protein content. Although among and within species variation in the nutritional quality of browse plants was apparently important determinants for NYWR moose food habitats, changes in crude protein, macronutrients, and ether extract content were not statistically correlated with seasonal diet shifts, indicating that other factors, such as snow conditions (see Chapter 5) and plant densities, may have been more important in regulating what moose ate.

Loope and Gruell (1973) were also correct in their speculation. Most mid- and late winter foraging was done in mature lodgepole pine forests where moose browsed subalpine fir. As a shade tolerant species and part of the lower layer in double canopy forests, nearly all browsed subalpine fir were <5 m tall and most were < 1m tall. Subalpine fir was used in proportions greater than availability in all ages and types of forests, while other conifer species were used less. Subalpine fir was an indicator of foraging conditions. Browsing intensity on subalpine fir increased during situations with more difficult foraging conditions due to deeper snow and loss of cover and foraging habitat, including late winter, after the 1988 fires, and in the areas where fire impacts were the greatest.

Moose response to the 1988 fires included changes in diet and foraging locations. Post-fire, moose abandoned burned coniferous forests in favor of nearby willow areas less affected by fire resulting in more intense early winter browsing on willow. However, use of willow stands declined in mid- and late winter to below pre-fire levels. Because these areas are spatially limited, available forage was probably exhausted in early winter with the additional browsing pressure. For example, in the SC study unit where fire effects on mature lodgepole pine and spruce-fir forests were greatest (see Chapter 2), increases in willow and lodgepole pine browsing and declines in subalpine fir browsing were also the greatest. In addition to heavy

use of remaining willow stands, moose concentrated browsing on the adjacent small stands of unburned young lodgepole pine. Use of forest dependent shrubs such as buffaloberry and gooseberry decreased post-fire with the decrease in available mature coniferous forests. In response to difficult foraging conditions, moose browsed twigs of burned trees but only where fire effects were extensive.

Ellis et al. (1976) theorized that as the disparity between forage availability and animal requirements widens, diet expansion is expected as the animal becomes less selective. In these situations an animal is expected to utilize less preferred and less nutritionally valuable forage. Food habits among NYWR moose support this theory. I found that use of burned plant material and other foraging anomalies were greatest in SC, where fire impacts were greatest (see Chapter 2) and preferred pre-fire food items were least available. This pattern was most evident in late winter when snow conditions made searching for food the most difficult (see Chapter 5). Diet composition and foraging patterns in the BC study unit, an unburned area, changed little pre- and post-fire suggesting that changes seen in the fire affected study units were fire related and not advantageous to moose.

Risenhoover (1987) reported that moose winter foraging movements provided a sensitive indicator of the amount of acceptable foods along a foraging path. As measured by the number of bites taken per meter traveled, I found that NYWR moose browsed the most stems in the shortest distance while foraging in habitats where willow was either dominant or a co-dominant with conifers. Foraging was next most efficient in the oldest coniferous forests where browsing was primarily on subalpine fir. It was significantly less efficient in the youngest conifer stands and open areas. Feeding efficiency was lowest in areas that burned in 1988.

Risenhoover (1987) concluded that moose diet varies among habitats in relationship to forage palatability and relative abundance, and that moose are quite selective about the plant and plant parts they consume. Saether and Anderson (1990) theorized that moose select the highest quality food from usable biomass in the best available habitats. Renecker and Schwartz (1997) stated that the combination of food selected and movements while foraging provide the best predictors of how moose in a given environment balance energy tradeoffs. The best foraging strategy for NYWR moose involves use of willow until snow conditions preclude access to this limited resource. The harshest winter months are spent minimizing travel by pursuing subalpine fir where snow depths are lowest in mature lodgepole pine forests (see Chapters 5 and 6). NYWR moose appear to be choosing willow and subalpine fir because, in part, they are locally plentiful in patches and require less foraging effort (see Chapters 6 and 8). Other plants such as gooseberry and buffaloberry are comparatively rare and may be worth searching for in early and late winter, respectively, because of nutritional benefits. Lodgepole pine, an abundant species browsed only

during more difficult conditions, may represent a simple attempt to maintain rumen fill. Use of lodgepole pine appears to be directly related to the magnitude of fire effects and loss of preferred foraging areas.

The reliance of NYWR moose on mature coniferous forests for winter foods makes them susceptible to natural or human-induced disturbance. Loss of these areas during the 1988 fires required moose to adopt less energy efficient foraging strategies. Where unburned woody vegetation becomes sparse or widely dispersed as occurred in 1988, moose are unlikely to prosper (Renecker and Schwartz 1997). Moose shifting to less nutritionally valuable forage and spending more time foraging illustrated this. Food shortages may compound problems for remaining moose because limited food supplies may be over-utilized. Riparian habitats with live woody vegetation tend to concentrate moose when other foraging areas are unproductive. The resulting browsing pressure may deplete food in the short term and long-term ecological changes may also ensue (Oldemeyer 1983). Because of the importance of mature conifer forests with shade-tolerant subalpine fir understories, fires had negative consequences for NYWR moose forage availability that may take centuries to erase (Loope and Gruell 1973).

Moose have evolved to survive in harsh northern climates where winter conditions require precise foraging strategies, including the use of patches of preferred food to minimize travel. NYWR moose displayed habitat use patterns commensurate with other North American moose populations by browsing rare high quality foods when available but relying on biomass concentrations of woody plants to balance energy budgets. However, the characteristics unique to NYWR moose diet and foraging patterns reveal strategies for survival specific to this environment. Unlike most populations, NYWR moose benefited from favorable foraging opportunities in mature forests rather than post-fire shrubfields (Loope and Gruell 1973).

MOOSE COVER TYPE USE
ON THE NORTHERN YELLOWSTONE WINTER RANGE

Introduction

Moose are considered "selective generalists" because they can occupy a wide variety of habitats. They are also capable of using habitat components in higher proportion than they occur and selecting seasonally advantageous areas within those environments (Neu et al. 1974, Peek 1997). The selection of cover types by moose reflects the location of resources needed to meet habitat requirements (Neu et al. 1974, Van Horne 1983, Hobbs and Hanley 1990, Peek 1997).

Cover type use patterns have implications beyond forage availability for moose. The quality of thermal and hiding cover and differences in snow conditions also influence moose habitat use (Kelsall and Telfer 1974, Coady 1982, Telfer 1984, Renecker and Schwartz 1997, Schwartz and Renecker 1997, Peek 1997). Requirements and availability of these resources may vary with environmental changes (Geist 1971, 1974, Neu et al. 1974, Kelsall et al. 1977, Oldemeyer et al. 1977). In managed forests, cover type is routinely manipulated through a variety of silvicultural practices that affect moose winter survival strategies. In addition, moose habitat in boreal forests is often substantially altered by fire requiring moose to adapt to a radically different environment (Spencer and Chatelain 1953, Spencer and Hakala 1964, Peek et al. 1976, Coady 1982, Risenhoover and Maass 1987, Thompson and Stewart 1997). Peek (1997) concluded that general descriptions are available for moose habitat use patterns in most regions but also indicated the need to determine habitat components preferred by moose in local situations, especially where significant habitat alterations have occurred.

Recent landscape level habitat alterations, primarily the 1988 Yellowstone fires, have changed about 30% of the NYWR from mature conifer forests (143,856 ha pre-fire) to early seral stages, dramatically affecting proportions of successional communities available to moose. Romme and Despain (1989) postulated that the GYA experienced a similar major fire event or series of events about 1700 followed by a period that lacked comparable disturbances. In 1988 when the fire cycle apparently repeated, more >300-year-old lodgepole pine forests existed than at any time in the past 3 centuries (Romme and Despain 1989). The 1988 Yellowstone fires affected 35% of my study area, including 29% of mature forests. In addition, although GNF timber harvesting over the past 50 years has involved <1.0% (885 ha) of the mature forests in the study area, it has added cumulatively to fire effects by increasing the proportion of young forests in moose winter range.

Across most of North America, fire and logging in mature forests are considered beneficial for moose winter range because removal of conifer competition can stimulate growth of post-disturbance shrub fields providing concentrations of deciduous moose browse and efficient foraging opportunities (Peterson 1955, Geist 1971, Kelsall and Telfer 1974, Coady 1982). However, the effects of disturbances on NYWR moose cover type use patterns have not been investigated, and others have speculated that moose habitat relationships in this area may be anomalous. Loope and Gruell (1973) hypothesized that GYA moose do not benefit from early seral stages but rather are associated with mature conifer forests where double canopies ameliorate snow conditions and provide browse. They forwarded the idea that GYA moose numbers have increased due to a general lack of stand replacing fires over several centuries. They believe subalpine fir, a shade-tolerant tree that reaches its greatest densities in the oldest forests (see Chapter 6), is the primary food item of GYA moose. In support of this theory, McDowell and Moy (1942) and Peek (1974a) speculated that NYWR moose cover type use involves an early winter association with permanent streamside willow stands until snow accumulation forces a mid-winter move to adjacent forested mountainsides where dense cover and abundant conifer browse provide for habitat needs.

Because a greater variety of cover types may be available post-disturbance in boreal forest landscapes for moose to select from, moose habitat use patterns following fires or logging can help identify critical habitat components; i.e. post-disturbance landscapes may have a greater mix of forest types and ages than more uniform undisturbed environments allowing for an assessment of moose proportional use of available successional stages (Neu et al 1974). I used the 1988 Yellowstone fires as an opportunity to examine the theories of Loope and Gruell (1973), McDowell and Moy (1942), and Peek (1974a), and contrast NYWR moose cover type use with other North American populations, the preponderance of which are associated with post-disturbance shrub fields. Results of this investigation have implications for management of moose populations and remaining NYWR mature forest habitats.

Peek (1997) maintained that a significant shortcoming in moose research and management has been the inability to determine accurately the limits of adaptability of moose to habitat alteration. To rectify this he recommended investigating patterns of moose habitat use illustrating variation among seasons, years, and areas, and determining reasons for variation. Generally, habitat use patterns for moose are obtained by comparing frequency distributions of tracks, pellet groups, or radiolocations within each habitat parameter of interest with the availability of that parameter to the population, the assumption being that there is a positive correlation between moose abundance and habitat quality (Neu et al. 1974, Van Horne 1983, Bookhout 1994, Peek 1997). Although commonly accepted, the techniques used to collect moose habitat

use data and the assumption that these data represent disparities in habitat quality have inherent drawbacks that must be taken into account (Van Horne 1983, Hobbs and Hanley 1990, Bookhout 1994, Peek 1997).

In order to identify which cover types were important for NYWR moose winter survival, I developed 4 data sets involving cover type use by radiocollared moose, pellet group and bed locations found while back-tracking moose, cover type use by moose along a road transect, and fixed linear transects to record track data by cover type. Because all of these techniques have potential biases, I used multiple methods, expanding beyond reliance on 1 technique to make sure patterns I found were generalized and accurate. I also analyzed data at various spatial and temporal scales as a cross-check on consistency among and within data sets. I was also able to use the fixed linear transects to identify overlap in cover type use between moose and other ungulates in the system. Some hypotheses were tested by more than 1 method. They included: 1) moose use of cover type did not vary by winter period; 2) moose use of cover type did not vary among study units with different vegetation characteristics; 3) moose use of cover types was not affected by landscape level changes in amount and distribution of mature coniferous forests following the catastrophic 1988 fires.

Methods

Descriptions of time intervals are: early winter = November-December, mid-winter = January-February, late winter = March-April, pre-fire = November 1986-June 1988, and post-fire = July 1988-April 1990. I used the Mattson and Despain (1985) cover type key for describing vegetation patterns, a system specific to the GYA and the accepted standard for vegetation mapping by the Departments of Interior and Agriculture. It characterizes forested areas by dominant tree species and successional stage. Descriptions for shrublands and grasslands are based on dominant vegetation. Mattson and Despain called discrete vegetation patterns "cover types". Where I combined several similar cover types, I called the result "cover categories". Rather than pooling data from the major forest types (lodgepole pine, Douglas fir, spruce-fir, and whitebark pine) by successional stages (early, mid-, and late) I kept these cover category distinctions because of potentially important environmental differences for moose among forest types and ages.

Lists of cover categories used to represent available habitat to moose varied among techniques and were affected by spatial scale, terrain differences, means of travel, and the need to keep category numbers low. For example, aircraft radio locations and bed and pellet group backtracking counts were collected at the largest spatial scale (entire study area), so cover categories are broad and represent the full range of forest types and ages potentially available. However, road transect data were obtained from vehicles along a corridor bisecting the study area through lower elevations. Consequently, cover categories for this

method reflect more available open habitat and valley bottoms and a finer data collection resolution. Track data on fixed transects were collected from skis and snow machines on roads and trails through higher elevation logged and unlogged forests. Therefore, cover categories for track-intercept transects are mostly forest types with mixes of treated and untreated stands, also at a finer resolution. In spite of differences in technique-specific cover categories, I designed the respective recording systems with sufficient commonality for comparisons among data sets.

Variation in Cover Category Use by Radiocollared Moose

Radio locations from 14 instrumented moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were collected from fixed-wing aircraft a minimum of 2 times per month, 1986-1990, and classified by 20 cover categories (Table 5). I compared cover type use data at several spatial and temporal scales, including the pre- and post-fire periods for the entire study area and for each of the 4 study units individually, and the entire study area for the early, mid-, and late winter periods. Radiocollared moose found in areas burned in 1988 were reported by burned cover category. I addressed fire effects by summarizing use of burned areas in each of the 20 cover categories and the use of areas that burned at different levels of intensity in increments of 25%. I also tested to determine if use was in proportion to availability (Neu et al. 1974). Hectares of available habitat were obtained using GIS technology and existing cover type (Mattson and Despain 1985) and 1988 burn area maps (R. Renkin, YNP, personal communication; C. Stein, GNF, personal communication).

Location of Pellet Groups and Moose Beds by Cover Category

The second data set included pellet groups and beds I encountered while back-tracking moose (Table 5). Fourteen instrumented moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were available for back-tracking. Fresh tracks from a minimum of 2 radiocollared and 2 uncollared moose were located monthly (November-April) in each study unit from 1986 to 1990. These animals were back-tracked through snow to record locations of moose pellet groups and beds. I did not follow moose because I did not want the animals to respond to my presence. I tried to get a minimum sample size of 2 pellet groups and 2 beds for each tracking effort. Cover types where pellet groups and beds occurred were summarized into 20 cover categories (Table 5) (Mattson and Despain 1985), and I tested use patterns by pre-fire, post-fire, early winter, mid-winter, and late winter periods.

Variation in Cover Category Use by Moose Seen
Along the Cooke City Road

The third data set used in cover type analysis consisted of sightings of moose along a road transect from Gardiner to Cooke City. Moose locations were recorded during 700 trips along the corridor from January 1986 to June 1997. Descriptions of the route are given in Chapter 1. I compared data among 16 cover categories along the road corridor (Table 18) for the pre-fire (1987-1988), post-fire 1 (1988-1992), and post-fire 2 (1995-1997) periods. I also summarized the data for 2-month periods including November-December, January-February, March-April, and May-June. I could not arrive at methods to adequately quantify available cover categories along the road to test if use was in proportion to availability.

Table 18. Cover type categories (Mattson and Despain 1985) used to characterize moose sightings along the Cooke City road.

Cover categories	Description
Willow	Tall (>1.5 m) and low (<1.5 m).
Oldest lodgepole pine	100-300+ year old lodgepole pine; may also contain significant spruce and subalpine fir.
Aspen	Over mature aspen, may contain significant conifer encroachment or grasslands.
Oldest spruce-fir	Mature forest dominated by spruce and subalpine fir.
Open areas	Sagebrush grasslands and moist to wet meadows.
Oldest spruce-fir/meadow	Mature spruce-fir in a mosaic of moist to wet meadows.
Oldest Douglas fir	100-300+ year old lodgepole pine; may contain significant lodgepole pine, spruce, and subalpine fir.
Oldest Douglas fir/open areas	100-300+ year old Douglas fir and other conifers in a mosaic of sagebrush grasslands.
Burned lodgepole pine	300+ year-old lodgepole pine burned in 1988.
Wet area	Marsh and fen.
Oldest lodgepole pine and meadow	100-300+ year old lodgepole pine and other conifers in a mosaic of moist to wet grasslands and meadows.
Younger lodgepole pine	40-100 year old lodgepole pine.
Younger Douglas fir	0-40 year old Douglas fir.
Sagebrush	Moist to dry sagebrush grasslands.
Lodgepole pine/sagebrush	100-300+ year old lodgepole pine mixed with sagebrush grasslands.
Oldest conifer/willow	100-300+ year old conifer and tall and low willow.

Variation in Cover Category Selection of Moose
and Sympatric Cervids on Track-Intercept Transects

The fourth data set used in cover type analysis was a system of fixed linear track transects. This data set allowed me to determine if moose, elk, and deer used 10 cover categories (Table 19) in proportion to their availability. I grouped moose and elk track data for analysis into pre- (1986-1988) and post- (1988-

1990) fire periods and the early (November-December), mid- (January-February), and late winter periods (March-May). Because almost all mule deer tracks were in the BC study unit and it was the only one not affected by fire, I analyzed these data for the 4 years combined.

Table 19. Cover categories (Mattson and Despain 1985) along fixed transects where moose tracks were searched for. Percent indicates amount of cover category available.

Cover categories	Description
Willow (4.0%)	Sites dominated by <i>Salix</i> spp. typically occurring on floodplains, along streambanks, and on gently sloping seeps.
Young lodgepole pine (18%)	Forests dominated by lodgepole pine from 1 to 100 years post-disturbance.
Oldest lodgepole pine/sagebrush (7.3%)	Forests dominated by lodgepole pine 100+ years post-disturbance in combination with sagebrush shrublands.
Oldest lodgepole pine (14.9%)	Forests dominated by lodgepole pine 100+ years post-disturbance. Spruce, subalpine fir, and whitebark pine may also be strongly represented.
Oldest lodgepole pine/meadow (6.3%)	Forests dominated by lodgepole pine 100+ years post-disturbance in combination with unforested areas of diverse species of grasses and forbs. Spruce, subalpine fir, and whitebark pine may also be strongly represented.
Conifer/willow (17.2%)	Diverse <i>Salix</i> spp. in combination with a coniferous forest. The forests are in any stage of successional development and include any of the conifers found in this region including lodgepole pine, spruce, subalpine fir, Douglas fir, and whitebark pine.
Oldest lodgepole pine/young conifer (13.2%)	Forests dominated by lodgepole pine 100 years in combination with coniferous forests from 1 to 100 years post-disturbance. Spruce, lodgepole pine, and whitebark pine may be strongly represented in the oldest lodgepole pine component.
Oldest spruce-fir/young conifer (2.2%)	Stands dominated by mature spruce and subalpine fir in combination with coniferous forests 1 to 100 years post-disturbance.
Douglas fir/sagebrush (9.8%)	Forests dominated by Douglas fir in all stages of development post-disturbance in combination with sagebrush shrublands.
Oldest spruce-fir (6.6%)	Stands dominated by mature spruce and subalpine fir; these tree species form both the understory and overstory.

Jenkins (1985) described a protocol for using tracks in snow along fixed linear transects to investigate distribution and habitat selection of ungulates, including moose. I established transects based on this protocol in 3 of the 4 study units – SB, SC, and BC. I conducted a preliminary reconnaissance to determine the spatial limits of moose winter range along an elevation gradient. Transects were designed to extend above and below observed moose winter range. In SC and SB, transects roughly followed the stream course. In BC, the pattern was dendritic and followed a network of logging roads.

The same route was used with each sample. Travel was by skis, snowshoes, or snowmobiles depending on travel restrictions and convenience. Transects were sampled 2 to 4 times a month from November through May. Because the snow pack arrived and melted at different times annually, the initiation and conclusion dates for transects varied.

Transects were traveled approximately 24 hours after a snowfall. New snow provided a fresh surface to "read" tracks. Each time a track was intercepted, it was recorded. In addition to moose tracks, I recorded elk and mule deer because of the importance of winter distribution and habitat relationships of these species in sympatry (Cairns and Telfer 1980, Boonstra and Sinclair 1984, Jenkins 1985). If tracks were difficult to identify, they were followed off the transect until a distinguishing foot print, hair sample, or pellet group was located.

A track was recorded when it crossed the transect. The track of an animal walking down the path was recorded once. A track indicating an animal had crossed the path to browse and then re-crossed the path to browse on the other side was counted as many times as it crossed and re-crossed. The animal was expressing a behavioral link to that area by where it traveled. Therefore, each time it crossed the path the intercept was recorded to capture that behavior. This is a departure from the methods used by Jenkins (1985) where tracks were recorded once in these instances.

At each track, cover types were described by what was found on each side of the transect. This distinction was important in areas where timber harvesting or forest fires had occurred. Often, harvest boundaries or fire perimeters were found at the edge of the road used for the transect because the road defined the timber sale or served as a firebreak. I considered the cover type to be different each time the pattern of vegetation changed on either side of the road. The location of each cover type was mapped on an aerial photograph. Photocopies of these photos were carried in the field, and tracks were recorded at appropriate locations on the photocopy for later transfer to data forms.

I found 166 cover type combinations, which I consolidated into 10 cover categories for moose and elk tracks and 7 for mule deer tracks (Table 19). Because mule deer used fewer cover categories, I combined categories 1 and 6 (Table 19), 4 and 5, and 7 and 8 for a total of 7. The availability of each cover category was determined in the summer by measuring lengths with a hand operated odometer wheel.

Statistical Tests

Analysis of habitat selection is a common aspect of wildlife science and various methods were available. I reviewed several documents to determine appropriate tests and the best way to organize data

(Aldredge and Ratti 1986, White and Garrott 1990, Aldredge and Ratti 1992). A method associated with Chi-square goodness of fit test as described by Neu et al. (1974) best matched these data. Differences in use patterns were tested using Chi-square in conjunction with the Bonferonni Z-statistic when data on use and availability were recorded. To ensure that Chi-square tests were robust for the road transect data, I limited the number of categories representing what was available in the environment to 10. In addition, not more than 20% of the categories reflected 5% or less of the actual use data. Because it was more difficult to limit category numbers for the radio location data, I used similar but different rules to test proportional use by instrumented moose, i.e. cover types with <5% available or <5 moose locations were not included. To meet these assumptions, I sometimes pooled radio location data among 4 willow categories. To simplify reporting, I described habitat used in proportions greater than availability as preferred and habitat used proportionally less than availability as avoided, recognizing that these descriptors overstate the relationship of animals to their environment.

Results

Variation in Cover Category Use by Radiocollared Moose Among Winter Periods

Analysis of landscape level moose radio location data indicated important shifts in cover category use among winter periods. However, although the forest types moose were found in varied among the early, mid-, and late winter periods, they were associated with mature conifer forests winter-long. Of the cover categories with no or minimal forest cover, only willow was important and use in these areas was greatest in early winter.

Utilization of the oldest lodgepole pine cover category by radiocollared moose (n=609) increased throughout the winter with >50% of the mid- and late winter utilization in this type (Figure 23). Conversely, utilization of the oldest spruce-fir and willow types declined throughout the winter. Use of the oldest whitebark pine cover category and oldest Douglas fir cover category peaked in mid- and late winter, respectively, but neither type was >10% of utilization.

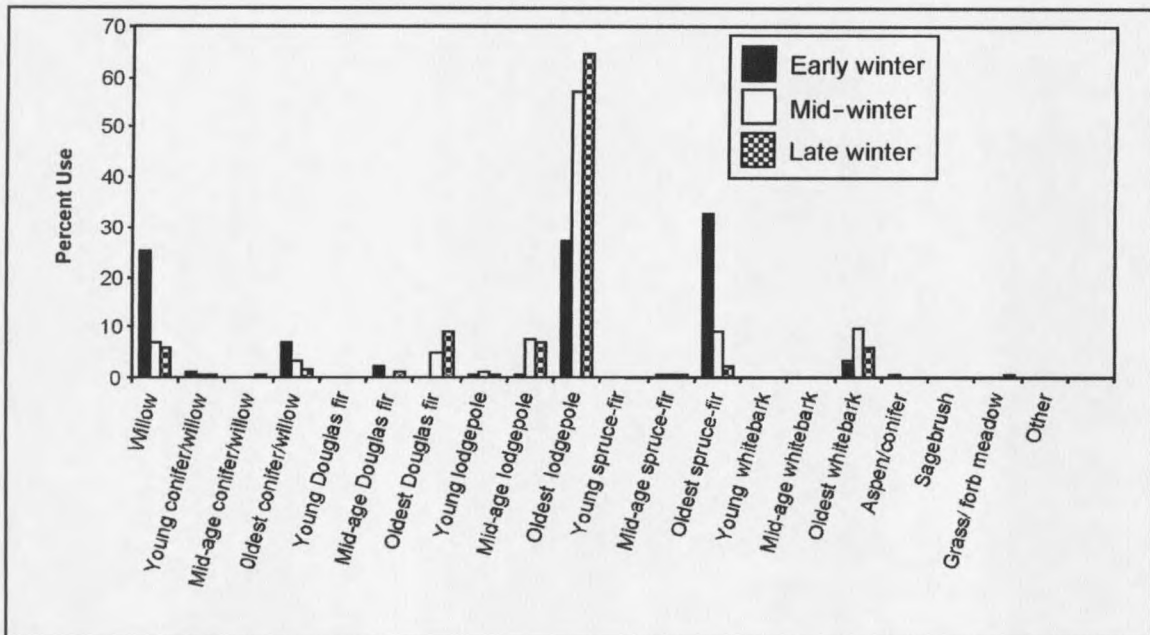


Figure 23. Winter cover type use by 14 radiocollared moose summarized in 20 categories (Table 5). Data are reported for the early (November-December), mid- (January-February), and late (March-April) winter periods and represent all radio locations over 4 winters; November through April 1987-1991. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).post-fire 2 – January 1995 to December 1997. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Variation in Cover Category Use by Radiocollared Moose Among Study Units

Analysis of radio location data at a smaller spatial scale (individual study units) provided an opportunity to cross-check moose landscape level cover category use patterns. These data also revealed an association of moose with mature conifer forests, especially lodgepole pine, and willow. Radiocollared moose in each study unit were found in the oldest lodgepole pine forests about 50% of the time (Table 20). In the SB and SC study units, about 20% of radio locations were in well-defined willow stands, while the remainder were in other mature coniferous forests. In YP and BC, which lacked comparable streamside willow stands, 20% and 16% of radio locations, respectively, were in the oldest spruce-fir forest, and the rest of the use was distributed among mature whitebark pine, lodgepole pine, and Douglas fir forests.

Table 20. Winter cover type use by 14 radiocollared moose summarized in 20 categories (Table 5). Data are reported for each study unit and represent all locations over 4 winters, November through April 1987-1991. Data are a percent of the total in each column. Young = 0-100, mid = 100-300 and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Numbers of radio location used to calculate percent appear in parentheses.

Cover categories	YP (177)	SB (224)	BC (179)	SC (89)
Willow	6.2	19.2	5.0	19.1
Young conifer/willow	0.0	0.0	0.6	3.4
Mid-age conifer/willow	0.0	0.4	0.0	0.0
Oldest conifer/willow	4.5	4.5	3.4	0.0
Young Douglas fir	0.0	0.0	0.0	0.0
Mid-age Douglas fir	4.0	0.0	0.0	0.0
Oldest Douglas fir	4.5	9.4	2.2	1.1
Young lodgepole pine	1.1	0.0	0.6	1.1
Mid-age lodgepole pine	2.8	1.8	7.8	13.5
Oldest lodgepole pine	51.4	49.6	52.5	52.8
Young spruce-fir	0.0	0.0	0.0	0.0
Mid-age spruce-fir	0.6	0.9	0.0	0.0
Oldest spruce-fir	20.3	8.0	16.2	9.0
Youngest whitebark pine	0.0	0.0	0.0	0.0
Mid-age whitebark pine	0.0	0.0	0.0	0.0
Oldest whitebark pine	2.8	6.3	11.7	0.0
Aspen/conifer	0.6	0.0	0.0	0.0
Sagebrush	0.0	0.0	0.0	0.0
Grass/forb meadow	1.1	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0

Variation in Cover Category Use by Radiocollared Moose Related to Fire Effects

The 1988 Yellowstone fires did not result in substantive shifts in cover category use by radiocollared moose. Although >10 times more early successional stage forests were available after the fires (4,469 ha versus 46,073 ha), the majority of radio locations in both the pre- and post-fire periods were in the oldest lodgepole pine cover category (Figure 24). The frequency of radio locations was also similar pre- and post-fire for the next 2 most commonly used cover categories – the oldest spruce-fir and willow. Total use of these 3 cover categories accounted for 69.9% and 80% of the pre- and post-fire locations, respectively, and instrumented moose used these cover categories in proportions greater than availability during both periods (Table 21). When radio location data for the young, mid-age, and oldest conifer/willow types were pooled, radiocollared moose also demonstrated a preference for this cover category pre- and post-fire. Before and after the fires they avoided all other cover categories except mid-age Douglas fir, an uncommon forest type, which was used in proportions equal to availability (Table 21) (Appendix N, Table 77-78).

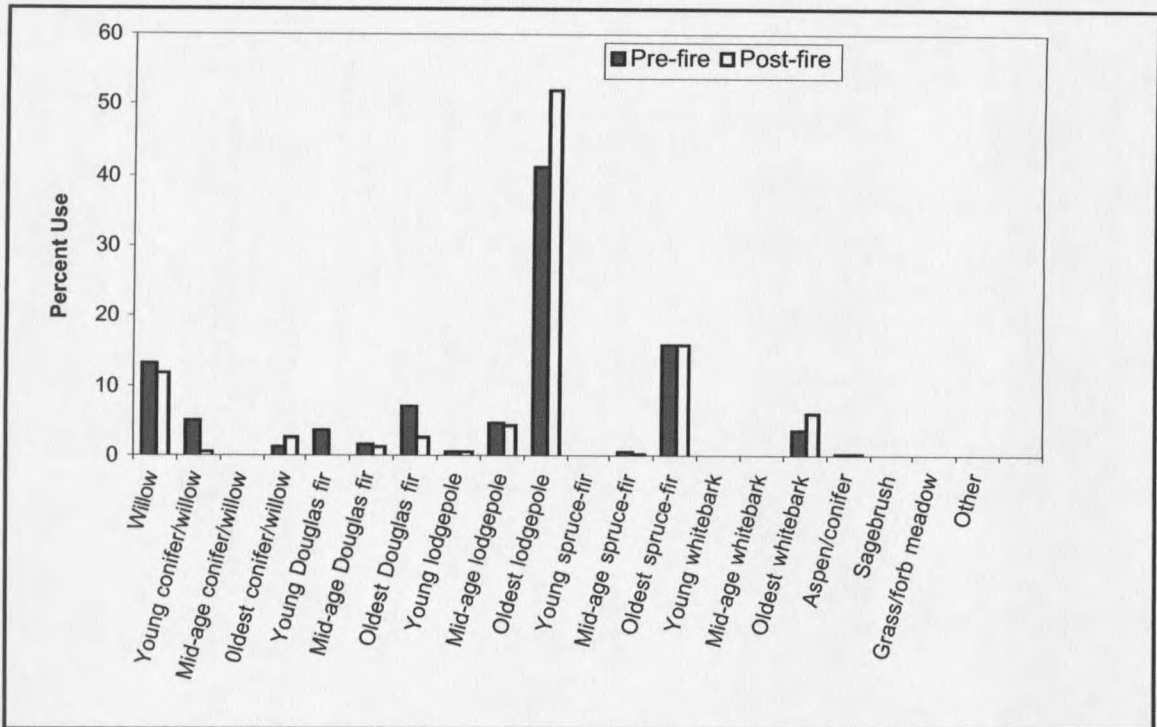


Figure 24. Winter cover type use by 14 radiocollared moose summarized in 20 categories (Table 5). Data are reported for the entire study area and represent all radio location points over 4 winters; November through April 1987-1991 pre- and post-1988 Yellowstone fires. Data are a percent of the total. Young = 0-100, mid = 100-300 and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Table 21. Percent of radio collared moose (use) found in 13 cover categories (Table 20) compared to percent of cover categories available. Data are reported for the entire study area and represent all radio location points over 4 winters; November through April 1987-1991 pre- and post-1988 Yellowstone fires. Symbols indicate habitat used in proportions greater than (+) less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix N, Tables 77-78. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses. Blanks indicated insufficient data.

Cover categories	Available Pre-Fire	Use Pre-Fire (279)		Available Post-fire	Use Post-Fire (475)	
Willow	0.2	13.3	+	0.2	12	+
Conifer/willow	0.1	6.4	+	0.1	3.5	+
Mid-aged Douglas fir	0.3	1.8	0	0.2	1.3	0
Oldest Douglas fir	18.3	11.1	-	16.1	2.7	-
Youngest lodgepole pine				13.3	0.8	-
Mid-age lodgepole pine	15.1	4.7	-	10.4	4.6	-
Oldest lodgepole pine	9.3	41.2	+	4.4	52.3	+
Oldest spruce-fir	7.1	16.1	+	4.7	16	+
Oldest whitebark pine	11.1	3.6	-	10.0	6.3	-
Aspen/conifer	6.2	0.4	-	6.6	0.2	-
Sagebrush	14.6	0	-	15.4	0	-
Grass/forb	7.7	0	-	8.1	0	-
Other	10.0	0	-	10.6	0	-

Again, I used radio location data from individual study units as a cross-check on moose cover category use at the landscape level. Pre- and post-fire trends at the 2 spatial scales were similar, moose in each study unit relied on mature conifer forests and willow stands to meet winter habitat needs before and after the fires. A post-fire shift to early successional stage (recently burned) forests was not observed in the 3 study units affected by the 1988 fires. Differences in cover category use among study units probably reflect variation in willow stand availability and proportional disparities in fire effects, especially in mature conifer forests.

The majority of pre- and post-fire radio locations in each study unit were in the oldest lodgepole pine cover category (Table 22) and use was in proportions greater than availability (Table 23, 24, 25). After the fire, frequency of locations in the oldest lodgepole pine category increased in all study units except SC where frequency of locations were about the same (Table 22) (Appendix O, Tables 79-82).

Prior to the fires, willow was preferred by instrumented animals in all study units, but was used most frequently by moose in SB and SC where larger willow stands were found (Table 22). The frequency of radio locations in this cover category decreased post-fire in all study units but it was still used in proportions greater than availability (Table 23, 24, 25) (Appendix O, Tables 79-82).

The number of radio locations in the oldest spruce-fir cover category generally ranked second or third in each study unit pre- and post-fire with more use occurring in YP and BC, study units without extensive riparian willow habitats (Table 22). Utilization in the oldest spruce-fir cover category declined post-fire in BC and SC, but increased in YP, and was about the same in SB (Table 22). Moose preferred this cover category pre- and post-fire in YP and otherwise used it in proportions equal to availability (Table 23, 24, 25) (Appendix O, Tables 79-82).

There was also an important post-fire use increase in the oldest whitebark pine cover category in BC (Table 22), although use was in proportions equal to availability both before and after the fires (Table 23, 24, 25). A decrease in use of the oldest Douglas fir cover category in SB occurred post-fire (Table 22), and, instead of pre-fire use in proportions equal to availability, it was avoided (Table 23, 24, 25) (Appendix O, Tables 79-82).

Although early successional stage forests were adequately represented on the landscape, there were insufficient pre- and post-fire radio locations in these cover categories to analyze proportional use. Limited data showed that moose avoided the youngest lodgepole pine forests before and after the fires (Table 23, 24, 25) (Appendix O, Tables 79-82).

Table 22. Winter cover type use by 14 radiocollared moose summarized in 20 categories (Table 5). Data are reported for each study unit and represent all radio location points over 4 winters; November through April 1987-1991 pre- and post-1988 Yellowstone fires. Data are a percent of the total in each column. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Numbers of locations are given in parentheses.

Cover categories	YP pre- (86)	YP post- (120)	SB pre- (109)	SB post- (142)	BC pre- (72)	BC post- (124)	SC pre- (12)	SC post- (89)
Willow	12.8	1.7	24.8	21.8	12.5	5.6	33.3	19.1
Young conifer/willow	0.0	0.0	0.0	0.0	0.0	0.8	0.0	3.4
Mid-age conifer/willow	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0
Oldest conifer/willow	8.1	2.5	1.8	6.3	6.9	0.8	0.0	0.0
Young Douglas fir	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age Douglas fir	5.8	5.0	0.0	0.0	0.0	0.0	0.0	0.0
Oldest Douglas fir	4.7	3.3	14.7	3.5	1.4	2.4	0.0	1.1
Young lodgepole pine	1.2	1.7	0.0	0.0	0.0	0.8	0.0	1.1
Mid-age lodgepole pine	2.3	3.3	3.7	0.0	11.1	4.8	0.0	13.5
Oldest lodgepole pine	43.0	50.8	38.5	51.4	37.5	54.0	50.0	52.8
Young spruce-fir	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age spruce-fir	0.0	0.8	1.8	0.0	0.0	0.0	0.0	0.0
Oldest spruce-fir	17.4	26.7	9.2	10.6	25.0	16.9	16.7	9.0
Youngest whitebark	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age whitebark pine	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oldest whitebark pine	1.2	3.3	4.6	6.3	5.6	13.7	0.0	0.0
Aspen/conifer	1.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Sagebrush	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Grass/forb meadow	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 23. Percent of moose radio locations (use) found in 12 cover categories (Table 5) compared to percent of cover categories available. Data were recorded during the winters of 1986-87 and 1987-88 (pre-1988 Yellowstone fires) and are reported by study unit. Data in SC were insufficient for analysis. Symbols indicate habitat used in proportions greater than (+) less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix O, Tables 79-80. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses. Blanks indicate insufficient data.

Cover categories	YP available (88)	YP use		SB available (109)	SB use		BC Available	BC use (72)	
Willow	0.1	20.9	+	0.3	27.5	+	0.1	19.4	+
Mid-age Douglas fir	0.1	5.8	0						
Oldest Douglas fir	27.9	4.7	-	20.2	14.7	0	10.6	1.4	-
Young lodgepole							5.4	0.0	-
Mid-age lodgepole	21.5	2.3	-	11.6	3.7	-	18.9	11.1	0
Oldest lodgepole	7.6	43.0	+	16.8	38.5	+	7.0	37.5	+
Oldest spruce-fir	4.2	17.4	+	7.8	9.2	0	15.5	25.0	0
Oldest whitebark				29.9	4.6	-	10.1	5.6	0
Aspen/conifer	8.3	1.2	-						
Sagebrush	24.1	0.0	-				20.5	0.0	-
Grass/forb	6.3	2.3	0	13.4	0.0	-			
Other							12.0	0.0	-

Table 24. Percent of moose radio locations (use) found in 13 cover categories (Table 5) compared to percent of cover categories available. Data were recorded during the winters of 1988-89 and 1990-91 (post-1988 Yellowstone fires) and reported by study unit. Symbols indicate habitat used in proportions greater than (+) less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix O, Tables 81 and 82. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses. Blanks indicate insufficient data.

Cover categories	YP Av.	YP Use (120)		SB Av.	SB Use (142)		BC Av.	BC Use (124)		SC Av.	SC Use (89)	
Willow	0.1	4.2	+	0.4	28.1	+	0.1	7.2	+	0.8	22.5	+
Mid-age Douglasfir	0.1	5	+									
Oldest Douglas fir	22.0	3.3	-	22.1	3.5	-	10.7	2.4	-			
Young lodgepole	15.8	1.7	-				5.4	0.8	-	17.5	1.1	-
Mid-age lodgepole	12.7	3.3	-	11.3	0.0	-	18.9	4.8	-	3.8	13.5	+
Oldest lodgepole	2.4	50.8	+	15.8	51.4	+	7.0	54.0	+	6.6	52.8	+
Young spruce-fir										11.7	0.0	-
Oldest spruce-fir	3.1	26.7	+	7.0	10.6	0	15.5	16.9	0	6.5	9.0	0
Oldest whitebark	6.8	3.3	0	28.7	6.3	-	13.7	10.1	0	15.4	0.0	-
Aspen/conifer	7.9	0.8	-							16.0	0.0	-
Sagebrush	23.1	0.0	-				20.5	0.0	-			
Grass/forb	6.0	0.0	-	14.7	0.0	-						
Other							12.0	0.0	-	21.6	0.0	-

Table 25. Comparison of pre- and post-fire radio collared moose use of 13 cover categories (Table 5) in 4 study units. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Pre-fire includes the winters 1986-87 (pre-1988 Yellowstone fires). Post-fire includes the winters 1989-90 (post-Yellowstone fires). Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Blanks indicate insufficient data.

Cover categories	YP Pre-	YP Post-	SB Pre-	SB Post-	BC Pre-	BC Post-	SC Pre-	SC Post-
Willow	+	+	+	+	+	+		+
Mid-age Douglas fir	0	+						
Oldest Douglas fir	-	-	0	-	-	-		
Young lodgepole		-			-	-		-
Mid-age lodgepole	-	-	-	-	0	-		+
Oldest lodgepole	+	+	+	+	+	+		+
Young spruce-fir								-
Oldest spruce-fir	+	+	0	0	0	0		0
Oldest whitebark		0	-	-	0	0		-
Aspen/conifer	-	-						-
Sagebrush	-	-			-	-		
Grass forb	0	-	-	-				
Other					-	-		-

In the 3 study units that burned, <10% of winter utilization was in burned sites; 5.3% of utilization after the fire was in the burned oldest lodgepole pine cover category, 2.5% in burned mid-age lodgepole pine cover category, and 0.8% in burned oldest Douglas fir cover category. Burned areas of other cover categories were not utilized by radiocollared moose. In the YP study unit, 3.3% of utilization was in burned areas in the oldest lodgepole pine, 2.5% in burned mid-age lodgepole pine, and 2.5% in burned oldest Douglas fir. Utilization of burned areas in SB occurred only in the oldest lodgepole pine (0.7%) and oldest Douglas fir (0.7%) categories. The largest number of radio locations in burned forests occurred in SC, and most of these were located in the oldest lodgepole pine category (22.5%). Another 10.1% were in burned mid-age lodgepole pine.

Use by radio collared moose was not evenly distributed among areas with different fire intensity (n=418); 4.3% of utilization was in areas that were about 1/2 burned, 2.9% in areas that were about 1/4 burned, and 2.4% in areas that were 3/4 burned. In the YP study unit (n=118), 5.9% of utilization was in areas that were 1/4 burned, 1.7% in areas that were 1/2 burned, and <0.1% in areas that were completely burned. Less than 2.0% of radio locations in SB were in burned areas (n=111). The highest percentage of utilization in burned areas was in SC (n=72). Most utilization after the fire was in unburned areas (59.7%), but 22.2% was in areas that were 1/2 burned, 12.5% in areas that were 3/4 burned, and 5.6% in areas that were 1/4 burned.

Radio collared moose generally avoided burned areas regardless of burn intensity. In the burned study units least affected by fire (YP and SB, with 70% and 92% unburned, respectively) moose avoided burned areas and preferred unburned habitat. Fire effects were greatest in SC and moose in this study unit selected burned and unburned areas in proportion to availability (Table 26) (Appendix P, 83-84).

Table 26. Percent of moose radio locations (use) found in burned and unburned areas compared to percent of available fire affected areas. Data were recorded during the winters of 1988-89 and 1990-91 (post-1988 Yellowstone fires). Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974).

Fire effects	YP Available	YP Use (118)		SB Available	SB Use (111)		SC Available	SC Use (72)	
Unburned	70	92	+	92	98	+	65	60	0
Burned 1-49%	15	6	-	4	1	-	14	6	0
Burned 50-100%	15	2	-	4	1	-	21	34	0

Distribution of Moose Pellet Groups and
Beds Among Cover Categories

Moose pellet group and bed location data provided a second method for assessing NYWR moose cover category use, and, because they involved the same spatial scale and instrumented animals, an opportunity to cross-check radio location data. Results were similar between the 2 methods and confirmed a pattern of moose using willow and mature conifer forests, especially the oldest lodgepole pine and spruce-fir types, in various proportions during the winter to meet resource needs. Moose daily activities, as represented by pellet group and bed locations, were not usually conducted in young conifer forests.

Locations of moose pellet groups and beds among 20 cover categories (Table 5) were similar during pre- and post-fire periods (Table 27 and 28). However, there was variation in seasonal use. In early winter, >35% of pellet group and bed locations were in the oldest spruce-fir cover category and >10% in both the willow and the oldest lodgepole pine cover categories. As winter progressed, use of the oldest spruce-fir and willow cover categories decreased until by late winter about 11% of pellet group and bed locations were in the oldest spruce-fir and <1.0% were in the willow cover categories. Use of the oldest lodgepole

Table 27. Percentages of pellet groups found while back-tracking radiocollared and uncollared moose during the winter. Data are reported by cover category (Table 5) and the time frames of the early (November-December), mid- (January-February), and late (March-April) periods of four winters (1986-1990) and the two years before (1986-1988) and after (1988-1990) the 1988 fires. Young = 1-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Numbers of pellet groups appear in parentheses.

	Early (111)	Mid- (380)	Late (415)	Pre-fire (296)	Post-fire (610)
Willow	13.5	6.8	0.0	2.4	5.6
Young conifer/willow	7.2	2.6	4.1	6.1	2.8
Mid-age conifer/willow	0.0	1.1	0.5	1.4	0.3
Oldest conifer/willow	2.7	5.3	1.9	6.4	2.0
Young Douglas fir	0.0	1.6	2.2	2.4	1.3
Mid-age Douglas fir	1.8	2.4	1.9	0.0	3.1
Oldest Douglas fir	0.0	5.5	15.2	10.5	8.5
Young lodgepole pine	6.3	5.0	2.2	0.7	5.4
Mid-age lodgepole pine	8.1	17.4	28.9	19.3	22.6
Oldest lodgepole pine	11.7	35.5	26.3	28.7	28.2
Young spruce-fir	0.0	0.0	0.0	0.0	0.0
Mid-age spruce-fir	2.7	0.0	1.2	1.7	0.5
Oldest spruce-fir	38.7	14.7	11.8	17.9	15.6
Young whitebark pine	0.0	0.0	0.0	0.0	0.0
Mid-age whitebark pine	0.0	0.0	0.2	0.3	0.0
Oldest whitebark pine	0.0	0.0	2.4	2.0	0.7
Aspen/conifer	0.0	0.5	0.0	0.0	0.3
Sagebrush	7.2	0.5	0.5	0.0	2.0
Grass/forb meadow	0.0	0.0	0.5	0.0	0.3
Other	0.0	1.1	0.2	0.0	0.8

pine cover category increased through the winter. By late winter, about 70% of use was in the oldest lodgepole pine, mid-age lodgepole pine, and oldest Douglas fir cover categories.

In both the pre- and post-fire periods, most pellet groups and beds were found in the oldest lodgepole pine, mid-age lodgepole pine, and oldest spruce-fir cover categories (about 30%, 20%, and 15% respectively) (Table 27 and 28). About 9% of pellet groups pre- and post-fire were located in the oldest Douglas fir cover category, but use, as reflected by bed locations, declined from 16% to 8% in this category. Willow use was about 4% pre- and post-fire.

Table 28. Percentages of beds found while back-tracking radiocollared and uncollared moose through the snow. Data are reported by cover category (Table 5) and the time frames of the early (November-December), mid- (January-February), and late (March-April) periods of four winters (1986-1990) and the two years before (1986-1988) and after (1988-1990) the 1988 fires. Young = 0-100, mid = 00-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Numbers of beds appear in parentheses.

	Early (68)	Mid- (237)	Late (262)	Pre-fire (218)	Post-fire (349)
Willow	10.3	4.6	0.4	2.3	4.0
Young conifer/willow	2.9	1.7	4.2	4.6	2.0
Mid-age conifer/willow	1.5	0.4	0.0	0.5	0.3
Oldest conifer/willow	8.8	3.0	3.1	4.6	3.2
Young Douglas fir	0.0	0.8	1.1	0.9	0.9
Mid-age Douglas fir	1.5	2.1	1.9	0.0	3.2
Oldest Douglas fir	0.0	4.6	22.1	18.4	8.3
Young lodgepole pine	7.4	4.2	1.9	0.5	5.4
Mid-age lodgepole pine	4.4	19.4	20.6	16.1	19.5
Oldest lodgepole pine	19.1	42.6	29.8	31.7	35.2
Young spruce-fir	0.0	0.0	0.0	0.0	0.0
Mid-age spruce-fir	0.0	0.0	1.1	1.4	0.0
Oldest spruce-fir	35.3	14.8	11.1	16.5	14.9
Young whitebark pine	0.0	0.0	0.0	0.0	0.0
Mid-age whitebark pine	0.0	0.0	0.4	0.5	0.0
Oldest whitebark pine	0.0	0.0	1.9	1.8	0.3
Aspen/conifer	0.0	0.4	0.0	0.0	0.3
Sagebrush	7.4	0.0	0.0	0.0	1.4
Grass/forb meadow	0.0	0.0	0.4	0.0	0.3
Other	1.5	1.3	0.0	0.5	0.9

Variation in Cover Category Use by Moose Seen Along the Cooke City Road

Sightings along the Cooke City road provided a third method to assess moose cover category use, but results reflected observations made at a smaller spatial scale than locations of instrumented animals. While radio location data were collected throughout the study area, sightings from vehicles were made only along the road corridor between Gardiner and Cooke City. Consequently, moose cover category use along the

road disproportionately represented unforested habitat and valley bottoms associated with the lowest elevations, which may explain some differences in results between the 2 methods, e.g. a higher percentage of sightings in open meadows and willow along the road transect than with radio location data.

Nevertheless, findings from the road transect corroborated radio location data by demonstrating an association of NYWR moose with mature conifers and willow both pre- and post-fire but not with young forests, as well as a mid-winter transition from willow stands to mature lodgepole forests.

The majority of moose sightings in the pre- and post-fire periods along the road between Gardiner and Cooke City, Montana were in 3 cover categories (Table 29). About 50% during the pre-fire and immediate post-fire (1988-1992) periods and 30% during 1995-1997 were seen in the willow cover category.

Sightings of moose in the oldest lodgepole pine cover category increased post-fire and moose were also often seen in the open meadow cover category pre- and post-fire. Following the fires, moose evidently increased use of unburned mature Douglas fir forests but continued some use of burned mature lodgepole pine forests.

Table 29. Observations of moose along the Gardiner to Cooke City road, Yellowstone Park, summarized in 16 cover categories (Table 18). Data are a percent of the total in 3 time periods: 1) Pre-fire – January 1987 to June 1988, 2) Post-fire 1 – June 1988 to December 1992, 3) Post-fire 2 – January 1995 to December 1997. Numbers of observations used to calculate percent appear in parentheses.

	Pre-fire (135)	Post-fire 1 (317)	Post-fire 2 (233)
Willow	50.4	55.5	31.3
Oldest lodgepole pine	12.6	16.7	18.5
Aspen	5.9	1.0	0.0
Spruce-fir	0.0	1.0	4.7
Open meadows	12.6	6.0	15.9
Oldest spruce-fir/meadow	3.0	0.3	3.4
Douglas fir	0.7	1.0	1.3
Douglas fir/open areas	1.5	0.0	0.9
Burned lodgepole pine	0.0	4.7	6.4
Riparian meadows	6.7	1.9	10.3
Oldest lodgepole pine/meadow	0.0	1.9	2.6
Younger lodgepole pine	0.0	1.0	0.0
Younger Douglas fir	4.4	1.0	0.0
Sagebrush grasslands	2.2	2.5	0.0
Lodgepole pine sagebrush	0.0	1.3	0.0
Oldest conifer/willow	0.0	4.4	4.7

Cover categories where moose were observed changed throughout the year. In November-December pre- and post-fire, about 90% of the 174 moose sighted were in willow stands and the remainder were in the oldest lodgepole pine (Figure 25).

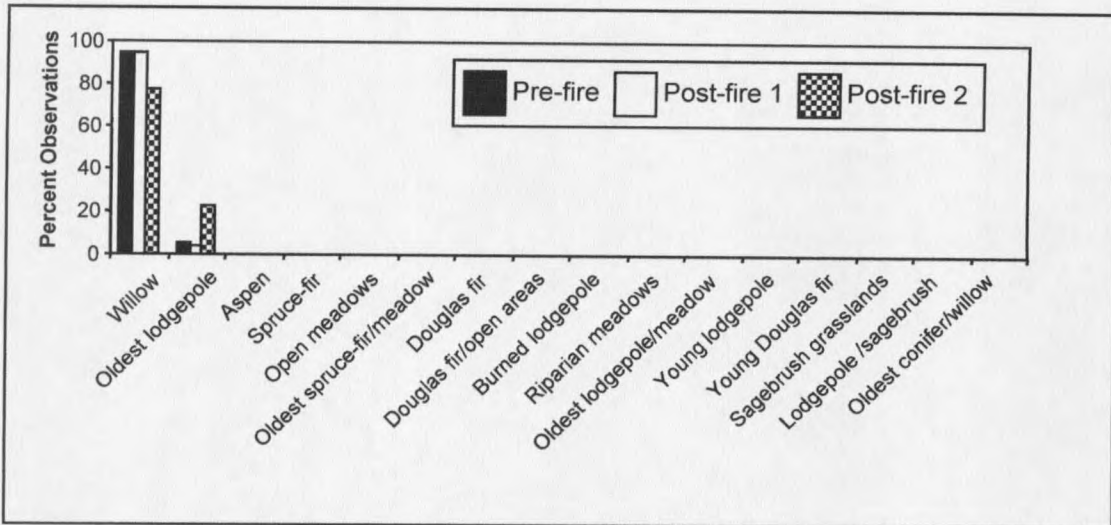


Figure 25. Observations of moose during November and December along the Gardiner to Cooke City road, Yellowstone Park, summarized in 16 cover categories (Table 18). Data are percent of the total seen in 3 time periods: 1) Pre-fire – January 1987 to June 1988, 2) Post-fire 1 – June 1988 to December 1992, and 3) post-fire 2 – January 1995 to December 1997. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

In January-February, moose were seen in a greater variety of cover categories than earlier in the winter, but almost all moose sightings ($n=47$) were in the oldest lodgepole pine and willow cover categories during both the pre-fire (41.2%, 58.8%) and 1 to 5 years post-fire periods (58.3%, 29.2%) (Figure 26). Eight to 10 years post-fire, only 6 moose were seen, and 5 were in the oldest lodgepole pine category.

In March-April before the 1988 fires, 53.1% of 32 moose were in willow stands, 12.5% in younger Douglas fir, and 9.4% in the oldest lodgepole pine and riparian meadows (Figure 27). More than 40% of moose seen along the road corridor 1 to 5 years after the fires were in the oldest lodgepole pine and >20% in willow stands. Eight to 10 years after the fires, the same cover categories were important to moose, but they were also found in burned lodgepole pine forests (56.0% were in the oldest lodgepole pine, 12% in burned lodgepole pine, and 24% were divided evenly between willow, open meadows, and riparian meadows).

In May-June ($n=289$), there was a similar pattern of moose observations in the pre-fire and 8-10 year post-fire period: about 30% in willow stands, 20% in open meadows, and 10% in the oldest lodgepole pine (Figure 28). During the period 1 to 5 years post-fire, the majority of moose observations were in open meadows (20.9%), followed by willow stands (16.4%), and the oldest lodgepole pine (11.9%).

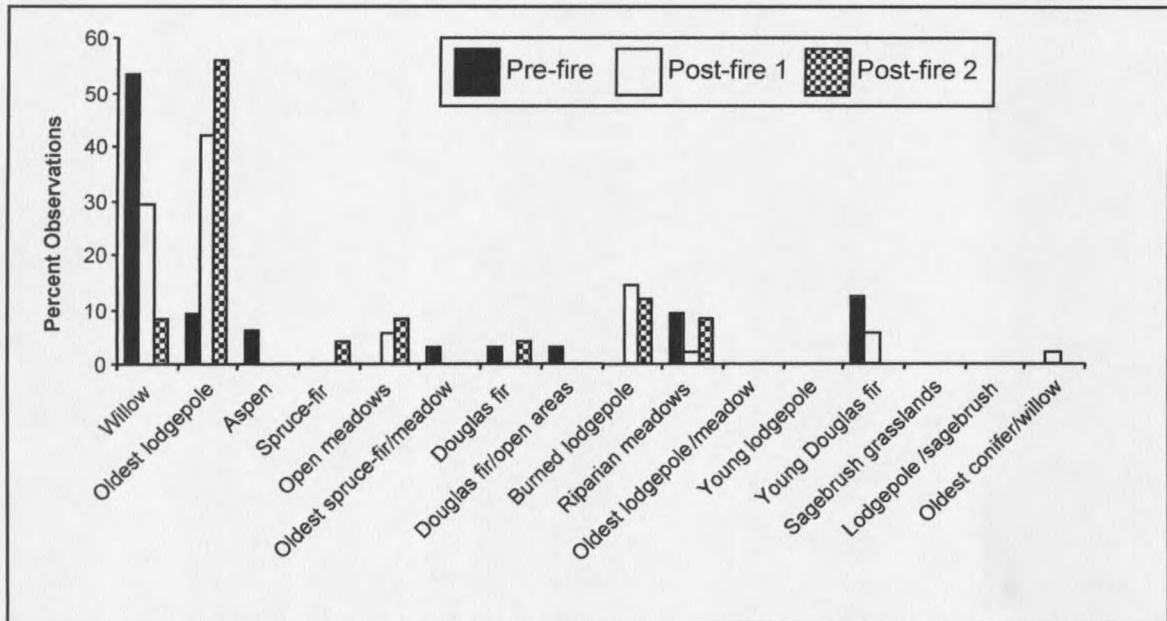


Figure 26. Observations of moose during January and February along the Gardiner to Cooke City road, Yellowstone Park, summarized in 16 cover categories (Table 18). Data are percent of the total seen in 3 time periods: 1) pre-fire – January 1987 to June 1988, 2) Post-fire 1 – June 1988 to December 1992, 3) Post-fire 2 – January 1995 to December 1997. Young = 0-100, mid = 100-300, and oldest = 300+ years post disturbance (Mattson and Despain 1985).

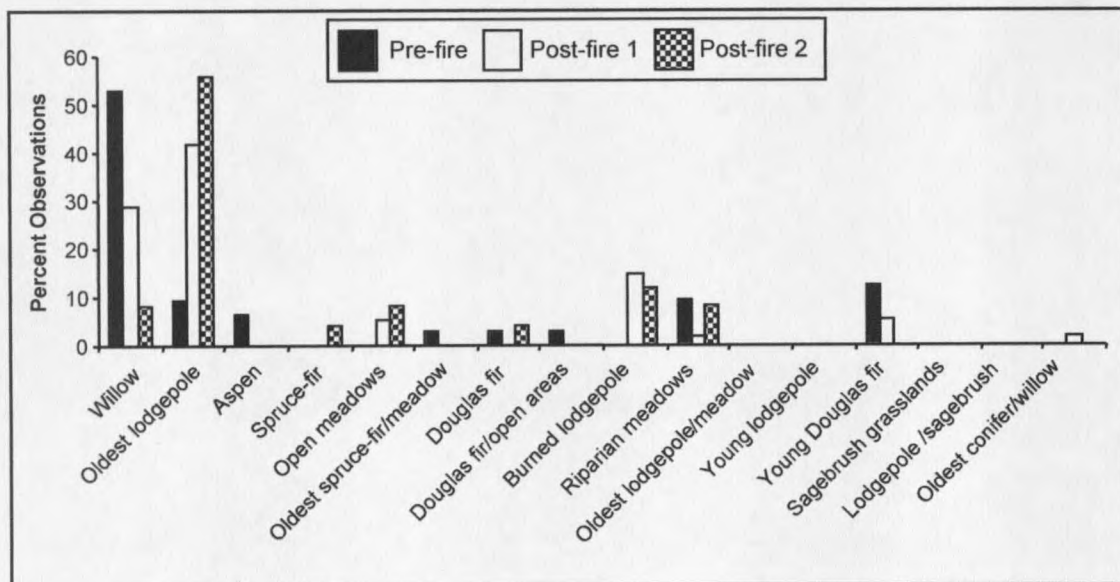


Figure 27. Observations of moose during March and April along the Gardiner to Cooke City road, Yellowstone Park, summarized in 16 cover categories (Table 18). Data are percent of the total seen in 3 time periods: 1) Pre-fire – January 1987 to June 1988, 2) Post-fire 1 – June 1988 to December 1992, 3) Post-fire 2 – January 1995 to December 1997. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

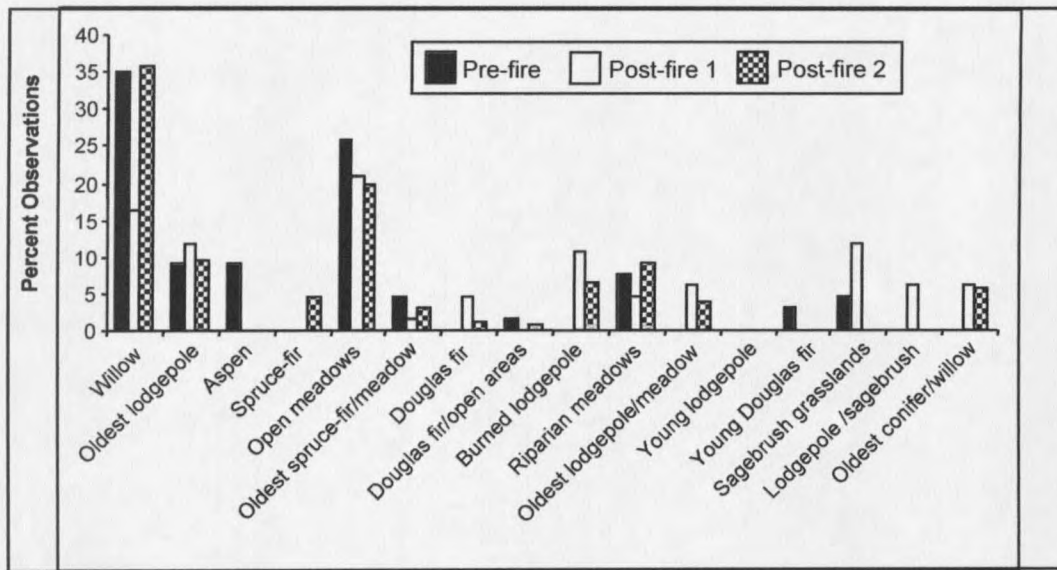


Figure 28. Observations of moose during May and June along the Gardiner to Cooke City road, Yellowstone Park, summarized in 16 cover categories (Table 18). Data are percent of the total seen in 3 time periods: 1) Pre-fire – January 1987 to June 1988, 2) Post-fire 1 – June 1988 to December 1992, 3) Post-fire 2 – January 1995 to December 1997. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Moose Cover Type Selection on Track-Intercept Transects

Recording moose tracks along fixed transects provided a fourth method and spatial scale for investigating moose cover category use and perhaps the most precise assessment on winter range. While radio location and bed and pellet group data were collected throughout the study area and sightings from vehicles were specific to the Gardiner-Cooke City road, track transect data were collected in areas with the highest moose densities. Results confirm a general pattern of moose cover type use involving a winter-long association with mature conifer forests and willow stands and a mid-winter shift from willow and spruce-fir types to the oldest lodgepole pine forests, a pattern followed pre- and post-fire and with minimal young conifer forest use.

There was a similar pattern of moose habitat use pre- and post-fire along fixed transects, including the selection of preferred cover categories (Table 30, 31, 32). Moose preferred 5 of 10 cover categories in at least 1 winter period. The willow cover category was preferred during every winter period pre- and post-fire except early winter pre-fire when it was used in proportion to availability. Use of the oldest lodgepole pine cover category pre- and post-fire progressed from avoidance in early winter to preference in late winter. Pre- and post-fire, moose preferred the conifer/willow and spruce-fir cover categories in early

winter and used them in proportion to availability in late winter. In mid-winter, these types were also preferred except post-fire the oldest spruce-fir cover category was used in proportion to availability. The oldest lodgepole/young conifer was preferred in mid-winter post-fire and otherwise usually avoided. The other 5 cover categories were avoided all or most winter periods pre- and post-fire (Appendix Q, Tables 85-88).

Table 30. Percent of moose tracks (use) found in 10 cover categories (Table 19) compared to percent of cover categories available. Data were recorded during the winters of 1986-87 and 1987-88 (pre-1988 Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than (+) less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix Q, Tables 85-86. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses.

Cover Categories	Available	Early winter use (486)		Mid- winter use (209)		Late winter use (167)	
Willow	4.0	8.9	0	10.5	+	25.8	+
Young lodgepole	18.0	1.1	-	3.3	-	4.5	-
Oldest lodgepole/sage	7.3	0.0	-	0.0	-	0.0	-
Oldest lodgepole	14.9	5.3	-	16.7	0	41.6	+
Oldest lodgepole/meadow	6.3	9.5	0	2.9	-	1.1	-
Conifer/willow	17.2	33.1	+	33.9	+	15.7	0
Oldest lodgepole/young conifer	13.2	2.2	-	13.9	0	4.5	-
Oldest spruce-fir/young conifer	2.2	5.3	0	3.3	0	0.0	-
Douglas fir/sage	9.8	0.0	-	0.0	-	0.0	-
Oldest spruce-fir	6.6	34.7	+	14.8	+	4.5	0

Table 31. Percent of moose tracks (use) found in 10 cover categories (Table 19) compared to percent of cover categories available. Data were recorded during the winters of 1988-89 and 1989-90 (post-1988 Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix Q, Tables 87-88. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses.

Cover Categories	Available	Early winter use (486)		Mid- winter use (209)		Late winter use (167)	
Willow	4.0	28.7	+	12.6	+	16.8	+
Young lodgepole	18.0	0.8	-	4.4	-	11.4	0
Oldest lodgepole/sage	7.3	0.1	-	0.2	-	0.0	-
Oldest lodgepole	14.9	9.2	-	10.8	0	35.9	+
Oldest lodgepole/meadow	6.3	1.9	-	5.0	-	1.8	-
Conifer/willow	17.2	24.4	+	33.8	+	16.2	0
Oldest lodgepole/young conifer	13.2	11.4	0	25.8	+	5.4	-
Oldest spruce-fir/young conifer	2.2	0.9	-	1.1	0	1.2	0
Douglas fir/sage	9.8	0.0	-	0.4	-	0.6	-
Oldest spruce-fir	6.6	21.2	+	5.5	0	10.8	0

Table 32. Comparison of pre- and post-fire use by moose of 10 cover categories (Table 19) as indicated by tracks. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Pre-fire includes the winters 1986-87 (pre-1988 Yellowstone fires). Post-fire includes the winters 1989-90 (post-Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Cover Categories	Pre- Early	Pre- Mid-	Pre- Late	Post- Early	Post- Mid-	Post- Late
Willow	0	+	+	+	+	+
Young lodgepole	-	-	-	-	-	0
Oldest lodgepole/sage	-	-	-	-	-	-
Oldest lodgepole	-	+	+	-	0	+
Oldest lodgepole/meadow	0	-	-	-	-	-
Conifer/willow	+	+	0	+	+	0
Oldest lodgepole/young conifer	-	0	-	0	+	-
Oldest spruce-fir/young conifer	0	0	-	-	0	0
Douglas fir/sage	-	-	-	-	-	-
Oldest spruce-fir	+	+	0	+	0	0

Elk Cover Type Selection on
Track-Intercept Transects

There were similarities in elk habitat use pre- and post-fire along fixed transects, including the selection of preferred cover categories (Tables 33, 34, and 35). Elk preferred 4 cover categories during at least 1 winter period. Sample size (n=8) was too small for a meaningful assessment of cover category use during early winter in the pre-fire period. The oldest lodgepole pine/sagebrush cover category was preferred during early and mid-winter pre-and post-fire but was avoided in late winter. During the early winter, elk preferred forests with mature spruce trees mixed with post-logging early successional conifers (oldest spruce-fir/young conifer category), but this cover category was avoided in mid-winter and used in proportion to availability in late winter. The Douglas fir/sagebrush cover category was preferred during every winter period pre- and post-fire except the mid-winter pre-fire period. The oldest spruce-fir cover category was preferred during late winter after the 1988 fires, used in proportion to availability in mid-winter post-fire, and otherwise avoided. Willow was generally used in proportion to availability. The 5 other cover categories were generally avoided, but 3 mixed conifer types were used in proportion to availability during late winter in both pre- and post-fire. The oldest lodgepole pine cover category and 2 of the mixed conifer types were also used in proportion to availability during mid-winter post-fire (Appendix Q, Tables 89-92).

Table 33. Percent of elk tracks (use) found in 10 cover categories (Table 19) compared to percent of cover categories available. Data were recorded during the winters of 1986-87 and 1987-88 (pre-1988 Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix Q, Tables 89-90. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses.

Cover categories	Available	Early winter use (n=8)		Mid- winter use (n=1,616)		Late winter use (n=161)	
Willow	4.0	0.0	-	0.4	0	2.5	0
Young lodgepole	18.0	12.5	0	0.4	-	2.5	-
Oldest lodgepole/sage	7.3	0.0	-	85.9	+	0.0	-
Oldest lodgepole	14.9	0.0	-	2.7	-	6.2	-
Oldest lodgepole/meadow	6.3	87.5	+	2.6	-	5.0	0
Conifer/willow	17.2	0.0	-	1.5	-	5.6	-
Oldest lodgepole/young conifer	13.2	0.0	-	1.3	-	15.0	0
Oldest spruce-fir/young conifer	2.2	0.0	-	0.2	-	3.1	0
Douglas fir/sage	9.8	0.0	-	4.1	-	60.2	+
Oldest spruce-fir	6.6	0.0	-	0.9	-	0.0	-

Table 34. Percent of elk tracks (use) found in 10 cover categories (Table 19) compared to percent of cover categories available. Data were recorded during the winters of 1988-89 and 1989-90 (post-1988 Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix Q, Tables 91-92. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985). Sample sizes are given in parentheses.

Cover categories	Available	Early winter use (n=2,173)		Mid- winter use (n=1,286)		Late winter use (n=124)	
Willow	4.0	3.9	0	0.8	-	2.4	0
Young lodgepole	18.0	3.0	-	1.0	-	4.0	-
Oldest lodgepole/sage	7.3	25	+	23.6	+	0.0	-
Oldest lodgepole	14.9	11.5	-	13.0	0	6.5	-
Oldest lodgepole/meadow	6.3	2.9	-	7.6	0	5.6	0
Conifer/willow	17.2	9.4	-	12.2	-	9.7	-
Oldest lodgepole/young conifer	13.2	3.1	-	6.8	-	21.0	0
Oldest spruce-fir/young conifer	2.2	3.5	+	1.1	-	0.8	0
Douglas fir/sage	9.8	34.5	+	27.7	+	26.6	+
Oldest spruce-fir	6.6	2.9	-	6.3	0	23.4	+

Table 35. Comparisons of pre- and post-fire use by elk of 10 cover categories (Table 19) as indicated by tracks. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Pre-fire includes the winters 1986-87 (pre-1988 Yellowstone fire). Post-fire includes the winters 1989-90 (post-1988 Yellowstone fires). Early winter is November-December, mid-winter is January-February, and late winter is March-May. Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Cover categories	Pre- Early	Pre- Mid-	Pre- Late	Post- Early	Post- Mid-	Post- Late
Willow	-	0	0	0	-	0
Young lodgepole	0	-	-	-	-	-
Oldest lodgepole/sage	-	+	-	+	+	-
Oldest lodgepole	-	-	-	-	0	-
Oldest lodgepole/meadow	+	-	0	-	0	0
Conifer/willow	-	-	-	-	-	-
Oldest lodgepole/young conifer	-	-	0	-	-	0
Oldest spruce-fir/young conifer	-	-	0	+	-	0
Douglas fir/sage	-	-	+	+	+	+
Oldest spruce-fir	-	-	-	-	0	+

Mule Deer Cover Type Selection on Track-Intercept Transects

Most mule deer tracks (372 of 396) were found in the BC study unit, so analysis was restricted to this sample. Again, to insure an adequate sample size and because the area did not burn, analysis was conducted for all the years combined. Most use occurred in the Douglas fir/meadow mosaic cover category (Table 36). Use was greater than availability in that cover category and for the Douglas fir/sagebrush cover category. Willow/conifer and the oldest spruce-fir/meadow cover categories were used in proportion to availability, and the rest were avoided (Appendix Q, Table 93).

Table 36. Selection by mule deer of 7 cover categories (Table 20) along BC transects as indicated by tracks. Sample size = 372. Symbols indicate habitat used in proportions greater than (+), less than (-), or in proportion to (0) availability based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974) (Appendix Q, Table 93). Data are from the years 1986-1990. Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

Cover category	Percent available	Percent use	
Willow/conifer	7.0	10.2	0
Young lodgepole	34.8	10.8	-
Oldest lodgepole	18.7	4.0	-
Oldest conifer/young conifer	22.5	11.0	-
Douglas fir/sage	3.8	28.5	+
Oldest spruce-fir/meadow	3.9	2.9	0
Douglas fir/meadow	9.4	32.6	+

Discussion

Variation in Moose Cover Category Use

Many moose habitat studies have compared seasonal advantages of forest successional stages and cover type combinations. In these investigations, North American moose have consistently been associated with early successional communities growing on burned sites (Peterson 1955, Coady 1982, Peek 1997). Natural and human-induced disturbances that create early successional stage forest are often considered necessary to replenish moose habitat across this continent (Geist 1971, 1974, Coady 1982, Thompson and Stewart 1997).

Geist (1971) hypothesized that fire effects explain the cyclic nature of moose populations in boreal forests. Permanent habitat found along watercourses, deltas, and high elevation dwarf shrub communities may provide refugia for moose to persist until they can expand into more favorable transient habitat created by fire (Geist 1971). Peek (1974c) found that burned areas in boreal forests were rapidly colonized when moose populations were nearby.

Studies indicate that moose habitat is often enhanced post-disturbance by a temporary increase in available forage. Parker and Morton (1978) demonstrated that woody biomass peaked 8 years following a clearcut in Newfoundland. On the Kenai Peninsula, Alaska, important browse species peaked 15 (Spencer and Hakala 1964) and 10 years (Oldemeyer and Regelin 1987) post-fire. Based on fluctuations in browse biomass and moose populations in boreal forests, Kelsall et al. (1977) concluded that the optimum successional stages for moose were 11 to 30 years after burning. Thompson and Stewart (1997) reported that moose need young successional stands in boreal forests but that their value is transient, lasting less than 30 years. Peek et al. (1976) found that the effects of logging in fire-prone Minnesota forests were similar to burning, comparable vegetation mosaics and increases in forage and moose populations resulted.

North American moose are also occasionally associated with habitats where fire is infrequent. High-density moose populations can exist where fire is either not a major influence or is detrimental to habitat availability (Peek 1997). Examples include river delta systems in Alaska (Doerr 1983, MacCracken 1992), habitats at or above timberline in central Alaska (Miquelle and Van Ballenberghe 1989, Risenhoover 1989), and mesic maritime forests of eastern Canada (Telfer 1984). In central Idaho, moose inhabit areas of densely forested steep terrain with limited riparian vegetation that burn infrequently (Peek et al. 1987). These forests have double canopies with Pacific yew (*Taxus brevifolia*) as a subcanopy beneath mixed conifers that are >150 years old. The yew provides food and cover and the double canopy intercepts snowfall. In other areas of Idaho where yew is not abundant, spruce-fir forests provide similar habitat with a mixture of seral and climax species including subalpine fir, Engelmann spruce, western larch (*Larix occidentalis*), lodgepole pine, and Douglas fir (Peek et al. 1987, Peek 1997).

Where moose are associated with mature boreal forests with intact canopies, as opposed to recently disturbed areas, juxtaposition of food and shelter during late winter may be essential for their survival. This spatial relationship between cover and food becomes limiting because snow makes low growing forage unavailable (Coady 1974, Telfer 1978, Welsh et al. 1980, Thompson and Vukelich 1981, Eastman and Ritcey 1987, Peek et al. 1987) (see Chapter 5). In Alberta, Stelfox (1981) found that regrowth of adequate winter shelter did not begin until 25 years after logging, and moose did not use the disturbed area in winter before that time (Stelfox et al. 1976). Welsh et al. (1980) showed that moose in boreal Ontario migrated from previously occupied habitat that was recently clearcut to mature forests as much as 50 miles (80.5 km) away. In response to progressively deeper snows and less accessible food in open areas, a mid-winter shift into closed canopy habitats has been documented in Alberta (Rolley and Keith 1980), British Columbia (Eastman 1974), Wyoming (Houston 1968), Montana (Stevens 1970), eastern Minnesota (Peek et al. 1976), western Minnesota (Phillips et al. 1973), Ontario (Thompson and Vukelich 1981), and Nova Scotia (Telfer 1970).

Vegetation in the study area and surrounding Yellowstone region is an artifact of fire cycles (Romme and Despain 1989), which has implications for moose habitat and populations. Using cross sections from fire-scarred Douglas fir to construct a chronology, Houston (1973, 1982) concluded that the interval between successive fires on the NYWR was 20 to 25 years. He also believed that fire suppression in the 20th century disrupted natural cycles causing important vegetation changes, including a decrease in deciduous vegetation and an increase in older forests. Romme and Despain (1989) mapped vegetation in YNP and noted that coniferous forests characterized by patches in different stages of post-fire development dominated the landscape. They also reported that, in 1988, >300-year-old lodgepole forests were more prevalent than at any time in the past 3 centuries. The quantity of these older forests, which are considerably more flammable than earlier successional stages, in combination with extreme weather conditions, resulted in the 1988 fires (Romme and Despain 1989). Based on a reconstruction of successive forest composition from about 1700 to 1985, they concluded that a comparable fire event or series of events occurred in the early 1700's. In their opinion, fire suppression beginning in 1886 with the U.S. Army and continuing through the 20th century had a minimal effect on fuels and fire behavior in 1988, at least in the more remote high plateaus and mountains. The 1988 fires may have been an inevitable event in a long-term fire cycle. Data I collected prior to 1988 allowed me to assess the effects of landscape level habitat alterations on NYWR moose cover type use patterns.

I used multiple techniques, all of which had inherent biases (Van Horne 1983, Hobbs and Hanley 1990, Gasaway et. al. 1986, Bookhout 1994, Peek 1997), to determine NYWR moose proportional use of cover types during winter periods and before and after the 1988 Yellowstone fires. Using several methods at various spatial scales insured that data were generalized and accurate and also allowed me to assess the efficacy of sampling protocols. Radio location data demonstrated cover type use patterns across the study area, but locating instrumented animals in dense forests can be imprecise (Gasaway et. al. 1986). Back-tracking the same collared moose as well as uncollared animals to record bed and pellet count locations among cover types cross-checked radio location data, although bed and pellet group location data may or may not represent areas where most daily activities are performed. However, results were comparable indicating that both methods may adequately reflect moose cover type use patterns in this environment. Nevertheless, using radio locations and back-tracking in combination, increased confidence in the data. Roadway moose sightings allowed for direct observations of animals in cover types, but only along an unrepresentative study area cross section. Peek (1997) emphasized the need to obtain habitat selection data over a period of years to account for use patterns related to weather variables, a major influence of habitat use change. In spite of limitations, the road transect, as the most convenient and least expensive technique,

allowed for the most years of sampling. Track data from fixed transects through high moose density areas provided records from optimal moose winter range that offset biases from the road transect data.

In addition to cover type use data collection techniques, others have voiced concern over the fundamental assumption in associated studies, i.e. are species abundance and habitat quality always positively correlated (Van Horne 1983, Hobbs and Hanley 1990)? For example, habitat use patterns may be difficult to determine or may change unpredictably because of variation in population density or the temporal and spatial influence of weather. In addition, patchy, widely scattered habitat may require moose to move often and over long distances creating seemingly erratic and cryptic cover type use patterns (Van Horne 1983, Peek 1997). Hobbs and Hanley (1990) recommended addressing these issues with parallel studies investigating the underlying processes controlling animal response to change. Coady (1982) and Peek (1997) identified snow conditions, changes in plant nutrient content, vulnerability to predators, and interspecific competition as possible habitat determinants affecting moose cover type use patterns (see Chapters 2, 3, 5, 6, 7, and 8).

As postulated by Loope and Gruell (1973), I found that NYWR moose did not occupy transitory early successional stage habitats but were instead associated with forests that had probably begun development following fires in the early 1700's. This preference for older forests was consistent in radio location, pellet count, bed count, roadside, and track data. Moose did use willow stands that formed concentrations of deciduous browse, but most use was during the early winter. Most willow stands were relatively stable streamside types, not transitory post-fire habitats. NYWR moose began winter predominantly in the open willow types and nearby oldest spruce-fir forests. In study units without well-defined willow stands, the oldest spruce-fir forests and other mature coniferous forests were used comparatively more. Consistent with the theories of McDowell and Moy (1942) and Peek (1974a), moose shifted use to mature, double canopy lodgepole pine forests as winter progressed, and they spent the hardest winter months in these types. There was some movement back to willow areas in early spring. This pattern suggests that snow conditions strongly influenced cover use by NYWR moose (see Chapter 5). Preferred willow areas were too limited in size and inaccessible in deep snow to provide browse through the winter (see Chapter 8), and forage in early successional forest communities at elevations used by moose were buried in snow for most of the winter (see Chapter 5).

In spite of a >10-fold increase in early successional stage forests after the 1988 fires, moose cover type use was similar pre- and post-fire, suggesting that moose deviated from normal movement patterns and locations post-fire to find unburned areas and continue traditional season-specific habitat use. This could have resulted in moose concentrating in limited unburned areas and/or a loss of moose because of the

energy costs involved with displacement. There is evidence that both occurred. Starvation of 3 radiocollared moose (see Chapter 2) in heavily burned study units indicates that some moose could not find adequate browse post-fire. A negative relationship between extent of fire effects and moose use demonstrates that moose shifted out of burned areas. Unburned forests received the most use post-fire, while the forests most impacted by the 1988 fires, as described by the percent of burned canopy, received the least. Changes in cover use patterns were also influenced by area-specific burn patterns. For example, in the SB study unit, the oldest Douglas fir cover type burned extensively, and moose use decreased after the 1988 fires. Stands of the oldest lodgepole pine cover category in SB were mostly unaffected, and moose use of these areas increased. Moose in SC shifted from burned areas of the oldest spruce-fir to areas of mid-age lodgepole pine that did not burn. Use of burned forests among study units was related to the amount of that unit that burned. The most use by moose of burned forests was in SC where forests were most significantly affected.

Most North American moose use transitory habitats created by fire or logging. In these areas, a post-disturbance proliferation of deciduous browse enhanced moose habitat for about 30 years. In a few habitats, including the NYWR, moose rely instead on late successional stage coniferous forests to meet late winter food requirements. Removing mature forests in this environment decreases available moose winter range and negatively affects populations. Logging in BC and SB began in the early 1900's and continues to the present. Replacement of optimum moose winter range on lands devoted primarily to timber production is unlikely because they are generally reharvested every 25 to 120 years, and NYWR coniferous forests require at least 200 years to develop old-growth characteristics most favorable to moose (Mattson and Despain 1985, Thomas et al. 1988). As forest plantations, harvested areas in the BC and SB study units will be maintained as early to mid-seral stages which, compared to late successional forests, are structurally simple having a single canopy layer, a limited number of tree species, and relatively little understory (Hayes et al. 1997).

The fires of 1988 also removed extensive late successional stage forests in wilderness and managed forests. The 1988 Yellowstone fires may be an iteration of an approximately 300-year fire cycle. Just as the fires of the early 1700's created a successional trajectory for 300 years, the fires of 1988 may have established a pattern of vegetation that will be apparent for centuries. Replacement forests will not be optimum moose winter range for several hundred years. Therefore, unlike other North American moose populations that potentially peak and crash in several decades in response to the ephemeral availability of transitory habitats, the NYWR moose numbers may fluctuate on a cycle comparable to the stochastic fire events characteristic of the Yellowstone region.

Moose are highly adaptable animals, but the limits of moose adaptability to habitat alteration in specific environments are difficult to determine. The effects of habitat changes on moose numbers and densities may appear minor initially but become critical as they accumulate, and the time lag may vary among populations. In addition, factors other than cover type change (predation, disease, weather variation, climate change) may limit, override, or exacerbate the ultimate consequences of habitat alteration (Peek 1997). Recent changes in proportions of successional stages do not appear to favor NYWR moose and population declines are expected (see Chapters 1 and 2). However, the adaptability of NYWR moose and population thresholds for change are unknown.

Variation in Cover Category Use Among
Sympatric Cervids on Moose Winter Range

Moose may share habitat spatially and temporally with a variety of browsers, including elk and mule deer. Where this occurs, competition may exist in the form of joint exploitation of essential resources such as food, or they may simply occupy the same area without true competition occurring (Wiens 1977, Boer 1997). Others have investigated competition among large herbivores by measuring the niche overlap of sympatric species (Stevens 1974, Anthony and Smith 1977, Schwartz and Ellis 1981, Jenkins 1985). Although niche overlap measures the degree of resource use two species hold in common, equating overlap with competition requires verification that resources are limiting (Wiens and Rottenberry 1979, Abrams 1980). High niche overlap in a period of resource shortage is generally taken as evidence for competition (Jenkins 1985). If niche overlap increased during the lean period, it implies that species are forced to specialize on the limited available resource and thus to compete.

Mule deer are associated with open shrubby areas and adjacent forest ecotones, and competition between mule deer and moose is not thought to be great (Boer 1997). Elk are primarily grazers, but their food preferences can shift in response to food availability, and they appear to be successful browsers as well (Houston 1982). On the NYWR, elk follow the typical use patterns of grazers but also capitalize on deciduous trees and shrubs where available, especially willow. Flexible foraging habits, the ability to use a wide variety of terrain, and high fecundity allow elk to be effective competitors. They have the potential to out-compete moose for food (Wiens 1977, Telfer and Cairns 1986). Moose can use scattered winter forage more efficiently than large herds of elk, but concentrations of elk can quickly deplete limited food, such as willow, that is important to moose (Wiens 1977, Houston 1982).

Jenkins (1985) evaluated habitat and niche relationships between white-tailed deer, elk, and moose in bottomlands along the North Fork of the Flathead River, Montana. Spatial and temporal variation in the

North Fork environment and interspecific differences in foraging requirements ameliorated competitive relations both within and between years and in so doing, enhanced coexistence among cervids. White-tailed deer concentrated on forage quality, moose on forage quantity, and elk were intermediate. Deep snow appeared to limit many options for forage and habitat selection that may have resulted in temporary competition between elk and white-tailed deer and elk and moose during harsh winters. Stevens (1974) also found ecological separation between moose and elk in Montana and Wyoming, with moose occurring in areas of deeper snow.

I found limited habitat niche overlap in moose winter range among 3 cervid species. When cover category use was shared, it generally occurred between moose and elk and elk and mule deer. However, all 3 species had some association with one important resource, the willow cover category. Elk preferred the oldest lodgepole pine/sagebrush cover category in the early and mid-winter periods. Elk and mule deer preferred the oldest Douglas fir/sagebrush cover category. Moose avoided both cover categories during all winter periods. Elk preferred the oldest spruce fir/young conifer cover category in early winter, and moose used this type in proportion to availability during the same winter period. Elk and mule deer generally used willow in proportion to availability, while moose preferred this type throughout the winter. Because all 3 species browse willow, the potential for competition exists for the willow resource. Otherwise, competition among moose and the other cervids, as defined by use of a common limited resource in late winter, did not occur.

CHAPTER 5

THE EFFECTS OF SNOW
ON MOOSE HABITAT USE
ON THE NORTHERN YELLOWSTONE WINTER RANGEIntroduction

Unfavorable snow conditions tend to make locomotion difficult and restrict activity of many wild ungulates. However, moose are considered "chionophyls", or snow lovers, and are morphologically better adapted to snow environments than other boreal browsers (Peterson and Allen 1974, Coady 1982, Telfer and Kelsall 1984, Peek 1997). Superior size and strength and longer legs enable moose to negotiate deep, dense snows, reach high vegetation (Peek 1997), remain active in inclement weather, and exploit widely dispersed food resources (Telfer and Kelsall 1984, Schwartz 1992). In addition, the relative costs of movements are less for moose than for smaller ungulates (Taylor et al. 1970, Kelsall and Prescott 1971). However, in spite of their favorable adaptations to snow, snow conditions are still a major determinant of moose habitat suitability in northern climates (Kelsall 1969, Peek 1971, Coady 1982, Peek 1997).

As ruminants with a large body size, moose require a large quantity of food (trees and shrubs) and are usually constrained by the time required to obtain it (Peterson 1955, Krefting 1974, Renecker and Schwartz 1997). The amount of available food often determines moose density. Consequently, trade-offs between time and energy constraints and food acquisition influence foraging strategies (Peek et al. 1992, Renker and Husdon 1992). Because snow conditions affect access to food, snow depth and hardness are primary determinants of moose foraging activities (Peek 1971, Telfer and Kelsall 1984, Peek 1986).

Snow depth thresholds that affect moose foraging habits are of particular ecological significance and have been widely studied (Peek 1997). For example, consistent exposure to deep snow because of severe winters or habitat alterations that reduce cover can negatively affect moose winter survival, especially for weaker cohorts (Peterson 1977, Coady 1982, Mech et al. 1987). Snow depth thresholds have been described for the 3 larger North America moose subspecies, but less is known about snow depths selected by the smaller Shiras moose (Peek 1997). Regardless of the subspecies involved, 2 thresholds are usually recognized because of their effect on moose movements. When snow reaches a critical depth, moose usually avoid open areas and seek forests, presumably because movements without cover to ameliorate snow conditions are energetically too costly (Des Mueles 1964, Kelsall 1969, Telfer 1970, Peek et al. 1976, Rolley and Keith 1980, Thompson and Vukelich 1981). In areas where snow annually becomes too deep in

unforested areas for optimum foraging, cover may be a limiting factor (Kelsall and Prescott 1971). Another threshold represents the maximum depth moose can tolerate with or without cover. Depths that exceed this threshold preclude sustained activity (Des Mueles 1964, Peek 1997). This snow depth threshold can determine the upper elevational limit of moose winter range (Jenkins 1985, Peek 1986, Peek 1997).

North American moose demonstrate regional habitat use differences related to obtaining adequate food in snowy northern climates. Many studies have demonstrated that North American moose benefit from the enhancement of shrubfields following fire or logging in boreal forests (Peterson 1955, Taber 1966, Krefling 1974, Kelsall and Telfer 1974, LeResche et al. 1974, Irwin 1975, Peek et al. 1976, Peek 1997). In these environments, forest canopy removal promotes growth of woody browse species by reducing competition between trees and shrubs, and large quantities of food accessible above the snow minimize moose foraging costs (Spencer and Hakala 1964, Dyrness 1973, Kelsall et al. 1977, Whittinger et al. 1977, Parker and Morton 1978, Irwin and Peek 1979, Oldemeyer and Regelin 1987, Thompson and Stewart 1997). For these reasons, natural and human-induced disturbances that create early successional stage forests are often considered necessary to replenish moose habitat across the continent (Coady 1982, Thompson and Stewart 1997).

However, North American moose are also occasionally associated with habitats where fire is infrequent and even a detriment to habitat quantity and quality. In these locations, post-fire shrub growth is not prevalent and intact forest canopies are critical for providing browse and ameliorating snow conditions. For example, Peek (et al. 1987) found that moose in central Idaho inhabit forests with a sub canopy of Pacific yew browse beneath an overstory of >150 year old mixed conifers. He believed that these double-canopy forests reduced snow depth by intercepting falling snow and prevented crusting by providing shade. Loope and Gruell (1973) hypothesized that moose in the GYA, also an anomaly, were similarly associated with mature conifer forests. McDowell and Moy (1942) and Peek (1974a) speculated that, by mid-winter, NYWR moose are forced from riparian willow stands by deepening snow to near-by densely forested mountainsides where they find abundant conifer browse and less snow.

In boreal forests, like the NYWR, where post-disturbance shrub proliferation does not occur (see Chapter 7), moose have presumably developed foraging strategies for surviving in double-canopy conifer forests. Because mature forests are vulnerable to disturbance, moose in these environments are also vulnerable. Replacing mature forests with early successional stages could reduce available browse and opportunities for moose to find relief from deep snow. Wildfires in mature forests are inevitable, but planned events such as prescribed fire, creation of firebreaks through fuel reduction, logging, and road

building are discretionary. Therefore, it is important for managers to understand the relationship between moose and snow conditions in these forested environments.

Sympatric cervid winter distribution is another important factor in boreal forest management. Moose may share habitat spatially and temporally with a variety of browsers, including elk and mule deer. Where this occurs, competition may exist in the form of joint exploitation of essential resources such as food, or they may simply occupy the same area without true competition occurring (Anthony and Smith 1977, Schwartz and Ellis 1981, Jenkins 1985, Boer 1997). Competition and spatial overlap among large herbivores in northern climates can be strongly influenced by snow depths which either separate the species and enhance coexistence or limit forage and habitat selection causing temporary competition (Jenkins 1985, Boer 1997).

I used multiple methods to investigate the relationship between NYWR Shiras moose and snow depth at several spatial and temporal scales. By recording moose tracks on an extensive system of fixed transects, I addressed moose winter range habitat selection in response to variation in snow depth among winter periods, as well as upper limit snow depth thresholds. I also included records of elk and mule deer tracks to examine species-specific distribution in the context of snow depth variation.

According to the untested hypothesis of Loope and Gruell (1973), McDowell and Moy (1942), and Peek (1974a), NYWR moose winter foraging strategies result from a lack of available deciduous browse and the advantages afforded by double-canopy conifer forests. Snow depths in forested environments may vary because of tree canopies and other factors that ameliorate snow conditions providing moose routes with less snow and easier traveling while foraging in forests. Snow depth can affect the ability of moose to access browse and balance energy demands. For these reasons, I compared snow depths at moose beds and along travel routes with the average available snowpack in the 2 most important types of double-canopy conifer forests available to NYWR moose (mature lodgepole pine and spruce-fir) (see Chapter 3 and 4). I also assessed variation in snow depth and the availability of deciduous browse species (see Chapter 3) among winter periods in these same forests.

Methods

Variation in Snow Depth at Moose Beds and Travel Routes Among Winter Periods

I recorded snow depths at beds found while back-tracking collared and uncollared moose through the snow and compared the differences among the early, mid-, and late winter periods as an expression of

variability of snow depth on winter range. Snow depths were recorded about 2 m from the edge of the moose bed crater. Fourteen instrumented moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were available for back-tracking. Fresh tracks from a minimum of 2 radiocollared and 2 uncollared moose were located monthly (November - April) in each study unit from 1986 to 1990. I did not follow moose because I did not want the animals to respond to my presence. I located a minimum of 2 beds for each tracking effort.

While back-tracking collared and uncollared moose through the snow, I recorded the species and height of browsed trees and shrubs and also measured the snow depth where moose stood to reach each browsed plant. I continued tracking efforts until 500 bites had been counted. On each route where moose concentrated browsing, I randomly placed a cluster of 3 plots, 3 m in radius. I determined the height and species of each tree and shrub in the plots and the snow depth past the drip line (outer most edge of branches). This allowed for a comparison of the average snow pack present versus the snow depth where moose traveled. I summarized the data for the early (November-December), mid- (January-February), and late (March-April) winter periods for all years in the oldest lodgepole pine and spruce-fir forests, the 2 most important forested cover types for wintering moose in the study area (see Chapters 3 and 4). I considered the hypothesis that there is no difference in the depth of snow where moose traveled and browsed versus random locations in the same area.

Average Height of Browsed Shrubs Compared to Average Snow Depth

Snow depths at 3-m radius plots placed along moose travel routes and measurements taken next to browsed trees and shrubs found while back-tracking moose were used to determine an average depth for the early, mid-, and late winter periods. This was compared with the average heights of shrubs browsed by moose (see Chapter 3) to determine which shrub species would likely be exposed above the snow pack and available as browse during different winter periods.

Variation in Snow Depth by Moose and Sympatric Cervids on Track-Intercept Transects

I compared snow depths at tracks found on fixed transects with snow depths available along the length of the transects to test if moose, elk, and deer used snow depths in proportion to their availability. I grouped moose, elk, and mule deer track data for analysis into the early, mid-, and late winter periods. I tested the hypothesis that snow depths used by moose, elk, and mule deer did not differ significantly from

snow depths available along transects through moose winter range in the early, mid-, and late winter periods.

Jenkins (1985) described a protocol for using tracks in snow along fixed linear transects to investigate distribution and habitat selection of ungulates, including moose. I established transects based on this protocol in 3 of the 4 study units- SB, SC, and BC. I conducted a preliminary reconnaissance to determine the spatial limits of moose winter range along an elevation gradient. Transects were designed to extend above and below observed moose winter range. In SC and SB, transects roughly followed the stream course. In BC, the pattern was dendritic and followed a network of logging roads.

The same route was used with each sample. Travel was by skis, snowshoes, or snowmobiles depending on travel restrictions and convenience. Transects were sampled 2 to 4 times a month from November through May, 1986-1990. The annual date of initiation and conclusion varied because of different arrival and melting times of the snow pack.

Transects were traveled approximately 24 hours after a snowfall. New snow provided a fresh surface to "read" tracks. Each time a track was intercepted it was recorded. In addition to moose tracks, I recorded elk and mule deer because of the importance of winter distribution and habitat relationships of these species in sympatry (Cairns and Telfer 1980, Boonstra and Sinclair 1984, Jenkins 1985). If tracks were difficult to identify, they were followed off the transect until a distinguishing foot print, hair sample, or pellet group was located. The snow depth at each track set was also recorded.

A track was recorded when it crossed the transect. The track of an animal walking down the path was recorded once. A track indicating an animal had crossed the path to browse and then re-crossed the path to browse on the other side was counted as many times as it crossed and re-crossed. The animal was expressing a behavioral link to that area by where it traveled. Therefore, each time it crossed the path the intercept was recorded to capture that behavior. This is a departure from the methods used by Jenkins (1985) where tracks were recorded once in these instances.

Track-intercept transects were also divided into 55 sections with common slope, aspect, elevation, and vegetation. The 55 sections were close to equal length and represented my best effort to break the transects into areas with similar habitat features. The length of each section was measured using a hand-operated odometer wheel during the summer. Five snow depth measurements were taken in each section and averaged each time the transect was traveled to determine snow depth available per section. The percent of each transect available in each snow depth category was calculated based on the number of times the transect was traveled each month. Snow depth categories were described in 20-cm increments from 0-200 cm.

Differences in use patterns were tested using Chi-square in conjunction with Bonferonni Z-statistic (Neu et al. 1974) when data on use and availability were recorded. Results appear in Appendix R. To ensure that Chi-square tests were robust, I limited the number of categories representing what was available in the environment to 10. In addition, not more than 20% of the categories reflected 5% or less of the actual use data. To simplify reporting I described habitat used in proportions greater than availability as preferred and habitat used proportionally less than availability as avoided, recognizing that these descriptors overstate the relationship of animals to their environment. I used Spearman's rank correlation test to quantify the associations among moose, elk, and mule deer selection of snow depths.

Results

Variation in Snow Depth at Moose Beds and Travel Routes Among Winter Periods

Average depths at moose beds varied by winter period and were commensurate with snow depths along moose travel routes. They increased from 38.3 cm in early winter (n=68) to 59.1 cm in mid-winter (n=236) and decreased to 56.6 cm in late winter (n=262). These were similar to the range of snow depths utilized by moose during feeding and other daily activities.

Snow depths were consistently greater in lodgepole pine forests than in spruce-fir stands, and average available snow depths in these 2 cover types were consistently greater than snow depths used by browsing moose (Figure 29). The difference between available and used snow depth increased as winter progressed and snow depths increased in both cover types. The average snow depth used by moose in the 2 types varied through the early, mid-, and late winter periods (38.4 cm, 59.9 cm, 57.4 cm, and 22.3 cm, 41.8 cm, 40.1 cm, respectively).

In early winter, average snow depths along routes taken by browsing moose varied by < 2 cm from available depths in the oldest lodgepole pine (used n=484, available n=169) and the oldest spruce-fir (used n=4,067, available n=1,588) (Figure 29). Snow depths in early winter were about 16 cm less in the oldest spruce-fir than the oldest lodgepole pine. By mid-winter, the average depth of the snow pack where moose traveled was 5.4 cm less than the mean depth in the oldest lodgepole pine (used n=1,784, available n=1,330) and 11.4 cm less in the oldest spruce-fir (used n=1,273, available n=540). Compared to the oldest spruce-fir, snow depths used by moose in the oldest lodgepole pine were 18.1 cm greater and available snow depths were 12.1 cm greater. During late winter, the difference between used and available snow depths increased to 22.2 cm in the oldest lodgepole pine (used n=1,155, available n=419) and 26.8 cm in

the oldest spruce-fir (used $n=412$, available $n=71$) (Figure 29). Snow depths associated with moose tracks in the oldest lodgepole pine were 17.3 cm greater than in the oldest spruce-fir type, while the difference in available snow depths between the 2 types was 12.7 cm.

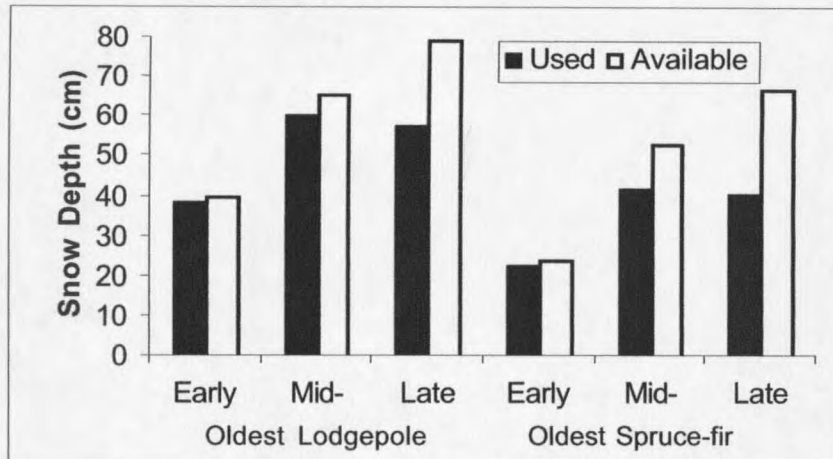


Figure 29. Average available snow depth (cm) in the oldest lodgepole pine and the oldest spruce-fir forests during early (November-December), mid- (January-February) and late (March-April) winter compared with snow depths along routes used by browsing moose.

Average Height of Browsed Shrubs Compared to Average Snow Depth

Snow depths affected the availability of several browse species to moose. Grouse whortleberry (*Vaccinium scoparium*) was consistently buried during early, mid-, and late winter by snow (Figure 30). Six other species, Labrador tea, honeysuckle (*Lonicera* spp.), skunkbush sumac (*Rhus trilobata*), gooseberry, snowberry (*Symphoricarpos albus*), and huckleberry (*Vaccinium globulare*) were, on average, unavailable to moose for browsing during mid- and late winter. Three species, Rocky Mountain maple (*Acer glabrum*), ninebark, and buffaloberry, were, on average, available all winter above the snow pack. The sample size for serviceberry (*Amelanchier alnifolia*) was inadequate, and willow was not sampled.

Variation in Snow Depth Selection by Moose on Track-Intercept Transects

During early winter, snow depths of 0-20 cm and 60-140 cm were avoided by moose, while snow depths of 20 to 40 cm were preferred and snow depths of 40-60 cm were used in proportion to availability (Table 37) (Appendix R, Tables 94-95). In mid-winter, moose preferred snow depths of 60-80 cm. Snow

depths of 20-60 cm were used in proportion to availability, but other depths were avoided. In late winter, moose preferred snow depths from 40-60 cm. Depths from 0-40 cm and 60-100 cm were used in proportion to availability while the remainder were avoided.

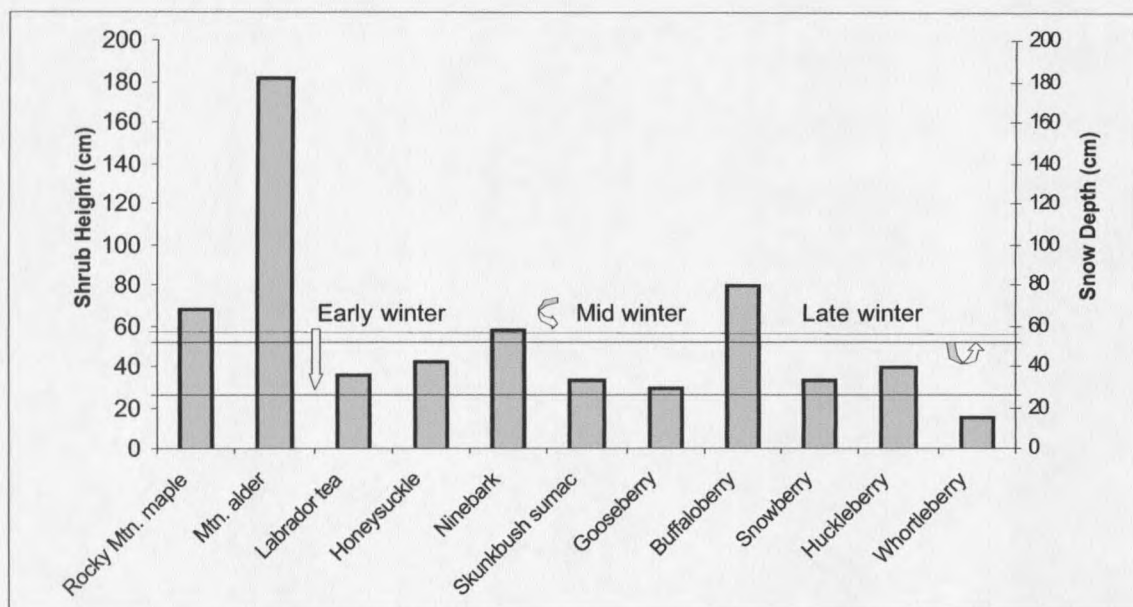


Figure 30. Average height of 11 shrub species recorded from plants browsed by moose in comparison with the average early (November-December), mid- (January-February), and late (March-April) winter snow depth in areas browsed by moose.

Table 37. Percent of moose tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available. Data were recorded during the winters 1986-1991. Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than availability (+), habitat used proportionally less (-) or habitat use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix R, Tables 94-95. Numbers of tracks in each winter period appear in parentheses.

Snow depth	Early use (932)	Early available	Mid- use (645)	Mid- available	Late use (256)	Late available
0-20	5.4 (-)	10.0	0.0 (-)	0.1	3.2 (0)	2.4
20-40	46.5 (+)	32.0	4.9 (0)	2.8	4.6 (0)	2.4
40-60	37.0 (0)	38.3	12.1 (0)	10.2	27.3 (+)	8.9
60-80	10.7 (-)	14.1	64.9 (+)	31.2	25.4 (0)	18.4
80-100	0.3 (-)	3.7	16.6 (-)	27.2	21.5 (0)	23.2
100-120	0.0 (-)	0.6	1.6 (-)	16.6	13.3 (-)	20.4
120-140	0.0 (-)	0.6	0.2 (-)	6.1	4.7 (-)	13.5
140-160	0.0	0.0	0.0 (-)	3.1	0.0 (-)	4.4
160-180	0.0	0.0	0.0 (-)	1.3	0.0 (-)	4.1
180-200	0.0	0.0	0.0 (-)	0.4	0.0 (-)	2.0

Moose did not select the lowest snow depths on the winter range, but throughout the winter they did, on average, use sites with less snow than was available (Figure 31). The difference in the available and selected snow depths ranged from 4.3 cm in early winter ($n=932$) to 18.3 cm in mid- winter ($n=645$) to 25.3 cm in late winter ($n=256$). The average depths at tracks in early winter was 39.5 cm, and it increased as winter progressed to 68.3 m in mid-winter and 70.4 cm in late winner. The maximum snow depth used was consistently much less than the maximum available with the differences ranging from 50 cm in early winter, 105 cm in mid- winter, and 96 cm in late winter. The deepest snow used by a moose was 139 cm in late winter.

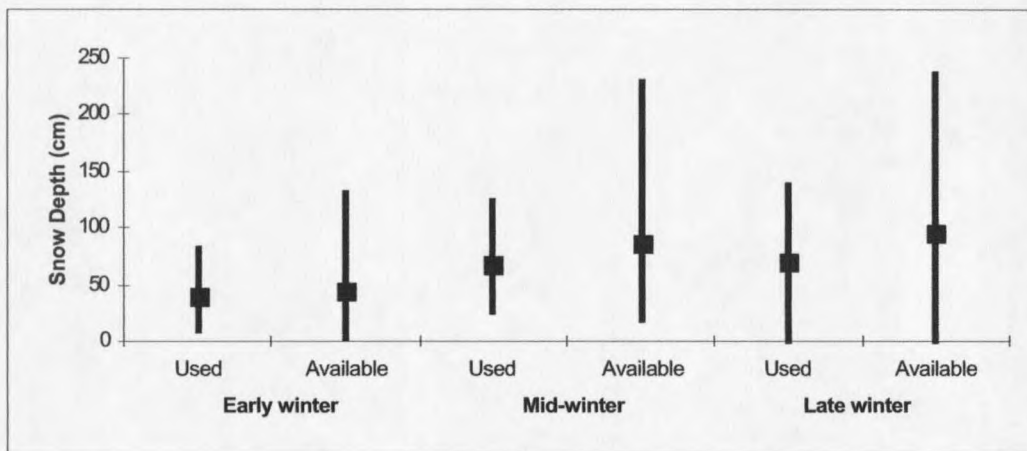


Figure 31. Maximum, minimum, and average snow depth (cm) in habitats used by and available to moose as determined by track encounters.

Variation in Snow Depth Use by Elk on Track-Intercept Transects

During early winter, elk avoided snow depths from 0-20 cm and 60-140 cm, while snow depths from 20-60 cm were preferred (Table 38) (Appendix R, Tables 96-97). In mid-winter, elk preferred snow depths 40-80 cm and avoided the remainder. In late winter, elk preferred snow depths from 0-20 and 40-80 cm. Depths from 20-40 cm were used in proportion to availability, but others were avoided.

Like moose, elk did not select the lowest snow depths on the winter range, but throughout the winter they did, on average, use areas with less snow than the average available snow pack (Figure 32). Elk, on average, used areas with much less snow than moose. Consequently, the difference in the average available and selected snow depths was greater for elk than moose. The mean difference in snow depth at elk tracks ranged from 3.5 cm in early winter ($n=2,182$), 32.3 cm in mid-winter ($n=2,902$), and 44 cm in late winter

(n=290). In early winter, the average snow depth at elk tracks was 40.3 cm, and it increased to 54.5 cm in mid-winter and 51.7 cm in late winter. The average snow depth at an elk track was about 19 cm less than the average depth at a moose track during the critical late winter period. The maximum snow depth used was consistently much less than the maximum available with the differences ranging from 60 cm in early winter, 123 cm in mid-winter, and 107 cm in late winter. The deepest snow used by an elk was 128 cm in late winter, about 10 cm less than the maximum snow depth for a moose.

Table 38. Percent of elk tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available. Data were recorded during the winters 1986-1991. Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than availability (+), habitat used proportionally less (-) or habitat use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix R, Tables 96-97. Numbers of tracks in each winter period appear in parentheses.

Snow depth	Early use (2,181)	Early available	Mid- use (2,902)	Mid- available	Late use (290)	Late available
0-20	0.7 (-)	10.0	0.0 (-)	0.1	26.2 (+)	2.4
20-40	35.2 (+)	32.0	1.4 (-)	2.8	5.9 (0)	2.4
40-60	63.9 (+)	38.3	53.6 (+)	10.2	15.9 (+)	8.9
60-80	0.1 (-)	14.1	39.7 (+)	31.2	32.4 (+)	18.4
80-100	0.0 (-)	3.7	5.1 (-)	27.2	15.9 (-)	23.2
100-120	0.0 (-)	0.6	0.2 (-)	16.6	2.8 (-)	20.4
120-140	0.0 (-)	0.6	0.0 (-)	6.1	1.0 (-)	13.5
140-160	0.0	0.0	0.0 (-)	3.1	0.0 (-)	4.4
160-180	0.0	0.0	0.0 (-)	1.3	0.0 (-)	4.1
180-200	0.0	0.0	0.0 (-)	0.4	0.0 (-)	2.0

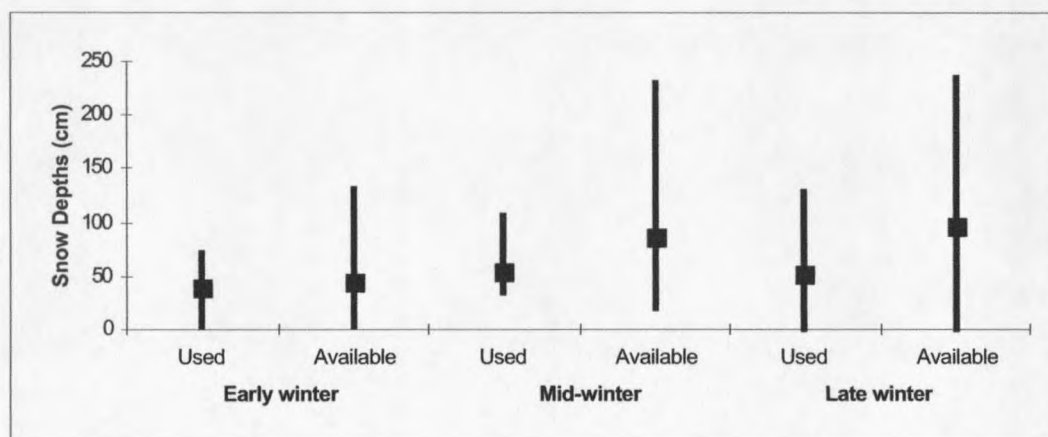


Figure 32. Maximum, minimum and average snow depth (cm) in habitats used by and available to elk as determined by track encounters.

Variation in Snow Depth Use by Mule Deer
on Track-Intercept Transects

During early winter, snow depths 0-20 cm were used in proportion to availability by mule deer, 20-40 cm were preferred and snow depths from 40-140 cm were avoided (Table 39) (Appendix R, Tables 98-99). Snow deeper than 140 cm was not found in areas used by deer. During mid-winter, snow depths from 20-60 cm were preferred and the rest were avoided. Tracks were not found in snow depths deeper than 60 cm and no mule deer tracks were found during late winter.

Table 39. Percent of mule deer tracks (use) found at various snow depths compared to percent of the transect with various snow depths available. Data were recorded during the winters 1986-1991. Early winter is November-December, mid-winter is January-February, and late winter is March-May. Symbols indicate habitat used in proportions greater than availability (+), habitat used proportionally less (-) or habitat use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$, Neu et al. 1974). Chi-square statistics and confidence intervals are reported in Appendix R, Tables 98-99. Numbers of tracks in each winter period appear in parentheses.

Snow Depth	Early Use (313)	Early available	Mid-use (59)	Mid-available	Late use (0)	Late available
0-20	14.7 (0)	10.0	0.0 (-)	0.1	0.0	2.4
20-40	81.4 (+)	32.0	69.5 (+)	2.8	0.0	2.4
40-60	3.8 (-)	38.3	30.5 (+)	10.2	0.0	8.9
60-80	0.0 (-)	14.1	0.0 (-)	31.2	0.0	18.4
80-100	0.0 (-)	3.7	0.0 (-)	27.2	0.0	23.2
100-120	0.0 (-)	0.6	0.0 (-)	16.6	0.0	20.4
120-140	0.0 (-)	0.6	0.0 (-)	6.1	0.0	13.5
140-160	0.0	0.0	0.0 (-)	3.1	0.0	4.4
160-180	0.0	0.0	0.0 (-)	1.3	0.0	4.1
180-200	0.0	0.0	0.0 (-)	0.4	0.0	2.0

The minimum snow depths used by mule deer were comparable to the minimum snow depths available (Figure 33). No mule deer tracks were found in late winter when the average available snow depth was 95.7 cm. In early winter ($n=313$), the average snow depth used by mule deer (28.5 cm) was about 15 cm less than the average available snow depth (43.8 cm). In mid-winter ($n=59$), the average depth at tracks (38.1 cm) was 48.7 cm less than the average available snow pack (86.8 cm). In early winter, the difference in the maximum depth at tracks and maximum snow depth was 88 cm, but by mid-winter it increased to 170 cm. The maximum snow depth at a mule deer track was 59 cm.

Moose early winter snow depth selection was not correlated with selection by elk ($r_s = 0.6$, $P = 0.4$) or mule deer ($r_s = 0.4$, $P = 0.6$) and elk snow depth selection was not correlated with mule deer selection ($r_s = 0.4$, $P = 0.6$). Similarly, there were no correlations between the same ungulate species for mid-winter ($r_s =$

0.8, $P = 0.2$; $r_s = -0.105$, $P = 0.895$; $r_s = 0.211$, $P = 0.789$), or late winter ($r_s = 0.4$, $P = 0.6$; $r_s = 1.0$, $P = 1.0$; $r_s = 1.0$, $P = 1.0$) snow depth selection.

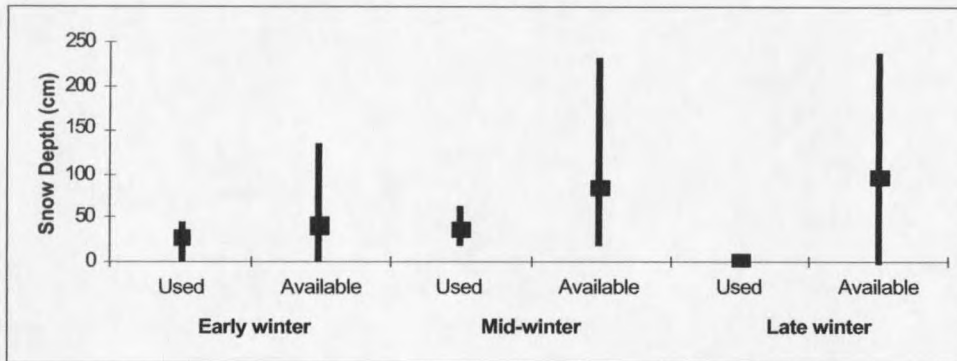


Figure 33. Maximum, minimum, and average snow depths (cm) in habitats used by and available to mule deer as determined by track encounters.

Discussion

Moose survival strategies in boreal forest habitats are significantly affected by snow depth. Moose may be forced to change foraging patterns if snow buries food supplies or if preferred browse becomes energetically too expensive to reach. Because the costs of locomotion increases exponentially in accumulations > 60 cm (Renecker and Schwartz 1997), energy expended by moose to move in deep snow can be greater than energy derived from food intake (Renecker and Hudson 1985). Therefore, moose may restrict their movements or select areas of relatively shallow snow depth rather than expend the energy necessary to travel through deep snow (Peck 1971, Coady 1982, Telfer and Kelsall 1984, Hundertmark 1997). Moose in southeast Alaska reacted to deep snow by confining their activities to those areas within their ranges that had significantly lower snow depths (Hundertmark et al. 1990). In Sweden, 25 cm of snow buried dwarf shrubs, an important winter food item, and 40 cm of snow triggered migration to more favorable winter range (Sandegren et al. 1985).

An inverse relationship between moose survival and fecundity and snow depth has been observed in other populations. Peterson (1977) and Mech et al. (1987) stressed the role of snow accumulation as a limiting factor for Isle Royale moose. Peterson (1977) documented poor calf survival during winters of deep snows, primarily associated with increased wolf predation. He also observed residual negative effects on calves born after severe winters. Bishop and Rausch (1974) documented substantial winter mortality of

mainly calves for several Alaskan populations at high density when snow exceeded a critical depth. They found calf growth and development retarded and survival reduced in subsequent years. Coady (1982) reviewed differential moose mortality resulting from deep snows and resulting malnutrition and concluded that calves, adults > 8 years, and adult males were more affected by nutritional stress than other age groups.

Snow characteristics that affect moose habitat use include temperature, density, hardness, and depth (Peek 1986). Snow provides moose insulation against extremes because snowpack temperatures fluctuate less and never drop below ambient temperatures. Snow density, the relative compaction of individual snow crystals, typically increases during snow pack maturation. Hardness, the degree to which individual snow crystals fuse to one another, also increases with time. Hardness and density jointly influence the ability of a snow pack to support an animal that travels through or on snow. Light, powdery snow permits greater ease and range of movements than does wet, packed snow. Crusted snow can make movements extremely difficult and cause injuries to lower legs and hooves (Kelsall and Prescott 1971, Peek 1997). Snow depth is the easiest determinant to measure and the one most frequently linked to moose habitat relationships (Peek 1997).

Although I was unable to relate temperature, density, and hardness to NYWR moose habitat use, I did address snow depth effects. Generally, northern ungulates do not tolerate snow depths greater than chest height and movements are impeded when snow is metatarsal deep. Limited or restricted movements and access to food have been observed for the 4 subspecies of moose at snow depths ranging from 70-100 cm (Des Meules 1964, Kelsall 1969, Kelsall and Prescott 1971, Coady 1974, Thompson 1987, Peek 1997).

Moose respond to snow depth thresholds with various strategies to conserve energy, including reducing home range size and/or seeking better cover, or moving to winter range at lower elevations. On many winter ranges, moose cope with harsh snow conditions by a greater use of forest cover that ameliorates snow and weather influences (Peek 1971, Peek 1997). The distribution of snow between forests and open areas and within forests influences moose habitat use patterns by affecting forage availability and travel routes. Because deep snow restricts moose mobility, the food found under or near shelter provided by a conifer canopy is important (Coady 1974, Peterson and Allen 1974, Poliquin et al. 1977, Welsh et al. 1980). In northeastern Minnesota (Peek 1971), snow depth and hardness were lower under dense forests than in openings. Where moose travel in forests may be affected by snow distribution, snow tends to drift to greater depths between trees than beneath them (Peek 1997). Snow falling on tree branches, especially branches of fine-needled firs and spruces, tends to be retained and is called *qali* (Pruitt 1959). *Qali* produces a lower snow depth immediately beneath the tree canopy called a tree well or *qamaniq*. The

qamaniq offers moose opportunities to seek forage protruding through the lower snow depth (Coady 1974, Peek 1997).

Habitat use patterns related to snow depth selection indicate that NYWR moose were affected by snow conditions and balanced winter energy needs using strategies similar to other North American populations. They did not use the areas with the least snow on their winter range but did, at all spatial and temporal scales, find areas with less than the average available snow depth. Others have determined that at 60 - 70 cm of snow moose activity is restricted and energy investments for foraging increase significantly (Kelsall and Prescott 1971, Thompson 1987, Peek 1997, Renecker and Schwartz 1997). During the 4 years I collected snow depth data, average annual available snow depths on moose winter range reached or exceeded that threshold by mid-winter and persisted into the late winter period, indicating that snow depth limited options for moose feeding and habitat selection. However, on average, NYWR moose were able to find and utilize locations with snow depths at or below that threshold across the study area. Moose also attempted to balance winter energy needs during foraging activities by taking routes in 2 important forest types that had less snow than the average snowpack available. They likely used the uneven distribution of snow created by canopy effects and drifting patterns between and around trees to find the least energy consumptive paths. They encountered less snow in the oldest spruce-fir forests than in the oldest lodgepole pine forests, probably because the oldest spruce-fir forests had a more complete canopy for intercepting snow.

Snow conditions also affected availability of winter food for moose, and, presumably, moose foraging strategies. Seven of 10 deciduous shrub species commonly available on the NYWR were likely buried by mid-winter and remained buried through the late winter period. The annual pattern of increasing snow depths and corresponding loss of access to food items was reflected in seasonal shifts in winter diet (see Chapter 3) and foraging locations (see Chapter 4).

I found little overlap between moose and mule deer in the NYWR but moderate overlap between elk and moose, although the correlation was not statistically significant. Others have found habitat niche separation among cervids due to species-specific thresholds for snow conditions. However, separation is rarely complete and some amount of spatial and temporal overlap normally exists during winter (Cairns and Telfer 1980, Jenkins 1985). I found that sympatric cervids were partitioned along a snow depth gradient with mule deer predictably using the shallowest snow depths, moose the deepest, and elk intermediate depths. Mule deer were effectively excluded from moose winter range by deep snow during the late winter period, eliminating any potential for interspecific competition with elk and moose for resources during the most difficult winter conditions. Although elk did not demonstrate the same ability as moose to negotiate

snow depths, they were able to access most moose winter range during early winter and portions during the remainder of the winter. Jenkins (1985) found temporary competition between elk and moose in certain shared critical habitats, including coniferous shelter, especially during harsh winters when greater snow depths limited habitat use options. Similarly, there is the potential for competition between elk and moose on the NYWR when both species seek resources such as cover or deciduous browse that are within the snow depth thresholds of each.

I did not measure the effects of snow conditions on moose numbers. However, I did document that NYWR moose had the opportunity to find and utilize snow depths below reported critical thresholds, which should enhance survival, at least during years with similar favorable snow conditions. Results of all methods indicated that at several spatial and temporal scales moose selected areas with less snow than the average available snow pack. At microsites for bedding, along routes used for foraging in several forest types, and across their winter range inclusively, moose utilized snow conditions during all winter periods that were less restrictive than those found in the majority of their environment. As winter progressed, the average selected snow depth increased as did the average available snow depth and the difference between the 2 measurements. Average selected and available snow depths varied among cover types. Snow depths were less in dense canopied spruce-fir forests and greatest along fixed transects with variable or no forest cover. Snow depths routinely encountered in my study area were sufficient to cover average height plants of most deciduous browse species used by moose and force them to use alternative foods (see Chapter 3).

As predicted by Loope and Gruell (1973), McDowell and Moy (1942), and Peek (1974a), mature double-canopy conifer forests play an important role in ameliorating snow conditions for wintering NYWR moose. As such, availability of these forests could be a population-limiting factor, and a decrease would likely result in lower moose densities. In this context, events such as the 1988 Yellowstone fires and logging on the Gallatin Forest could negatively affect moose numbers (see Chapters 1 and 2). Because wild fire is inevitable in mature GYA conifer forests (Romme and Despain 1989) there is little that managers can do to protect moose winter range beyond restricting discretionary activities that open forest canopies. If the objective is retention of moose winter range, resource extraction, road building, and manipulation of mature forests should be relegated to elevations below moose winter range, areas where snow accumulations exceed moose limits, or nonforested cover types. More proactive solutions, such as construction of fuel breaks to prevent landscape level wild fires in unburned landscapes, could also be employed.

FACTORS INFLUENCING THE DISTRIBUTION OF MOOSE IN CONIFER FORESTS
ON THE NORTHERN YELLOWSTONE WINTER RANGE

Introduction

In North America, some moose populations are associated with mature coniferous forests where high densities of small trees beneath double-canopies provide browse (Pierce 1984, Pierce and Peek 1984, Peek et al. 1987), but most use transitory habitats created by fire and logging where concentrations of palatable deciduous vegetation are stimulated by disturbance (Geist 1971, Coady 1982, Thompson and Stewart 1997). In either case, the distribution of moose on winter range is related to the availability of browse (Peterson 1955, Renecker and Schwartz 1997).

McDowell and Moy (1942) and Peek (1974a) speculated that NYWR moose are anomalous because, unlike most North American populations, they spend mid- and late winter on densely forested mountainsides where coniferous cover and browse are abundant. They believed that a pervasive lack of accessible deciduous shrubs across the NYWR and snow conditions (see Chapter 5) promoted this behavior. These theories have not been tested.

Moose winter forage usually occurs as a series of biomass patches of different kinds and sizes unequally distributed in space and time and with varying seasonal value. Moose select habitats with patches of food that favor energy conservation (Renecker and Hudson 1992, Peek 1997). The characteristics of forage concentrations may vary among regions and among forests of different types and ages and may not be distributed uniformly in the habitats that moose prefer. Patterns and densities of browse may, therefore, determine moose distribution. These concepts have not been investigated in landscapes dominated by the oldest age class of lodgepole pine forests. The results would clarify NYWR moose foraging strategies and identify the characteristics of important winter habitat.

I used 2 approaches to understand the factors that influence the winter distribution of NYWR moose in conifer forests. First, I examined the differences in tree and shrub characteristics among moose feeding sites in 7 conifer cover types to determine availability of various food items. As an indicator of the value of the cover type for moose foraging, I examined the browsing rate on various size classes of 5 conifer species.

Second, I tested to see if differences in subalpine fir density in 4 successional stages of lodgepole pine forests helped explain moose winter distribution in this forest type. Loope and Gruell (1973) speculated

that GYA moose rely on mature coniferous forests for winter habitat because of the abundance of subalpine fir browse in the understory.

Subalpine fir, a shade-tolerant species and the primary food item of NYWR moose (see Chapter 3), increases as coniferous forests (predominantly lodgepole pine) mature. It commonly reproduces by layering; the low branches that touch the ground establish roots and then grow vertically. The result is a proliferation of small, branch-like trees centralized around a larger, parent tree. Together they form a dense, pyramid-shaped patch in the forest. Therefore, addressing the characteristics of subalpine fir in forests of different ages involves a representation of these patches. I used the relative density of pellets and intensity of browsing on subalpine fir to represent moose abundance.

Loupe and Gruell (1973) also postulated that GYA moose numbers have increased since the 1800's (see Chapters 1 and 2), in part, because conifer forests matured with human efforts to suppress fires. Romme and Despain (1989) maintained that, although fires have been episodic in the past 300 years, at the time of the 1988 Yellowstone fires, there were more mature lodgepole pine forests in the GYA than in previous centuries. A proportionally greater abundance and size of subalpine fir patches in the oldest lodgepole pine forests would support the theory that there is a direct relationship between NYWR moose density and the amount of mature forests available as winter range.

Methods

Tree and Shrub Characteristics of NYWR Moose Feeding Sites in Forests

I recorded species, height, and browse status of 5 coniferous trees species at moose feeding sites in 7 cover types (Table 40) utilized by wintering moose (see Chapters 3 and 4). Cover types were 3 successional stages of Douglas fir and lodgepole pine forests and the oldest spruce-fir forests. I used the Mattson and Despain (1985) cover type key for describing vegetation patterns. This system is specific to the GYA and accepted by the Departments of Agriculture and Interior. It characterizes forested areas based on dominant tree species and successional stage.

Data were collected during the summer at 160 moose winter feeding sites using circular 0.02-ha plots. The feeding sites were found while back-tracking moose through the snow. I tested the hypothesis that there were no differences among cover types in the average number of trees of each species in each size class. I also recorded the average percent canopy cover and height of shrub species utilized by moose (see

Chapter 3) in the same 7 cover types. I tested the hypothesis that there was no difference in shrub canopy cover and height among cover types at moose feeding sites.

Fourteen instrumented moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were available for back-tracking to find feeding sites. Fresh tracks from a minimum of 2 radiocollared and 2 uncollared moose were located monthly (November-April) in each study unit from 1986 to 1990. I did not follow moose because I did not want the animals to respond to my presence. I continued tracking efforts until 500 bites had been counted. On each route, where moose concentrated browsing I flagged the site and determined UTM coordinates to return for summer sampling.

Despite the overwhelming evidence that subalpine fir is the primary browse of NYWR moose (see Chapter 3), I collected data on all conifer species at identified moose feeding sites, not just subalpine fir. Earlier observational studies reported NYWR moose utilizing Douglas fir, lodgepole pine, subalpine fir, and spruce (USDA 1936, McDowell and Moy 1942, McDowell and Smart 1945a), and I wanted to assess the accuracy of these reports. In addition, recording all tree species found in study plots allowed me to validate results of the back-tracking technique. This method showed that, while subalpine fir was the dominant browse species, lodgepole pine and Douglas fir comprised >5.0% and whitebark pine >1.0% of the diet during at least 1 winter period in at least one study unit (see Chapter 3). However, in spite of the 1936-1945 observations, I did not find NYWR moose I back-tracked utilizing spruce.

Each tree in the study plots was described as browsed or unbrowsed and by height class. Results of measurements for the height classes <1m and 1-5m appear in the text and the remainder in Appendix S. A tree was classified as browsed if any evidence of browsing was found.

Height and cover of important shrub browse species (see Chapter 3) were quantified along line transects at the feeding sites. A 6.1-m (20 ft) baseline was established perpendicular to the slope at the edge of the 0.02 circular plot. Five 20.1-m (66 ft) transects were laid out at 45 degrees to the baseline. The origin of each line along the baseline was selected using random numbers. The number of centimeters of each shrub species intersecting the plain defined by the tape was recorded to determine percent canopy cover (Elzinga et al. 1998). I recorded average shrub height by measuring 5 plants along each line.

Ungulate Activity and Subalpine Fir Characteristics in Representative Lodgepole Pine Forests of Different Ages

I used an additional series of study plots to test the hypothesis that there is no difference in the abundance of subalpine fir or moose activity in lodgepole pine forests of different ages. After searching the

study units, I chose sampling sites that best represented 4 successional stages of lodgepole pine forests (Mattson and Despain 1985)(Table 41). The sampling sites were located in 3 of the 4 study units - BC, SC, and SB. No data collection for this part of the study was done in the YP study unit. To insure selected sites were available to wintering moose, sampling occurred within an area used by >2 radiocollared animals. To minimize differences in floristic site potential, sampling was done in the same habitat type (*Abies lasiocarpa/Vaccinium globulare*) (Pfister et al.1977) and at similar elevations (2,408 m - 2,530 m). For convenience and clarity I use the accepted symbols (LP0, LP1, LP2, and LP3) to represent the cover types in the text (Mattson and Despain 1985).

Table 40. Cover type descriptions for moose feeding sites discovered while back-tracking moose.

Categories	Description
DF0	0-40 years post-disturbance, Douglas fir seedling to sapling stage before canopy closure.
DF2	100-200 years post-disturbance, closed canopy dominated by Douglas fir, understory of small to medium Douglas fir seedlings and saplings.
DF3	300+ years post-disturbance, canopy ragged, predominantly mature to over-mature Douglas fir but containing some spruce, subalpine fir, or whitebark pine in the pole size class, understory of small to large spruce and subalpine fir.
LP1	40-100 years post-disturbance, closed canopy of even-aged lodgepole pine.
LP2	100-300 years post-disturbance, closed canopy dominated by lodgepole pine, overstory mostly intact, understory usually small to medium spruce and subalpine fir seedlings and saplings but also may be mostly lodgepole pine.
LP3	300+ years post-disturbance, ragged canopy of over-mature lodgepole pine but containing some spruce, subalpine fir, and whitebark pine in pole size, understory of small to large spruce and subalpine fir seedlings and saplings.
SF	Mature forests dominated by spruce and subalpine fir in both overstory and understory lodgepole pine. Douglas fir or whitebark pine may be present but are a minor component.

Table 41. Characteristics of 4 successional stages of lodgepole forests.

Successional stages	Characteristics
LP0 (0-40 post-disturbance)	Recently burned or harvested lodgepole pine stands in the grass to seedling/sapling stage before canopy closure.
LP1 (40-100 post-disturbance)	Closed canopy of even-aged, usually dense, lodgepole pine.
LP2 (100-300 post-disturbance)	Closed canopy dominated by lodgepole pine. Overstory still largely intact. Mature lodgepole pine successional stage. Understory usually small to medium spruce and subalpine fir seedlings and saplings but also may be mostly lodgepole pine
LP3- (300 + post-disturbance)	Canopy quite ragged, predominately of overmature lodgepole pine but containing some spruce, subalpine fir, and whitebark pine in the pole sized class. Old growth lodgepole pine successional stage. Understory of small to large spruce and subalpine fir seedlings and saplings.

Sampling included 4 square 0.25-ha plots per study unit - 1 each in LP0, LP1, LP2, and LP3 - for a total of 12 or 3 per cover type. The 0.25-ha plots were used to describe patches of subalpine fir. In addition, there were 15 circular 0.02-ha plots in each cover type in each study unit for a total of 180, 45 per cover type. They were scattered in and around the 0.25-ha plot and were used to determine characteristics of individual subalpine fir.

In the 0.25-ha plots, mature subalpine fir trees and the size of subalpine fir patches were quantified. All subalpine fir >5 m in height were aged with an increment borer, DBH was determined, and the height was measured using a clinometer. Subalpine fir patches were located and the size determined with 4 measurements: major axis or the widest portion of the patch, minor axis or widest portion of the patch perpendicular to the major axis, and 2 measurements at 45 degrees to the intersection of the major and minor axis. The portion of each 0.25-ha plot included in subalpine fir patches was calculated as a percent of the total area.

In the circular 0.02-ha plots, I recorded subalpine fir by size class. Winter pellet groups (Murie 1975, Halfpenny and Biesiot 1986) for moose, elk, and deer were counted and averaged for each cover type. In the sampling area (defined as the area where the 0.25-ha and 15 0.02-ha plots were clustered), 10 of the largest trees were aged with an increment borer.

Statistical Tests

Data were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met ANOVA, Kruskal-Wallis ANOVA by ranks, Newman-Keuls post hoc test, Student's t-test, and Mann-Whitney U test were used to test for differences among and between data ($P < 0.05$) (see Chapters 1 and 2). Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance are reported in the text, P-values only appear in appendices.

Results

Tree and Shrub Characteristics of Moose Feeding Sites in Forests

Moose tracked through the snow utilized 7 major forest types (Mattson and Despain 1985) where 5 coniferous tree species were potentially available as browse. Figures 34-39 show study plot results for

browsed and unbrowsed trees in the height categories <1 m and 1-5 m. The remainder of the data appear in Appendix S, Tables 100-109.

Conifer tree numbers and browsing rates varied significantly among moose feeding sites in the 7 cover types. Subalpine fir was the most heavily browsed tree species (Figure 34). Numbers of subalpine fir trees increased with forest age, and it was the most common tree species in the oldest successional stages of lodgepole pine, Douglas fir, and spruce-fir forests, reaching its highest density in the oldest lodgepole pine forests. Browsing frequency ranged from about 20% to 35% among older forest types where it was common (230-335 trees per plot, on average) to 50% in types where it was rare (1.3 trees per plot, on average), such as young lodgepole pine forests (Appendix S, Tables 100-104).

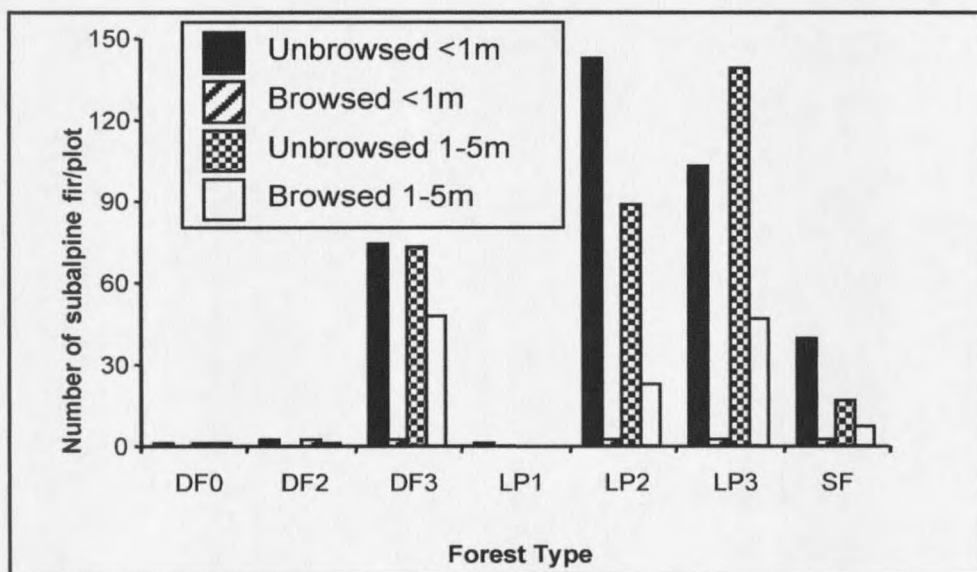


Figure 34. Average number of subalpine fir per 0.02-ha plot by height size class at moose feeding sites in 7 forest types (Table 40): young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests (Appendix S, Table 100). Young = 0-100, mid-=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

Other conifer species generally had lower densities of trees and lower frequencies of browsing at feeding sites than subalpine fir. Lodgepole pine <5 m tall provided browse in young lodgepole pine forests (Figure 35). On average, 75% of 28 lodgepole pines per plot were browsed in this forest type. In older forest types where both lodgepole pine and subalpine fir were common, browsing rates were much higher on subalpine fir (Appendix S, Table 105).

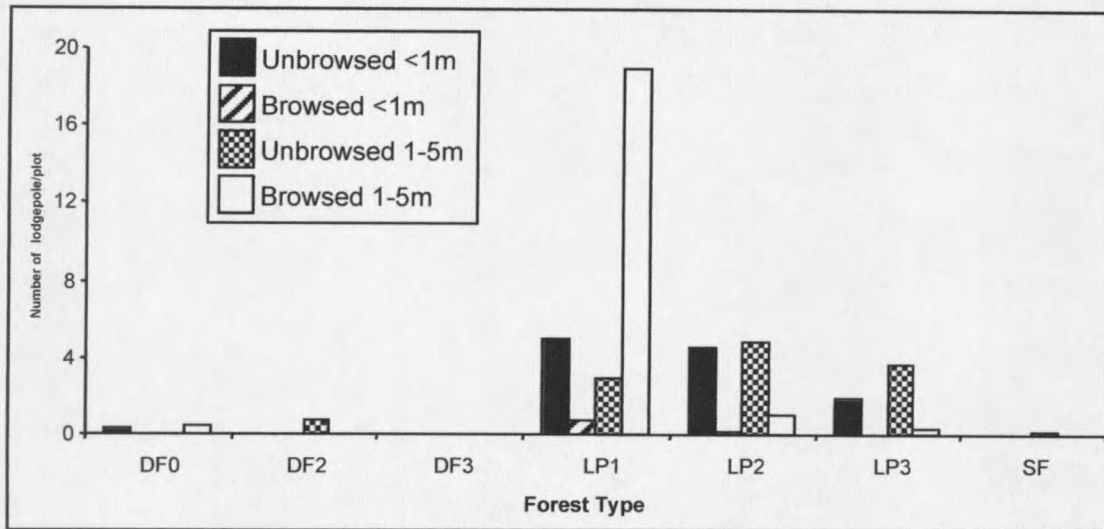


Figure 35. Average number of lodgepole pine per 0.02-ha plot by height size class at moose feeding sites in 7 forest types (Table 40): young (DF0), mid-age (DF2), and oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and oldest lodgepole (LP3) and oldest spruce-fir (SF) forests (Appendix S, Table 105). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

Spruce was not browsed (Figure 36), and browsing rates on Douglas fir were comparatively low (Figure 37). The highest browsing rate for Douglas fir trees was 15% in mid-age Douglas fir stands (39 trees per plot, on average, <5m tall) (Appendix S, Tables 106-107).

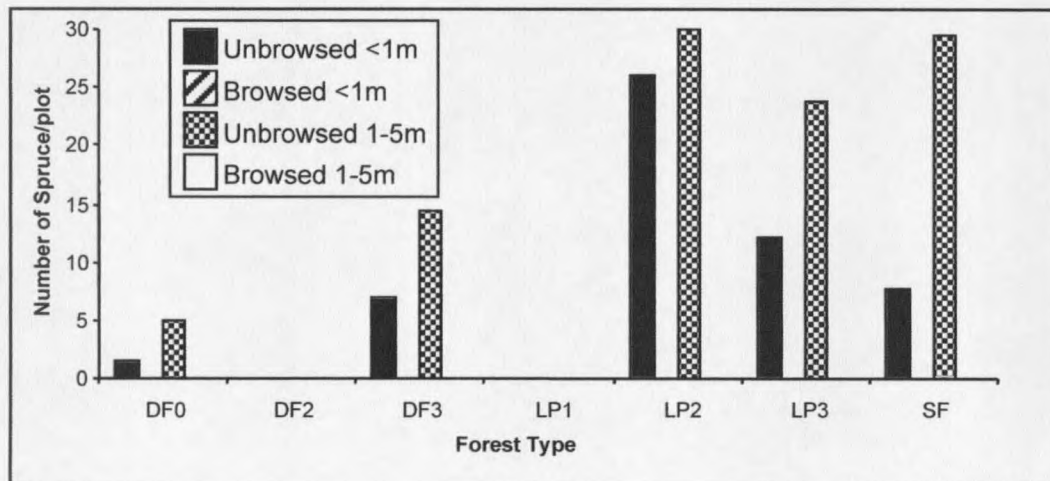


Figure 36. Average number of spruce per 0.02-ha plot by height size class at moose feeding sites in 7 forest types (Table 40): young (DF0), mid-age (DF2), and oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and oldest lodgepole (LP3) and oldest spruce-fir (SF) forests (Appendix S, Table 106). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

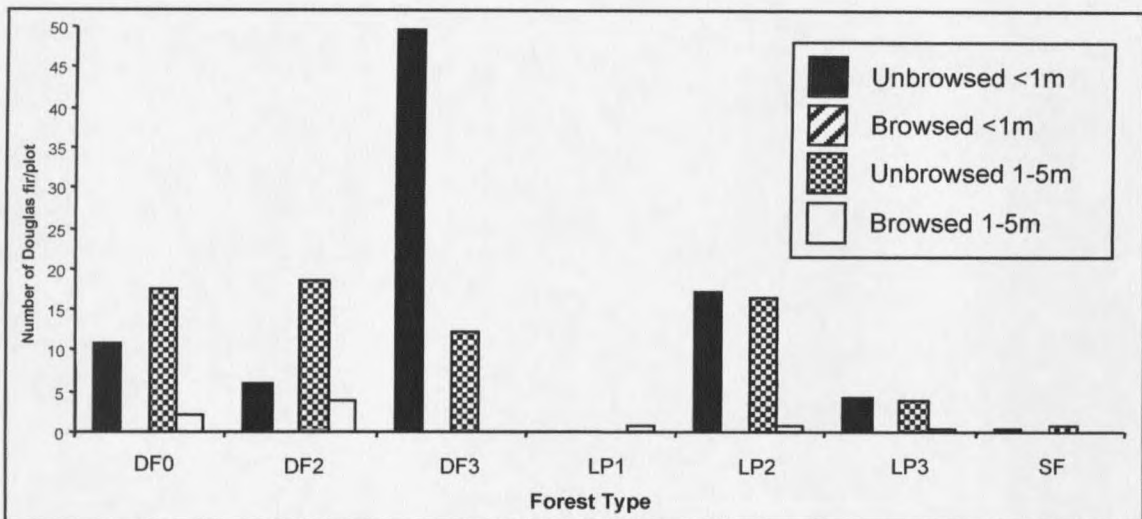


Figure 37. Average number of Douglas fir per 0.02-ha plot by height size class at moose feeding sites in 7 forest types (Table 40): young (DF0), mid-age (DF2), and oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and oldest lodgepole (LP3) and oldest spruce-fir (SF) forests (Appendix S, Table 107). Young = 0-100, mid = 100-300, and oldest = 300+ years post-disturbance (Mattson and Despain 1985).

Whitebark pine was uncommon at feeding sites in most forest types (Figure 38). The highest average number per plot was found in mid-age and the oldest lodgepole pine forests where whitebark pine <5 m tall had some importance as a browse species (33% and 37% browsed of an average 23 and 18 trees per plot, respectively) (Appendix S, Table 108).

A comparison of the abundance of the 5 conifer species at feeding sites among the 7 forest types (Appendix S, Table 109) showed that Douglas fir was the most common tree in young Douglas fir forests (Figure 39) and mid-age Douglas fir, but the advanced successional stage of this forest type was dominated by subalpine fir. A similar pattern was true for forests in the lodgepole pine cover type. Lodgepole pine was the most common tree in young lodgepole pine forests, but subalpine fir was much more abundant than lodgepole pine in the mid-age and the oldest lodgepole pine forests. Also, subalpine fir was the most common tree in the oldest spruce-fir forests followed by spruce.

Deciduous shrubs were generally uncommon at forested winter feeding sites and provided relatively limited forage biomass (Tables 42-43 and Appendix T, Tables 110-122). Only 5 of 12 species comprised > 5% canopy cover in at least 1 forest type, including ninebark, gooseberry, whortleberry, buffaloberry, and snowberry (Table 42). Of these, only buffaloberry and snowberry had >5% canopy cover in more than 1 forest type. Buffaloberry was found in each type, but canopy cover was significantly different in only the mid-age lodgepole pine (7.5% canopy cover) and young Douglas fir (5.7% canopy cover) where it was

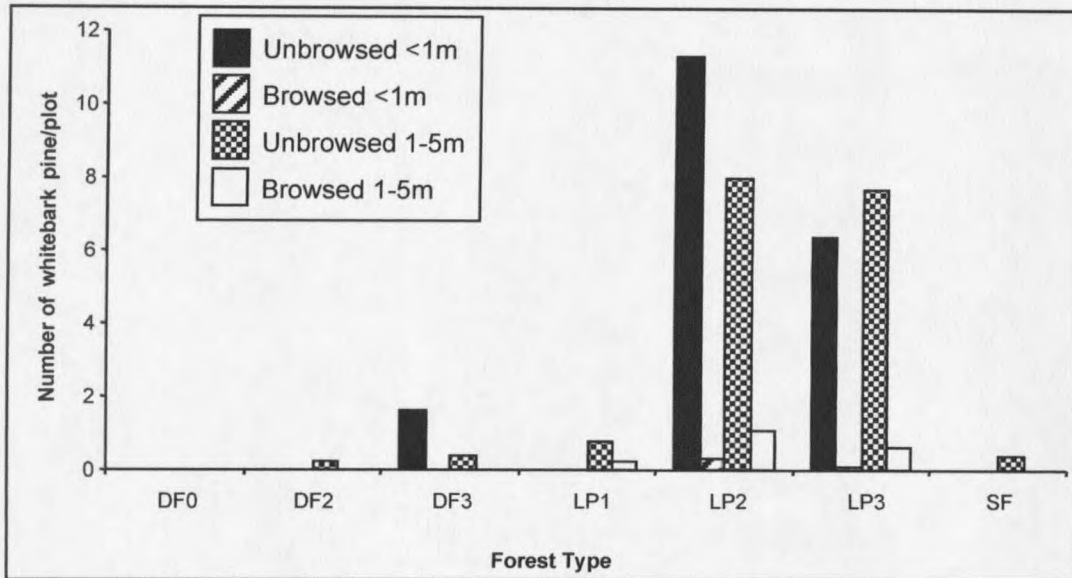


Figure 38. Average number of whitebark pine per 0.02-ha plot by height size class at moose feeding sites in 7 forest types (Table 40): young (DF0), mid-age (DF2), and oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and oldest lodgepole (LP3) and oldest spruce-fir (SF) forests (Appendix S, Table 108). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

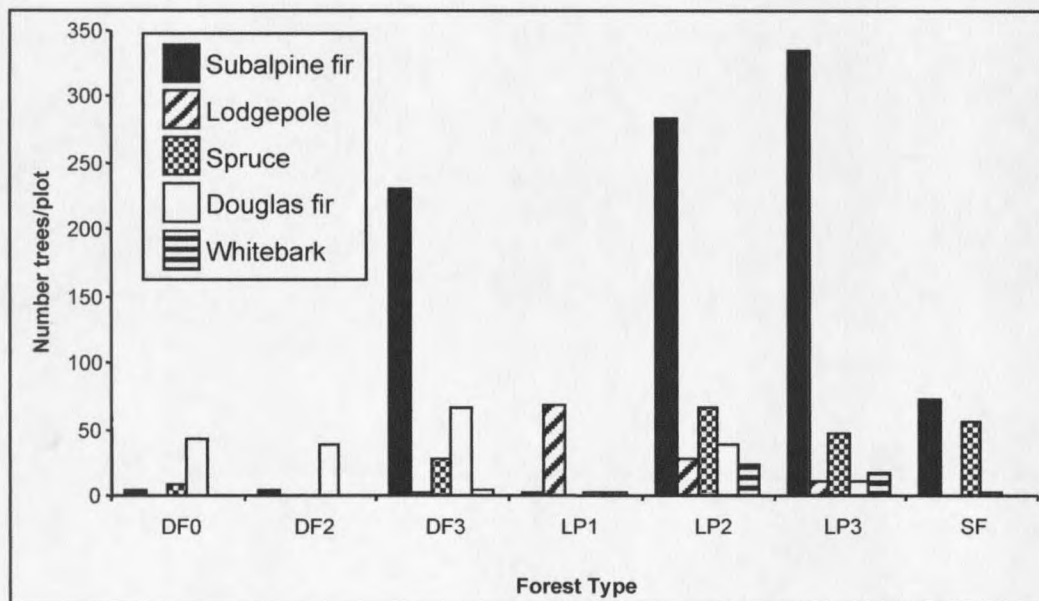


Figure 39. Average number of trees per plot 0.02-ha of the 5 tree species found in the study area for each of the 7 cover types where moose browsing occurred (Table 40): young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests (Appendix S, Table 109). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

most abundant. The canopy cover for snowberry was significantly different in all ages of Douglas fir forest (about 5% canopy cover). Ninebark was significantly more common in the youngest Douglas fir type (37% canopy cover) but was otherwise uncommon or absent. Gooseberry was present in low densities in all types but canopy cover was significantly greater in the oldest spruce-fir type (10% canopy cover). Canopy cover differences were also significant between the young and oldest Douglas fir types (2.2% and 1.86%, respectively) and the lodgepole pine types. Grouse whortleberry was present in the oldest forest types and was most abundant in the oldest lodgepole pine type (9.2% canopy cover).

Table 42. Average percent canopy cover of deciduous shrub species in 7 forest types where moose browsing was recorded (Table 40): young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF). Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Blanks indicate insufficient data. Scientific names appear in Appendix D, Table 54. F and P of tests values are given in the table.

	DF0	DF2	DF3	LP1	LP2	LP3	SF	F	P<
Maple	3.2	0.0	0.4	0.0	0.1	0.0	0.0	20.6	0.001
Alder	0.0	0.0	0.0	0.0	2.8	1.2	3.1	2.18	0.115
Serviceberry	1.1	0.2	0.0	0.0	0.1	0.0	0.0	48.01	0.001
Labrador tea	0.0	0.0	0.0	0.0	0.0	0.4	0.4		
Honeysuckle	0.1	0.0	2.3	0.0	2.9	1.4	0.9	10.36	0.001
Ninebark	37.6	1.8	0.1	0.1	0.0	0.0	0.0	338.19	0.001
Gooseberry	2.2	1.1	1.9	0.1	0.3	0.6	10.0	64.07	0.001
Willow	0.0	0.0	0.0	0.0	0.0	0.0	1.5		
Buffaloberry	5.7	1.2	1.2	0.4	7.5	2.1	0.2	29.83	0.001
Snowberry	6.5	5.1	5.1	0.1	0.0	0.4	0.1	63.36	0.001
Huckleberry	0.0	0.0	2.3	0.0	3.5	3.2	1.9	1.01	0.413
Whortleberry	0.0	0.0	0.3	0.0	2.4	9.2	2.1	12.43	0.001

In environments where snow depth affects moose access to shrubs, shrub height is an important determinant of browse availability (see Chapter 5). Of the 12 shrub species browsed by moose in these forest types, the average height of 9 was <1 m, too short to provide moose with an important food source in mid- and late winter (Table 43). Mountain maple, alder (*Alnus* spp.), and willow were the only shrubs that had average heights >1m in any forest type. Mountain maple was significantly taller, on average, in the LP2 type. Height differences in alder were not significant, but it grew tallest in the LP3 type. Willow was only found in the SF type. The LP2 forests were the best location for moose to search for the tallest plants. Average heights were significantly greater for 4 shrub browse species in LP2, 3 in SF, 1 in LP3, 1 in DF2, and 1 in DF0. However, of the shrub species with the tallest plants located in the LP2 type, 3 of 4 were < 75 cm tall, on average.

Table 43. Average height (cm) of 12 deciduous shrub species in 7 forest types where moose browsing was recorded (Table 40): young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3), and the oldest spruce-fir (SF). Young = 0-100, mid-=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985). Blanks indicate insufficient data. F and P values of tests are given in the table.

	DF0	DF2	DF3	LP1	LP2	LP3	SF	F/H	P<
Maple	95.0		84.6		126.0			H8.89	0.012
Alder					180.8	217.4	204.3	F0.39	0.684
Serviceberry	44.5	34.7			71.5	27.1		H30.87	0.001
Labrador tea						21.9	28.6		
Honeysuckle	59.3		49.2		60.5	53.9	58.5	F3.82	0.005
Ninebark	70.4	60.6	37.5	18.9		36.7		H31.02	0.001
Gooseberry	38.5	52.7	35.3	25.5	63.5	44.9	49.7	F17.31	0.001
Willow							134.9		
Buffaloberry	66.5	71.4	76.1	57.8	93.2	86.3	93.5	F29.83	0.001
Snowberry	31.9	48.1	42.4			38.0	46.3	H14.95	0.005
Huckleberry			29.6		40.8	39.5	41.1	F13.43	0.001
Whortleberry			9.7		13.5	15.2	13.1	F5.8	0.001

Ungulate Activity and Subalpine Fir Characteristics in Representative Lodgepole Pine Forests of Different Ages

Forest characteristics, subalpine fir densities, and average pellet group numbers varied among the stands chosen to represent the 4 successional stages of lodgepole pine forests in moose winter range. Average ages of the 10 largest trees (LP0-8.4, LP1-93.0, LP2-185.4, to LP3-226.4 years) were significantly different ($P < 0.001$, $H = 93.33$) (*post hoc* tests, Appendix U, Table 123). The average number of moose pellet groups per plot was also significantly different ($F = 46.91$, $P < 0.001$) (Figure 40). *Post hoc* tests demonstrated that the results for LP3 were significantly higher than for the other successional stages (Appendix T, Table 124). The average number of elk pellet groups per plot differed significantly with the highest average occurring in LP1 ($F = 13.48$, $P < 0.001$) (*post hoc* tests, Appendix U, Table 125). The average number of pellet groups for mule deer did not differ significantly among forests of different ages ($F = 1.08$, $P = 0.359$) (*post hoc* tests, Appendix U, Table 126).

The average number of subalpine fir per 0.02-ha plot was significantly different among forests of different ages for every measurement category (Figure 41) (Appendix U, Table 127). The highest number of subalpine fir was found in the LP3 sites in each size class. *Post hoc* tests (Appendix U, Tables 128-141) showed that, for most summary categories, the average number of trees per plot was not significantly different between LP0 and LP1. However, the average number of trees per plot was different between LP2 and each of the other forest types and LP3 and each of the other forest types.

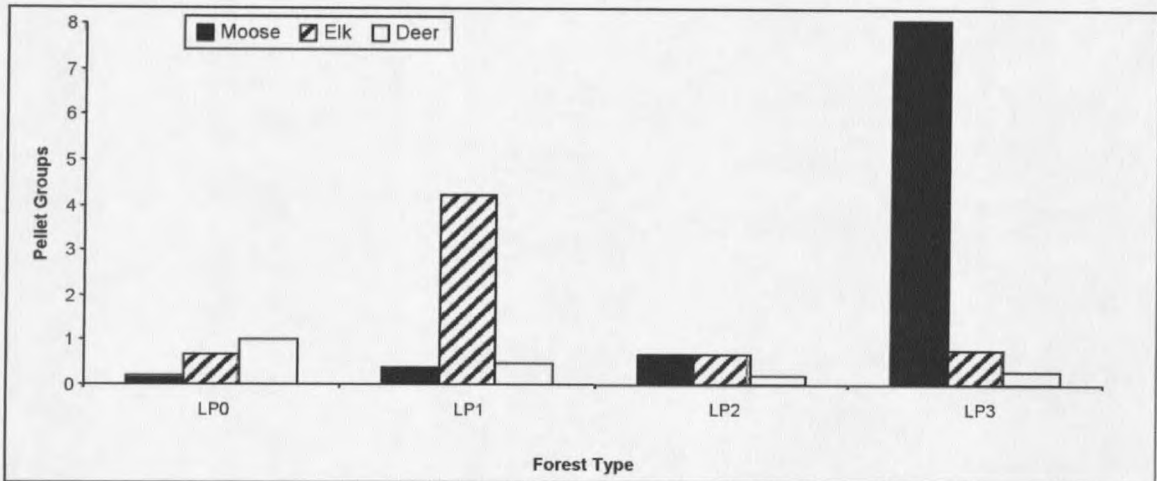


Figure 40. Average number of pellet groups of three ungulate species per 0.02-ha plots in lodgepole pine forests of different ages (Table 40): LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance.

All measurements of subalpine fir >5 m tall and patches of subalpine fir in 0.25-ha plots among the 4 ages of lodgepole pine forests were significantly different, and the greatest average for each parameter was found in LP3 sites (Table 44). Specifically, *post hoc* tests (Appendix U, Table 142) showed the average age of subalpine fir >5 m tall in LP0 was significantly lower than the averages for each of the other sites. *Post hoc* tests (Appendix U, Table 143) also showed that the average DBH of subalpine fir >5 m in LP3 differed

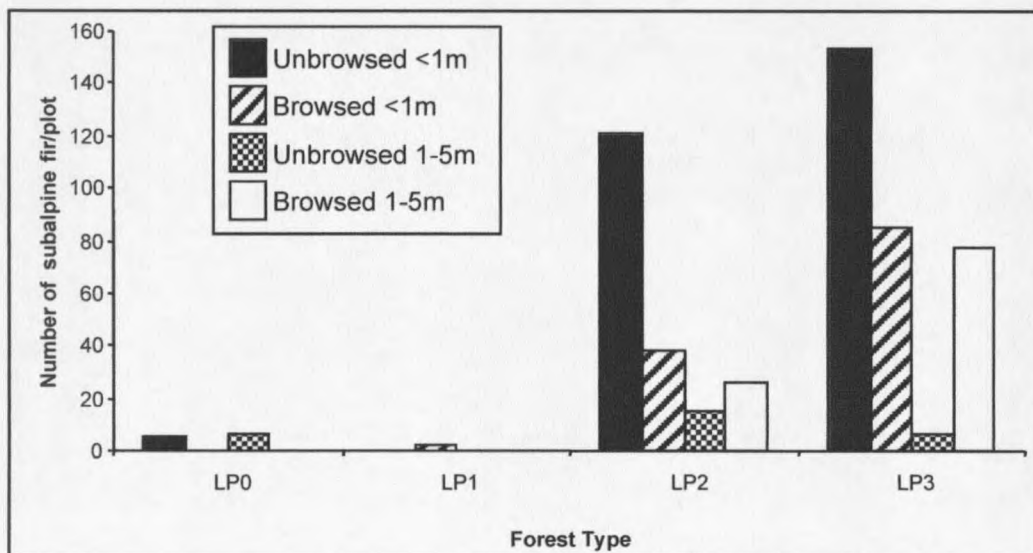


Figure 41. Average number of browsed and unbrowsed subalpine fir per 0.02-ha plot by height size class in lodgepole forests of different ages (Table 40): LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance.

from those in LP0. LP3 had the highest average number of trees >5 m tall, and *post hoc* tests (Appendix U, Table 144) showed it differed from the average for each of the other sites. Although, the average tree height was greatest in LP3, *post hoc* tests (Appendix U, Table 145) showed that the average height of trees in LP3 differed only from LP0. The average number of subalpine fir patches was greatest in LP3. *Post hoc* tests showed the average number of patches in LP3 was greater than in the other successional stages (Appendix U, Table 146). The average size of subalpine fir patches was also largest in LP3. However, *post hoc* testing did not show significant differences (Appendix U, Table 147) among successional stages.

Table 44. Average age, DBH, number, and height of subalpine fir trees >5 m tall per 0.25 ha plot as well as number and m² of subalpine fir patches in lodgepole forests of different ages (Table 40): LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance. F and P values of tests are given in the table.

	LP0	LP1	LP2	LP3	F	P
Average age	15.6	44.8	56.9	70.7	11.51	0.001
Average DBH	1.5	3.2	3.9	4.8	6.68	0.001
Average # of trees	1.2	1.5	21.8	64.0	34.61	0.001
Average height	5.1	5.9	8.7	10.4	6.97	0.001
Average # of patches	0.0	0.7	6.0	49.3	0.941	0.005
Average m ²	0.0	3.3	4.4	13.1	4.44	0.005

Discussion

Forage Characteristics of Forested Moose Winter Range

Significant differences in conifer tree numbers and browsing rates among feeding sites may explain why NYWR moose selected specific locations for foraging. As the most abundant and heavily browsed conifer tree species among all moose feeding sites in 7 forest types, subalpine fir provided NYWR moose the preponderance of the coniferous forage they consumed. Numbers of subalpine fir trees at feeding sites increased with forest age, and it was the most common tree in the oldest successional stages of lodgepole pine, Douglas fir, and spruce-fir forests, reaching its highest density in the oldest lodgepole pine forests. Even though it was preferred, less than 50% of subalpine fir was browsed in most forest types.

Feeding sites usually had lower numbers of trees and lower frequencies of browsing for conifers other than subalpine fir, and the abundance of the other conifers did not appear to explain moose attraction to feeding sites in most cases. Lodgepole pine <5 m tall may have drawn moose to young lodgepole pine forests or been utilized opportunistically. In older forest types where both lodgepole pine and subalpine fir

were common, browsing rates were much higher on subalpine fir. Spruce was not browsed, and browsing rates on Douglas fir were comparatively low, with the highest in mid-age Douglas fir stands. The importance of whitebark pine as a browse species was limited. Trees <5 m tall had some importance as a browse species in the mid-age and oldest lodgepole pine forests.

Deciduous shrubs were generally uncommon at forested moose feeding sites and provided limited forage biomass. Only 5 of 12 shrub species comprised >5% canopy cover in at least 1 forest type and canopy cover rarely exceeded 10%. Only buffaloberry and snowberry had >5% canopy cover at feeding sites in more than 1 forest type. At most, some shrubs in specific cover types could influence moose distribution. For example, the highest canopy cover of gooseberry was found in the oldest spruce-fir forests, habitats moose utilize in the early winter (see Chapters 3 and 4).

Deciduous shrubs at NYWR moose feeding sites were also relatively low-statured. Height is an important determinant of browse availability in environments where snow affects moose access to shrubs (see Chapter 5). Across North America where moose are associated with post-disturbance shrub fields, deciduous species such as aspen, birch, and willow grow to heights several times greater than moose and average snow depths (Spencer and Hakala 1964, Wolff 1978, Eastman and Ritcey 1987, Oldemeyer and Regelin 1987, Peek 1997, Thompson and Stewart 1997). However, of the 12 shrub species found at NYWR moose feeding sites, the average height of 9 was <1 m, too short to provide moose with an important food source in mid- and late winter. Only mountain maple, alder, and willow had average heights in any forest type >1 m and only alder had an average height >2 m. LP2 had the tallest plants of 4 shrub species, but, of these, 3 averaged <75 cm tall.

The distribution of moose pellet groups among lodgepole pine forests of different ages showed that moose utilized the oldest successional stages significantly more than the younger successional stages of this forest type, while elk pellet group distribution was significantly greater in the youngest successional stage, and differences in mule deer pellet group distribution were insignificant but greatest in the youngest lodgepole pine forest. The average number of moose pellet groups was about 8 times greater than elk pellet groups in the oldest lodgepole pine.

Subalpine fir formed discrete patches with dense clusters of small trees around a larger parent tree or trees. Subalpine fir patches had formed sufficiently to be distinct in mid-age lodgepole pine forests, and the number and size of patches increased significantly as the forest matured to a late successional stage. The oldest lodgepole pine forests also provided the greatest biomass of subalpine fir as individual trees <5 m tall and the greatest number of subalpine fir trees >5 m tall, trees large enough to potentially ameliorate snow conditions (see Chapter 5). Frequency of browsing was greater on subalpine fir 1-5 m tall than on

those <1 m tall, probably because trees in the larger size class were more consistently accessible above the snow pack.

The distribution and abundance of subalpine fir may explain moose winter habitat selection. NYWR moose apparently invested the greatest foraging effort at locations with the greatest concentrations of subalpine fir. Subalpine fir was most abundant in the oldest forests as were moose pellet groups. Canopy cover and height data for deciduous browse species did not present a clear pattern to explain moose winter foraging strategies or habitat selection.

Foraging Theory and NYWR Moose Winter Distribution in Conifer Forests

Morphology and energy needs help explain moose foraging patterns. Moose require greater absolute quantities of lower quality but more abundant food than other ruminants (Coady 1982, Peek et al. 1992, Renecker and Schwartz 1997). Food resources in moose boreal forest habitats are not continuous or particularly dense but rather exist as scattered biomass patches. In these environments, moose are limited by the time and energy required to find and consume sufficient food. To exploit resources, moose must move from one food patch to the next, which, with long legs and a large body, they are morphologically adapted to do, even in snow. In response to reduced forage biomass and the impediments of snow conditions during winter, moose travel as little as possible and consume readily available food, occupying habitats where the availability of plants permits high foraging rates and nutrient return (Renecker and Hudson 1993). Therefore, patches of woody browse are the critical component of moose habitat. Moose home range size is probably determined, in part, by a sufficient number and/or size of patches spatially distributed in a way that allows for energy needs to be met (Hundertmark 1997). Presumably, to minimize travel and maximize energy return, the selection of food patches also occurs at smaller spatial scales. In addition to selecting large patches such as shrub fields, moose should also search for species of plants and individual plants with clumped growth forms that provide patches of food at the microsite level.

Renecker and Hudson (1992) examined the influence of moose body size on seasonal energy balances and foraging time as an explanation for moose use of patchy environments. On the basis of moose metabolic needs and digestive capacity, they concluded that a larger body size imposes longer foraging times and also energy budgets that must be balanced more carefully. This is probably achieved by efficient foraging and thermoregulatory tradeoffs, i.e. correctly choosing when and where to feed (Pianka 1994). Low feeding rates and or low amounts of usable biomass cause moose to spend more time moving and looking for food and less time eating.

According to Risenhoover (1987) moose foraging movement rates can be strongly affected by the amount of usable biomass along chosen foraging paths. Success at locating patches of food is critical to moose in attempts to minimize search costs and balance energy budgets. If unsuccessful at obtaining more or sufficient forage, moose may leave one clump of plants in favor of another or abandon a patch and disperse, sometimes over long distances, in search of resources to satisfy the need for large quantities of food.

Johnson (1980) suggested that animal habitat selection occurs at various spatial scales. To reduce forage investments, moose should select habitat at the appropriate scale to include browse patches. Although NYWR moose winter range contained available woody perennial browse at all spatial levels, I found that moose distribution was determined primarily by biomass concentrations of subalpine fir in mature coniferous forests. The distribution and density of subalpine fir varied significantly among forests of different ages, but it was consistently present where moose foraged. NYWR moose winter ranges were in the upper reaches of drainages where the landscape was dominated by dense coniferous forests rather than the more open terrain of lower elevations (see Chapter 4). Moose spent winters in late successional stage lodgepole pine forests. Within these stands, moose selected the densest understories of subalpine fir and concentrated on areas where patches of these trees provided the greatest biomass.

My data support the theory of Danell et al. (1991) that moose food selection occurs primarily at the tree level within stands. They concluded that, in the northern coastal region of Sweden, moose utilized individual trees, not stands, as patches of food. In addition, browse use in relation to availability was disproportionately directed towards the more profitable (largest biomass within reach) tree types. Similarly, use by NYWR moose of areas with high densities of subalpine fir patches also supports the theory of Gross et al. (1995) regarding herbivore foraging patterns. They postulated that, when plants are apparent to the herbivore and are embedded in a matrix producing a high contrast, movements of herbivores are governed by local, small-scale patterns, i.e. during searches for food, herbivores select the "nearest neighbor" when food items are within view, rather than conducting random searches for browse at a larger spatial scale.

Subalpine fir patches may have the appropriate characteristics, including physical structure, to provide what Haukioja and Lehtila (1992) theorized moose required from browse patches - food of sufficient quality and quantity to meet energy needs. The most productive home ranges presumably contain the greatest percent cover of subalpine fir (see Chapter 2). Moose concentrated activity in areas where patches of subalpine fir were relatively dense, which allowed moose to choose foraging routes with high levels of usable biomass along them (Risenhoover 1987). The particularly dense growth form of many small

subalpine fir trees around a parent tree allowed moose to minimize search time for browse (Pyke et al. 1977) and maximize energy capture (Belovsky 1978). Because the number and size of these patches increased with the forest age, density varied among lodgepole pine stands. In the most productive habitats, moose should be able to significantly reduce travel costs in areas that approximate an optimal number of patches (McArthur and Pianka 1966, Danell et al. 1991, Gross 1995).

According to the marginal limits theorem, moose should browse a subalpine fir patch until a threshold of utilization is reached, and it is more efficient to find another patch than continue browsing (Charnov 1976, Astrom et al. 1990). In all ages and types of NYWR moose winter range forests I sampled, browsing on subalpine fir did not exceed 50% of available trees. The frequency of browsed trees was highest in the early successional stages of lodgepole pine, forest where subalpine fir was the least common and the number and size of patches were the smallest. Moose were presumably forced to abandon patches more quickly and use more energy in searching for subalpine fir in these young forests.

In summary, using data on browse abundance and ungulate activity at moose feeding sites and in lodgepole pine forests of different ages, I investigated NYWR moose winter habitat use patterns in relationship to factors that may affect their distribution, including patchy food resources and forest types and ages. My findings validate the theories by Loope and Gruell (1973) McDowell and Moy (1942) and Peek (1974a) that describe NYWR moose utilizing conifer browse in mature forests in an environment with limited available deciduous shrubs.

Like other North American populations, NYWR moose foraging strategies involved utilizing forage biomass patches to balance energy budgets. However, instead of feeding in transitory brushfields created by disturbance, they located environments with the greatest size and density of subalpine fir biomass clusters. These data demonstrate the importance of subalpine fir as a food source for NYWR moose. With its unique growth form of lower branch layering around a parent tree, subalpine fir provides moose with opportunities to minimize travel time and maximize energy capture. Because the number and size of subalpine fir patches and the overall number of trees within reach for browsing increased with forest age, the oldest coniferous forests provided the optimum patch arrangement for meeting energy needs. Other conifer species received little or no browsing. Shrub species were uncommon and did not form sizeable or abundant browse patches in forested moose winter range, including mature forests and recently disturbed areas.

CHAPTER 7

IMPACTS OF CLEARCUTS ON
MOOSE HABITAT USE IN LODGEPOLE PINE FORESTS
ON THE NORTHERN YELLOWSTONE WINTER RANGEIntroduction

In winter, moose attempt to select habitats with concentrations of food that favor energy conservation (Geist 1971, Coady 1982, Peek 1997). Therefore, moose habitat is usually a series of forage patches of different kinds and sizes unequally distributed in space and time and with varying seasonal value. Because forage biomass varies with seral ages of forests, there is a critical link between forest age, food abundance, and moose density (Telfer 1978, Telfer and Kelsall 1984, Renecker and Schwartz 1997).

In North America, some moose populations are associated with more permanent mature coniferous forests where high densities of small trees provide efficient foraging opportunities in double-canopy forests (Pierce 1984, Pierce and Peek 1984, Peek et al. 1987), but most use transitory habitats created by fire and logging where disturbance has stimulated concentrations of palatable woody vegetation (Peterson 1955, Geist 1971, Coady 1982). Because the highest moose densities are often associated with early successional stages, managers use human-induced disturbances to create or maintain habitat (Peterson 1955, Coady 1982, Thompson and Stewart 1997).

On most moose winter range, removal of conifers reduces competition for resources and promotes prolific growth of deciduous vegetation. However, shrub fields are comparatively ephemeral and are replaced by shade-producing conifers (Kelsall et al. 1977, Coady 1982, Risenhoover 1987, Thompson and Stewart 1997). For example, Kelsall et al. (1977) concluded that the optimum successional stages for moose were 11 to 30 years post-disturbance, and Thompson and Stewart (1997) reported that the value of disturbed areas to moose is transient, lasting less than 30 years.

Disturbances in mature forests can also create edges, the interface between two successional stages. In terms of ecological effects, edge is defined as a zone of influence extending into each of the adjacent communities, not as a linear feature. Edge width varies depending on forest type and the habitat needs of the wildlife species considered (Franklin and Forman 1987, Yahner 1988, Morrison et al. 1998). Managers have traditionally considered edges favorable for wildlife because species diversity often increases in these environments (Pianka 1994). Explanations for the edge effect include greater vegetative complexity and

the simultaneous availability of more than one landscape feature, i.e. availability of two different habitats in close proximity (Leopold 1933, Coady 1982, Franklin and Forman 1987, Yahner 1988, Morrison et al. 1998). The edge effect is considered beneficial for most North American moose populations, and edge creation is viewed as either a favorable byproduct or deliberate objective when using fire or logging to enhance moose winter range (Coady 1982, Thompson and Stewart 1997, Peek 1997).

However, more recently, edge effect values for wildlife have been questioned, particularly for species that require forest interior habitat. For example, edges can be detrimental for species needing large, undisturbed areas because increases in edge generally result in concomitant reductions in available interior habitat and corridors (Franklin and Forman 1987, Yahner 1988, Pianka 1994, Morrison et al. 1998).

Some portions of the GNF associated with the NYWR are managed for timber production. Based on the reputed benefits of post-disturbance shrub production and edge effect, the GNF Management Plan (USDA 1987) advocates logging as an ungulate habitat enhancement tool on winter range. However, the effects of these practices on moose have not been tested, and others (McDowell and Moy 1942, Loope and Gruell 1973, Peek 1974a) have postulated that, unlike most North American populations, NYWR moose are forest interior species negatively affected by disturbances.

Loope and Gruell (1973) hypothesized that GYA moose numbers increased through most of the 20th century as conifer forests aged in the absence of disturbances, especially landscape level fires. They believed that mature forests provided moose winter browse concentrations in the form of subalpine fir, a conifer that increases in density under closed canopies. Similarly, Peek (1974a) and McDowell and Moy (1942) forwarded the idea that NYWR moose survive winters in an environment depauperate of deciduous vegetation by retreating to forested mountainsides where dense conifers ameliorate snow conditions and provide browse. Several observational studies of moose food habits conducted between 1936 and 1945 north of Yellowstone Park emphasized the importance of conifer browse in mature forests and listed subalpine fir, lodgepole pine, Douglas fir and spruce as food items (USDA 1936, McDowell and Moy 1942, McDowell and Smart 1945a).

Disturbances in forests and the resulting vegetative structure can affect moose. The forest edge created by clearcutting, and the logged and forested areas on each side have unique characteristics. The relationship between moose and these distinct vegetative patterns provide insights into foraging strategies. I investigated the quantifiable differences in vegetation important to NYWR moose among logged, forested, and forest edge environments of lodgepole pine dominated landscapes to determine how human manipulation of succession affected both moose use of habitat and growth of plants that provide forage.

Given the abundance of elk and mule deer on the NYWR and their potential interaction with moose, I also looked at how these species distributed themselves in relation to edge and the associated vegetative components. Competition among NYWR ungulates for deciduous vegetation, a limited resource, is of significant interest to managers (Tyers 1981, Houston 1982, Yellowstone National Park 1997).

Methods

Data were collected at the abrupt boundaries between 25-year-old clearcuts and ≥ 300 year-old lodgepole pine forests in BC, the only study unit with timber harvests 11-30 years-old, reputedly the optimum post-disturbance age for moose habitat (Kelsall et al. 1977, Thompson and Stewart 1997). To insure the selected sites were available to moose, sampling occurred within an area used by ≥ 2 radiocollared animals. To minimize differences in floristic site potential, sampling was done in the same habitat type (*Abies lasiocarpa/Vaccinium globulare*) (Pfister et al. 1977) and at similar elevations (2,408-2,530 m). I sampled only along clearcut/forest boundaries oriented parallel to the slope. I randomly placed study plot groups at 15 locations along the 4 km of boundary that met these criteria.

Each of the 15 sample sites had 6 circular plots (0.02-ha) for a total of 90 (Figure 42). The circular plots were arranged in rows (6 in each) positioned perpendicular to the slope and extending across a clearcut/forest boundary to include the clearcut and adjacent mature forest. The study plots were positioned relative to the boundary to reflect habitat options available to moose, i.e. clearcut and forest locations within the edge, at the transition between edge and interior habitat, and within interior habitat.

Edge width is variously defined depending on the dominant vegetation and wildlife habitat needs (Franklin and Forman 1987, Yahner 1988, Morrison et al. 1998). At boundaries between open areas and forest, edge width is related to the height and structure of the forests and, when site and species-specific edge effects are unknown, may be interpreted as twice the length of average tree height (Franklin and Forman 1987). In mature NYWR lodgepole pine forests, average height of canopy trees is about 25 m (R. Gowan, GNF, personal communication). Therefore, to sample the range of variation associated with edges, I placed the center of one study plot at the boundary but in the forest (4.0 m from the boundary), while its counterpart was placed at the boundary but in the clearcut (Figure 42). These two represented the area most influenced by edge with and without a forest canopy. Another was placed with its center 50 m from the boundary inside the forest and its counterpart at the same distance from the boundary but in the clearcut. These represented areas with and without forest canopies at the transition between edge and

interior environments. Another was located 100 m from the boundary in the forest and its counterpart at the same distance into the clearcut. These represented forest and clearcut interiors.

I determined abundance and height of conifers in the study plots. While back-tracking radiocollared and uncollared moose through snow to record browsed stems, I found that 4 of 5 conifer species common on winter range were browsed by NYWR moose (see Chapter 3). Although subalpine fir was the dominant browse species, lodgepole pine and Douglas fir comprised >5.0% and whitebark pine >1.0% of the diet during at least 1 winter period in at least 1 study unit. I did not find moose utilizing spruce. With the exception of whitebark pine, these species and spruce were reported in earlier observational studies to be important moose browse on the NYWR (USDA 1936, McDowell and Moy 1942, McDowell and Smart 1945a). To ensure that the back-tracking technique did not misrepresent moose diet at forest edge environments and to clarify the results of the 1936-1945 observations, I recorded all tree species found in study plots, not just subalpine fir.

Each tree found in a study plot was placed in a height class (<1 m, 1-5 m, >5 m tall) and classified as browsed or unbrowsed. I presented data for the 2 smallest size classes in the figures. The remainder of the data appear in appendices (Appendix V, Tables 155-169). Pellet groups of wintering ungulates were also counted (Murie 1975, Halfpenny and Biesiot 1986), these and evidence of browsing on conifers were used as indicators of ungulate activity.

I also quantified height and cover of deciduous shrub browse species (see Chapter 3) along line transects (Figure 42). A 6.1 m (20 ft) baseline was established parallel to the slope at the perimeter of each study plot. Five 20.1 m (66 ft) transects were laid out perpendicular to the baseline. The origin of each line along the baseline was selected using random numbers. The number of centimeters of each shrub species intersecting the plane defined by the tape was recorded to determine percent canopy cover (Elzinga et al. 1998). I recorded average shrub height by measuring 5 plants along each line.

To assess edge effect on ungulate distribution and potential moose browse, I compared pellet group density, and shrub (canopy cover and height) and tree characteristics (height class and browsing rate) at 3 spatial scales. First, to test for differences in these measures across a landscape mosaic of clearcuts, edges, and mature forests, I combined data from all study plots, i.e. data collected at all distances from the clearcut/forest boundary. Second, to assess the existence of edge effect within clearcuts and forests as distinct environments, I examined variation among study plots at the 3 distances from the boundary in clearcuts and in forests separately. Third, to examine differences between the clearcut and forest environments, I pooled data from the 3 locations in clearcuts and compared the results with pooled data from the 3 forest locations.

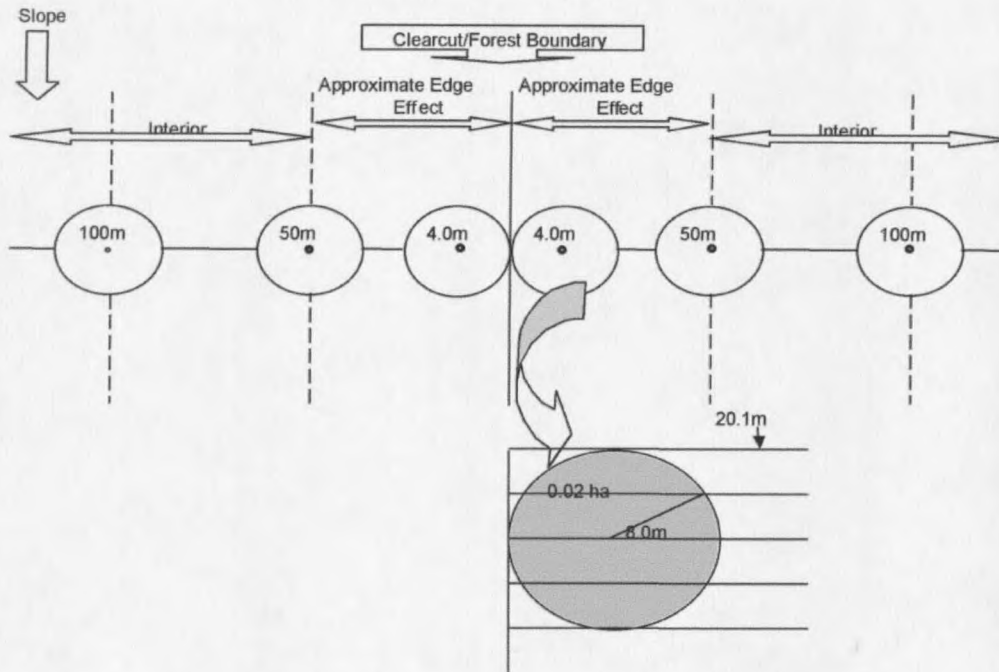


Figure 42. Arrangement of study plots for measuring tree density in relationship to the clearcut/forest boundary and line transects for determining shrub canopy cover and height at each plot.

Statistical Tests

Data were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met, ANOVA, Kruskal-Wallis ANOVA by ranks, the *post hoc* test Newman-Keuls, Student's t-test, and Mann-Whitney U were used to test for differences among and between data ($P < 0.05$) (see Chapters 1 and 2). Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance are reported in the text, P-values only appear in appendices.

Results

Pellet Group Distribution

Ungulate pellet groups were not evenly distributed across all distance classes. Moose pellet group distribution differed significantly ($P < 0.001$, $H = 23.01$) (Figure 43) (Appendix V, Table 148), and the highest averages were found in forested plots. The same was true of elk pellet groups ($P = 0.003$, $H = 18.1$). The difference in average number of deer pellet groups among treatments was not significant ($P = 0.188$, $H = 7.47$), although the highest averages were found in forested locations.

The distribution of pellet groups did not demonstrate an edge effect within clearcuts or forest environments. The average number of pellet groups per plot for the 3 ungulate species was not significantly different among the 3 distance categories in clearcuts (moose $P = 0.543$, $H = 1.22$; elk $P = 0.993$, $H = 0.02$; deer $P = 0.891$, $H = 0.23$). Similarly, when the average number of pellet groups per plot were compared for distance classes in forests, the difference was not significant for moose ($P = 0.343$, $H = 1.08$), elk ($P = 0.701$, $H = 0.71$), or deer ($P = 0.935$, $H = 0.13$).

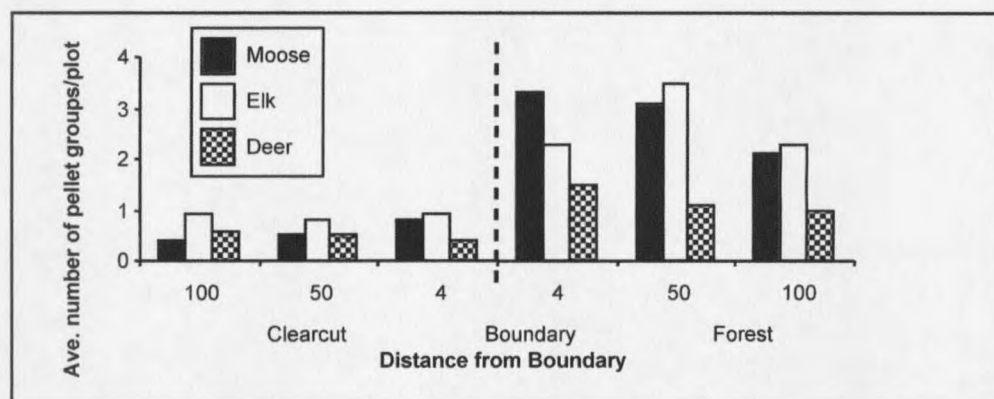


Figure 43. Average number of moose, elk, and deer pellet groups per 0.02-ha plot at different distances from a clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 148).

When I eliminated edge as a classification category and compared only clearcut with forest, differences were significant for all species (moose- $t = 4.94$, $P < 0.001$; elk- $t = 4.31$, $P < 0.001$; deer- $t = 2.76$, $P = 0.009$)(Figure 44). Pellet group counts indicated about 5 times more moose and elk use of forests and 3 times more deer use.

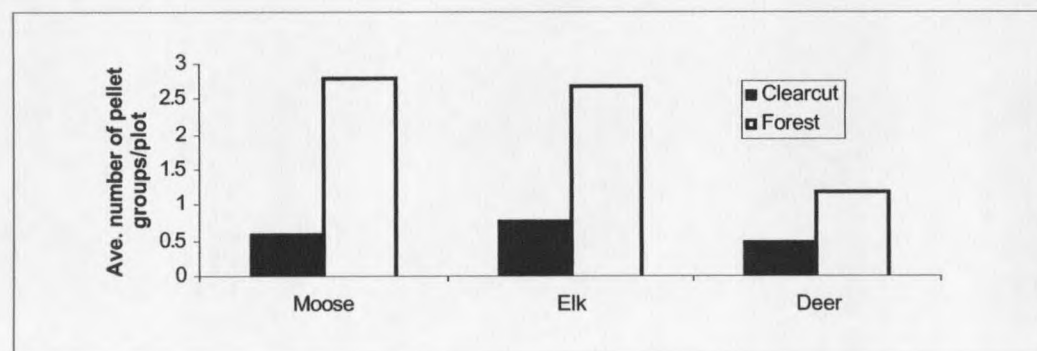


Figure 44. Average number of moose, elk, and deer pellet groups per 0.02-ha plot at different distances from a clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 148).

Shrub Characteristics

Fourteen shrub species are important to NYWR moose (see Chapter 3). Seven were encountered in these sample plots, including alder, buffaloberry, honeysuckle, huckleberry, gooseberry, whortleberry, and willow. The most common species among all sites, as measured by canopy cover, was grouse whortleberry (Figure 45).

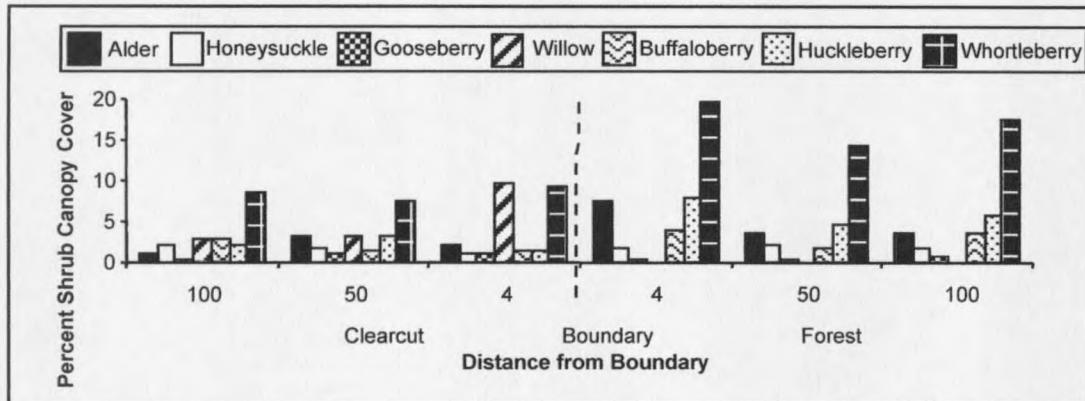


Figure 45. Average percent canopy cover per 0.02-ha plot of shrub species browsed by moose in clearcut and forest locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 149).

There was no clear pattern in shrub canopy cover among the clearcut, edge, and forest plots. The difference in average percent canopy was not significant for alder ($P = 0.757$, $H = 2.63$), honeysuckle ($P = 0.898$, $H = 1.63$), buffaloberry ($P = 0.209$, $H = 7.15$), and whortleberry ($P = 0.39$, $H = 5.22$) (Appendix V, Table 149). Average canopy coverages for gooseberry ($P = 0.005$, $H = 16.61$) and willow ($P = 0.009$, $H = 15.11$) were highest in clearcuts, and willow was not found in forested study plots. Huckleberry ($P = 0.002$, $H = 19.24$) canopy cover was highest in forested locations.

Shrub canopy cover did not demonstrate an edge effect within clearcut or forest environments. Distance from the clearcut/forest boundary was not associated with differences in shrub canopy cover in clearcuts for any shrub species. The edge did not have greater percent canopy cover of shrubs than the distances further into the clearcut (Appendix V, Table 150). Similarly, within forested locations, sites at increasing distance from the boundary did not have a significantly different percent canopy cover for any shrub species, nor was there a greater shrub canopy cover associated with the edge (Appendix V, Table 150).

When I compared all forested plots with all clearcut plots (Figure 46) (Appendix V, Table 151), there was a significantly greater percent canopy cover per plot of huckleberry ($t = 3.97$, $P < 0.001$) and whortleberry ($t = 2.81$, $P = 0.006$) in the forested environment and a significantly greater canopy cover of gooseberry ($t = -2.27$, $P = 0.026$) and willow ($t = -2.26$, $P = 0.026$) in the clearcut areas. Differences were not significant for alder ($t = 1.37$, $P = 0.173$), honeysuckle ($t = 0.38$, $P = 0.703$), and buffaloberry ($t = 1.44$, $P = 0.155$).

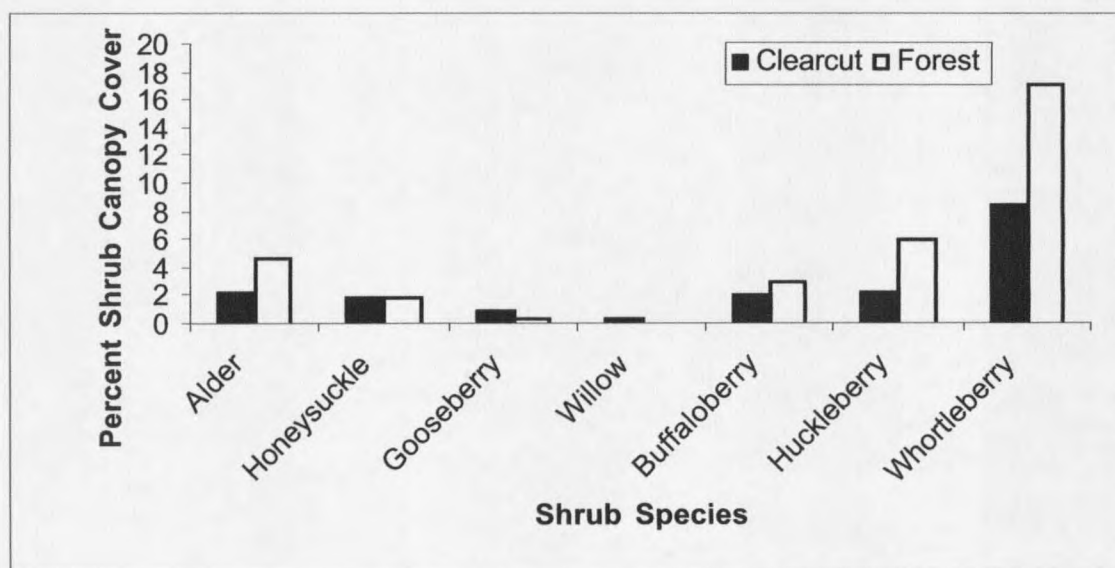


Figure 46. Average percent canopy cover per 0.02-ha plot of shrub species browsed by moose in clearcuts and forests. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 151).

Shrub height is an important factor in determining browse availability in snowy regions (see Chapter 5). For all shrub species except huckleberry, there were no important height differences among clearcuts, edges, and forests. This indicated that moose would not find taller, more accessible shrubs in any specific part of this environment. The differences in the average heights of shrub species per plot, was significant only for huckleberry ($H = 26.1$, $P < 0.001$) (Figure 47) (Appendix V, Table 152) where heights were greater in the forested locations.

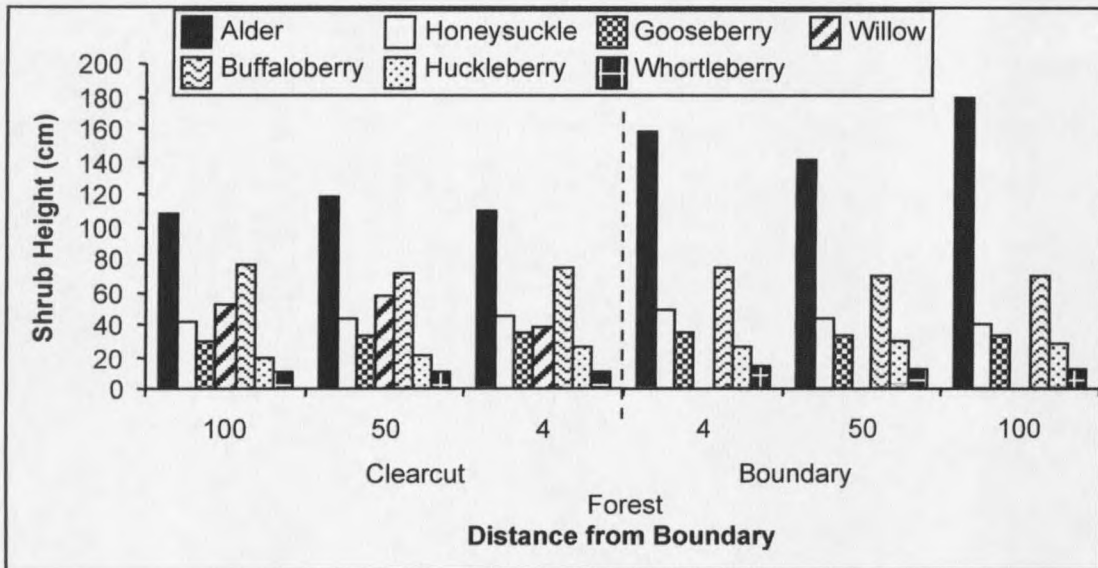


Figure 47. Average height per 0.02-ha plot of shrub species browsed by moose in clearcut and forest locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 152).

When only shrub heights within clearcuts were considered, I found no difference in height at different distances from the clearcut edge except for huckleberry ($H = 7.01$, $P = 0.03$) (Appendix V, Table 153). The greatest average height of huckleberry per plot was at the clearcut locations furthest from the boundary. Similarly, the average height of shrub species per plot was not significantly different when just forested locations were compared and an edge effect on the forested side was not apparent (Appendix V, Table 153).

A comparison of all forested with all clearcut plots indicated that moose could find taller plants, on average in the forests versus the clearcuts for several species. The average height per plot in forested areas was greater for alder ($t = 2.17$, $P = 0.039$), huckleberry ($t = 4.27$, $P = 0.001$) and whortleberry ($t = 2.13$, $P = 0.037$) (Figure 48) (Appendix V, 154).

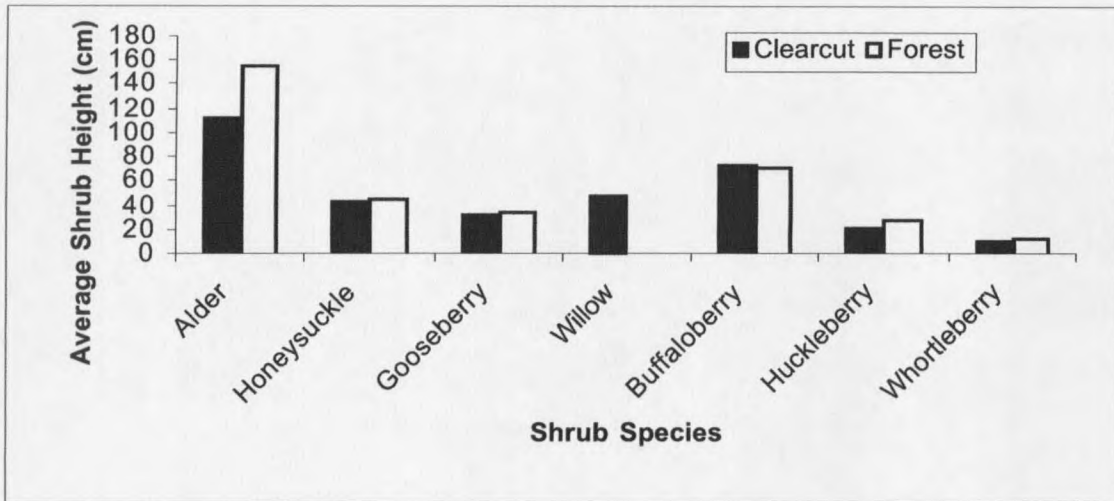


Figure 48. Differences in average shrub height per 0.02-ha plot of shrub species browsed by moose between forests and clearcuts. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 154).

Tree Characteristics

The average number of subalpine fir per plot was significantly different among forested, edge, and clearcut plots for most variables I measured (Figure 49) (Appendix V, Table 155). As expected, there were more subalpine fir and more evidence of browsing on this species in the forested locations. The highest rate of browsing was on subalpine fir between 1 and 5 meters tall, and subalpine fir was the most common tree species in all categories.

Density of subalpine fir and browsing rate did not demonstrate an edge effect. The number of browsed and unbrowsed subalpine fir per plot was not significantly different at different distances from the boundary in the clearcut or the forest (Appendix V, Table 156). Although the differences were not significant, more subalpine fir were found at the forest edge, but browsing intensity was greatest at the location farthest from the boundary.

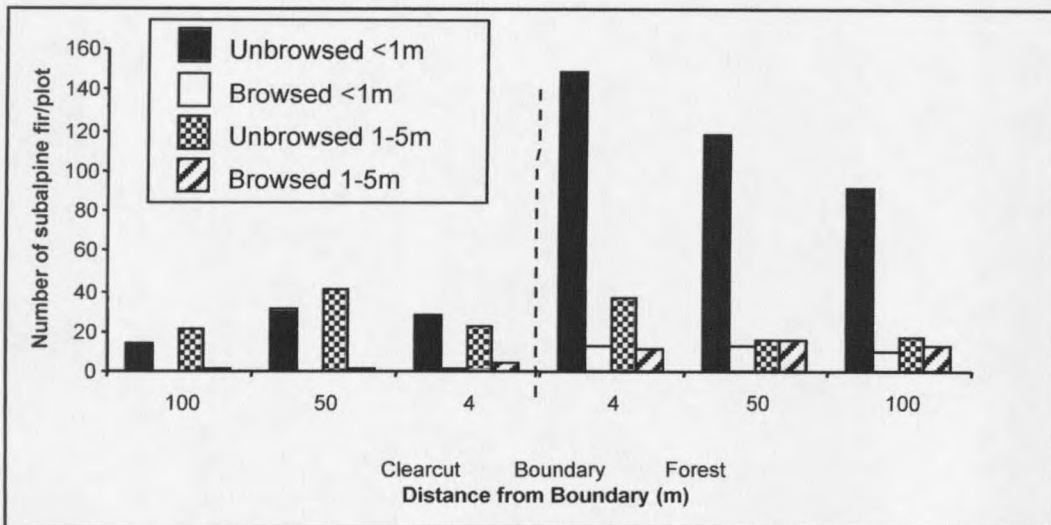


Figure 49. Average number of browsed and unbrowsed subalpine fir per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 155).

When only forest and clearcut environments were compared, the average number of subalpine fir per plot was higher in all measurement categories in the forests (Figure 50) (Appendix V, Table 157). Except for unbrowsed 1-5 m trees, values in forested plots were higher than values in clearcut plots.

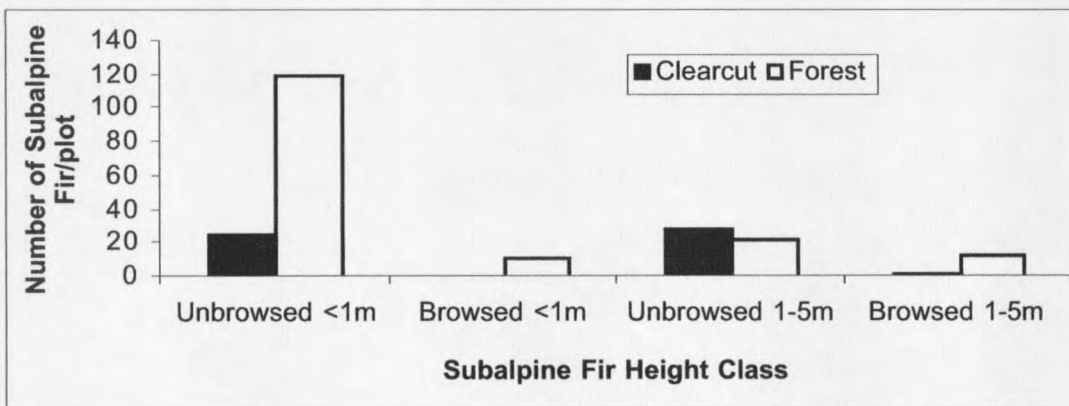


Figure 50. Differences in average number of browsed and unbrowsed subalpine fir per 0.02-ha plot in clearcut and forested locations. Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. In this analysis, results were compared between clearcut and forest sites combined (Appendix V, Table 157).

The number of lodgepole per plot differed significantly among sampling locations in clearcuts, edges, and forests for all analysis categories except those that quantified browsing (Figure 51) (Appendix V, Table 158). More lodgepole pine were found in the clearcut locations than the forest. Little browsing occurred on lodgepole pine compared with subalpine fir, and the amount of browsing was not significantly different among forested and clearcut locations.

Density of lodgepole pine trees did demonstrate an edge effect, more lodgepole pine were found at the boundary in clearcut locations. The difference was significant for the smallest tree size class (<1 m tall) ($H = 9.62$, $P = 0.008$) (Appendix V, Table 159). However, an edge effect was not apparent on the forest side where the number of lodgepole pine was not significantly different between plots at varying distances from the boundary (Appendix V, Table 159).

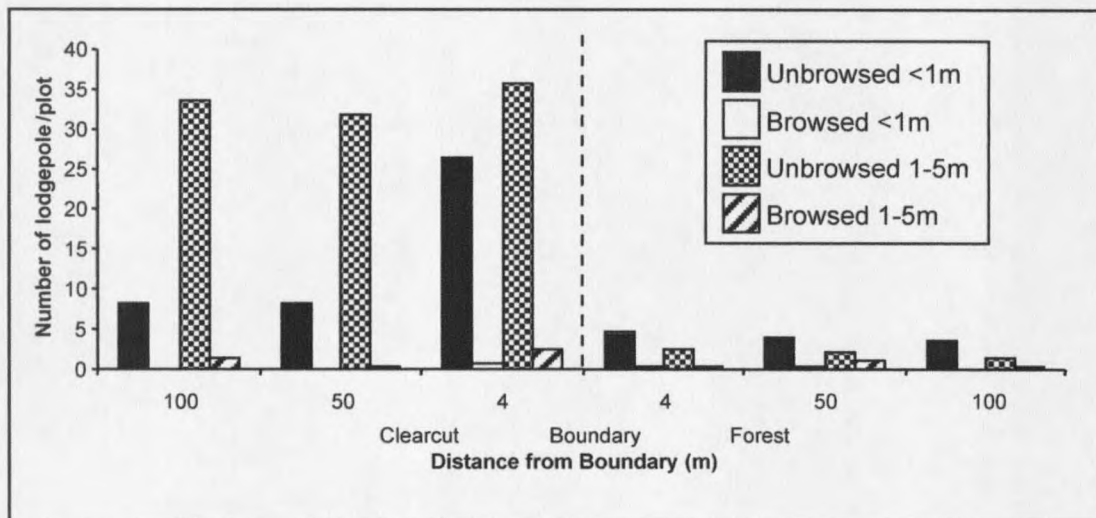


Figure 51. Average number of browsed and unbrowsed lodgepole pine per 0.02-ha plot in clear cut and forested locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 158).

When only forest and clearcut plots were compared, there were significantly more lodgepole in the clearcut than the forest in all size classes except 'trees >5 m tall' (Figure 52) (Appendix V, Table 160). Generally, the amount of browsing that occurred on lodgepole pines in clearcuts versus forests was not significantly different.

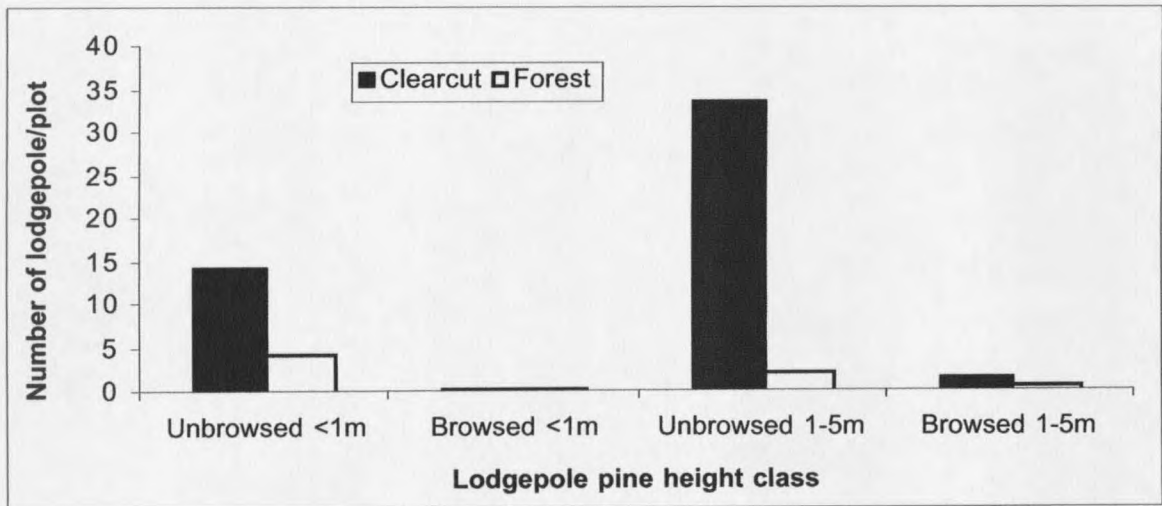


Figure 52. Differences in average number of browsed and unbrowsed lodgepole pine per 0.02-ha plot in clearcut and forested locations. Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. (Appendix V, Table 160).

As expected, across the forest, edge, clearcut landscape, there were more spruce in forested than clearcut locations (Figure 53) (Appendix V, Table 161). The difference was significant when the number of smallest trees (<1 m tall) ($H = 11.7$, $P = 0.039$) and tallest trees (>5 m tall) ($H = 39.9$, $P < 0.001$) were compared. Browsing on spruce did not occur.

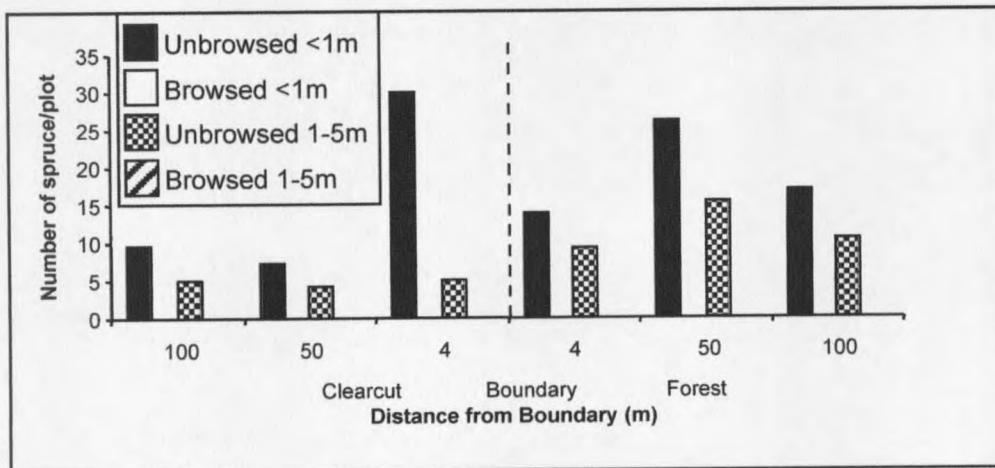


Figure 53. Average number of browsed and unbrowsed spruce per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 161).

The density of small spruce (<1 m tall) showed an edge effect in the clearcut ($H = 7.24$, $P = 0.027$) (Appendix V, Table 162). However, there was no demonstration of edge effect with any size class in the forest (Appendix V, Table 162).

There was more spruce found in the forest environment than in the clearcuts (Figure 54). The difference was significant for the larger tree sizes (Appendix V, Table 163).

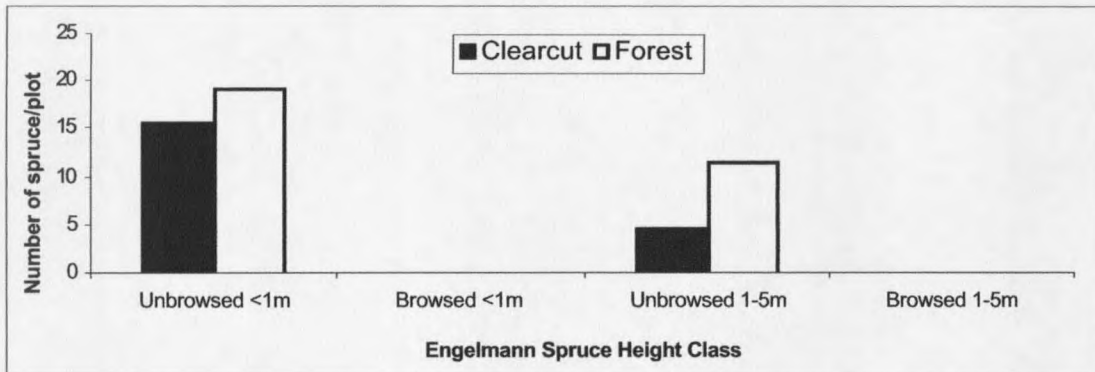


Figure 54. Differences in average number of browsed and unbrowsed spruce per 0.02-ha plot in clearcut and forested locations. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 163).

Douglas fir received very little browsing compared to subalpine fir, regardless of location in relationship to the clearcut/forest boundary (Figure 55). There were more trees in the forested portion of the landscape, and the difference was significant for every size class (Appendix V, Table 164).

Density of Douglas fir did not demonstrate an edge effect. There were almost no Douglas fir found in the clearcut (Appendix V, Table 165), and the difference in the low number of trees at various distances from the boundary was not significant. Most Douglas fir occurred away from the forest perimeter on the forest side study plots (Appendix V, Table 165). The difference in the number of trees was significant only for 'unbrowsed 1-5 m tall' ($H = 7.11$, $P = 0.029$), and the greatest number of trees in that class was at the location farthest from the boundary.

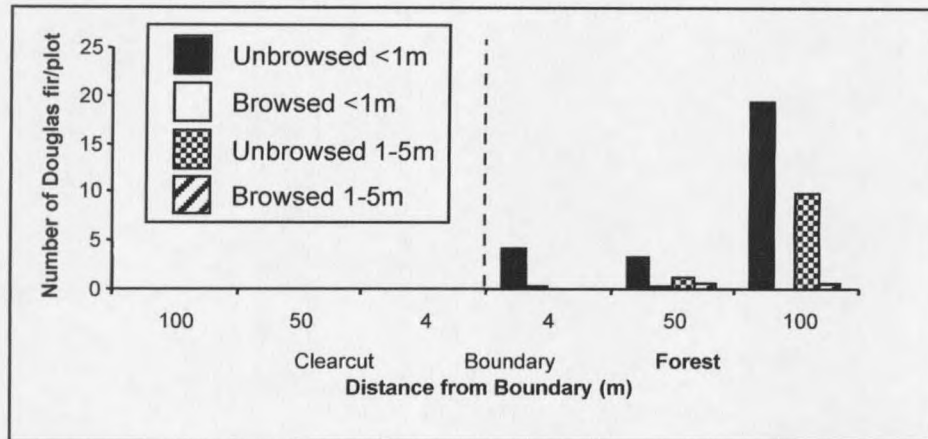


Figure 55. Average number of browsed and unbrowsed Douglas fir per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 164).

Douglas fir was uncommon relative to other conifer species in the clearcut and forest environments. More trees were found in the forests, but the difference was significant only when the number of browsed trees <1 m and 1-5 m tall ($t = -2.07$, $P = 0.041$ and $t = -2.8$, $P = 0.006$, respectively) and trees >5 m tall ($t = -4.12$, $P < 0.001$) were compared (Figure 56) (Appendix V, Table 166). The slight amount of browsing on Douglas fir took place in the forest where the largest number of Douglas fir >5 m tall was also found.

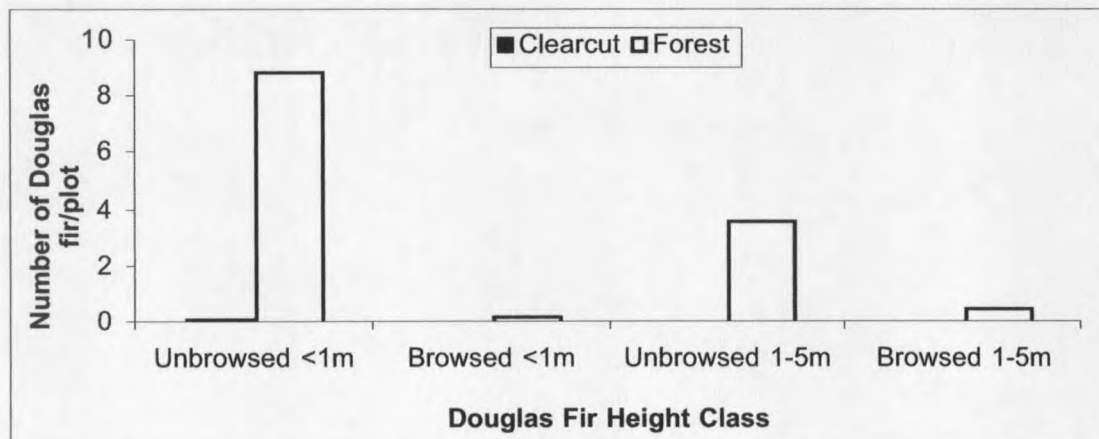


Figure 56. Differences in average number of browsed and unbrowsed Douglas fir per 0.02-ha plot in clearcut and forested locations. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 166).

At the landscape level, whitebark pine was also uncommon. More were found per plot in the forested locations (Figure 57) (Appendix V, Table 167), and the difference was significant for most measurement categories. Compared to subalpine fir, whitebark were not an important source of browse for moose.

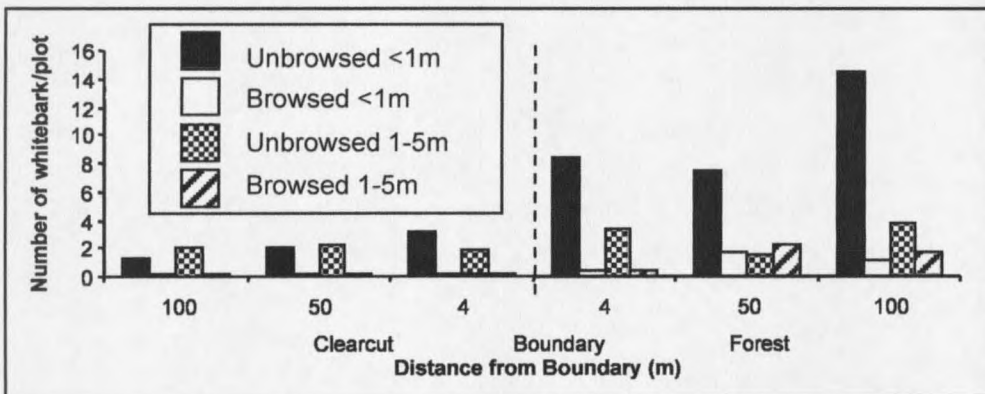


Figure 57. Average number of browsed and unbrowsed whitebark per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the boundary (Appendix V, Table 167).

Whitebark pine did show some response to edge effect in the clearcut (Appendix V, Table 168). The highest number of whitebark pine on the clearcut side was found next to the boundary. There were no whitebark pine >5 m tall found in the clearcut. There was no edge effect on the forest side either in tree density or browsing intensity (Appendix V, Table 168).

When forested and clearcut plots were contrasted, whitebark pine was more common in the forest than the clearcut (Figure 58). The difference was significant for most categories (Appendix V, Table 169). Significantly more browsing occurred in the forest on trees 1-5 m tall ($t = -2.94$, $P = 0.005$).

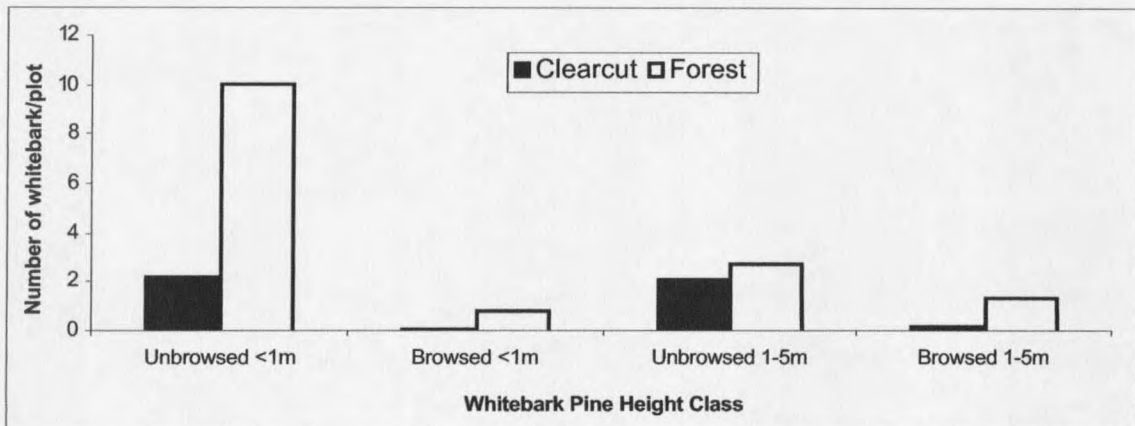


Figure 58. Differences in average number of browsed and unbrowsed whitebark per 0.02-ha plot in clearcut and forested locations. Sample plots were paired in 25-year-old clearcuts and mature lodgepole pine forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined (Appendix V, Table 169).

Discussion

The association of moose with early stages of post-fire succession in boreal forests is commonly accepted (Peterson 1955, Geist 1971, Coady 1982). Transitory seral shrub communities that follow fire can provide extensive concentrations of moose forage (Wolff 1978, Oldemeyer 1983, Oldemeyer and Regelin 1987, Risenhoover 1985, Peek 1997). For example, there is evidence from portions of Alaska of dramatic moose population increases as a result of new brush fields created by wildfires in 1947 and 1969 (Spencer and Hakala 1964, Schwartz and Franzmann 1989). Logging in boreal forests can create similar effects. In north central British Columbia, Westworth et al. (1989) found that moose were drawn to high densities of forage in a 10-year-old clearcut. In northern British Columbia, moose were most abundant in areas of high biomass created by logging 10 to 25 years previous (Eastman 1974). Similarly, moose numbers in Newfoundland grew rapidly in deciduous forests created by pulp logging (Pimlott 1963). Historically, fire was a significant ecological force in northeast Minnesota, but in the 1970's logging was a more important habitat influence (Peek et al. 1976). Nevertheless, moose habitat use patterns were similar in mosaics created by logging or fire. Habitat use appeared to be governed primarily by the availability of palatable forage except when winter severity forced occupation of closed canopy forests.

Although moose usually occur where fire or logging create transitory patches of food, they can also be found in permanent habitats where fire is infrequent. In Idaho, moose occupy double-canopy forests where

concentrations of small Pacific yew provide browse beneath trees >150 years old (Peek et al. 1987, Pierce 1984, Pierce and Peek 1984).

Fire or logging can also enhance habitat by creating features of high value to moose such as edge, the interface between forests and disturbance areas. The advantages to wildlife of the "edge effect" are widely accepted and are often associated with the tendency for communities to be more dense and diverse in ecotonal situations (Leopold 1933, Naiman et al. 1988, Naiman et al. 1993, Morrison et al. 1998, Szaro et al. 1999). Most work suggests that edges may benefit moose by providing the juxtaposition of food and shelter in late winter, an important and possibly limiting time period (Coady 1982, Thompson and Stewart 1997). Moose use of shrubfields immediately juxtaposed to conifers is expected across North America, especially when deep snow is common and movements are restricted (Coady 1982, Peek 1997). Moose demonstrated higher use of areas within about 90 m of the forest edge at recent burns in Alaska (Bangs et al. 1985) and Minnesota (Neu et al. 1974). Mastenbrook and Cumming (1989) showed that, in Ontario, moose preferred edge provided by corridors of 100 to 200 m wide strips of uncut timber to the clearcut interior.

In North America, attempts to create or improve moose habitat have mostly involved enhancing edge and converting timber stands to young age classes through harvesting or prescribed fire. Habitat manipulation of this nature must be repetitive; the value of young successional forest is transient, perhaps lasting less than 30 years in boreal forests (Coady 1982, Thompson and Stewart 1997). Although increasing productivity and size of moose herds can be a general habitat management goal, in most areas where moose exist, fiber production is the dominant land use; therefore, moose are a by-product (Stewart and Thompson 1997).

Recommended sizes for clearcuts for moose habitat management range from 20 to 140 ha (Stewart and Thompson 1997), but to meet habitat requirements, prescriptions should be area-specific. For example, in northern Minnesota where moose utilize transitory shrub fields, Peek et al. (1976) proposed that 40% to 50% of management units (93km²) be maintained in clearcuts <20 years old, 5% to 15% in mature spruce/balsam fir, and 35% to 55% in water and mature trembling aspen/white birch stands. However, in Idaho where Pacific yew dominated the understory, Peek et al. (1987) favored very different guidelines, including the recommendation that logging should remove <50% of the canopy and maintain 50 to 60% of the yew subcanopy. In addition, they advocated a harvest rotation of about 210 years with >45% of the total area in trees >90 years old and <14% of the entire winter range logged during any 30-year period.

Unlike most North American moose populations, pellet group counts in logged portions of moose winter range in the Bear Creek area indicated a significant association of moose, elk, and deer with the

oldest lodgepole pine forests but not to the adjacent 25-year-old clearcuts or to the forest edge.

Instrumented moose confirmed this cover type relationship by using mature lodgepole pine forests in proportions greater than availability and clearcuts in proportions less than availability (see Chapter 4).

Differences in shrub canopy cover and height did not appear to be important enough to account for differences in winter moose distribution between clearcuts and forests. Shrubs were uncommon across the sampling area, and the data did not reveal an edge-effect pattern of greater shrub canopy cover or height.

Seven of 14 deciduous browse species used by NYWR moose were present in the plots I sampled (see Chapter 3). Alder, huckleberry, willow, and whortleberry were common (5%-10% canopy cover in at least 1 sampling distance) in clearcut and/or forested sites I measured, while buffaloberry, gooseberry, and honeysuckle were relatively sparse (<5% canopy cover in all sites). There were some significant species-specific differences in shrub canopy cover and height between clearcuts and forests, but none reflected important disparities in browse concentrations.

Differences in the distribution of subalpine fir trees and browsing rates provided a possible explanation for greater moose activity in the forest as opposed to the clearcut. Subalpine fir was the most common tree in all clearcut and forested locations, but it was significantly more common in forested locations. Browsing rates were significantly higher in forested plots. The highest rate of browsing among species, size classes, and sampling sites was on subalpine fir trees 1-5 m tall at locations farthest from the edge in the forest.

There were some species-specific differences in the distribution of various size classes of lodgepole pine, spruce, Douglas fir, and whitebark pine between clearcuts and forests and among sampled distances from the forest edge. However, because there was little or no browsing on these species, such differences could not account for differences in moose distribution. Low browsing rates on these conifer species and comparatively heavy browsing on subalpine fir confirmed the results of diet investigations conducted by back-tracking moose through the snow (see Chapter 3). Moose utilization of coniferous browse was apparently similar between the edge environment and the unlogged habitats in the remainder of the study area.

Current Forest Service direction (USDA 1987) for timber harvesting in the study area requires management of winter range for big game, including moose, to meet species-specific forage and cover needs but relies on conventional wisdom to meet objectives. As a result, past and proposed timber harvesting has targeted mature lodgepole pine forests utilized by wintering moose.

GNF timber harvesting protocol conceptually resembles standards proposed by Peek et al. (1976) for moose winter range in northern Minnesota where moose are associated with post-disturbance shrubfields. This protocol is not appropriate for the NYWR. Retention of 30% of old growth forests is currently required in the

study area, emphasizing, by priority, Douglas fir, whitebark and wet spruce-subalpine fir types (USDA 1987). The remainder of the mature forest can potentially be removed to "promote production of browse species". By contrast, implementing timber harvesting standards proposed by Peek et al. (1987) for moose winter range in the mature, double-canopy Idaho forests would favor NYWR moose by protecting forest canopies and understory coniferous browse and allowing for a forest rotation of >200 years.

The ecological consequences of these and other forest management practices can be substantial. For example, the number, size, and arrangement of cutting units and remaining forest patches affect forest structure, including edge length and forest interior amount (Franklin and Forman 1987). Patch number and edge length are directly related, the number of patches and edge length increase concomitantly. However, interior habitat quantity and quality are negatively affected by decreased patch size (Franklin and Forman 1987). Smaller patch size and the corresponding increase in edge can benefit species associated with edge environments (edge species) but negatively affect species that conduct daily activities away from edges (interior species) (Franklin and Forman 1987, Yahner 1988, Pianka 1994, Morrison et al. 1998). My investigations suggest that NYWR moose are forest interior species during winter and are, therefore, negatively affected by disturbances and the associated reduction in patch size.

Although an over-simplification, there are 2 common models for timber harvest layout, dispersed patch and single unit. A dispersed patch forestry model for harvest units involves interspersed cut and uncut forests in a checkerboard pattern. This model has been widely used during recent decades in the western U.S. to replace harvest patterns typified by larger, single unit, cut blocks (Smith 1985, Franklin and Forman 1987). Although many variations in patch size and configuration have been employed, a relative patch number and edge length increase and forest interior decrease occurs when timber harvesting follows the dispersed patch model. A better understanding of edge effect, forest fragmentation, and the habitat needs of forest interior species has revealed some disadvantages to this practice (Franklin and Forman 1987, Yahner 1988, Morrison et al. 1998). While historic timber harvesting in Bear Creek created large clearcuts, current GNF silvicultural standards and practices allow for retention of more mature timber but also promote smaller patch size and encourage edge creation (USDA 1987), landscape structural characteristics detrimental to wintering moose and possibly other ungulates. Single unit cuts that maximize forest interior environment may have fewer negative effects on moose winter range.

Causes of forest fragmentation in moose habitat are not limited to timber harvesting. Natural and prescribed fire, road building, and other disturbances capable of creating mosaic vegetation patterns while reducing mature forest interior environments could have similar negative effects on forest structure.

In summary, like other North American populations, NYWR moose foraging strategies involved utilizing forage biomass patches to balance energy budgets. However, instead of feeding in transitory brush fields created by disturbance, they utilized environments with the greatest density of available subalpine fir trees. These data confirm the hypotheses of Loope and Gruell (1973), McDowell and Moy (1942), and Peek (1974a) by demonstrating the importance of subalpine fir as a food source for NYWR moose. Other conifer species received little or no browsing. Shrubs species were uncommon and did not form sizeable or abundant browse patches in forested moose winter range, recently disturbed areas, or edge environments. There was no evidence that forest edges had a greater habitat value for moose in terms of available forage, and clearcutting of mature forests removed moose winter range. To maintain or increase moose densities, managers should protect interior environments in mature conifer forests.

CHAPTER 8

WILLOW AVAILABILITY
AND WILLOW AS A DETERMINANT OF MOOSE HABITAT USE
ON THE NORTHERN YELLOWSTONE WINTER RANGE

Introduction

As browsers, moose feed primarily on woody vegetation during the winter months when availability of digestible food is lowest (Geist 1971, Peek et al. 1992). Among the many tree and shrub species moose utilize, willow is a significant and, in some areas, primary determinant of moose habitat relationships because of its ability to provide critical forage (Peterson 1955, Wölff and Zasada 1979, Coady 1982, Risenhoover 1989, Renecker and Schwartz 1997, Peek 1997). In a comprehensive review of North American food studies, Renecker and Schwartz (1997) found that moose used 221 different plant species and/or genera. However, moose ate large quantities of only a few species, including aspen, birch, and willow. Coady (1982) summarized North American moose ecology and concluded that, from Wyoming to Alaska, shrub communities, particularly riparian willow stands, are the most critical winter habitat, the importance of which "can not be overstated". Peek (1974a,b), in his review of Shiras moose food habit studies, used the relationship of moose to willow as the primary criterion in characterizing 5 categories of winter range. Peek (1997) also reported that in 5 of 8 studies assessing the distribution of Shiras moose among cover types in Montana, Wyoming, and Idaho, the majority of observations were in willow stands.

Specific to the GYA, McDowell and Moy (1942) postulated that willow was the principle food item of Yellowstone moose and that moose distribution was associated with willow abundance. Peek (1974a) theorized that NYWR moose were dependent upon willow stands to meet early winter foraging needs before deep snows force them to adjacent mature conifer forests where double canopies ameliorate snow conditions and provide late winter browse.

Although the ecological status of willow stands in the GYA has been studied extensively (Grimm 1939, Gruell 1980, Houston 1982, Singer et al. 1994, Chadde and Kay 1996, Yellowstone National Park 1997), the relationship of NYWR moose to willow has not been investigated or widely discussed. Willow stands make up <0.5% of the NYWR, and significant decreases in overall willow distribution and individual plant height and canopy size have been measured over the past 100 years. Reasons for the decline in NYWR willow have been the source of intense discussion and have been variously assigned, but no authors deny that changes are occurring (Grimm 1939, Gruell 1980, Houston 1982, Chadde and Kay 1996, Yellowstone

National Park 1997). The extent of spatial and temporal overlap of moose and elk in willow stands on moose winter range, and the importance of browsing by moose and elk in these plant communities, has been debated but not adequately measured (McDowell and Moy 1942, Chadde and Kay 1988, Yellowstone National Park 1997).

My study was not designed to examine the ecological status of NYWR willow or determine reasons for a perceived decline in abundance and vigor. Instead, using a variety of methods, I investigated the winter availability of willow as a moose food source and foraging strategy determinant in an environment where significant changes in willow stands are in progress.

The ability of moose to meet energy needs utilizing willow varies with available biomass. The best foraging opportunities should be where willow canopy is greatest and shrubs are of sufficient height to consistently extend above the snow pack (Eastman and Ritcey 1987, Joyal 1987, Oldemeyer and Regelin 1987, Thompson and Euler 1987, Schwartz and Franzmann 1989). Because willow abundance and height may vary between permanent and transitory willow stands, moose foraging efficiency may likewise vary (Geist 1971, Kelsall and Telfer 1974). To address these issues, I compared willow canopy cover and height among moose feeding sites with different vegetative characteristics (presence or absence of a forest canopy, forest type, and age of forest) to determine the range of willow stand variation that affects moose forage availability.

Willow stand availability for moose may vary by month and elevation because of differences and changes in snow depth and crusting (Telfer and Kelsall 1984). Elk access to moose winter range willow stands is also unknown. To determine effects of snow conditions on willow availability, I described the winter-long relationship between ungulate activity and snow conditions in 8 willow stands ranging in elevation from 2,070 to 2,682 meters.

Willow stands may be relatively stable habitats, but they are vulnerable to episodic environmental changes and stochastic events. Because of its growth form, association with riparian habitats, and high food value, willow may be substantially altered by fire, flooding, sediment movement, drought, and ungulate browsing (Peek 1997). Fire may promote twig production and is often advocated as a management tool to enhance willow vigor (Wolff 1978, USDA 1987). Willow in riverine habitats is subjected to periodic flooding and uprooting, and the nutrient influx in floodwaters and mechanical damage can enhance new willow sprouting. Willow stands require moist soil and are vulnerable to changes in the water table. Ungulate browsing can have variable effects on willow. Some research has shown that willow are generally tolerant of browsing and increase production at intermediate browsing intensities, while heavy and repeated utilization may lead to increased mortality (Wolf 1978, Suter and Gillingham 1990).

The 1988 Yellowstone fires, drought, and post-fire flooding and erosion allowed me to observe willow response to environmental extremes, i.e. the potential positive and negative effects of fire on willow stands exposed to ungulate browsing and weather variability. In the same 8 stands where I assessed the effects of snow conditions on willow browse availability, I measured annual variation in willow browse production (2 of 8 stands were combined for a total of 7 for production and utilization sampling). In addition, I determined variation in utilization rates to assess ungulate activity in willow stands in the context of substantial 1988 fire effects to moose winter range and a post-fire moose population decline (see Chapters 1 and 2).

Finally, to assess long-term changes in willow availability on moose winter range, I used a permanent SC study unit willow exclosure established in 1961. This allowed me to examine the status of willow with and without protection from browsing to determine changes in the availability of this important moose food source over a 35-year period.

Methods

Characteristics of Moose Feeding Sites With Willow

I summarized the average percent willow canopy and height at moose feeding sites where willow was present. These sites were found while back-tracking moose. Fourteen instrumented moose (4 in SB, 3 in SC, 3 in BC, and 4 in the YP study unit) were available for back-tracking. Fresh tracks from a minimum of 2 radiocollared and 2 uncollared moose were located monthly (November-April) in each study unit from 1986 to 1990. I did not follow moose because I did not want the animals to respond to my presence. I continued tracking efforts until 500 bites had been counted. On each route, where moose concentrated browsing on willow, I flagged the site to return for summer sampling.

To measure summer willow shrub height and canopy cover, a 6.1 m (20 ft) baseline was established across the flagged feeding site (see Chapter 7). Five 20.1 m (66') transects were laid out perpendicular to the baseline. The origin of each line along the baseline was selected using random numbers. The number of centimeters of willow intersecting the plane defined by the tape was recorded to determine percent canopy cover (Elzinga et al. 1998). I measured 5 plants along each line to record average willow height.

Six willow cover categories were involved (Mattson and Despain 1985): 1) tall willow (stands with willow >1.5 m), 2) low willow (stands with willow <1.5 m), 3) oldest conifers/tall willow, 4) young conifers/tall willow, 5) young conifers/low willow, and 6) oldest conifers/low willow. I tested the

hypothesis that there was no difference in the average percent canopy cover and height of willow among cover types that moose selected for browsing.

Although willow height in the 6 types is implicit in the definition of "tall" and "low" willow (Mattson and Despain 1985), I tested for height differences because of potential variation within the height classes and in feeding site characteristics (i.e. presence or absence of conifers and conifers of different ages) that might affect willow height. I used the Mattson and Despain (1985) cover type descriptions approved by the USDA and USDI to classify "young" and "old" conifers (<100 and >300 years post-disturbance, respectively). Although interpretation of willow stand successional stage can be ambiguous (Houston 1968, Peek 1997), I considered sites with conifer encroachment as transitory habitat (categories 3-6) and alluvial and stream valley willow stands without conifers as permanent habitat (categories 1 and 2) (Geist 1971, Telfer 1974, Kelsall and Telfer 1974, Coady 1982, Peek 1997).

Monthly Variation in Snow Conditions and Ungulate Activity in Willow Stands

I investigated the winter relationship between moose and 8 willow stands in 2 study units, SB and SC (Table 45), under varying snow conditions. The 8 willow stands were all of the major willow areas available to moose in each of the study units. Two stands were adjacent, Bannock-riverside and Bannock-terrace. The former was in the flood plain, and the later was on a terrace about 2 m above the river. I investigated which winter months moose and elk used willow stands at various elevations on moose winter range and attempted to establish the determinants of use. Tracks were used as evidence of ungulate activity. Determinants included snow depth, snow crust, and availability of willow above the snow pack.

Stands were sampled a minimum of two times each month, November-April, 1986-1990. Each was bisected along its longest axis with a track-intercept transect (Jenkins 1985). The presence or absence of moose and elk tracks was recorded on each visit. Snow depth was determined by averaging 10 measurements collected at 10-m intervals along the transect. Snow consistency was described by subjectively indicating "yes" or "no" to the presence of a crust that would impede travel by ungulates. To determine how moose responded to snow conditions that buried most willow, I recorded when >95% of average plant height was buried by snow. I determined if snow covered >95% of willow by visual observation (no willow visible above the snowpack) or by comparing the height of 50 plants above the snow with a previously determined average height of the stand. Track data (present or absent) were summarized according to classes reflecting snow depth (>70 cm, >120 cm), snow crust (present or absent), and availability of willow above the snowpack.

Because of the potential for substantial annual, monthly, and even weekly variation in snow conditions, I attempted to determine a conservative overall trend in ungulate use and snow conditions in each willow stand by summarizing monthly data over 4 years. For example, I reported that a snow depth threshold had been reached for a given month if it was exceeded each of 4 years during that month, i.e. if the average snow depth exceeded 70 or 120 cm during each November over 4 winters, the threshold was reported as reached for that month. Likewise, a report on the presence or absence of moose tracks in November represented sampling over 4 winters. I recorded moose tracks "present" if a track was found in the willow stand each November, 1986-1990.

Snow depth thresholds were arrived at by a review of literature (Kelsall and Prescott 1971, Peek 1971, Kelsall 1969, Thompson and Vukelich 1981, Des Mueles 1964, Peek 1997). At other North American winter ranges, 65-90 cm of snow caused moose to leave open areas and seek forest canopies, and in several studies the threshold was about 70 cm, a conservative estimate for the smaller Shiras moose. Snow >120 cm is reported to preclude most moose activity.

Table 45. Eight willow stands in SB and SC study units were used for sampling. Stands were distinguished as tall (>1.5 m) or low (<1.5 m) (Mattson and Despain 1985).

Willow Stand	Study Unit	Elevation	Willow type
Fisher Creek	SB	2682 m	low willow
Soda Butte Campground	SB	2365 m	tall willow
Bannock-riverside	SB	2286 m	tall willow
Bannock-terrace	SB	2286 m	low willow
Warm Creek	SB	2219 m	low willow
Frenchy's meadow	SC	2089 m	tall willow
Lost Creek	SC	2073 m	low willow
Slough Creek Cabin	SC	2070 m	tall willow

Variation in Willow Survival, Height,
Percent Browsing, and Twig Production

In May 1988, 265 plots were established and sampled in the same 8 willow stands available to wintering moose (Table 45). For analysis purposes, I combined the Bannock-riverside and Bannock-terrace stands and reported results for only 7 stands. Willow species were identified in each stand. About 10 plots were chosen for each willow species present in a stand. Plots were tagged and mapped to allow resampling. Sampling included counting all browsed and unbrowsed twigs within a 0.5-m radius circular plot to determine total number of twigs, percent of twigs browsed, and the height of the tallest live leader in centimeters. Twig height data were discarded for plots that burned in 1988. I analyzed twig production

data twice, once with plots where plants died during the course of the study and once without. The former allowed me to assess annual variation in the total number of twigs potentially available for browsing and the later showed yearly changes in twig production on plants alive throughout the study. Data were collected in 1988, 1989, 1990, 1995, 1996, and 1997.

Fire (in 1988) and other environmental influences affected plants in some plots. These were sampled to determine if willow persisted, recovered (resprouted), or died. I also used the vegetation cover type base map prepared by the USDI and USDA for the GYA (Mattson and Despain 1985), 1988 burn area maps, and GIS technology (R. Renkin, YNP, personal communication; C. Stein, GNF, personal communication) to determine hectares of willow stands available in each study unit and relative proportions affected by fire.

Average height, percent browsing, and twig production among species, locations, and years were tested for significant differences. I tested the hypotheses that there is no annual difference in the average height, utilization, and twig production among willow species and willow stands. Because sampling was initiated before the 1988 fires, I was able to assess fire effects.

Variation in Willow Height and Percent Cover In and Out of the Slough Creek Exclosure

An exclosure was established at the south end of Frenchy's Meadow (SC) in 1961. Two transects were inside the fence bearing diagonally from corner to corner (25 m and 26 m long). Two were placed outside originating at the eastern corners (21.6 m 27.6 m long). I could not find data for 1961 and 1962. The site was sampled in 1964 and 1965 and partially sampled in 1979 (Erickson 1979 in: Chadde and Kay 1988). In 1986, 6 new transects each 30.5 m long were established outside the exclosure and data were collected from these and existing transects (Chadde and Kay 1988). Individual plant locations were also mapped. I resampled these same transects in 1995 and 1997.

The percent canopy cover of willow was calculated along transects in and out of the exclosure. Willow identification was generic before 1986 and by species in 1986 and subsequent years. Average height of willow was determined by measuring each plant along the lines.

Statistical Tests

Data were analyzed using Statistica software (StatSoft 1995). StatSoft (1995) and Zar (1999) were consulted for appropriate statistical tests. When assumptions were met, ANOVA, Kruskal-Wallis ANOVA by ranks, and Newman-Keuls *post hoc* test were used to test for differences among data sets ($P < 0.05$) (see

Chapter 1). Results of *post hoc* tests appear in the Appendices. P, F, Z, and H statistics appear in the text in relevant places in addition to appendices. However, if a series of tests for significance are reported in the text, P-values only appear in appendices.

Results

Characteristics of Moose Feeding Sites With Willow

Willow availability on moose winter range differed by as much as 3 times among stands with permanent and transitory vegetative characteristics. Tall willow stands without conifers provided the greatest biomass accumulation. The average percent canopy cover of willow at sites where moose browsed varied significantly among willow types ($P < 0.001$, $H = 80.34$) (Figure 59). The willow types without conifers had the highest average percent canopy cover, and the tall willow types with conifers had more willow canopy cover than low willow types with conifers. The tall willow types had the highest average percent cover (65%), followed by low willow (49.1%), oldest conifers/tall willow (33.4%), young conifers/tall willow (26.29%), young conifers/low willow (22.1%), and oldest conifers/low willow (2.1%). When just willow canopy cover of the 3 tall willow types were compared, the difference was significant ($P < 0.001$, $H = 36.67$). It was also significant when just cover of the 3 low willow types were compared ($P < 0.001$, $H = 38.95$).

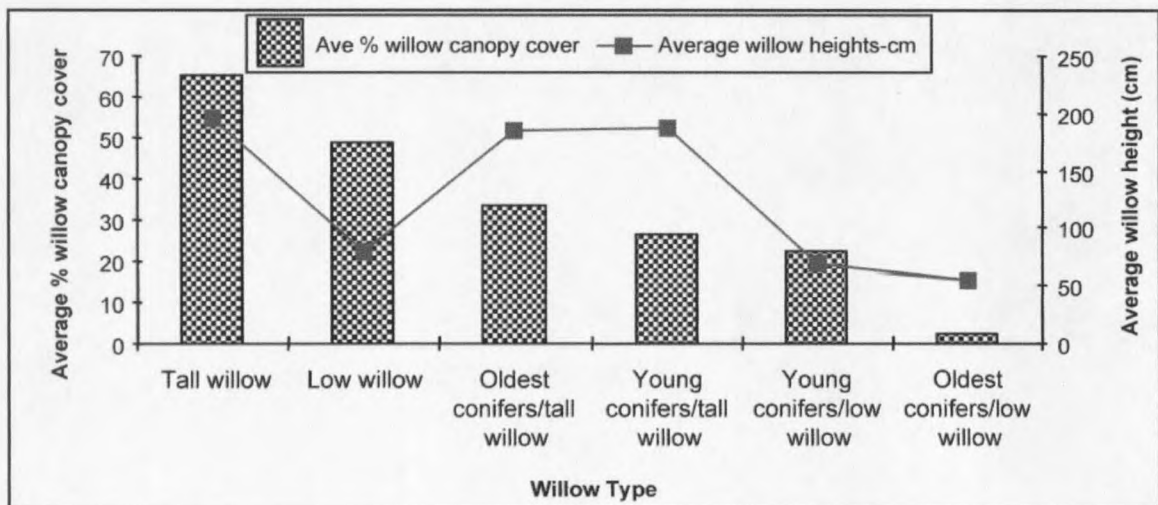


Figure 59. Average percent willow canopy cover and height in 6 categories of moose feeding sites with willow present. Feeding sites were located while back-tracking moose through the snow. Sites were categorized as low or tall based on average height: low willow sites were <1.5 m and tall willow were >1.5 m on average (Mattson and Despain 1985).

In addition, willow availability for moose is affected by height, which, as expected, also varied significantly among willow types ($P < 0.001$, $H = 108.22$) (Figure 59). Tall willow communities had the highest average height (195.0 cm), followed by young conifers/tall willow (186.5 cm), oldest conifers/tall willow (184.5 cm), low willow (80.0 cm), young conifers/low willow (69.8 cm), and oldest conifers/low willow (54.3 cm). When the average height of 3 tall willow types were compared, the difference was not significant ($P = 0.732$, $H = 0.62$). There were also no significant differences in height among low willow types ($P = 0.055$, $H = 5.79$).

Monthly Variation in Snow Conditions and Ungulate Activity in 8 Willow Stands

Snow conditions had a substantial affect on the availability of willow to moose, burying willow plants in some situations and precluding access to stands for all or portions of 4 winters. Tracks indicated ungulates were not present in the SB or SC study unit willow stands winter-long and the duration of use of each stand differed by ungulate species (Table 46). Snow conditions among months and stands also varied and influenced the ability of ungulates to browse willow. Generally, over a 4-year period, ungulates were displaced from willow stands by December or January and no activity occurred in March.

Over 4 winters, moose and elk activity was not found in the Fisher Creek willow stand, a low willow (<1.5 m) type with the highest elevation (2,682 m) and greatest snow depth. On average, the snow depth exceeded 70 cm by December and the stand was buried by January. Moose and elk utilized Soda Butte, the next highest stand (2,365 m), during November and December but not the remainder of the winter during 4 years. The average snow depth exceeded 70 cm in January and 120 cm by February, but with the average height of willow >1.5 m, stems were available above the snowpack winter-long. Moose were active in the Bannock riverside willow stand (2,286 m), a tall willow type, through January and elk through December. Average snow depth exceeded 70 cm by January but did not reach an average depth of 120 cm any month. Conditions were similar at the Bannock riverside and terrace willow stands except for April when snow depth was less and moose were present at the Bannock terrace stand (low willow type). Moose utilized the Warm Creek stand (elevation 2,219 m) only in December while elk were present through January. Average snow depth exceeded 70 cm only in February, and willow (low willow type) was entirely buried that month.

The 3 stands in SC were spaced along Slough Creek but at comparable elevation (2,089 m, 2,073 m, and 2,070 m, respectively). Moose were found in Frenchy's Meadow, a tall willow stand, through February and elk only in November. Average snow depths exceeded 70 cm by January but did not reach 120 cm any

month. Moose activity was found through December in the low willow Lost Creek stand but elk only in November. The average monthly snow depth did not reach 70 cm, but willow was essentially buried January through March. Moose and elk activity was found in the Slough Creek willow stand in November and December where the average willow height was >1.5 m. Average snow depth did exceed 70 cm part of the winter but not 120 cm.

Table 46. Monthly snow conditions and presence of ungulate tracks, November-April, in 8 moose winter range willow stands, 1987-1991. Snow depths reflect a monthly average during all years >70 cm or >120 cm. Crust was present or absent each month during all years as were moose and elk tracks. The willow stand was buried if >95% of the average height was beneath snow.

Stand	Measurement	November	December	January	February	March	April
Fisher Creek	Snow depth		>70 cm	>70 cm	>120 cm	>120 cm	>120 cm
	Crust					Crust	Crust
	Willow			Buried	Buried	Buried	Buried
	Tracks						
Soda Butte	Snow depth			>70	>120 cm	>120 cm	>70 cm
	Crust					Crust	Crust
	Willow						
	Tracks	Moose, elk	Moose, elk	Moose			
Bannock Riverside	Snow depth			>70 cm	>70 cm	>70 cm	>70 cm
	Crust					Crust	
	Willow						
	Tracks	Moose, elk	Moose, elk	Moose			
Bannock Terrace	Snow depth			>70 cm	>70 cm	>70 cm	
	Crust					Crust	Crust
	Willow						
	Tracks	Moose, elk	Moose, elk	Moose			Moose
Warm Creek	Snow depth				>70 cm		
	Crust					Crust	
	Willow			Buried	Buried	Buried	Buried
	Tracks	Elk	Moose, elk	Buried Elk			
Frenchy's Meadow	Snow depth			>70 cm	>70 cm	>70 cm	
	Crust					Crust	
	Willow						
	Tracks	Moose, elk	Moose	Moose	Moose		Moose
Lost Creek	Snow depth						
	Crust					Crust	
	Willow			Buried	Buried	Buried	
	Tracks	Moose, elk	Moose				
Slough Creek	Snow depth					>70	>70
	Crust					Crust	
	Willow						
	Tracks	Moose, elk	Moose, elk	Moose	Moose		

Willow Height Variation in 7 Stands

Annual variation in willow height over a 10-year period was not an important factor in determining the availability of browse for moose. In the 7 willow stands where I measured height, the average annual height of willow, all species combined, did not vary significantly ($F = 0.4$, $P = 0.876$) among the years 1988 to 1997 (Appendix W, Table 170). The greatest average annual height per plot of willow species occurred pre-fire, followed by a slight downward trend (Figure 60).

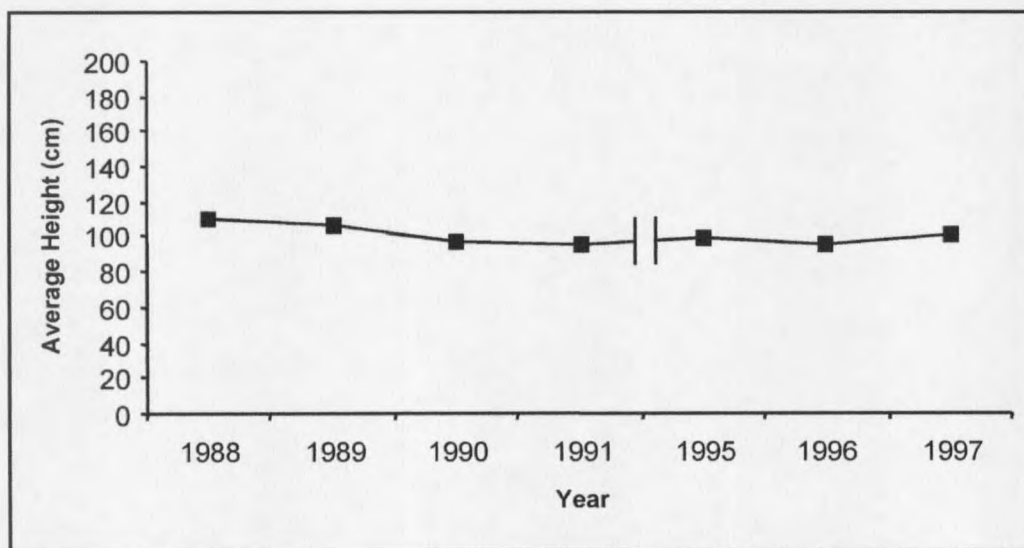


Figure 60. Average annual height (cm) per plot of 7 willow and 1 birch species combined among the years 1988-1991 and 1995-1997; 265 study plots at 7 willow stands in the SB and SC study units.

Similarly, over 10 years, most willow species did not demonstrate significant annual height variation. When species were tested separately for differences in average annual height among years (Figure 61) (Appendix W, Table 170) annual variation was significant for 3: Farr's (*S. farrae*) ($F = 2.97$, $P = 0.009$), Geyer's (*S. geyeriana*) ($H = 50.95$, $P < 0.001$), and Eastwood's (*S. eastwoodeae*) ($F = 10.48$, $P < 0.001$). It was not significant for 4 other species: Wolf's (*S. wolfii*) ($F = 0.55$, $P = 0.768$), Booth's (*S. boothii*) ($F = 0.12$, $P = 0.993$), Drummond's (*S. drummondiana*) ($F = 0.17$, $P = 0.983$) and Barclay's (*S. barclayi*) ($F = 0.95$, $P = 0.472$). The greatest annual average height for Farr's willow was in 1988 followed by a downward trend. The highest average for Geyer's willow was in 1997, and the highest average for Eastwood's willow was in 1990. *Post hoc* tests for Eastwood's willow showed that the higher averages for 1988 to 1991 differed from averages for the years 1995 to 1997 (Appendix W, Table 171). *Post hoc* tests for Farr's willow did not show differences among yearly average heights (Appendix W, Table 172).

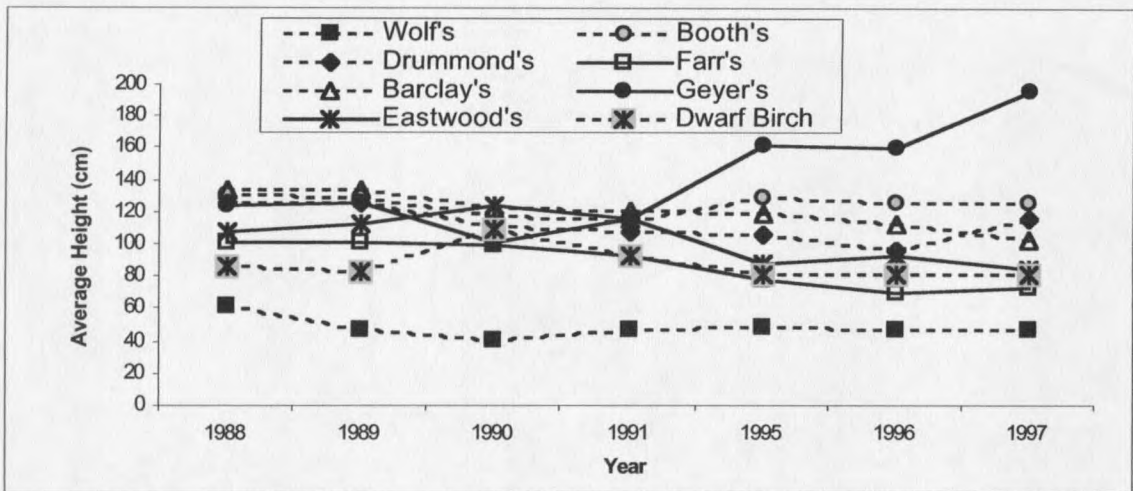


Figure 61. Average annual height (cm) per plot of 7 willow and 1 birch among the years 1988-1991 and 1995-1997; 265 study plots at 7 willow stands in the SB and SC study units.

Willow species composition was not uniform among the 7 stands where sampling occurred, as a result, given species-specific growth form differences, height varied among the stands by as much as 3 times. Differences were significant in average height of willow among the 7 willow stands when all species and all years were combined ($F = 16.04$, $P < 0.001$). Willow at Soda Butte had the greatest average height (140.3 cm) and those at Warm Creek had the lowest (44.5 cm). *Post hoc* tests revealed that the average height of willow at Soda Butte was greater than at all other sites (Appendix W, Table 173). Also, averages for Warm Creek, Lost Creek, and Frenchy's Meadow were lower than averages for Bannock, Fisher Creek, and Slough Creek.

In spite of substantial environmental changes between 1988 and 1997, willow height did not vary significantly in 5 of the 7 willow stands. Average height of willow, all species combined (Figure 62), did not vary significantly among the years 1988 to 1997 at Soda Butte ($H = 8.93$, $P = 0.178$), Bannock ($F = 0.96$, $P = 0.468$), Frenchy's ($F = 0.59$, $P = 0.633$), Lost Creek ($F = 0.87$, $P = 0.542$), or Slough Creek ($F = 1.2$, $P = 0.344$) (Figure 62) (Appendix W, Table 174). Average height did vary significantly at Fisher Creek ($F = 10.48$, $P < 0.001$) and Warm Creek ($H = 108.88$, $P < 0.001$). At Fisher Creek, the highest average was in 1990 followed by a downward trend. *Post hoc* tests showed that the high averages for 1988 to 1991 differed from the averages for 1995 to 1997 (Appendix W, Table 175). At Warm Creek, the highest average was in 1988 followed by a downward trend.

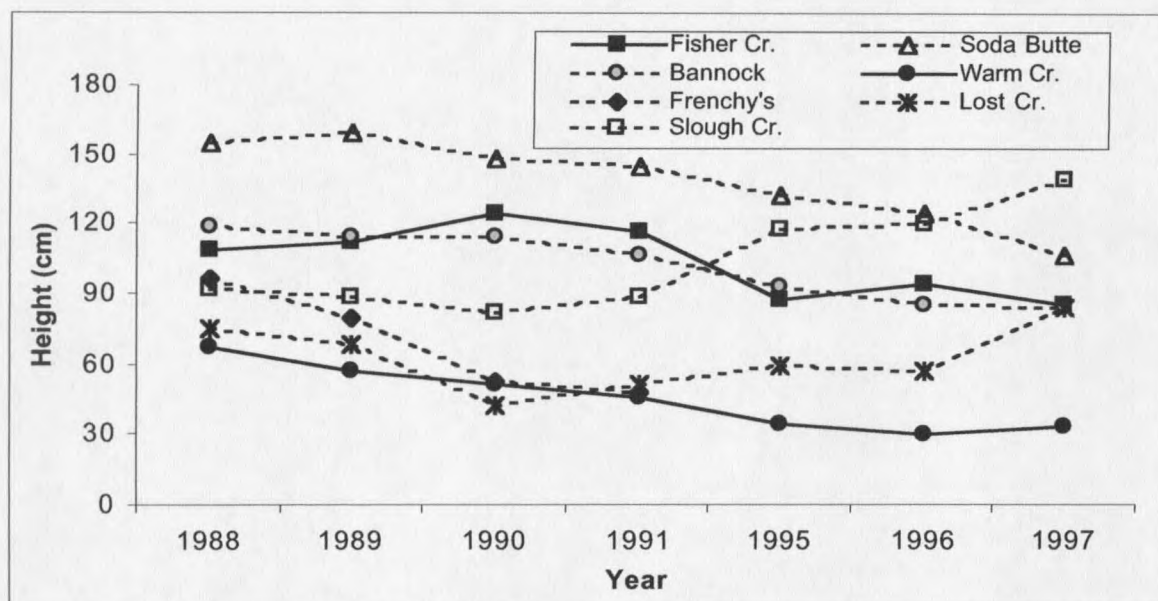


Figure 62. Average annual height (cm) of willow per plot, all species combined among the years 1988-1991 and 1995-1997; 265 study plots at 7 willow stands in the SB and SC study units.

Willow Browsing Rate Variation in 7 Stands

Variable environmental conditions over 10 years, including the 1988 fires, affected ungulate browsing intensity. Rates more than doubled during the years post-fire before returning to near pre-fire levels by 1997. Average annual utilization, all species combined, varied significantly among the years 1988 to 1997 ($F = 14.94$, $P < 0.001$) (Figure 63) (Appendix W, Table 176). The high average occurred in 1989 (49.7%), the year after the fires, followed by a downward trend. Results were as follows: 1988-16.2%, 1989-49.7%, 1990-30.9%, 1991-32.3%, 1995-20.5%, 1996-21.7%, and 1997-17.9%. *Post hoc* tests (Appendix W, Table 177) showed that the high average for 1989 was different from the averages for the other years. In addition, the average for 1988, the lowest sampled, was different from the averages for 1990 and 1991, and the average for 1991 was different from 1997.

The same utilization trend of a post-fire increase followed by a decline was consistent for each species considered individually except dwarf birch ($H = 9.23$, $P = 0.161$) (Figure 64) (Appendix W, 176). *Post hoc* tests revealed that the high average in 1989 was the source of most of the species-specific differences (Appendix W, Tables 178-180). Results of tests for significant differences in average annual utilization among years for each species were as follows: Wolf's ($H = 13.36$, $P = 0.038$), Booth's ($H = 20.56$, $P = 0.002$), Farr's ($F = 9.94$, $P = 0.001$), Drummond's ($F = 4.48$, $P = 0.005$), Barclay's ($F = 4.03$, $P = 0.003$), Geyer's ($H = 54.9$, $P = 0.001$), and Eastwood's ($H = 47.49$, $P < 0.001$).

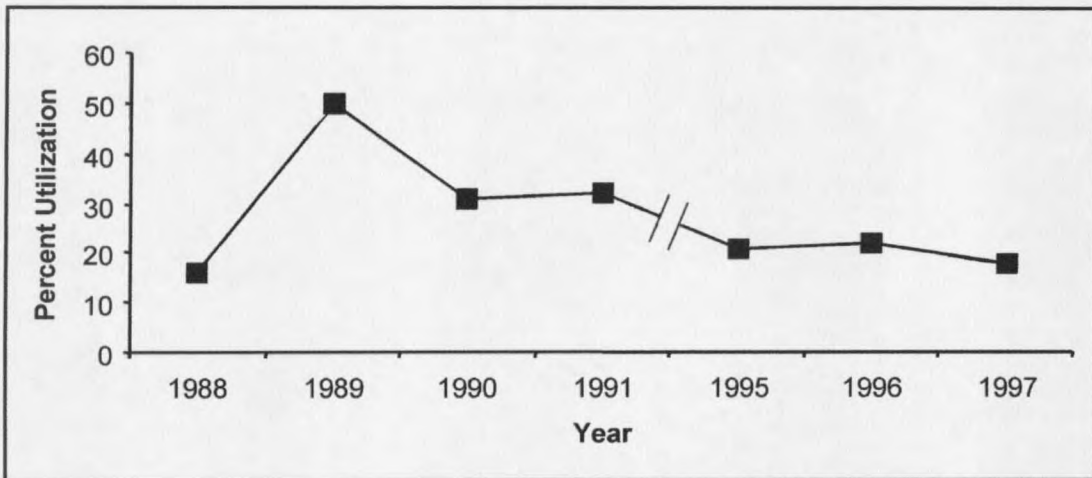


Figure 63. Average annual utilization per plot for 7 willow and 1 birch species combined among the years 1988-1992 and 1995-1997, 265 study plots at 7 willow stands in the SB and SC study units.

Average annual utilization varied significantly among the 7 willow and 1 birch species ($P = 0.001$, $F = 55.8$). The highest average was for dwarf birch (34.6%) and the lowest for Eastwood's willow (0.7%). Eastwood's willow was evidently either unavailable or undesirable as winter forage. *Post hoc* tests indicated that use of Eastwood's willow was lower than use of any other species (Appendix W, Table 181). Use of Geyer's and Farr's willows was also comparatively low, while use of Drummond's and Wolf's willows was intermediate. Results for the two species with the highest percent average, dwarf birch and Barclay's willow, were different from the averages for Farr's and Geyer's, and averages for Drummond's and Wolf's were different from the average for Farr's. When the average for Eastwood's was removed from the analysis, the difference was also significant ($P < 0.001$, $F = 3.73$). *Post hoc* tests showed that the difference between averages for Farr's and Drummond's willows were significant, as were differences between dwarf birch and Farr's willow and Geyer's and Drummond's willows (Appendix W, Table 182).

The stands where sampling occurred differed by elevation, snow accumulation, and willow species mixes. These and other factors contributed to average browsing rate differences among locations of >30 times over 10 years. The average annual utilization among the 7 locations across all years was significant ($P < 0.001$, $F = 5.19$) with the highest use occurring at Bannock (34.1%) and the lowest at Fisher Creek (0.7%). *Post hoc* tests revealed the source of the difference was Fisher Creek in comparison with each of the other locations (Appendix W, Table 183).

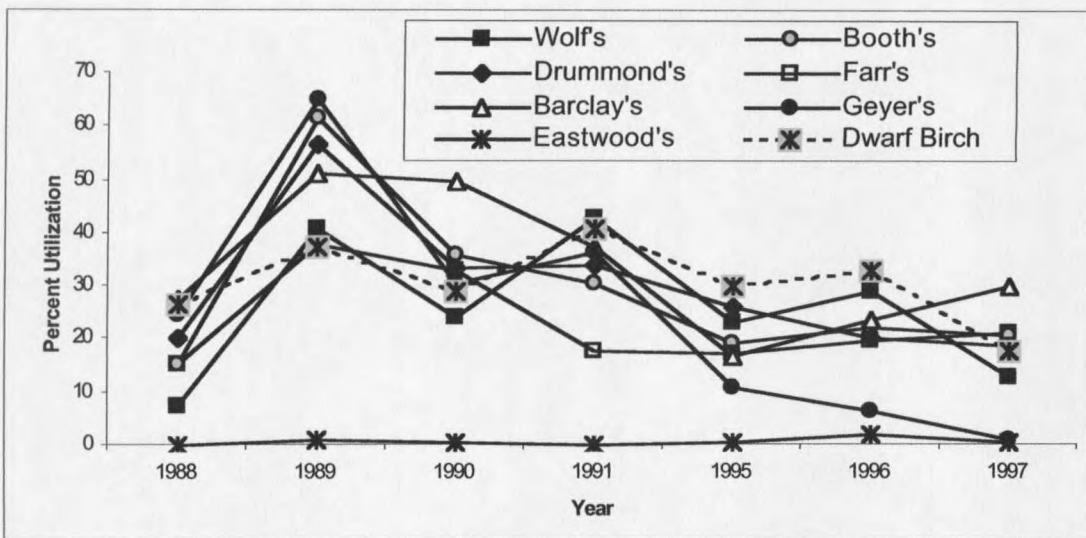


Figure 64. Average annual utilization per plot for 7 willow and 1 birch species among the years 1988-1992 and 1995-1997, 265 study plots at 7 willow stands in the SB and SC study units.

Stand-specific differences in willow utilization were also apparent. Again, the 10-year trend was for much higher utilization for several years after the fires followed by a decrease in browsing pressure. Variation in average annual utilization among years was significant at all willow stands except Frenchy's meadow ($F = 1.48$, $P = 0.29$) (Figure 65) (Appendix W, Table 184).

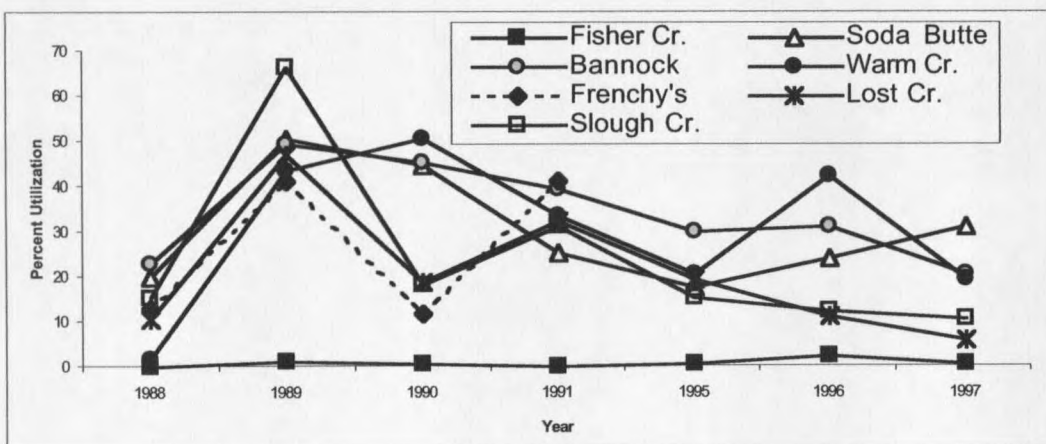


Figure 65. Average annual utilization among the years 1988-1992 and 1995-1997, 265 study plots at 7 willow stands in the SB and SC study units.

No data were available for Frenchy's meadow past 1991. Many of the plots at this location burned in 1988 and did not resprout. The rest were subsequently covered in a mudflow from the adjacent burned hillside and did not recover. Results of tests for significant differences among average annual utilization at each location are as follows: Fisher Creek ($H = 47.49$, $P < 0.001$), Soda Butte ($H = 22.12$, $P < 0.001$), Bannock ($H = 23.88$, $P < 0.001$), Warm Creek ($H = 101.36$, $P < 0.001$), Lost Creek ($H = 13.43$, $P = 0.036$), and Slough Creek ($H = 15.57$, $P = 0.016$).

Willow Twig Production Variation in 7 Stands

At the landscape level, willow browse production was susceptible to environmental variation, especially drought, over a 10-year period. The average number of twigs, all species combined, varied significantly among years at sample plots where the plants survived from project initiation to the end of the study ($F = 30.9$, $P < 0.001$) (Appendix W, Table 185). The general trend in these unburned plots was for the lowest average to occur in 1989, the year after the fires and severe drought, followed by a general increase through 1996 and then a decrease in 1997 (Figure 66). Results of *post hoc* tests for all species combined showed that the low averages for the years 1989, 1990, and 1991 were different from the other averages (Appendix W, Table 186), and the average for 1997 was different from all but the average for 1991.

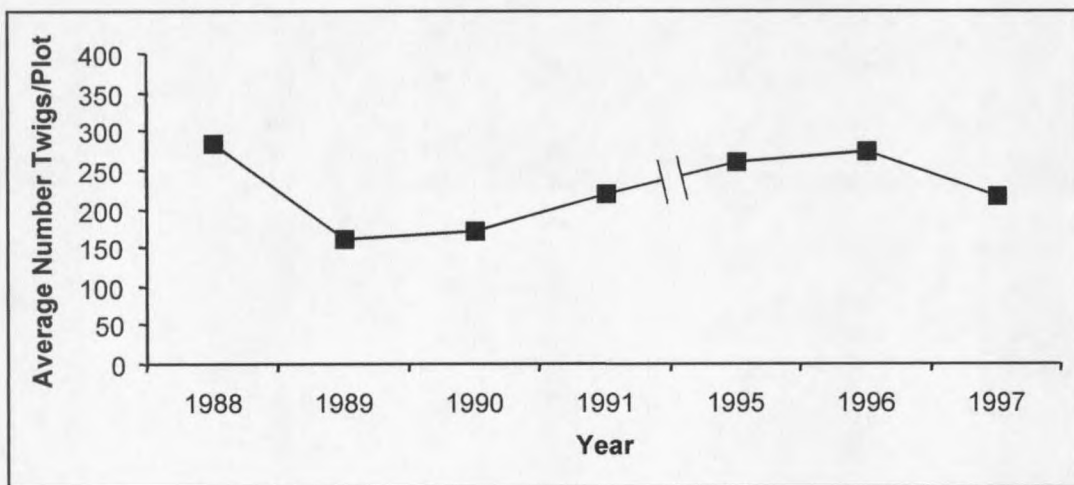


Figure 66. Average number of twigs per plot of 7 willow and 1 birch species combined among the years 1988-1992 and 1995-1997. Data excludes plots at 7 willow stands where willow died between project initiation and conclusion.

Annual species-specific availability of willow browse as measured by twig numbers was also substantial. The difference was significant for each species considered individually except for Barclay's ($F = 0.44$, $P = 0.846$) and dwarf birch ($H = 4.42$, $P = 0.62$). Eastwood's was an exception to the general pattern ($F = 5.16$, $P < 0.001$). Twig production for this species declined through the measurement period (Figure 67). *Post hoc* tests for individual species confirmed the general pattern of twig production and showed that the highest and lowest averages were different from the rest of the data (Appendix W, Tables 187-191). Results for tests of significant differences of average number of twigs in unburned plots among years are as follows: Wolf's ($F = 25.82$, $P < 0.001$), Booth's ($F = 8.93$, $P < 0.001$), Farr's ($F = 7.11$, $P < 0.001$), Drummond's ($F = 9.93$, $P < 0.001$), Geyer's ($H = 55.65$, $P < 0.001$).

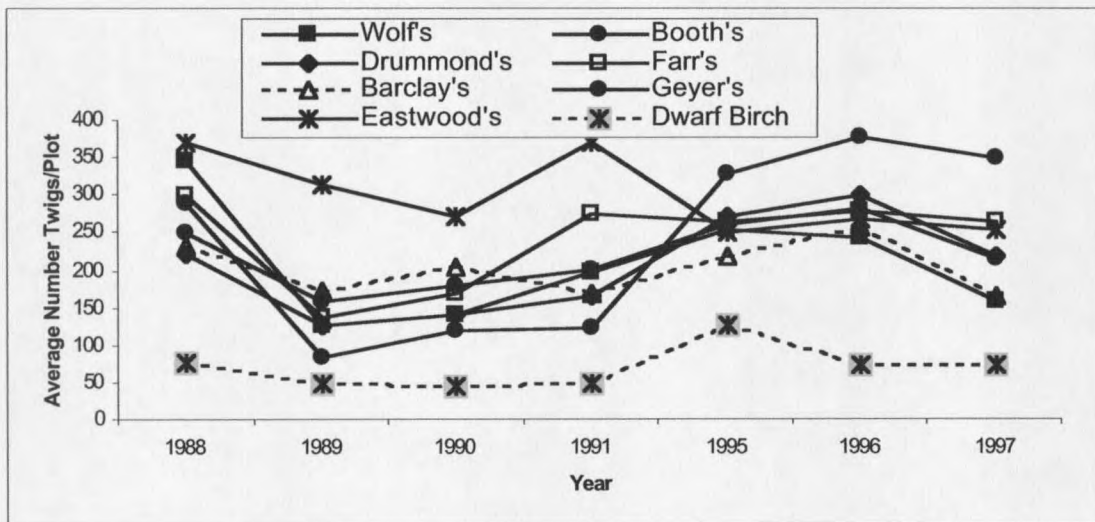


Figure 67. Average number of twigs per plot of 7 willow and 1 birch species among the years 1988-1992 and 1995-1997. Data excludes plots at 7 willow stands where willow died between project initiation and conclusion.

The average number of twigs also varied significantly among years when burned and unburned plots were analyzed together ($F = 41.16$, $P < 0.001$) (Figure 68) (Appendix W, Table 192). The same was true for each species considered individually except Booth's ($F = 0.44$, $P = 0.846$). The trend was for a decrease in 1989 followed by a gradual increase (Figure 69). The *post hoc* tests showed that the low averages for the years 1989, 1990, and 1991 were different from the higher averages for the other years, although the pattern varied (Appendix W, Table 193-200). Results of tests for species-specific among-year variation in average annual twig production, burned and unburned plots combined, are as follows: Wolf's ($F = 31.66$, $P < 0.001$), Booth's ($F = 0.44$, $P = 0.846$), Farr's ($F = 7.49$, $P < 0.001$), Drummond's ($F = 11.07$, $P < 0.001$), Barclay's ($F = 12.4$, $P < 0.001$), Geyer's ($F = 38.8$, $P < 0.001$), Eastwood's ($F = 5.18$, $P < 0.001$), and dwarf birch ($F = 2.36$, $P = 0.042$).

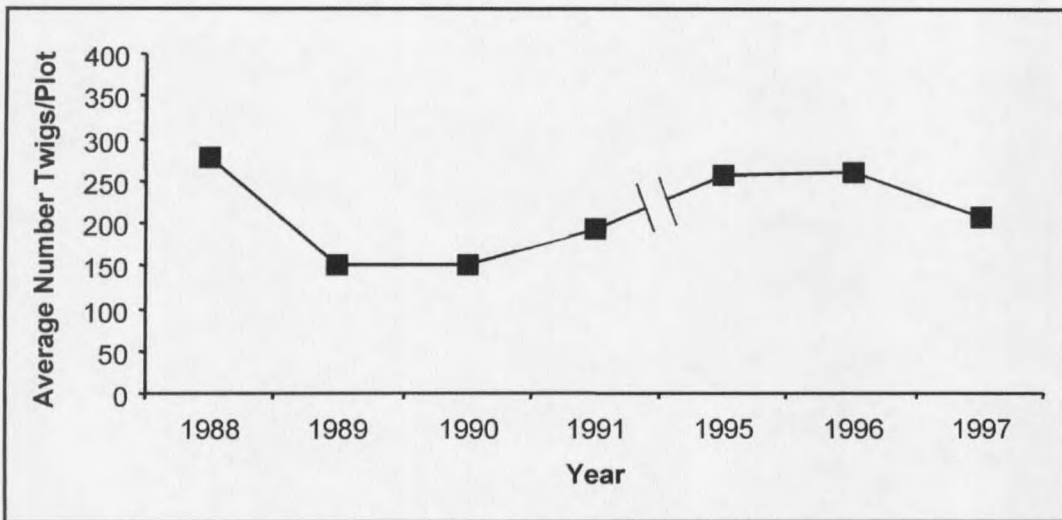


Figure 68. Average number of twigs per plot of 7 willow and 1 birch species combined among the years 1988-1992 and 1995-1997. Data includes plots at 7 willow stands where willow died between project initiation and conclusion.

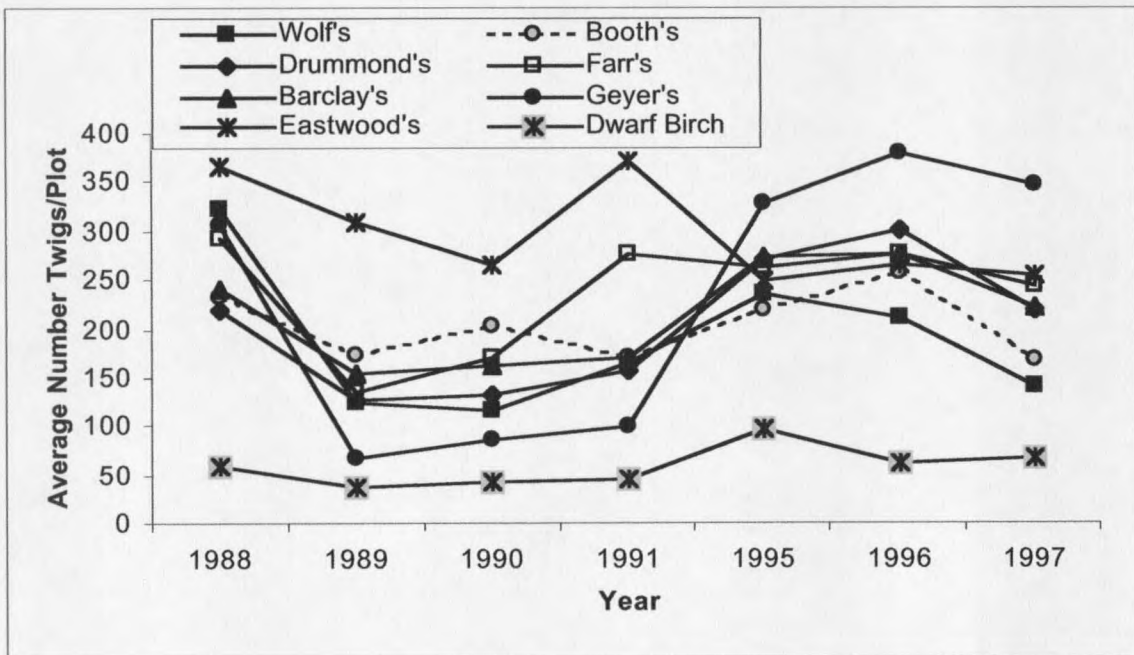


Figure 69. Average number of twigs per plot of 7 willow and 1 birch species among the years 1988-1992 and 1995-1997. Data includes plots at 7 willow stands where willow died between project initiation and conclusion.

Willow Survival Variation in 7 Stands

In addition to height and twig production, willow mortality was affected by environmental factors over a 10-year period. In spring, 1988, 265 plots were marked and sampled at 7 sites in the SC and SB study units. Later that summer, 46 plots burned (3 of 7 sites were involved) providing an opportunity to investigate the effects of fire disturbance on willow. Willow sprouted or resprouted in 18 of the 46 plots but not in 28 by the time data collection was discontinued in 1997 (Table 47). Willow in 12 unburned plots died between 1989 and 1997, possibly due to stress induced by drought and/or browsing impacts. Only one of these had plants that died and were replaced by new shoots. In 1992, the entire Frenchy's site was inundated by a mudflow emanating from a nearby burned hillside. All 35 plots, including 19 that burned and did not resprout, 7 that burned and did resprout, and 9 that were unburned, were buried. No willow was growing in any of these plots by 1997.

Table 47. Number of willow sampling plots at each site where plants were destroyed by the 1988 fires or drought/browsing stress compared with the number that reestablished by 1997.

	Burned in 1988	Reestablished	Dead from stress	Reestablished
Fisher	0	0	2	1
Soda Butte	0	0	0	0
Bannock	0	0	2	0
Warm Creek	9	9	0	0
Frenchy's	26	7	0	0
Lost Creek	11	2	4	0
Slough Creek	0	0	4	0

The species most heavily impacted by fire or drought/browsing stress in plots I measured was Wolf's willow. Wolf's willow in 24 of 72 plots where the plants died did not resprout (Table 48). Farr's, Barclay's, and Eastwood's willows and dwarf birch were not in plots that burned in 1988, while Booth's, Drummond's and Geyer's willow were. Willow in <1/3 of burned plots survived. One or 2 plots each of Farr's, Eastwood's willow and dwarf birch died from other causes and plants in only 1 of the affected plots survived. In addition, 10 Wolf's, 10 Booth's, and 15 Geyer's plots were buried by a mudflow at Frenchy's site in 1992 and did not reestablish by 1997.

Table 48. Number of plots of each willow species where plants were destroyed by the 1988 fires or drought/browsing stress compared with the number that reestablished by 1997.

	Total Plots	Burned in 1988	Reestablished	Dead from stress	Reestablished
Wolf's	72	25	10	9	0
Booth's	69	12	4	0	0
Farr's	19	0	0	1	0
Drummond's	33	2	0	0	0
Barclay's	6	0	0	0	0
Geyer's	26	7	4	0	0
Eastwood's	30	0	0	2	1
Dwarf birch	10	0	0	1	0

Variation in Willow Stand Fire Effects
Among Study Units

Although I could not assess how closely study plot survival data represented the post-fire fate of willow across the study area, I was able to calculate the percent of willow burned in each study unit. GIS queries contrasting pre-fire cover type hectares and 1988 burn area maps (Mattson and Despain 1985; R. Renkin, YNP, personal communication; C. Stein, GNF, personal communication) (Figure 70) revealed that SC had the largest total area of willow (342 ha or 0.68% of study unit), 18% (62 ha) of which burned. However, fire effects were greatest in the YP study unit where willow comprised only 0.12% of the vegetative cover. In the YP study unit, 88 of 168 ha of willow (53%) burned in 1988. Fire effects on willow were minimal in SB (70 ha or 0.22% of study unit in willow) where 9.8% (7 ha) of willow stands were affected. Fourteen ha (0.08% of study unit) of willow in BC did not burn.

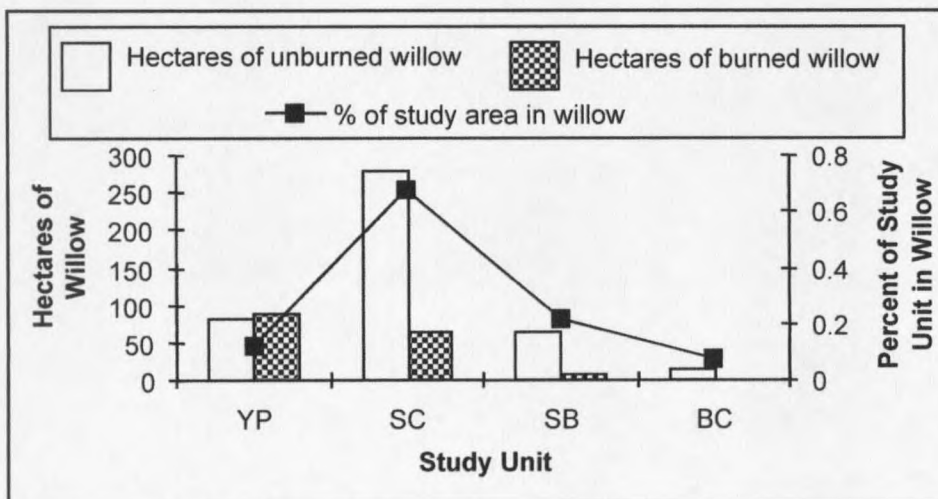


Figure 70. Hectares of burned and unburned willow in 4 study units after the 1988 fires and the percent of each study unit in willow.

Variation in Willow Height and Percent Cover
In and Out of the Slough Creek Exclosure

The Slough Creek willow exclosure, established in 1961, provided the only data on willow status north of YNP in the study area that predated this project. It was set up to compare willow growth patterns with and without moose browsing impacts. I could not find data prior to 1963. However, a 1962 report (Joy 1962) described the "recovery" (increase in canopy cover and height) of willow in the exclosure from 1961 to 1962 as "amazing", but changes were not quantified. It is unclear if percent canopy cover and average height of willow were initially greater inside the exclosure compared to outside. In 1963 they were. Canopy cover and height more than doubled inside the exclosure between 1963 and 1986 but increased only slightly outside (Table 49). Canopy cover was complete in the exclosure by 1986 and virtually 100% canopy cover persisted through 1997. Height appears to have reached a maximum in the exclosure by then as well. Percent canopy cover of willow and height were consistently less outside the exclosure than inside, but after 1986 willow canopy cover more than doubled outside.

Table 49. Percent willow canopy cover and average height (m) in and out of the Slough Creek Exclosure, Absoraka-Beartooth Wilderness, 1963-1997. Blanks indicate no data.

	% Canopy Cover-In	Average Height-In	% Canopy Cover-Out	Average Height-Out
1963	46	1.2	20	0.8
1964	55	1.2	32	0.7
1965	47	1.2	28	0.8
1979			36	1.9
1986	114	3.0	36	1.0
1995	108	2.0	54	1.2
1997	109	2.5	84	1.6

Data were not collected inside the exclosure by species until 1986. At that time, Wolf's willow was not present. It is unknown if it was originally there in 1961. Because it was found outside the exclosure in 1986, and the site was selected to be representative, I assumed it was present but disappeared between 1961 and 1986. Geyer's willow dominated the exclosure and canopy cover increased slightly from 1986 to 1997 (Figure 71). Canopy cover of Booth's willow and Drummond's willow decreased slightly inside the exclosure over the same period. Canopy cover doubled outside the exclosure between 1986 and 1997.

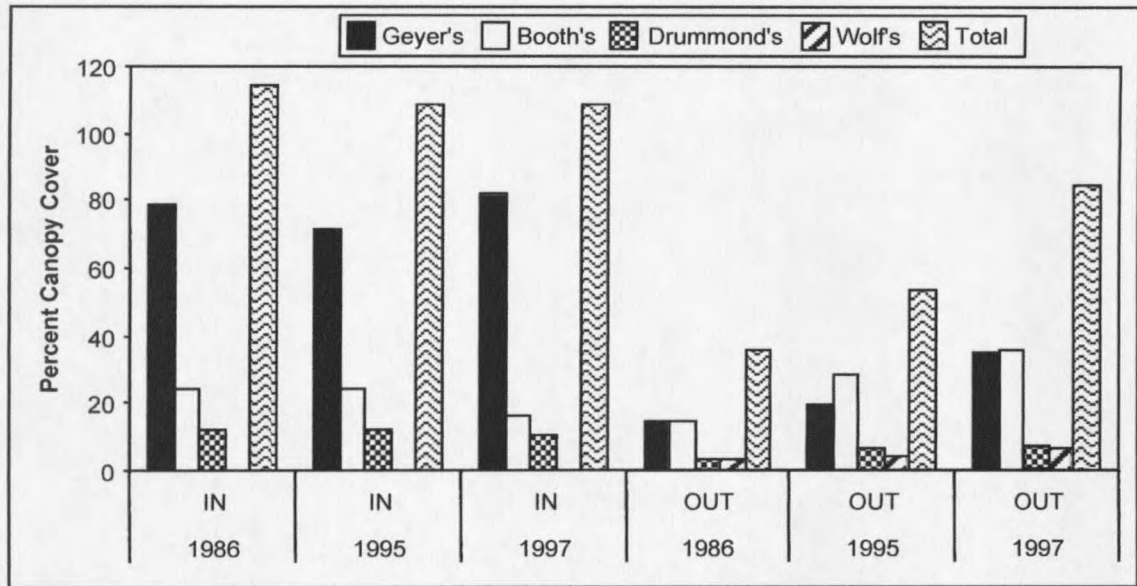


Figure 71. Percent canopy cover of willow by species inside and outside the Slough Creek Exclosure.

The average height of Geyer's willow inside the exclosure doubled from 1986 to 1997. However, the average height of Booth's willow and Drummond's willow decreased (Figure 72). Average height of individual willow species increased outside the exclosure from 1986 to 1997. Geyer's willow increased 52%, Booth's willow 45%, and Drummond's willow 46%, while Wolf's willow showed the least increase (21%).

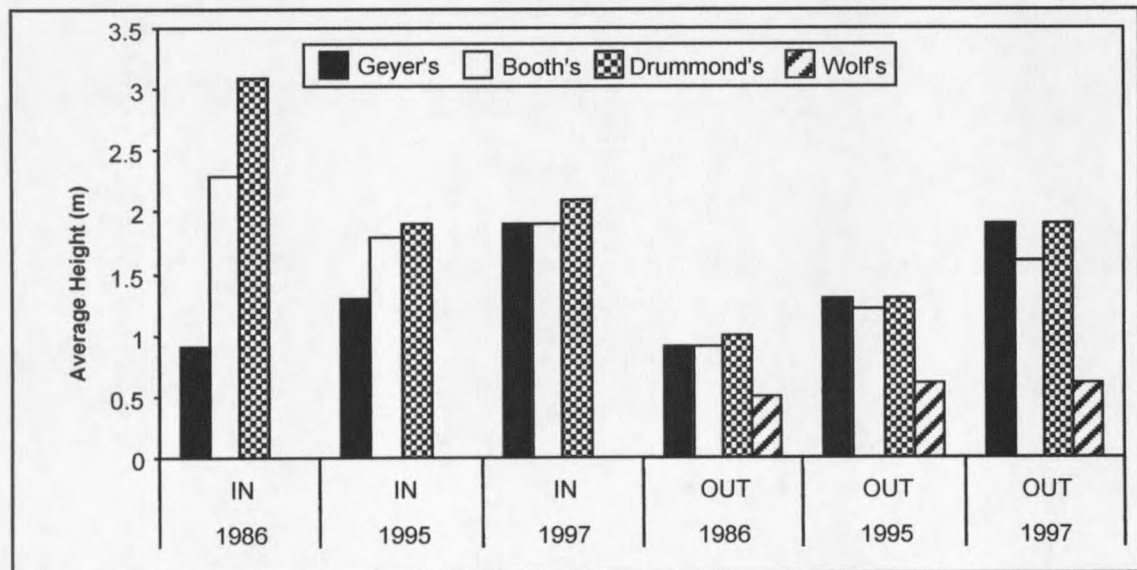


Figure 72. Average height (m) of willow by species associated with the Slough Creek Exclosure.

Discussion

Willow is considered a preferred moose food across North America because it is selected whenever and wherever it is available (Peterson 1955, Coady 1982, Renecker and Schwartz 1997). Moose population densities have been positively correlated to the abundance of willow, with the strongest associations occurring in the subalpine and subarctic habitats of Alaska (Machida 1979, Risenhoover 1989) and the montane regions of the Rocky Mountains (Peek 1974a, b).

As large-bodied ruminants, moose require large absolute amounts of food (Peek et al. 1992). In winter, moose are normally constrained by the time required to search for adequate quantities of comparatively rare foods that meet minimum digestibility requirements. Consequently, moose foraging strategies are determined by trade-offs between moose time-energy constraints and food density and quality (Hanley 1982). Deciduous shrubfields, which contain concentrations of relatively high quality food, are ideal locations for moose to maximize foraging effort (Peterson 1955, Wolff and Zasada 1979, Coady 1982, Risenhoover 1989, Renecker and Schwartz 1997, Peek 1997).

Because moose forage resources are unequally distributed in space and time, moose habitat is a series of patches of different kinds and sizes with the value of each type of patch varying though the year (Peek 1997). With a highly clumped growth form and concentration of biomass in stands, willow provides efficient foraging opportunities for moose throughout much of their range in summer and, given the alternative food array in most northern ecosystems, especially winter (Risenhoover 1985, Renecker and Hudson 1992).

Although classification can be ambiguous (Houston 1968, Peek 1997), willow stands may be stable or transitory. Geist (1971, 1974) recognized both habitats as important in the evolution of moose. Although large floodplain willow stands are dynamic in the sense that flooding and frequent streambed realignment produces a constantly changing system, they are considered relatively permanent because they persist through time without significant alteration (Houston 1968, Dorn 1970, Peek 1997). Stream valley willow stands characteristic of the Rocky Mountains represent another identifiable permanent moose willow habitat at a smaller scale (Stevens 1970, Stone 1971, Peek 1997). Peek's (1974a) classification of winter habitat for Yellowstone Shiras moose included willow bottom/stream conifer complexes along high-gradient streams. He postulated that these habitats are sufficiently permanent to have influenced the behavior, physiology, and morphology of the moose that evolved with them.

Transitory willow stands may be seral to conifers and show significant increases in biomass following disturbances such as fire. Moose populations associated with these habitats fluctuate with successional stages (Peterson 1955, Spencer and Hakala 1964, Wolff 1978, Schwartz and Franzmann 1989).

I found NYWR moose foraging in permanent willow stands as described by Peek (1974a) and also in transitory types. Some willow stands were devoid of conifers and were probably permanent while others contained conifer trees of various ages and were potentially seral to conifer dominance. Willow biomass in the transitory stands may decline if conifer growth continues.

The ability of moose to obtain browse from willow should vary with available biomass. Presumably, the best foraging opportunities are found where willow canopy cover is greatest and shrubs are of sufficient height to consistently extend above the snowpack. NYWR tall (>1.5m) and low (<1.5 m) willow stands (Mattson and Despain 1985) without conifers had greater canopy cover than stands with conifers, and tall willow stands had the greatest average height and at least 2 times the canopy cover of less productive sites.

Availability of willow also varied temporally with snow condition changes. Deep snows restricted opportunities for moose to use willow stands to meet foraging requirements. Moose tracks were found at every winter range willow stand during some portion of the winter except Fisher Creek, the highest elevation SB study unit site, but none was utilized winter-long, confirming Peek's (1974a) theory that snow conditions annually force NYWR moose from willow stands to adjacent conifers.

Higher elevation stands reached critical snow depth thresholds earliest, and utilization in all stands generally ended in December or January when one or more snow depth thresholds were reached. Other studies have determined that about 70 cm of snow forces moose to retreat from shrub fields to forests and that 120 cm or the presence of a crust can preclude use (Des Mueles 1964, Kelsall 1969, Pierce and Peek 1984, Thompson and Vukelich 1981). Use patterns in NYWR willow stands by Shiras moose, the smallest of the 4 North American subspecies, generally confirmed these thresholds. In addition, moose were typically not found in willow stands when >95% of the average shrub height was buried by snow.

The spatial and temporal extent of elk utilization of moose winter range willow stands has been discussed in an attempt to proportionally assign species-specific browsing impacts on the NYWR (McDowell and Moy 1942, Chadde and Kay 1988). The seasonal pattern of elk and moose use was similar in the willow stands I monitored, indicating the possibility of interspecific competition.

NYWR productivity for moose has been negatively affected by long-term changes in willow status. Houston (1982) estimated that willow had declined in the area from about 0.8% of the NYWR to about 0.4% in the past century. Explanations for the decline include over-browsing by elk (Grimm 1939, Patten 1968, Beetle 1974, Chadde and Kay 1996), declines in beaver (Singer et al. 1994), moose colonization

(Houston 1982, Chadde and Kay 1996), fire suppression (Houston 1982), and climatic variation, especially the drought of the 1930's (Houston 1982, Singer et al. 1994), or some combination of these factors. I found that the 1988 fires created additional substantive changes in willow stands on moose winter range with implications for short and long term moose foraging opportunities. Although post-fire changes in willow height were generally not significant, changes in browsing rates and twig production were. The effects of drought, fire, post-fire browsing impacts, and post-fire erosion combined to cause long-term changes in willow stands and variations in available forage for moose.

The average height of willow across moose winter range showed an insignificant post-fire downward trend, but decreases were not enough to affect willow availability to moose. Changes in willow height were significant at 2 of the 7 willow stands. Significant declines in willow height at the highest elevation willow stand, Fisher Creek, which is entirely Eastwood's willow, could be attributed to persistent mechanical damage from heavy snowmobile traffic. Because snow conditions severely limit winter moose access to this stand, these impacts were not consequential to moose. The cause of the decline in average willow height at the Warm Creek stand is unknown but may be attributed to drought stress. Reasons for a significant post-fire decrease in the average height of Farr's willow and an increase in Geyer's willow over all stands are also unknown. Both may have been negatively affected by drought and browsing impacts and, while Geyer's willow responded positively to a post-fire decrease in browsing pressure, Farr's willow did not.

Browsing intensity increased significantly in the winter following the 1988 fires. The percent of browsed willow stems was lowest pre-fire (16.2%), increased by 1.8 times in 1989 (49.7%), and remained high for several years after the fire. Browsing rates began to decline after 1990 and exhibited a downward trend to nearly pre-fire levels by 1997 (17.9%). Reasons for the post-fire increase in browsing intensity probably include a reduction in available food sources due to the fires. Substantial amounts of conifer stands used by moose in winter burned eliminating food items in these forests and forcing moose to browse willow stands more heavily and for a longer portion of the winter. This may have been energetically expensive to moose because of the comparatively deeper snows found in open areas as opposed to mature coniferous forests (see Chapter 5). Because the conifer stands have not had time to grow to pre-fire structure (see Chapter 4), the downward trend in utilization probably reflects a decrease in moose population post-fire rather than a shift to other foods or habitats (see Chapters 1 and 2).

Risenhoover (1985) found that moose in Alaska showed preferences for individual willow species. However, preference varied considerably among Alaskan habitat types and did not appear to be related to biomass, nutritional quality, or amounts of secondary compounds. Average annual utilization varied

significantly among 7 NYWR willow and 1 birch species, but I did not investigate reasons for moose preferences. Utilization was highest on dwarf birch and Barclay's willow and lowest on Eastwood's willow. Eastwood's willow received almost no browsing because it was found exclusively at the high elevation Fisher Creek willow stand, a site buried by snow winter-long.

Moose had significantly fewer willow twigs to browse during the critical post-fire period, a negative effect on moose attempting to substitute willow for forage destroyed in adjacent burned conifer stands. Willow twig production was highest pre-fire (284.1 stems per plot, on average), decreased significantly post-fire (161.2 stems), recovered to about pre-fire levels by 1996 (272.2 stems), and then declined again in 1997 (216.4 stems). Low post-fire production of willow twigs may have been exacerbated by the 1988 drought conditions.

Willow stands in moose winter range were smaller after the 1988 fires, which further reduced moose foraging opportunities. About 35% of 265 willow sample plots were affected by fire and/or post-fire events and 20% of these did not recover. Fire is generally expected to stimulate willow production (Wolff 1978, Guell 1980, MacCracken and Viereck 1990), although fire effects have been found to be detrimental where water table or climate conditions are not optimal (Singer et al. 1994, Singer et al. 1998). About 20% of 265 willow plots I monitored burned in 1988. Of these, <1/2 had any resprouting 10 years later, and none resprouted vigorously or to pre-fire levels. Willow in an additional 12 plots died post-fire, presumably from drought stress and browsing and also did not resprout. Thirty-five more plots were buried by a mudflow from post-fire erosion without resprouting. The greatest post-fire net loss was of Wolf's willow, a species that may be less tolerant of the environmental stresses present during this period.

Exclosure data trends seen prior to 1988 were consistent with the hypothesis that browsing impacts were important agents in the century-long decline in NYWR willow. Willow canopy cover and height inside the exclosure more than doubled from 1963 to 1986 but increased only slightly outside. When measurements were taken in 1986, canopy cover was complete (100%) inside and this high coverage persisted until the last data collection in 1997. Species composition of willow changed with protection from browsing. Wolf's willow presumably disappeared through competition as Geyer's willow became dominant. Willow status outside the exclosure changed substantially and favorably after the 1988 fires, possibly because of a decrease in moose numbers (see Chapters 1 and 2) and browsing pressure. The percent of willow canopy cover and height was consistently less outside the exclosure than inside, but post-fire willow canopy more than doubled outside. Wolf's willow showed the least increase outside, about 1/2 as much as other species.

Peek (1974a) theorized correctly that NYWR moose utilize permanent streamside willow communities at least part of the winter. These areas provide important concentrations of browse that probably play a critical role in moose foraging strategies. Scarcity of willow stands on winter range ($<0.7\%$ of any study unit) may be a limiting factor for NYWR moose populations. Although rare on this landscape, the demonstrated importance in other regions (Peterson 1955, Wolff and Zasda 1979, Coady 1982, Risenhoover 1989, Renecker and Schwartz 1997, Peek 1997) as well as the NYWR (see Chapters 3 and 4) shows that any decline in willow could reduce moose carrying capacity.

Long-term willow declines (see Chapter 1) exacerbated by the 1988 fires and drought may have reduced NYWR carrying capacity for moose, although interactions and trends are complex and cause and effect relationships difficult to determine. Current NYWR conditions may favor changes in individual willow plant production, including increases, but not new plant establishment or recovery of severely damaged plants. Although twig numbers in plants that survived the 1988 fires returned to near pre-fire levels by 1996, about 20% of plants in study plots affected by 1988 fire and/or post fire events did not resprout by 1997, representing an apparent permanent decrease in available moose winter range willow. Even at the SC exclosure, which did not burn in 1988, the doubling of canopy coverage between 1986 and 1997 was the result of increases in size of established plants rather than generation of new plants. At a larger spatial scale, GIS calculations indicated that the 1988 fires affected 26% of willow coverage in the study area. Based on results from my study plots, as much as 20% of burned plants may have died. If this occurred, moose that experienced a post-fire loss of important winter range conifer forests (see Chapters 3 and 4) also had to contend with decreases in willow stands that provided the most favorable NYWR foraging opportunities during early winter.

Conditions that would promote increases in NYWR willow plant and stand numbers and sizes are unknown but would presumably include more favorable growing conditions (wetter climate and concomitant higher water tables) and reduced browsing rates. The decline in moose population following the 1988 fires (see Chapters 1 and 2) may benefit willows in areas favored by moose and less favored by elk by relieving browsing pressure. It is uncertain but unlikely that this alone will restore willows on moose winter range to either pre-fire or early 20th century conditions.

Because the 1988 fires removed many mature conifer forests utilized by moose during mid- and late winter, it is also unlikely that an increase in willow browse, an early winter food source, will result in pre-fire moose numbers. As Peek (1974a) theorized, NYWR moose densities are dependent upon the combination of adjacent and seasonally available willow and mature forest habitats (see Chapters 3 and 4).

CONCLUSION

Moose Population Status

The 4 subspecies of North American moose have expanded their range considerably in the past several hundred years (Geist 1971, 1974, Kelsall and Telfer 1974, Peek 1974a, Coady 1982, Van Ballenberghe and Ballard 1997). For example, Peek (1974a) described important increases in territory by Shiras moose, the subspecies found in the GYA, during the 20th century and concluded that all suitable habitat in southwest Montana had been occupied by 1970. Kelsall and Telfer (1974) found evidence of a recent movement by Shiras moose into British Columbia and Alberta. Coady (1982) considered the Shiras moose to be stable or slightly increasing across its range in 1982.

Various theories have been forwarded to explain the phenomenon of moose range expansion. Most involve population increases in response to favorable changes in climate, predation rates, and habitat availability (Loope and Gruell 1973, Kelsall and Telfer 1974, Peek 1974a, Kay 1997). Loope and Gruell (1973) postulated that GYA moose numbers increased from the late 1800's to the mid- 1900's because conifer forests matured during a period of fire suppression. They believed that, unlike most North American populations, GYA moose are associated with late successional stage conifer forests rather than post-disturbance shrub fields.

Long-term studies in North America indicate that moose populations often erupt, crash, and then stabilize at various densities depending on prevailing ecological conditions (Peterson 1955, Geist 1971, 1974, Coady 1982, Van Ballenberghe and Ballard 1997). Geist (1971, 1974) attributed this pattern to changes in habitat quality. In his opinion, moose typically occur in comparatively low numbers in limited areas of permanent habitat and then rapidly colonize large areas of transitory habitat created periodically by fire. Therefore, periods of population growth often follow disturbances because substantial increases in available deciduous browse provide energy efficient foraging opportunities during winter. Conversely, population crashes have been documented when conifers succeed shrubs on moose winter range (Mech 1966, Peek et al. 1976, Schwartz and Fransmann 1989, Loranger et al. 1991, Messier 1991).

I found that NYWR moose population trends were anomalous. Numbers did fluctuate significantly in response to major habitat changes. However, as predicted by Loope and Gruell (1973), the 1988 Yellowstone fires were followed by important moose population declines, not increases.

Moose probably invaded the NYWR in the late 1800's (Houston 1982, Schullery and Whittlesey 1992). The lower elevation sagebrush grasslands they encountered were generally unfavorable winter

habitat, but coniferous forests that provided cover and browse dominated the higher elevations. Landscape level fires may have swept the region around 1700 (Romme and Despain 1989). Consequently, when moose arrived, coniferous forests were sufficiently developed to have intact canopies and understories of shade-tolerant conifer species, including subalpine fir (Mattson and Despain 1985), an important winter moose food (see Chapter 3). Willow stands were only a small part of the NYWR landscape, but they were robust (Houston 1982) and likely enhanced winter range productivity for moose (see Chapters 3 and 8).

Moose population increases in the early 1900's attracted the attention of managers who at first recorded moose as a curiosity and then attempted surveys as they perceived a substantial increase in numbers (McDowell and Moy 1942, Rush 1942, Gaab 1949, Keherberg 1964). Organized attempts to count moose began in the 1920's and continued until about 1950 (see Chapter 1). I was able to find survey records from this period only for areas north of Yellowstone Park. They were labor-intensive efforts on snowshoes or horseback and provided only trend data. Yellowstone Park was considered a reservoir of moose from which animals migrated to the surrounding national forests (McDowell and Moy 1942). The first count occurred during the winter of 1921-1922 and revealed 16 moose (Crane 1922). Count results increased to 65 in 1924-1925 (Johnson 1925) and 194 in 1942 (McDowell and Moy 1942).

The 1930's and early 1940's were characterized by increases in moose and elk numbers, drought, reduced willow vigor, beaver population declines, and ungulate feeding programs in Yellowstone Park. Deciduous browse species deterioration was variously assigned to overbrowsing or drought conditions (McDowell and Moy 1942, Rush 1942, Keherberg 1964, Houston 1982). During the period of perceived moose population increases, NYWR coniferous forests were about 200 to 250 years old and had double canopies (Mattson and Despain 1985), conditions advantageous to wintering moose in this environment (see Chapters 3, 4, 5, 6 and 7).

Moose quota hunting was initiated in 1945, in part, to preserve beleaguered willow stands and to control a population considered excessive for the habitat capacity (Montana Fish and Game 1945, Gaab 1948). The last concerted effort to survey moose in the upper drainages occurred in the late 1940's (Gaab 1950). It may have documented the beginning of a downward trend in moose numbers, which was attributed, primarily, to a loss of winter forage provided by willow (Gaab 1948, 1949, 1950). However, the effects of quota hunting were probably more consequential in causing the population decline. Horseback surveys recorded 106, 71, and 30 for the years 1947, 1948, and 1949, respectively (Gaab 1948, 1949, 1950).

Although the higher elevation moose habitat was excluded, moose were recorded incidental to fixed-wing aircraft elk surveys from 1968 to 1978 across elk winter range (Barmore 1980, Houston 1982). These data show moose widely distributed in pockets of preferred habitat of mature conifers and willow stands.

At the time of extensive fires in 1988, most coniferous forest moose habitat on the NYWR was about 250 to 350 years old. With high densities of shade-tolerant subalpine fir in the understory and well-developed double canopies (Mattson and Despain 1985), they provided ideal moose winter habitat in this environment (see Chapters 3, 4, 5, 6 and 7). The 1988 fires, which may have been the next major event in a 300-year fire cycle (Romme and Despain 1989), had substantial negative effects on NYWR moose populations by removing winter forage and cover. Moose populations during the 1980's and 1990's may have also been negatively impacted by an additional loss of winter range through logging, continued quota hunting, drought impacts to willow, and predation, including wolves reintroduced in 1995 and indigenous grizzly bears (see Chapters 1 and 2).

I attempted to assess the NYWR moose population using a suite of indices (see Chapter 1). My efforts to count NYWR moose using conventional fixed-wing aircraft survey techniques (Gasaway et al. 1986, Gasaway and Dubois 1987) were unsuccessful, but a combination of indices, including a horseback survey first employed during the 1940's (Gaab 1949, 1950), provided consistent and corroborative trend data. Based on comparisons with data from ground surveys in the 1940's (McDowell and Moy 1942, Gaab 1950) and observations from aircraft in the 1970's (Barmore 1980, Houston 1982), results suggest a decrease in moose numbers between 1947 and 1988. Pre- and post-fire assessments confirm a substantial decline after the 1988 fires.

For example, the average number of moose seen per observer day on horseback surveys was 2.63 during the 1940's when quota hunting began (Gaab 1950) but decreased by more than 2-fold to 1.15 in the early 1980's and by more than 7-fold to 0.34 post-fire (1990-2001, excluding 1988 and 1989 when survey conditions were atypical). Similarly, the probability of seeing a moose along the road between Mammoth and Roosevelt Junction, the portion of the Cooke City road most affected by the 1988 fires, decreased from 15% pre-fire to 4% post-fire. Between 1989 and 1992 moose seen on survey flights decreased by 78% from a high of 59 in November 1989 to a low of 13 in May 1992. Between 1968 and 1978, Houston (1982) and Barmore (1980) found an average of 13 moose per flight (annual high counts) in upper Slough Creek and 38.6 moose per flight in the southern part of the study area (roughly YP study unit), while I found an average of 10.3 and 4.5 per flight, respectively, in the same areas between 1988 and 1992.

The opportunity to find moose on the NYWR was affected by seasonal and daily timing and varied among vegetation types. Barmore (1980) found seasonal variation in moose sightability during attempts to count NYWR moose incidental to elk distribution flights between 1968 and 1970. He concluded that moose are difficult to observe in this environment but are most easily found when associated with willow, and he was most successful at finding them in these stands in May, early June, and December. My findings

were comparable. The probability of seeing a moose along the road between Gardiner and Cooke City was highest during May and June (54.5%) and November and December (40.4%) and lowest in July to October and January and February when the probability ranged from about 5% to 20%. Similarly, the average number of moose seen per over-flight in selected willow stands was highest in November (9.3) followed by December (8.6) and May (7.6), while averages ranged from 0 to about 4 during the remaining months. The highest average number of moose seen per 1/2 hour during daily observations of a willow stand in the SB study unit was highest in June (0.9) and December and May (0.6 in each). Predictably, mornings and evenings were the most productive times to search for moose.

Hunting has been reduced as a source of mortality for NYWR moose through significant decreases in quotas beginning in 1990. For example, when the project began in 1986 the quota was 55 either sex, but by 1996 it had been reduced to 15 antlered bulls. However, winter habitat quantity and quality will ultimately control NYWR moose population density. Extensive favorable moose winter habitat will not be present again until areas that burned in 1988 develop mature coniferous forests with canopies that ameliorate snow conditions and understories of subalpine fir, the preferred browse species of NYWR moose (see Chapter 3).

Reductions in hunting quotas after the 1988 Yellowstone fires and a shift from either sex to bulls only harvesting were appropriate responses to the substantial declines in NYWR moose numbers demonstrated by this study. However, hunting management strategies should be revisited periodically to address the need for implementing more conservative measures. For example, even hunting only antlered animals can have long-term negative effects on moose populations. Schwartz and Hundertmark (1993) and Schwartz (1997) hypothesized that, when sex ratios are highly skewed towards cows because bulls have been harvested, not all females will be bred and others may not breed or conceive during the first estrus. The result can be calves born too late to adequately prepare for winter; i.e. lower recruitment. Unfortunately, the minimum bull/cow ratio needed to ensure timely breeding and healthier calves is unknown (Schwartz 1997).

Moose Habitat Status

Moose habitat varies depending on season and the animal's sex, age, and life history (Telfer 1978, Coady 1982, Thompson and Stewart 1997). Moose populations may be limited at any given time by nutrition, predation, hunting, disease, and/or weather (Houston 1968, Fuller and Keith 1980, Ballard et al. 1991, Gasaway et al. 1992, Van Ballenberghe and Ballard 1997). However, food and cover and the animal's ability to access them ultimately regulate numbers (Coady 1982, Peek 1997). Locating food and cover requires movement and expenditure of energy (Moen 1973, Schwartz and Renecker 1997). During

winter, moose face low quality and quantity of food (Ammann et al. 1973, Messier and Crete 1984, Peek et al. 1992), as well as increased energetics costs associated with movement through deep snow and demands of severe cold (Kelsall 1969, Kelsall and Prescott 1971, Peek 1971, Telfer and Kelsall 1984). Renecker and Hudson (1992) and Cederlund and Okarma (1988) hypothesized that moose have developed foraging strategies involving use of concentrated patches of forage to deal with these conditions.

The wide array of habitat selection patterns described in the literature suggests that moose are highly adaptable animals (Peek 1974a,b; Coady 1982; Peek et al. 1992). Peek (1997) characterized moose as "selective generalists"- animals capable of using habitat components in higher proportions than they occur in the environment and adept at seeking seasonally advantageous foraging areas. However, he also indicated that the limits of the species' ability to withstand change in specific habitats are poorly understood, especially when major habitat alterations are involved. My study focused on delineating moose habitat use on the NYWR and their response to major habitat perturbations in the winter. I found 4 factors that were suspected of having impacts on moose habitat during the 1980's and 1990's: the 1988 fires, drought during the mid- to late 1980's, and the cumulative effects of logging and persistently high elk density.

Habitat currently occupied by North America moose has been characterized in various ways. Telfer (1984) placed moose habitat in 5 broad categories: boreal forests, mixed forests, large delta floodplains, tundra and subalpine shrub, and stream valleys. In addition, Peek (1974a) identified 5 types of winter habitat used specifically by the Shiras moose of the intermountain west, an area that includes the GYA. One of his categories characterized NYWR moose habitat, which he described as intermediate sized willow stands along meandering streams in association with adjacent forested slopes.

All moose habitat may be further categorized as permanent or transitory (Geist 1971, 1974, Coady 1982, Peek 1997). Throughout their range, moose are usually most abundant in transitory habitat where forest canopy removal promotes a proliferation of deciduous shrubs. The resulting brush fields in these early seral environments can provide high biomass concentrations of food for moose and energetically efficient foraging opportunities (Dryness 1973, Krefting 1974, Kelsall and Telfer 1974, LeResche et al. 1974, Peek et al. 1976, Irwin and Peek 1979). However, in a few locations, moose utilize mature coniferous forests where shade-tolerant conifers form a subcanopy of available browse, but these situations are considered anomalous (Pierce 1984, Pierce and Peek 1984, Peek et al. 1987, Peek 1997).

I found that NYWR moose are not associated with early seral vegetation or the habitats commonly used by other North American moose (Telfer 1984). Instead, they spend most of the winter in double

canopy coniferous forests in mountainous regions. As Peek (1974a) suspected, Shiras moose habitat in this part of the intermountain west consists of willow stands intermixed with or adjacent to forested slopes. I also found that, like other North American populations, NYWR moose seek concentrated browse. However, in addition to the predictable use of willow stands (Peek 1997), they were attracted to patches of subalpine fir, especially in lodgepole pine forests, rather than post-disturbance shrub fields.

Subalpine fir has a unique growth form that produces patches in the understory of the oldest coniferous forests; lower branches root to form an expanding cluster around the parent tree. This supports Loope and Gruell's (1973) explanation for expansion of moose in the GYA in the past 150 years. They believed that, with fire suppression, moose populations increased as forests aged and shade-tolerant subalpine fir proliferated. The loss of late successional subalpine fir patches in mature conifer forests was likely the most important reason for the decline in moose numbers in response to the 1988 Yellowstone fires. Approximately 29% (41,718 ha) of the mature conifer forests (143,856 ha pre-fire) in my study area burned in 1988.

Individual moose attempted to compensate for losses of subalpine fir after the large-scale 1988 fires in several ways. Three of 14 radiocollared moose were unsuccessful and starved the following winter. When pre-fire home ranges were extensively burned, these moose increased home range size and subsequently increased energy expenditure for foraging. Post-fire home range sizes were smallest for moose wintering in areas unaffected by the fires (see Chapter 2). Moose with burned areas in home ranges shifted to unburned willow stands and unburned hillsides of the oldest coniferous forests adjacent to the willows. The majority of radio locations before and after the 1988 fires (70% and 80%, respectively) were in the unburned oldest lodgepole pine, the oldest spruce-fir, and willow cover categories, even though there was a >3-fold decrease in the amount of available mature coniferous forests post-fire (see Chapters 2 and 4).

Had NYWR moose populations been high, intraspecific competition post-fire could have negatively affected the environment, including forest composition, soils, and primary browse (Risenhoover and Maass 1987, Pastor et al. 1988, Schwartz and Franzmann 1989). Post-fire browse effects on willow showed some evidence that this occurred in my study area (see Chapter 8). I believe high or excessive browsing rates on subalpine fir were also possible as moose concentrated in unburned areas, but I did not employ methods to quantify this occurrence.

Interspecific competition, specifically impacts of elk on moose, was more likely to have impacts on moose population biology in the NYWR. Interspecific competition can affect moose energetics and survival (Stevens 1974, Telfer and Cairns 1986, Boer 1997), although competitive overlap between

sympatric cervids is difficult to assess (Pianka 1976, Weins 1977). I was unable to define competitive relations but was able to investigate the degree of spatial overlap in winter among 3 cervids. Snow conditions and habitat location determined winter partitioning (see Chapters 4 and 5). Moose occupied the highest elevations where snow was deepest and boreal forests were most prevalent. Mule deer used the lowest elevations with less snow and more sagebrush grasslands and drier Douglas fir forests. Elk were restricted by snow from the highest elevations but ranged to the lowest. Separation of elevation and habitat use between mule deer and moose was nearly complete but only partial between elk and moose. Moose and elk use of major willow stands did overlap. This overlap included high elevation stands not typically considered to be within elk winter range (see Chapter 8). Given the importance of these areas to foraging moose, the presence of elk could be detrimental.

Elk have been reported to out-compete moose, especially for browse (Cowan 1950, McMillian 1953, Telfer and Cairns 1986, Wiens 1977). Moose and elk do not have to be present in the same area at the same time for competition to occur. Even infrequent high elk numbers in riparian habitat can reduce the amount of browse available to moose during critical winter periods (Martinka 1969, Telfer and Cairns 1986). Except for moose and elk use of willow, spatial and temporal variations in environment and interspecific differences in foraging requirements ameliorated competitive relations on the NYWR. This may represent evolutionary separation of niches to enhance coexistence among cervids (Cairns and Telfer 1980) or simply individual species responses to available habitat. Harsh winters may increase overlap and competition between elk and mule deer in open environments (Jenkins 1985). However, hard winters may actually decrease overlap between elk and moose when moose have access to late successional lodgepole pine, spruce-fir, or Douglas fir forests, a likely scenario on the NYWR.

Willow is an important moose food whenever and wherever it is found (Peek 1997). However, available willow biomass can vary among years with different levels of browsing pressure, frequency of disturbances, and variability in weather conditions. Because of its association with riparian areas, it is especially vulnerable to water table fluctuations (Peek 1997). Houston (1982) estimated that NYWR willow stands in elk winter range declined about 60% (1% -0.4%) during the 1900's. Most of the declines occurred during a period of pronounced drought between 1920 and 1940 that had long-term effects on willow plants and the overall environment (Jonas 1955, Engstrom et al. 1991, Singer et al. 1994, Singer et al. 1998). Singer et al. (1998) concluded that elk had a greater negative impact on willow on the NYWR than at Rocky Mountain National Park because of drier conditions in the former area. Frank and McNaughton (1992) determined that a severe drought of only one-year duration (1988) was sufficient to

have dramatic negative effects on NYWR grassland and shrub-grassland ecosystem function and productivity. Singer et al. (1994) measured willow moisture stress in the study area and concluded that some plants died as a result of the 1988 drought.

Similarly, I found that the 1988 drought produced critical short and long-term negative effects to willow within stands utilized by NYWR moose (see Chapter 8). Twig production was 1.8 times less after the 1988 fire and did not return to pre-fire levels until about 1997. Plants in 20% of sample plots that died in 1988 (Singer et al. 1994) had not resprouted when I discontinued monitoring 9 years later in 1997. A short-term decline in twig production and a long term decrease in willow plants induced by the 1988 drought and fires resulted in a loss of important winter forage for NYWR moose. The longevity of these effects is unknown but should be monitored.

Throughout most of their range in North America boreal forests, moose are associated with transitory shrub communities that grow following disturbances (Coady 1982, Peek 1997). Although the largest early seral stage shrub fields are usually created by fire, logging can produce similar effects. Thus fire and logging are tools commonly used to enhance moose winter range (USDA 1987, Thompson and Stewart 1997). However, I found that pellet group counts indicated a significant association of wintering moose to >300-year-old lodgepole pine forests rather than adjacent 25-year-old clearcuts, where there were 5 times fewer pellet groups. Deciduous shrub browse species were not an important habitat component in either the clearcut or the mature forests, and differences in shrub canopy cover did not indicate a post-disturbance proliferation of deciduous biomass. For example, of the deciduous shrub species that I measured in clearcuts (see Chapter 3 and 7), all had a canopy cover of <10% and most were <5%.

Differences in the distribution of conifer trees and browsing rates provided a possible explanation for the greater moose activity in the forest as opposed to the clearcuts. Subalpine fir was the most common tree among both clearcuts and mature forests, but it was significantly more abundant in the forest where browsing rates were also significantly higher. For example, there were about 5.5 more unbrowsed tree <1 m tall in forest than clearcuts as well as 10 times more browsed trees in that height class. On the NYWR, logging appears to remove moose habitat in the form of mature conifer forests as effectively as fire.

In addition to production of shrub fields, clearcuts are often created to provide forest edges, an ecotone purported to have many benefits for wildlife (Leopold 1933, Coady 1982, Yahner 1988, Naiman et al. 1988 and 1993, Morrison et al. 1998, Szaro et al. 1999). However, forest edge did not provide NYWR moose with greater forage amounts of either deciduous shrubs or conifers, and, as demonstrated by pellet group counts and conifer browsing rates, edges did not attract moose (see Chapter 7).

Moose Winter Strategy in the NYWR

Moose used characteristics of the oldest coniferous forests to cope with snow depths and reduce energy output while foraging. Moose found routes through snow with less accumulation as reported for Minnesota (Pruitt 1959, Peek 1997). For example, during late winter, moose used snow depths 22.2 cm less than average depths in the oldest lodgepole pine and 26.8 cm less in the oldest spruce-fir forests (see Chapter 5).

NYWR moose and other North American populations share the common problem of selecting food items of reasonable quality from an abundant array of vegetation of low quality (Peek et al. 1992, Renecker and Schwartz 1997). Diet and habitat use patterns recorded in this study reflected how moose balanced calorie intake and energy output on the NYWR. As noted in other studies (Peek 1974b, Renecker and Schwartz 1997), moose use a wide variety of food items but predominantly deciduous shrubs and trees. NYWR moose, however, selected subalpine fir as the dominant food item. It comprised 18.4%, 44.3%, and 49.4% of browsed stems found while backtracking moose in the early, mid- and late winter periods, respectively. Willow was the second most used browse species (early-47.7%, mid-22.4%, and late winter-13.2%). I found that these 2 species were central in foraging patterns of NYWR moose, and, with the addition of lodgepole pine, gooseberry, and buffaloberry, account for 85% of browsed stems recorded (see Chapter 3).

Willow formed the most concentrated patches of browse on the landscape. It was used most in early winter when snow conditions had less impact on moose movements. As snow made willow stands less accessible, use shifted to subalpine fir (see Chapters 3, 5, and 8). If snow had not restricted moose from many willow stands, it would probably have been the primary food item throughout the winter, or as long as unbrowsed twigs were available.

Foraging efficiency, as expressed by number of twigs browsed per meter traveled, was highest in areas with willow, whether they were mixed with conifers or were found as pure willow stands. Foraging efficiency, as measured by this standard, was next highest in 2 other cover types with patches of available food -aspen stands, another limited cover type on the NYWR, and the oldest coniferous forests where patches of subalpine fir were located (see Chapters 3 and 6).

NYWR moose utilization of biomass patches of willow and subalpine fir was commensurate with several optimal foraging theories. They selected habitat at the appropriate spatial scale to include browse patches which, according to the time minimization theory, is an advantageous strategy for moose persistently exposed to the risk of predation and/or cold stress (Pyke et al. 1977). The forage maximization theory postulates that, in harsh environments where food items tend to be of equal value, biomass patches

help moose maximize the capture of energy by providing the best logistical approach to foraging. When concentrations of forage such as subalpine fir patches are available, moose can make energy efficient choices for locating dense food supplies, searching for food within the patch, and consuming plant parts (Belovsky 1978). Moose are expected to become less selective about what plants to eat in a patch and what plants constitute a patch as the disparity between forage availability and animal movements increases (Ellis et al. 1976). Models of optimum patch choice theorize that animals search for optimal numbers and arrangements of feeding sites (McArthur and Pianka 1966). Moose travel costs should decline as more patches are included in their range; moose expand foraging range to include more patches until the cost of increased search time is greater than the savings from reduced travel. The marginal value theorem (Charnov 1976) explains the timing for abandonment of a particular patch. A moose should leave a patch when it has reduced the food supply by browsing to the point where intake is depressed and continued foraging is less efficient than searching for another patch.

NYWR moose minimized search time for food (Pyke et al. 1977) and maximized calorie intake (Belovsky 1978) by selecting landscapes with the most abundant food. These were the upper reaches of drainages dominated by late successional stage forests adjacent to willow stands. They utilized willow stands as long as snow conditions allowed and then retreated to the cover provided by double canopy forests. Within these forests they searched for areas with the optimal number of patches (McArthur and Pianka 1966) of small subalpine fir trees, usually the oldest (>300 years) lodgepole pine forest (see Chapter 6). Presumably, the larger the patch the longer a moose could browse before abandoning it in favor of another more efficient foraging opportunity (Charnov 1976).

Despite high dependence on 2 food items (subalpine fir and willow) that grew in dense patches, moose apparently selected quality over quantity in some cases. Gooseberry was the third most prevalent food item in the early winter. Because it grows as a few stems in scattered groups of plants, finding it took more energy than obtaining concentrated browse. However, it consistently provided a source of nutrients superior to other common browse species (see Chapter 3). It was most abundant in the oldest spruce-fir forest, which likely explained the association of moose with these areas in early winter. Although its nutritional value remained high through the winter, it was used less as winter progressed because snow depths made it unavailable. Buffaloberry was available all winter but was only important in the diet in late winter. Nutrient analysis showed it had the highest crude protein content of common browse species during that time, but it grew as scattered shrubs rather than in patches in most forest types. It was most common and most likely to have a large shrub or patch growth form in mid-age lodgepole pine forests, which may partially explain the association of moose with these forests in late winter.

Lodgepole pine was not an important browse item until after the 1988 fires (see Chapter 3). For example, 1.3% of browsed stems recorded pre-fire were lodgepole pine, but it was 20.5% of the diet post-fire. It was used most in areas most heavily impacted by fire. Because it was ubiquitous but not used unless habitat quality was diminished, it is probably a poor choice for avoiding energy deficits. It was most commonly browsed in nearly pure stands of lodgepole pine about 40-100 years post-disturbance where its growth form provided low branches and other food items were rare.

In spite of the fact that 35% of the study area burned, burned vegetation comprised only 1.8% of browsed twigs recorded post-fire (see Chapter 3). Browsing on burned vegetation was also a foraging pattern of moose in poor quality habitat. It was used the most in areas with the most fire impact, and use increased as winter progressed (1.8% of browsed stems in early winter and 4% in late winter). In addition, it was used only the first winter after the fire by moose whose home ranges burned extensively. Browsing efficiency, as measured by twigs browsed per meter traveled, was significantly lower in burned areas than unburned forests. For example, to obtain a comparable number of stems to browse moose traveled about twice as far in the oldest lodgepole pine forests that burned as opposed to unburned forests and 16 times farther in the oldest spruce-fir forests that burned than in unburned forests.

Most browsing in forested environments occurred in late successional stages of all forest types. Subalpine fir was most abundant in the oldest forests and, among these, was most abundant in the oldest lodgepole. In addition, moose selected subalpine fir in every successional stage of every forested cover type and avoided other conifer species. Specifically, nearly all subalpine fir browsed were <5 m tall and about 50% were <1 m (see Chapters 3, 4, and 6).

Browse intensity on subalpine fir was a reasonable indicator of habitat quality. Browsing on individual subalpine fir increased as habitat quality decreased through removal of the oldest forests in the 1988 fires (see Chapter 3). To balance energy needs, moose traveled less and browsed each plant more. More twigs per plant were browsed as winter progressed (7.3, 12.7, and 11.0 in early, mid-, and late winter, respectively) and pre-fire (8.5) versus post-fire (13.2). Also, proportionally more twigs were browsed in areas most heavily impacted by fire. Disturbances may negatively affect moose by increasing browsing pressure on remaining subalpine fir thus damaging plants and reducing habitat quality (Peek 1997). Although I did not employ methods to quantify the extent of over browsing, my observations confirm the potential.

Moose Habitat Management

Many studies have confirmed a common pattern of moose habitat use across North America and managers have responded by employing practices to enhance habitat quality and quantity commensurate with these findings (Peterson 1955, Coady 1982, Peek 1997, Thompson and Stewart 1997). For example, the association of moose with early stages of post-fire succession in boreal forests is commonly accepted (Peterson 1955, Geist 1971, Coady 1982). Transitory seral shrub communities that follow fire can provide extensive concentrations of moose forage (Wolff 1978, Oldemeyer 1983, Oldemeyer and Regelin 1987, Risenhoover 1985, Peek 1997). Logging in boreal forests can create similar effects (Pimlott 1963, Eastman 1974, Westworth et al. 1989, Peek et al. 1987).

In addition, fire and logging can also enhance habitat by creating features of high value to moose such as edge, the interface between forests and disturbance areas. The advantages to wildlife of the "edge effect" are widely acknowledged and are often associated with the tendency for communities to be more dense and diverse in ecotones (Leopold 1933, Naiman et al. 1988, 1993, Pianka 1994, Morrison et al. 1998, Szaro et al. 1999). Most work suggests that moose may benefit from edges because they provide a juxtaposition of food and shelter in late winter; both are important and possibly limiting factors (Neu et al. 1974, Coady 1982, Bangs et al. 1985, Mastenbrook and Cummings 1989).

As a result of these reports, attempts to create or improve moose habitat in North America have mostly involved enhancing edge and converting timber stands to young age classes through harvesting or prescribed fire (Coady 1982, Thompson and Stewart 1997). Managers of the NYWR and adjacent areas have likewise endorsed and implemented these practices (USDA 1987). However, my investigations suggest that NYWR moose habitat relationships are anomalous and that these methods of habitat enhancement are counterproductive in this environment. Instead of benefiting from disturbances and the edge effect, NYWR moose appear to be forest interior species that rely on late successional stage conifer forests for winter survival.

I found that moose foraging opportunities among logged, forested, and forest edge environments in lodgepole pine dominated landscapes were significantly different. Browsing rates on trees and pellet group densities indicated that logged areas were not used by moose in winter and, therefore, were not suitable winter range, while forested areas were (see Chapter 7). Neu et al. (1974) and Bangs et al. (1995) found moose associated with the edge between burns and forests. However, using the same measures (pellet group densities and browsing rates), I did not find differences in moose activity related to the clearcut/forest boundary either on the clearcut or the forested side in comparison with clearcut and forest interior

environments. In addition, I did not find important differences in numbers of trees or canopy cover and height of shrubs associated with the edge effect. These findings provide a context for managing timber on winter range for NYWR moose.

The number of cut and uncut stands of timber and the amount of edge length are related, i.e. the number of stands and edge length increase concomitantly. However, interior habitat quality and quantity are negatively affected by an increased number of stands (decreased stand size) (Franklin and Forman 1987). Smaller stand size and the corresponding increase in edge can benefit species associated with edge environments (edge species) but negatively affect species that conduct daily activities away from edges (interior species) (Franklin and Forman 1987, Yahner 1988, Pianka 1994, Morrison et al. 1998). As forest interior species during winter (see Chapter 7), NYWR moose are, therefore, negatively affected by disturbances in mature forests and the associated reduction in the size of uncut stands. Causes of forest fragmentation in moose habitat include timber harvesting, natural and prescribed fire, road building, and other disturbances capable of creating mosaic vegetation patterns while reducing mature forest interior environments.

Various sizes and arrangements of harvested blocks have been used for timber harvesting. Although an oversimplification, there are 2 common models for timber harvest layout, dispersed patch (checker board) and single unit. A dispersed patch forestry model has been widely used during recent decades in the western U.S. to replace harvest patterns typified by larger, single unit blocks (Smith 1985, Franklin and Forman 1987). Although many variations in patch size and configuration have been employed, patch number and edge length increase and forest interior decrease generally occurs when timber harvesting follows the dispersed patch model. Because NYWR moose appear to be forest interior species that do not benefit from the edge effect, single unit cuts that maximize forest interior environments may have fewer negative effects on moose winter range in this area.

Thompson and Stewart (1997) advocated that, to meet moose habitat requirements, timber harvest prescriptions should be area-specific. Recommended prescriptions vary substantially among geographic regions and are based on differences in moose habitat relationships. For example, in northern Minnesota where moose utilize transitory shrub fields that follow disturbances, Peek et al. (1976) proposed that 40% to 50% of each management unit (management units were 93 km²) be maintained in clearcuts <20 years old, 5% to 15% in mature spruce/balsam fir, and 35% to 55% in water and trembling aspen/white birch stands. However, in Idaho where moose are associated with double canopy conifer forests and browse Pacific yew in the understory, Peek et al. (1987) favored very different guidelines, including the recommendation that logging should remove <50% of the canopy and maintain 50 to 60% of the yew

subcanopy. In addition, they advocated a harvest rotation of about 210 years with >45% of the total area in trees >90 years old and <14% of the entire winter range logged during any 30 year period. Conditions on the NYWR are similar to what Peek et al. (1987) found in Idaho, except NYWR moose rely on understories of subalpine fir instead of Pacific yew for winter browse. Therefore, models for timber harvesting on the NYWR and adjacent areas should resemble prescriptions for Idaho, rather than Minnesota.

Renecker and Hudson's (1992) hypothesis that moose seek patches of food to optimize foraging energy has direct application to forest management practices on NYWR moose winter range. I found that in lodgepole pine dominated landscapes, quantity and location of subalpine fir appeared to be the major factor determining moose distribution and investment of foraging energy among forest types and ages (see Chapter 6). There was no apparent similar relationship with concentrations of deciduous shrubs other than willow.

Foraging opportunities related to subalpine fir at moose feeding sites (see Chapter 6) varied significantly between cover type and successional stage. Foraging opportunities, as measured by number of subalpine fir, were greatest in the oldest lodgepole pine followed by mid-age lodgepole pine, oldest Douglas fir, and oldest spruce-fir forests (334.5, 284.2, 229.8, and 71.6 trees per 0.02-ha plot, on average, respectively), while subalpine fir was a very minor component of early successional stage forests (1.3 and 3.6 trees per 0.02-ha plot in young lodgepole pine and Douglas fir forests, respectively). At feeding sites in the older forest cover types, subalpine fir was often the most common tree. Browsing on other conifer species was inconsequential by comparison.

Shrubs, other than willow, were a minor floristic component of NYWR moose feeding sites compared with other moose winter range in North America (Krefting 1974, LeResche et al. 1974, Eastman and Ritcey 1987, Loranger et al. 1991, Renecker and Schwartz 1997). Differences in height and cover of these shrub species were often significant among moose feeding sites, and there were differences in shrub species composition among forested cover types and among successional stages. However, there was no clear pattern demonstrating a greater abundance of shrubs overall in a particular type or age of forest. In addition, average snow depths buried most shrubs during most of the winter. I found that of the important shrub browse species that I measured, (excluding willow, which was not measured in conifer forests, and serviceberry and shrubby cinquefoil for which sample sizes were too small) grouse whortleberry was buried, on average, all winter, and Labradour tea, honeysuckle, shunkbush sumac, gooseberry, snowberry, and huckleberry were buried during mid- and late winter. Only Rocky Mountain maple, ninebark, and buffaloberry were, on average, available above the snow all winter (see Chapters 5 and 6).

Foraging opportunities related to subalpine fir in moose wintering areas varied significantly among lodgepole forests of different ages (see Chapter 6). More moose activity, as determined by pellet groups

and browsing rates, was found in the oldest forests. For example, there were about 32 times more moose pellet groups in study plots located in the >300 year-old forests than in the 0-40 year-old forests and about 16 times more than in the 40-100 and 100-300 year-old forest. More individual trees and more and larger subalpine fir patches were also found there. For example, there were almost 50 times more subalpine fir patches in study plots in >300 year-old forests than in 0-40 or 40-100 year-old forests and about 8 times more than in 100-300 year-old forests. Similarly, subalpine fir patch size was 3 to 13 times larger in study plots in the >300 year-old forests than in younger forests. In this context, the oldest forests provided the highest quality habitat by providing the largest quantities of browse and least distance between patches. Moose had the greatest chance to balance energy requirements in the oldest forests.

Fire can enhance moose habitat, including riparian vegetation such as willow (Wolff 1978, Thompson and Stewart 1997). Government agencies consider prescribed fire a tool to promote willow production (USDA 1987). However, under some conditions, fire impacts on willow can be undesirable from the standpoint of increasing moose browse. I found that the 1988 fires accompanied by severe drought negatively affected willow (see Chapter 8). Reductions in available willow biomass meant less forage for moose and increased foraging costs. The amount of willow decreased; portions or all of some stands burned or showed drought stress, and more died than reestablished or rejuvenated post-fire. Of all species of willow on the NYWR, Wolf's willow was most heavily impacted. While not all willow species at all sites showed a decrease in height following the fires, Farr's, Geyer's, and Eastwood's willow, and the willow at Fisher Creek and Warm Creek were shorter post-fire. Height of willow at Fisher Creek, which is entirely Eastwood's willow, was reduced through mechanical damage of snowmobile traffic, not fire effects.

These conclusions and management recommendations should be applicable to moose populations in environments comparable to the NYWR; i.e. mountainous regions in the northern latitudes dominated by double canopy coniferous forests that lack tall-statured shrub taxa. This includes much of the GYA and portions of the intermountain west.

Summary

The 1988 Yellowstone fires created a disturbance at a large landscape level and caused important declines in moose numbers. Replacement of moose winter range burned in 1988 could take several hundred years. Efforts to maintain remaining moose populations should concentrate on minimizing loss of unburned mature forests and careful management of hunting. Willow stands, particularly those adjacent to

these forests, should be retained as well. Moose populations should be carefully monitored, especially because the NYWR is an environment where multiple predators pursue this species.

Peek (1997) called moose selective generalists -animals capable of using forage and other habitat components in higher proportions than they occur in the environment and adept at selecting seasonally advantageous habitats. Moose on the NYWR fit that description in a way unique to this area. In simplest terms, in early winter, moose concentrated use in willow stands, a very limited resource. In addition, they sought gooseberry, a nutrient rich plant scattered in the greatest numbers throughout the oldest spruce-fir forests. Snow accumulation limited access to these browse species before the end of winter. As a consequence, moose sought the oldest forests with the largest aggregations of subalpine fir <5 m tall and less energetically expensive travel routes under dense canopies. Other shrubs, especially buffaloberry during late winter, were important browse. However, their abundance and availability were limited in this environment.

Shrubs, including willow, did not meet pre-fire winter foraging needs of NYWR moose. In addition, post-disturbance proliferation of shrub biomass common to moose winter range in much of North America does not occur in this area. Forest edges created by logging or fire did not benefit wintering moose; an increase in shrub biomass was not found along this ecotone. Removal of forest canopy on moose winter range in this environment reduced suitable habitat.

Several theories had been proposed to explain moose habitat relationships in the GYA and on the NYWR, but, prior to my investigation, they had not been tested. Loope and Gruell (1973) hypothesized that moose numbers increased in the GYA during the 20th century (prior to the 1988 fires) as a result of fire suppression and a concomitant increase in mature lodgepole pine forests. They believed that older conifer forests which provided concentrations of subalpine fir, a shade tolerant tree and important winter moose food, supported greater moose densities. Similarly, McDowell and Moy (1942) and Peek (1974a) postulated that NYWR moose begin the winter in streamside willow stands until forced to move to adjacent forested mountainsides where double canopy forest ameliorate snow conditions and provide understory concentrations of conifer browse. My findings confirmed these hypotheses and substantiated the importance of late successional stage lodgepole pine forests as winter range for NYWR moose.

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APPENDICES

APPENDIX A

POST HOC TEST DETERMINING SIGNIFICANT DIFFERENCES IN THE AVERAGE NUMBER
OF MOOSE SEEN PER 1/2 HOUR OVER A 64 WEEK PERIOD IN A SODA BUTTE WILLOW STAND

Table 50. Results of Newman-Keuls *post hoc* test determining significant differences among the 4 highest week averages of moose seen per 1/2-hour of observation at a SB willow stand over a 64-week period from April 1996 to June 1997 (* indicates significance at $P < 0.05$). Blanks indicate insufficient data.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8
Nov 24-30	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
Dec 1-7	0.019*	0.002*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 9	Week 10	Week 11	Week 12	Week 13	Week 14	Week 15	Week 16
Nov 24-30	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
Dec 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 17	Week 18	Week 19	Week 20	Week 21	Week 22	Week 23	Week 24
Nov 24-30	0.000*	0.001*	0.000*	0.000*	0.001*	0.000*	0.000*	0.000*
Dec 1-7	0.000*	0.074	0.003*	0.011*	0.059	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 25	Week 26	Week 27	Week 28	Week 29	Week 30	Week 31	Week 32
Nov 24-30	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
Dec 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 33	Week 34	Week 35	Week 36	Week 37	Week 38	Week 39	Week 40
Nov 24-30	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
Dec 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 41	Week 42	Week 43	Week 44	Week 45	Week 46	Week 47	Week 48
Nov 24-30	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	
Dec 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.149
June 1-7	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.038*
June 8-14	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.089
	Week 49	Week 50	Week 51	Week 52	Week 53	Week 54	Week 55	Week 56
Nov 24-30	0.149	0.000*	0.001*	0.000*	0.000*	0.003*	0.000*	0.133
Dec 1-7		0.000*	0.070	0.039*	0.000*	0.099	0.000*	0.632
June 1-7	0.001*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
June 8-14	0.002*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
	Week 57	Week 58	Week 59	Week 60	Week 61	Week 62	Week 63	Week 64
Nov 24-30	0.000*	0.000*	0.000*	0.038*	0.088	0.000*	0.000*	0.000*
Dec 1-7	0.018*	0.000*	0.000*	0.001*	0.002*	0.000*	0.000*	0.000*
June 1-7	0.000*	0.000*	0.000*		0.981	0.000*	0.000*	0.000*
June 8-14	0.000*	0.000*	0.000*	0.981		0.000*	0.000*	0.000*

APPENDIX B

NUMBER OF MOOSE SEEN ON SURVEY FLIGHTS ON THE
NORTHERN YELLOWSTONE WINTER RANGE
FROM 1968 - 1992

Table 51. Number of moose observed from aircraft on the northern portion of the study area (north of the Yellowstone River). Includes high counts from elk survey flights conducted by Barmore (1980) and Houston (1982) from 1968 to 1978 and 8 moose survey flights for this project 1988-92.

	Bear Creek	Hellroaring	Buffalo Fork	Upper S.C.	Soda Butte
68/69	No survey	No survey	No survey	14	No survey
69/70	No survey	No survey	No survey	10	No survey
70/71	No survey	No survey	No survey	13	No survey
71/72	No survey	No survey	No survey	27	No survey
72/73	No survey	No survey	No survey	14	No survey
73/74	No survey	No survey	No survey	23	No survey
74/75	No survey	No survey	No survey	6	No survey
75/76	No survey	No survey	No survey	3	No survey
76/77	No survey	No survey	No survey	9	No survey
77/78	No survey	No survey	No survey	11	No survey
12/06/88	3	9	4	13	24
05/18/89	0	4	2	28	4
11/30/89	0	10	7	21	21
05/02/90	0	11	0	6	8
12/12/90	1	2	6	6	7
05/17/91	0	4	0	8	4
05/07/92	0	0	0	0	3
05/12/92	0	5	0	0	6

Table 52. Number of moose observed from aircraft on the southern portion of the study area (south of the Yellowstone River). Includes high counts from elk survey flights conducted by Barmore (1980) and Houston (1982) from 1968 to 1978 and 8 survey flights for this project 1988-92.

Flight date	Total seen	Below MHS	Gardiner River-Mt. Everts	Above MHS-Gardiner's Hole	Blacktail Plateau	Tower Area	Lower Slough Creek	Lamar Valley
68/69	23	4	3	4	1	4	1	6
69/70	31	5	2	11	2	5	3	3
70/71	39	2	1	5	7	9	10	5
71/72	73	3	1	16	8	14	25	6
72/73	38	1	3	6	0	13	14	1
73/74	52	3	3	4	3	14	14	11
74/75	27	3	3	7	1	4	7	2
75/76	47	5	4	6	2	13	15	2
76/77	29	1	1	3	3	12	6	3
77/78	27	1	3	4	2	8	2	7
12/06/88	2	0	0	2	0	0	0	0
05/18/89	9	0	0	6	3	0	0	0
11/30/89	0	0	0	No survey	No survey	0	0	0
05/02/90	0	0	0	No survey	No survey	0	0	0
12/12/90	2	0	0	2	0	0	0	0
05/17/91	3	0	0	3	0	0	0	0
05/07/92	10	0	0	10	0	0	0	0
05/12/92	1	0	0	1	0	0	0	0

APPENDIX C

POST HOC TEST DETERMINING SIGNIFICANT DIFFERENCES IN
THE AVERAGE MOOSE HOME RANGE SIZE AMONG 4 STUDY UNITS

Table 53. Results of Newman-Keuls *post hoc* test determining significant differences among the average moose home range size in 4 study units (* indicates significance at $P < 0.05$).

	SB	SC	BC	YP
SB				
SC	0.003*			
BC	0.780	0.001*		
YP	0.004*	0.627	0.001*	

APPENDIX D

PLANT SPECIES APPEARING IN THE DIET OF MOOSE

Table 54. Plant species appearing in the diet of moose over 4 winters, 1986-1991.

<i>Abies lasiocarpa</i>	Subalpine fir
<i>Pinus albicaulis</i>	Whitebark pine
<i>Pinus contorta</i>	Lodgepole pine
<i>Picea engelmannii</i>	Engelmann spruce
<i>Pinus flexilis</i>	Limber pine
<i>Pseudotsuga menziesii</i>	Douglas fir
<i>Juniperus communis/scopulorum</i>	Common/Rocky Mt. Juniper
<i>Pinus contorta</i> -burned	Burned lodgepole pine
<i>Abies lasiocarpa</i> - burned	Burned subalpine fir
<i>Picea engelmannii</i> -burned	Burned Engelmann spruce
<i>Pseudotsuga menziesii</i> -burned	Burned Douglas fir
<i>Salix</i> spp.	Willow
<i>Ribes</i> spp.	Gooseberry
<i>Acer glabrum</i>	Rocky mountain maple
<i>Alnus tenuifolia</i>	Mountain alder
<i>Artemisia tridentata</i>	Big sagebrush
<i>Berberis repens</i>	Oregon grape
<i>Lonicera</i> spp.	Honeysuckle
<i>Physocarpus malvaceous</i>	Ninebark
<i>Populus</i> spp.	Cottonwood
<i>Populus tremuloides</i>	Aspen
<i>Potentilla fruticosa</i>	Shrubby cinquefoil
<i>Rhus trilobata</i>	Skunkbush sumac
<i>Rosa</i> spp.	Rose
<i>Shepherdia canadensis</i>	Buffaloberry
<i>Symphoricarpos albus</i>	Snowberry
<i>Vaccinium globulare</i>	Huckleberry
<i>Betula glandulosa</i>	Dwarf birch
<i>Vaccinium scoparium</i>	Grouse whortleberry
<i>Ledum glandulosum</i>	Labrador tea
<i>Compositae</i>	Annual composites
<i>Heracleum lanatum</i>	Cow parsnip
<i>Lupinus</i> spp.	Lupine
<i>Sambucus</i> spp.	Elderberry
<i>Mentha</i> spp.	Mint
<i>Calamagrostis rubescens</i>	Pine grass
<i>Achillea millifolia</i>	Western yarrow
<i>Stipa</i> spp.	Needle grass
<i>Delphinium occidentale</i>	Tall larkspur
<i>Epilobium angustifolium</i>	Fireweed
<i>Carex</i> spp.	Sedge

APPENDIX E

PLANT SPECIES EATEN BY MOOSE
EXPRESSED AS A PERCENTAGE OF THE TOTAL DIET
DURING THE EARLY, MID-, AND LATE WINTER PERIODS

Table 55. Plant species eaten by moose as determined by the percentage of the total number of browsed stems observed over 4 winters and for the early (November-December), mid- (January-February), and late (March-April) winter periods over 4 years (1986-1990).

Species	Early winter n=36,383		Mid- winter n=56,208		Late winter n=51,748	
	Percent	Rank	Percent	Rank	Percent	Rank
Subalpine fir	18.4	2	44.3	1	49.4	1
Whitebark pine	0.0	18	0.1	15	0.2	14
Lodgepole pine	4.2	5	13.8	3	11.7	3
Engelmann spruce	0.0	18	0.0	16	0.0	16
Limber pine	0.0	18	0.1	15	0.0	16
Douglas fir	0.0	18	2.5	7	3.2	5
Juniper	0.0	18	0.2	14	0.0	16
Burned lodgepole pine	0.0	18	0.4	13	1.0	10
Burned subalpine fir	0.0	18	0.1	15	0.8	11
Burned spruce	0.0	18	0.0	16	0.4	13
Burned Douglas fir	0.0	18	0.6	11	0.0	16
Willow	47.7	1	22.4	2	13.2	2
Gooseberry	12.1	3	3.3	4	0.6	12
Maple	0.1	7	1.2	8	2.9	7
Alder	0.4	14	3.1	5	3.1	6
Big sagebrush	0.0	18	0.0	16	0.0	16
Oregon grape	0.0	18	0.0	16	0.0	16
Honeysuckle	1.5	8	0.5	12	2.1	8
Ninebark	0.0	18	0.8	10	0.8	11
Cottonwood	0.0	18	0.4	13	0.0	16
Aspen	1.2	10	0.1	15	0.1	15
Shrubby cinquefoil	0.9	12	0.9	9	0.0	16
Sumac	0.0	18	0.8	10	1.4	9
Rose	0.0	18	0.0	16	0.1	15
Buffaloberry	1.0	11	2.7	6	7.6	4
Snowberry	0.0	18	0.2	14	0.8	11
Huckleberry	0.7	13	0.2	14	0.0	16
Dwarf birch	0.2	16	0.0	16	0.1	15
Grouse whortleberry	0.3	15	0.0	16	0.0	16
Labrador tea	2.4	7	0.0	16	0.0	16
Annual composites	4.5	4	0.9	9	0.1	15
Cow parsnip	0.0	18	0.2	14	0.0	16
Lupine	1.4	9	0.0	16	0.0	16
Elderberry	0.2	16	0.0	16	0.2	14
Mint	2.7	6	0.0	16	0.0	16
Others	0.1	17	0.1	15	0.0	16

APPENDIX F

PLANT SPECIES EATEN BY MOOSE
EXPRESSED AS A PERCENTAGE OF THE TOTAL DIET
PRE- AND POST-FIRE
DURING THE EARLY, MID-, AND LATE WINTER PERIODS

Table 56. Plant species in the diet of moose as determined by the percentage of the total number of browsed stems recorded before and after (1988-1990) the 1988 fires and the early (November-December), mid- (January-February), and late (March-April) winter periods.

Species	Early winter		Mid winter		Late winter	
	Pre-fire	Post-fire	Pre-fire	Post-fire	Pre-fire	Post-fire
n=	2,628	34,195	18,263	34,195	23,535	28,213
Subalpine fir	11.7	19.0	30.6	50.9	44.2	53.8
Whitebark pine	0.0	0.0	0.2	0.0	0.3	0.1
Lodgepole pine	0.0	4.6	2.5	19.3	1.3	20.5
Engelmann spruce	0.0	0.0	0.0	0.1	0.0	0.0
Limber pine	0.0	0.0	0.0	0.1	0.0	0.0
Douglas fir	0.0	0.0	0.0	3.7	4.6	2.1
Juniper	0.0	0.0	0.0	0.2	0.1	0.0
Burned lodgepole pine	0.0	0.0	0.0	0.6	0.0	1.9
Burned subalpine	0.0	0.0	0.0	0.2	0.0	1.4
Burned spruce	0.0	0.0	0.0	0.0	0.0	0.7
Burned Douglas fir	0.0	0.0	0.0	1.0	0.0	0.0
Willow	19.5	49.8	45.0	11.5	18.8	8.5
Gooseberry	14.2	11.9	8.6	0.8	1.3	0.0
Maple	0.0	0.1	0.0	1.7	4.7	1.4
Alder	1.6	0.3	2.0	3.6	5.7	1.2
Big sagebrush	0.0	0.0	0.0	0.0	0.0	0.0
Oregon grape	0.0	0.0	0.0	0.0	0.0	0.0
Honeysuckle	3.0	1.4	1.4	0.1	2.2	2.0
Ninebark	0.0	0.0	0.0	1.2	1.2	0.4
Cottonwood	0.0	0.0	0.0	0.6	0.0	0.0
Aspen	0.0	1.3	0.0	0.1	0.0	0.2
Shrubby cinquefoil	0.0	0.9	0.4	1.1	0.0	0.0
Sumac	0.0	0.0	0.0	1.1	0.0	2.5
Rose	0.0	0.0	0.0	0.0	0.1	0.1
Buffaloberry	0.5	1.0	4.9	1.6	14.1	2.2
Snowberry	0.0	0.0	0.0	0.3	1.0	0.7
Huckleberry	2.4	0.6	0.8	0.0	0.1	0.0
Dwarf birch	0.0	0.2	0.0	0.0	0.0	0.0
Grouse whortleberry	0.0	0.3	0.0	0.0	0.1	0.0
Labrador tea	22.8	0.8	0.0	0.0	0.1	0.0
Annual composites	24.3	3.0	2.7	0.0	0.1	0.0
Cow parsnip	0.0	0.0	0.7	0.0	0.0	0.0
Lupine	0.0	1.5	0.0	0.0	0.0	0.0
Elderberry	0.0	0.2	0.0	0.0	0.1	0.3
Mint	0.0	2.9	0.0	0.0	0.0	0.0
Others	0.0	0.1	0.2	0.0	0.0	0.0

APPENDIX G

PLANT SPECIES EATEN BY MOOSE
EXPRESSED AS A PERCENTAGE OF THE TOTAL DIET
PRE- AND POST-FIRE IN 4 STUDY UNITS

Table 57. Plant species in the winter diet of moose as determined by the percentage of the total number of browsed stems recorded before (1986-1988) and after (1988-1990) the 1988 fires in the SB, YP, SC and BC study units.

Species	SB		YP		SC		BC		
	n=	Pre 16,311	Post 25,618	Pre 5,663	Post 23,219	Pre 5,257	Post 25,016	Pre 17,381	Post 26,294
Subalpine fir		28.4	46.8	45.5	36.1	56.6	16.8	51.5	53.6
Whitebark		0.3	0.2	0.1	0.0	0.3	0.0	0.0	0.1
Lodgepole pine		0.5	10.9	4.2	13.6	7.9	34.8	0.1	0.0
Engelmann spruce		0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Limber pine		0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Douglas fir		6.2	0.8	0.7	6.6	0.0	0.3	0.4	0.2
Juniper		0.1	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Burned lodgepole		0.0	0.0	0.0	0.3	0.0	3.0	0.0	0.0
Burned subalpine fir		0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Burned spruce		0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
Burned Douglas fir		0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0
Willow		28.6	30.6	24.7	12.3	21.5	33.9	24.2	25.0
Gooseberry		2.7	2.9	10.4	4.9	3.3	0.0	8.1	8.5
Maple		5.1	0.1	4.6	4.5	0.0	0.0	0.1	0.0
Alder		0.8	1.6	0.1	0.0	6.8	2.5	4.5	3.5
Big sagebrush		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oregon grape		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Honeysuckle		2.8	0.6	1.3	0.3	0.2	0.0	2.7	2.0
Ninebark		0.1	0.0	5.0	2.4	0.0	0.0	0.0	0.0
Cottonwood		0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Aspen		0.0	0.0	0.0	2.1	0.0	0.1	0.1	0.0
Shrubby cinquefoil		0.0	0.0	0.0	3.1	1.2	0.0	0.0	0.0
Sumac		0.0	0.0	0.0	4.9	0.0	0.0	0.0	0.0
Rose		0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0
Buffaloberry		16.3	2.9	0.4	1.4	1.9	0.0	4.4	4.6
Snowberry		0.7	0.0	1.9	1.4	0.0	0.0	0.0	0.0
Huckleberry		0.3	0.7	0.2	0.1	0.0	0.0	0.4	0.2
Dwarf birch		0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Grouse whortleberry		0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.3
Labrador tea		0.4	0.7	0.0	0.4	0.0	0.0	1.2	1.0
Annual composites		5.7	0.9	0.1	1.0	0.1	0.0	1.8	0.6
Cow parsnip		0.6	0.0	0.4	0.0	0.1	0.0	0.1	0.1
Lupine		0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0
Elderberry		0.2	0.1	0.0	0.4	0.0	0.0	0.1	0.1
Mint		0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0
Other		0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.1

APPENDIX H

CHI-SQUARE ANALYSIS DETERMINING IF 5 TREE SPECIES ARE BROWSED BY MOOSE
IN PROPORTION TO AVAILABILITY IN SUCCESSIONAL STAGES
OF 3 FORESTS TYPES

Table 58. Percent of 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in the early, mid-, and late successional stages of lodgepole pine forests. Symbols indicate use proportionally greater than availability (+), use proportionally less than availability (-), or use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$).

	Young lodgepole % used n=194	Young lodgepole %available n=194	Mid- lodgepole % used n=1,357	Mid- lodgepole %available n=1,537	Oldest lodgepole % used n=2,438	Oldest lodgepole %available n=1,928
Subalpine fir	36.0 (+)	18.1	78.4 (+)	40.9	88.7 (+)	53.6
Lodgepole	63.4 (-)	69.5	18.4 (-)	35.4	9.8 (-)	24.3
Spruce	0.0 (-)	7.8	0.0 (-)	14.8	0.1 (-)	18.5
Douglas fir	0.6 (-)	3.0	2.3 (-)	6.4	0.8 (-)	2.1
Whitebark	0.0 (-)	1.6	0.9 (-)	2.5	0.6 (-)	1.5

Table 59. Chi-square values from 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in early, mid-, and late successional stages of lodgepole pine forests.

	Young lodgepole	Mid-age lodgepole	Oldest lodgepole
Subalpine fir	34.398	627.066	34.398
Lodgepole	133.565	543.730	133.565
Spruce	15.132	227.476	15.132
Douglas fir	5.808	98.322	5.808
Whitebark	3.104	38.407	3.104

Table 60. Bonferroni Z-statistic intervals for 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in early, mid-, and late successional stages of lodgepole pine forests.

	Young lodgepole		Mid-age lodgepole		Older lodgepole	
	Lower	Upper	Lower	Upper	Lower	Upper
Subalpine fir	0.274	0.446	0.758	0.810	0.869	0.905
Lodgepole	0.548	0.720	0.159	0.209	0.081	0.115
Spruce	0.000	0.000	0.000	0.000	-0.001	0.003
Douglas fir	-0.008	0.020	0.013	0.033	0.003	0.013
Whitebark	0.000	0.000	0.003	0.015	0.002	0.010

Table 61. Percent of 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in early, mid-, and late successional stages of Douglas fir forests. Symbols indicate use proportionally greater than availability (+), use proportionally less than availability (-), or use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$).

	Young Douglas fir % used n=243		Young Douglas fir %available n=220		Mid-age Douglas fir % used n=330		Mid-age Douglas fir %available n=403		Oldest Douglas fir % used n=575		Oldest Douglas fir %available n=504	
Subalpine fir	12.2	(+)	5.0		3.6	(+)	1.9		90.9	(+)	59.3	
Lodgepole	6.7	(-)	15.1		0.0	(-)	2.8		0.4	(-)	7.5	
Spruce	0.0	(-)	10.0		0.0	(-)	6.9		0.0	(-)	5.7	
Douglas fir	79.0	(-)	70.0		96.4	(+)	88.4		7.8	(-)	22.2	
Whitebark	0.0		0.0		0.0		0.0		0.8	(-)	5.2	

Table 62. Chi-square values from 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in early, mid-, and late successional stages of Douglas fir forests.

	Young Douglas fir		Mid-age Douglas fir		Oldest Douglas fir	
Subalpine fir	0.870		7.585		297.057	
Lodgepole	33.086		11.284		37.792	
Spruce	22.000		27.807		28.728	
Douglas fir	152.424		356.252		111.732	
Whitebark	0.000		0.000		26.192	

Table 63. Bonferroni Z-statistic intervals for 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in early, mid-, and late successional stages of Douglas fir forests.

	Young Douglas fir		Mid-age Douglas fir		Oldest Douglas fir	
	Lower	Upper	Lower	Upper	Lower	Upper
Subalpine fir	0.067	0.177	0.009	0.009	0.876972	0.941028
Lodgepole	0.025	0.109	0.013	0.013	-0.00303	0.011029
Spruce	0.000	0.000	0.003	0.003	0.0	0.0
Douglas fir	0.721	0.859	0.000	0.000	0.048137	0.107863
Whitebark	0.000	0.000	0.012	0.012	-0.00192	0.01792

Table 64. Percent of 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in the late successional stage of spruce-fir forests. Symbols indicate use proportionally greater than availability (+), use proportionally less than availability (-), or use in proportion to availability (0) based on Bonferroni confidence intervals ($P < 0.05$).

	Oldest spruce-fir % used n=1,154		Oldest spruce fir %available n=1,132	
Subalpine fir	98.0	(+)	65.6	
Lodgepole pine	1.0	(-)	3.1	
Spruce	0.0	(-)	30.7	
Douglas fir	0.7	(0)	0.4	
Whitebark	0.3	(0)	0.2	

Table 65. Chi-square values and Bonferroni Z intervals from 5 tree species browsed and available as determined in 3-m radius plots at moose feeding sites in the late successional stage of spruce-fir forests.

	Chi-square statistic	Bonferroni Z interval	
		Lower	Upper
Subalpine fir	740.633	0.970	0.990
Lodgepole	35.090	-0.001	0.003
Spruce	347.524	0.000	0.000
Douglas fir	4.514	0.001	0.013
Whitebark	0.000	-0.001	0.007

APPENDIX I

DISTRIBUTION OF MOOSE BROWSING AMONG COVER CATEGORIES
DURING THE EARY, MID-, AND LATE WINTER PERIODS

Table 66. Percent of browsed stems found in 20 cover categories over four winters (1986-1990) and the early (November-December), mid- (January-February), and late (March-April) winter periods ranked in descending order. Young = 0-100, mid=100-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

Cover category	Early winter n=36,823		Mid-winter n=56,246		Late winter n=51,782	
	Percent	Rank	Percent	Rank	Percent	Rank
Willow	30.8	1	12.4	4	2.9	7
Young conifer/willow	3.9	7	4.5	7	6.4	5
Mid-age conifer/willow	2.0	9	1.5	10	1.0	12
Oldest conifer/willow	7.9	4	6.6	5	3.7	6
Young Douglas fir	0.0	12	1.7	9	1.5	10
Mid-age Douglas fir	1.4	10	1.0	11	0.9	13
Oldest Douglas fir	0.0	12	4.7	6	18.2	3
Young lodgepole pine	4.3	6	4.3	8	2.5	9
Mid-age lodgepole pine	3.3	7	16.2	2	24.6	2
Oldest lodgepole pine	9.7	3	31.4	1	25.0	1
Young spruce-fir	0.0	12	0.0	14	0.0	16
Mid-age spruce-fir	2.4	8	0.0	14	0.8	14
Oldest spruce-fir	28.4	2	13.4	3	7.7	4
Young whitebark pine	0.0	12	0.0	14	0.0	16
Mid-age whitebark pine	0.0	12	0.0	14	0.6	15
Oldest whitebark pine	0.0	12	0.0	14	2.7	8
Aspen/conifer	1.2	11	0.8	12	0.0	16
Sagebrush	4.7	5	0.7	13	0.0	16
Meadow	0.0	12	0.0	14	0.0	16
Other	0.0	12	0.7	13	1.3	11

APPENDIX J

DISTRIBUTION OF MOOSE BROWSING AMONG COVER CATEGORIES
PRE- AND POST-FIRE
DURING THE EARLY, MID-, AND LATE WINTER PERIODS

Table 67. Cover categories where stems browsed by moose were found expressed as a percentage of the total for the early (November-December), mid- (January-February), and late (March-April) winter periods before (1986-1988) and after (1988 -1990) the 1988 fires. Young = 0-100, mid-=101-300, and oldest=301+ years post-disturbance (Mattson and Despain 1985).

n=	Early Winter		Mid winter		Late winter	
	Pre-fire 2,628	Post-fire 34,195	Pre-fire 18,263	Post-fire 37,983	Pre-fire 23,569	Post-fire 28,213
Willow	7.5	32.6	21.0	8.3	4.8	1.2
Young conifer/willow	8.6	3.5	4.1	4.7	10.3	3.2
Mid-age conifer/willow	3.5	1.9	4.6	0.0	0.0	1.9
Oldest conifer/willow	0.0	8.5	18.8	0.7	3.4	3.9
Young Douglas fir	0.0	0.0	0.0	2.5	2.1	1.1
Mid-age Douglas fir	0.0	1.5	0.1	1.5	0.0	1.7
Oldest Douglas fir	0.0	0.0	0.0	6.9	21.0	16.0
Young lodgepole	0.0	4.7	0.3	6.2	0.0	4.6
Mid-age lodgepole	20.6	1.9	4.3	21.9	21.7	27.0
Oldest lodgepole	9.4	9.7	30.7	31.9	18.2	30.8
Young spruce-fir	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age spruce-fir	0.0	2.6	0.0	0.0	1.8	0.0
Oldest spruce-fir	50.4	26.7	16.1	12.2	12.6	3.7
Young whitebark	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age whitebark	0.0	0.0	0.0	0.0	1.4	0.0
Oldest whitebark	0.0	0.0	0.0	0.0	2.6	2.7
Aspen/conifer	0.0	1.2	0.0	1.2	0.0	0.0
Sagebrush	0.0	5.1	0.0	1.0	0.0	0.0
Meadow	0.0	0.0	0.0	0.1	0.0	0.0
Other	0.0	0.0	0.0	1.0	0.0	2.3

APPENDIX K

DISTRIBUTION OF MOOSE BROWSING AMONG COVER CATEGORIES
PRE- AND POST-FIRE IN 4 STUDY UNITS

Table 68. Cover categories where stems browsed by moose were found during winter expressed as a percentage of the total for the SB, YP, SC, and BC study units before (1986-1988) and after (1988-1990) the 1988 fires. Young = 0-100, mid-=101-300, and oldest=300+ years post-disturbance (Mattson and Despain 1985).

Cover Category	SB		YP		SC		BC	
n=	Pre-fire 16,365	Post-fire 25,646	Pre-fire 5,663	Post-fire 23,219	Pre-fire 5,257	Post-fire 25,016	Pre-fire 17,381	Post-fire 26,294
Willow	17.3	16.7	25.9	11.7	8.1	21.4	5.3	6.2
Young conifer/willow	0.0	1.3	0.0	0.0	4.3	10.6	8.9	9.4
Mid-age conifer/willow	1.8	2.5	0.0	0.0	5.4	2.2	0.4	0.8
Oldest conifer/willow	9.0	9.5	0.0	0.0	3.1	0.6	13.2	9.7
Young Douglas fir	0.5	0.0	7.1	5.5	0.0	0.0	0.0	0.0
Mid-age Douglas fir	0.0	0.0	0.0	6.6	0.0	0.0	0.5	0.1
Oldest Douglas fir	24.8	9.9	9.9	8.5	0.0	2.1	4.4	5.5
Young lodgepole	0.0	2.0	0.0	2.5	1.1	10.6	1.1	3.5
Mid-age lodgepole	5.8	6.6	0.0	18.7	9.5	20.6	20.5	23.8
Oldest lodgepole	19.2	30.2	30.4	18.2	49.9	20.9	28.0	21.9
Young spruce-fir	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age spruce-fir	2.6	0.7	0.0	3.0	0.0	0.0	0.0	0.0
Oldest spruce-fir	13.2	17.9	26.8	13.6	18.7	6.1	17.0	18.5
Young whitebark	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mid-age whitebark	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oldest whitebark	3.8	2.0	0.0	0.0	0.0	0.0	0.7	0.6
Aspen/conifer	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0
Sagebrush	0.0	0.0	0.0	3.9	0.0	4.9	0.0	0.0
Meadow	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Other	0.0	0.5	0.0	3.9	0.0	0.0	0.0	0.0

APPENDIX L

POST HOC TEST DETERMINING SIGNIFICANT DIFFERENCES IN
THE AVERAGE NUMBER OF TWIGS BROWSED PER SUBALPINE FIR AMONG WINTER
PERIODS AND STUDY UNITS AND PRE- AND POST-FIRE

Table 69. Results of Newman-Keuls *post hoc* test to determine significant differences in the average number of twigs browsed per subalpine fir in the early, mid-, and late winter periods (* indicates significance at $P < 0.05$).

	Early winter	Mid-winter
Early winter		
Mid-winter	0.001*	
Late winter	0.001*	0.0

Table 70. Results of Newman-Keuls *post hoc* test to determine significant differences in the average number of twigs browsed per subalpine fir pre-fire among study units (* indicates significance at $P < 0.05$).

	BC	YP	SB
BC			
YP	0.0001*		
SB	0.136	0.001*	
SC	0.223	0.001*	0.019*

Table 71. Results of Newman-Keuls *post hoc* test to determine significant differences in the average number of twigs browsed per subalpine fir post-fire among study units (* indicates significance at $P < 0.05$).

	BC	YP	SB
BC			
YP	0.550		
SB	0.459	0.553	
SC	0.001*	0.001*	0.001*

APPENDIX M

PROXIMATE AND ELEMENTAL NUTRITIONAL ANALYSIS OF 5 MOOSE BROWSE SPECIES

Table 72. Nutrient (proximate and elemental) analysis of subalpine fir summarized for 4 winter periods, 1998-99, BC study unit.

	Nov-Dec	Jan-Feb	March	April
Calcium	2,600 ppm	4,090 ppm	5,000 ppm	4,900 ppm
Potassium	9,600 ppm	8,600ppm	8,700 ppm	10,000 ppm
Magnesium	1,100 ppm	990 ppm	980 ppm	910 ppm
Sodium	14 ppm	16 ppm	19 ppm	8.7 ppm
Phosphorus	1,900 ppm	1,900 ppm	1,700 ppm	2,000 ppm
Ash	3.4 %	3.6 %	3.5%	3.6%
Crude fiber	21.8 %	27.5 %	22.8%	22.2%
Crude protein	6.9 %	6.9 %	7.2%	7.8%
Ether extract	11.7 %	11.9 %	12.4%	2.4%
Total moisture	55.8%	55.9%	54.1%	55.2%

Table 73. Nutrient (proximate and elemental) analysis of willow summarized for 4 winter periods, 1998-99, BC study unit.

	Nov-Dec	Jan-Feb	March	April
Calcium	4,600 ppm	6,000 ppm	4,500 ppm	2,900 ppm
Potassium	4,100 ppm	4,000 ppm	4,200 ppm	4,700 ppm
Magnesium	1,000 ppm	1,000 ppm	1,100 ppm	1,200 ppm
Sodium	14 ppm	15 ppm	16 ppm	19 ppm
Phosphorus	1,300 ppm	1,300 ppm	1,300 ppm	1,600 ppm
Ash	2.4 %	2.7 %	2.2 ppm	2.8 ppm
Crude fiber	35%	20 %	33.8%	32.5 ppm
Crude protein	6.9 %	6.9 %	7.3%	7.8%
Ether extract	7.6 %	6.9 %	3.3%	4.1%
Total moisture	52.5%	48.1%	45.4%	49.1%

Table 74. Nutrient (proximate and elemental) analysis of lodgepole pine summarized for 4 winter periods, 1998-99, BC study unit.

	Nov-Dec	Jan-Feb	March	April
Calcium	420 ppm	20 ppm	2,200 ppm	1,800 ppm
Potassium	4,400 ppm	4,900 ppm	4,700 ppm	5,300 ppm
Magnesium	720 ppm	1,060 ppm	1,200 ppm	1,000 ppm
Sodium	32 ppm	41 ppm	24 ppm	19.3 ppm
Phosphorus	1,400 ppm	1,200 ppm	1,200 ppm	1,300 ppm
Ash	1.8 %	1.9 %	2.0%	1.9%
Crude fiber	24.7 %	26.8 %	27.4%	28.4%
Crude protein	16.8 %	6.9 %	6.7%	8.7%
Ether extract	1.6 %	11.5 %	6.7%	10.4%
Total moisture	55.9%	55.8%	50.8%	54.8%

Table 75. Nutrient (proximate and elemental) analysis of gooseberry summarized for 4 winter periods, 1998-99, BC study unit.

	Nov-Dec	Jan-Feb	March	April
Calcium	4,020 ppm	4,300 ppm	7,200 ppm	6,900 ppm
Potassium	9,500 ppm	9,900 ppm	1,200 ppm	1,200 ppm
Magnesium	1,200 ppm	1,130 ppm	1,600 ppm	1,500 ppm
Sodium	34 ppm	80 ppm	47 ppm	46 ppm
Phosphorus	2,400 ppm	2,300 ppm	2,300 ppm	2,500 ppm
Ash	3.9%	3.6%	4.3%	4.2%
Crude fiber	19.8%	46.8%	47.4%	46.9%
Crude protein	7.2%	6.4%	7.7%	7.7%
Ether extract	0.82%	0.77%	1.1%	0.77%
Total moisture	56.3%	53.5%	52.5%	48.3%

Table 76. Nutrient (proximate and elemental) analysis of buffaloberry summarized for 4 winter periods, 1998-99, BC study unit.

	Nov-Dec	Jan-Feb	March	April
Calcium	600 ppm	460 ppm	2,100 ppm	2,000 ppm
Potassium	3,100 ppm	4,500 ppm	5,300 ppm	5,400 ppm
Magnesium	1,050 ppm	740 ppm	810 ppm	720 ppm
Sodium	15 ppm	49 ppm	19 ppm	22 ppm
Phosphorus	1,200 ppm	1,600 ppm	1,600 ppm	1,700 ppm
Ash	2.0 %	3.1 %	1.9%	1.8%
Crude fiber	21.8 %	22.6 %	26.1%	25.6%
Crude protein	6.4 %	17.4 %	18.1%	18.5%
Ether extract	9.9 %	2.5 %	1.6%	0.93%
Total moisture	48.6%	49.2%	43.2%	16.0%

APPENDIX N

CHI-SQUARE ANALYSIS DETERMINING IF RADIOCOLLARED MOOSE IN THE STUDY AREA
WERE FOUND DURING THE WINTER IN COVER CATEGORIES PRE- AND POST-FIRE
IN PROPORTION TO THEIR AVAILABILITY

Table 77. Chi-square values from pre- and post-fire moose winter radiolocations in the study area and 20 cover categories. Blanks indicate insufficient data.

	Pre-fire	Post-fire
Willow	2415.641	3314.163
Willow/conifer (3 cover categories combined)	1142.457	576.179
Young Douglas fir		
Mid-age Douglas fir	21.128	26.923
Oldest Douglas fir	7.421	52.529
Young lodgepole pine		55.296
Mid-age lodgepole pine	19.595	15.114
Oldest lodgepole pine	312.682	2473.84
Young spruce-fir		
Mid-age spruce-fir		
Oldest spruce-fir	33.238	129.547
Young whitebark pine		
Mid-age whitebark pine		
Oldest whitebark pine	13.801	6.387
Aspen/conifer	15.109	29.316
Sagebrush	40.15	72.996
Grass/forb meadow	21.175	38.394
Other	27.5	50.244

Table 78. Bonferonni Z-statistic intervals for pre- and post-fire chi-square values from moose winter radiolocations in the study area and 20 cover categories. Blanks indicate insufficient data.

	Pre-fire		Post-fire	
	Lower	Upper	Lower	Upper
Willow	0.076	0.194	0.077	0.163
Willow/conifer (3 combined)	0.023	0.108	0.011	0.061
Young Douglas fir				
Mid-age Douglas fir	0.0	0.041	0.0	0.028
Oldest Douglas fir	0.058	0.167	0.006	0.049
Young lodgepole pine			0.0	0.021
Mid-age lodgepole pine	0.011	0.084	0.018	0.074
Oldest lodgepole pine	0.333	0.503	0.457	0.59
Young spruce-fir				
Mid-age spruce-fir				
Oldest spruce-fir	0.1	0.228	0.112	0.209
Young whitebark pine				
Mid-age whitebark pine				
Oldest whitebark pine	0.004	0.069	0.031	0.096
Aspen/conifer	0.0	0.014	0.0	0.008
Sagebrush	0.0	0.002	0.0	0.001
Grass/forb meadow	0.0	0.002	0.0	0.001
Other	0.0	0.002	0.0	0.001

APPENDIX O

CHI-SQUARE ANALYSIS DETERMINING IF RADIOCOLLARED MOOSE WERE FOUND DURING
THE WINTER IN COVER CATEGORIES PRE- AND POST-FIRE AMONG 4 STUDY UNITS IN
PROPORTION TO THEIR AVAILABILITY

Table 79. Chi-square values from pre-fire moose winter radiolocations in 4 study units and 20 cover categories. Blanks indicate insufficient data.

	YP	SB	BC	SC
Willow (4 categories combined)	3821.23	2744.06	2694.29	
Young Douglas fir				
Mid-age Douglas fir	287.7			
Oldest Douglas fir	16.12	1.46	5.76	
Young lodgepole pine			3.88	
Mid-age lodgepole pine	14.28	5.7	2.31	
Oldest lodgepole pine	146.83	32.11	95.68	
Young spruce-fir				
Mid-age spruce-fir				
Oldest spruce-fir	37.3	0.33	4.19	
Young whitebark pine				
Mid-age whitebark pine				
Oldest whitebark pine		22.78	1.47	
Aspen/conifer	5.12			
Sagebrush	20.24		14.76	
Grass/forb meadow	2.05	14.34		
Other			8.64	

Table 80. Bonferonni Z-statistic intervals for pre-fire chi-square values from moose winter radiolocations in 4 study units and 20 cover categories. Blanks indicate insufficient data.

	YP		SB		BC		SC	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Willow (4 categories)	0.09	0.338	0.164	0.397	0.065	0.324		
Young Douglas fir								
Mid-age Douglas fir	0.0	0.131						
Oldest Douglas fir	0.0	0.112	0.057	0.242	0.052	0.106		
Young lodgepole pine					0.003	0.054		
Mid-age lodgepole pine	0.0	0.07	0.0	0.087	0.008	0.214		
Oldest lodgepole pine	0.29	0.591	0.266	0.52	0.217	0.533		
Young spruce-fir								
Mid-age spruce-fir								
Oldest spruce-fir	0.63	0.294	0.018	0.169	0.108	0.392		
Young whitebark pine								
Mid-age whitebark pine								
Oldest whitebark pine			0.0	0.102	0.0	0.130		
Aspen/conifer	0.0	0.083			0.0	0.3		
Sagebrush	0.0	0.003			0.0	0.003		
Grass/forb meadow	0.07	0.063	0.0	0.003				
Other					0.0	0.003		

Table 81. Chi-square values from post-fire moose winter radiolocations in 4 study units and 20 cover categories. Blanks indicate insufficient data.

	YP	SB	BC	SC
Willow (4 categories combined)	200.203	2737.469	635.350	528.886
Young Douglas fir				
Mid-age Douglas fir	290.64			
Oldest Douglas fir	18.791	22.179	7.946	
Young lodgepole pine	15.015		4.845	13.465
Mid-age lodgepole pine	8.172	16.046	12.972	22.406
Oldest lodgepole pine	1183.727	113.956	391.846	292.145
Young spruce-fir				10.296
Mid-age spruce-fir				
Oldest spruce-fir	217.271	2.576	0.165	0.909
Young whitebark pine				
Mid-age whitebark pine				
Oldest whitebark pine	2.069	24.742	1.6	13.552
Aspen/conifer	7.507			
Sagebrush	27.489		25.420	
Grass/forb meadow	7.140	20.874		14.080
Other			14.880	19.008

Table 82. Bonferonni Z-statistic intervals for post-fire chi-square values from moose winter radiolocations in 4 study units and 20 cover categories. Blanks indicate insufficient data

	YP		SB		BC		SC	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Willow (4 categories)	0.0	0.094	0.18	0.383	0.008	0.137	0.103	0.351
Young Douglas fir								
Mid-age Douglas fir	0.0	0.107						
Oldest Douglas fir	0.0	0.08	0.0	0.077	0.0	0.062		
Young lodgepole pine	0.0	0.05			0.0	0.03	0.0	0.043
Mid-age lodgepole pine	0.0	0.08	0.0	0.002	0.0	0.102	0.035	0.238
Oldest lodgepole pine	0.383	0.643	0.401	0.627	0.416	0.664	0.387	0.682
Young spruce-fir							0.0	0.003
Mid-age spruce-fir								
Oldest spruce-fir	0.154	0.384	0.036	0.175	0.076	0.263	0.006	0.176
Young whitebark pine								
Mid-age whitebark pine								
Oldest whitebark pine	0.0	0.08	0.008	0.118	0.051	0.223	0.0	0.003
Aspen/conifer	0.0	0.032						
Sagebrush	0.0	0.003			0.0	0.003		
Grass/forb meadow	0.0	0.003	0.0	0.002			0.0	0.003
Other					0.0	0.003	0.0	0.003

APPENDIX P

CHI-SQUARE ANALYSIS DETERMINING IF RADIOCOLLARED MOOSE IN 4 STUDY UNITS
WERE FOUND DURING THE WINTER IN AREAS WITH DISPARATE FIRE EFFECTS
IN PROPORTION TO THEIR AVAILABILITY

Table 83. Chi-square values from pre- and post-fire moose winter radiolocations in 3 study units and areas with disparate fire effects.

	YP	SB	SC
Unburned	8.438	0.464	0.001
Burned 1-49%	6.468	2.665	0.024
Burned 50-100%	13.7	2.665	0.011

Table 84. Bonferonni Z-statistic intervals for post-fire chi-square values from moose winter radiolocations in 3 study units and areas with disparate fire effects.

	YP		SB		SC	
	Lower	Upper	Lower	Upper	Lower	Upper
Unburned	0.865	0.982	0.952	1.012	0.459	0.736
Burned 1-49%	0.007	0.111	0.0	0.03	0.0	0.12
Burned 50-100%	0.0	0.045	0.0	0.03	0.213	0.482

APPENDIX Q

CHI-SQUARE ANALYSIS DETERMINING IF MOOSE, ELK, AND MULE DEER TRACKS APPEAR
DURING THE WINTER IN COVER CATEGORIES ALONG FIXED TRANSECTS
IN PROPORTION TO THEIR AVAILABILITY

Table 85. Chi-square values from pre-fire winter encounters with moose tracks along fixed transects in 10 cover categories.

	Early winter	Mid-winter	Late winter
Willow	7.42	8.15	3.06
Young lodgepole pine	34.18	37.55	15.93
Oldest lodgepole/sage	13.87	15.26	6.50
Oldest lodgepole pine	28.20	30.81	12.44
Oldest lodgepole/meadow	11.78	13.11	5.59
Conifer/willow	32.02	35.27	15.00
Oldest lodgepole/young conifer	25.04	27.31	11.66
Oldest spruce-fir/young conifer	4.07	4.53	1.96
Douglas fir/sage	18.62	20.48	8.72
Oldest spruce-fir	11.86	13.50	5.78

Table 86. Bonferroni Z-statistic intervals for pre-fire chi-square values from winter encounters with moose tracks along fixed transects in 10 cover categories.

	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
Willow	0.031	0.147	0.045	0.165	0.128	0.388
Young lodgepole pine	-0.010	0.032	-0.002	0.068	-0.017	0.107
Oldest lodgepole/sage	0.000	0.000	0.000	0.000	0.000	0.000
Oldest lodgepole pine	0.007	0.099	0.095	0.239	0.269	0.563
Oldest lodgepole/meadow	0.035	0.155	-0.004	0.062	-0.020	0.042
Conifer/willow	0.235	0.427	0.247	0.431	0.049	0.265
Oldest lodgepole/young conifer	-0.008	0.052	0.072	0.206	-0.017	0.107
Oldest spruce-fir/young conifer	0.007	0.099	-0.002	0.068	0.000	0.000
Douglas fir/sagebrush	0.000	0.000	0.000	0.000	0.000	0.000
Older spruce-fir	0.250	0.444	0.079	0.217	-0.017	0.107

Table 87. Chi-square values from post-fire winter encounters with moose tracks along fixed transects in 10 cover categories.

	Early winter	Mid-winter	Late winter
Willow	29.11	17.15	6.35
Young lodgepole pine	133.54	78.21	29.83
Oldest lodgepole/sage	54.16	31.75	12.19
Older lodgepole pine	110.37	64.60	24.17
Oldest lodgepole/meadow	22.22	13.04	4.97
Conifer/willow	127.14	74.15	28.40
Oldest lodgepole/young conifer	97.72	56.91	21.94
Oldest spruce-fir/young conifer	16.31	9.55	3.65
Douglas fir/sage	72.72	42.62	16.35
Oldest spruce-fir	48.55	28.60	10.81

Table 88. Bonferonni Z-statistic intervals for post-fire chi-square values from winter encounters with moose tracks along fixed transects in 10 cover categories.

	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
Willow	0.240	0.334	0.081	0.171	0.087	0.249
Young lodgepole pine	-0.001	0.017	0.016	0.072	0.045	0.183
Oldest lodgepole/sage	-0.002	0.004	-0.004	0.008	0.000	0.000
Oldest lodgepole pine	0.062	0.122	0.066	0.150	0.255	0.463
Oldest lodgepole/meadow	0.005	0.033	-0.005	0.015	-0.011	0.047
Conifer/willow	0.200	0.288	0.274	0.402	0.082	0.242
Oldest lodgepole/young conifer	0.081	0.147	0.199	0.317	0.005	0.103
Oldest spruce-fir/young conifer	-0.001	0.019	-0.003	0.025	-0.012	0.036
Douglas fir/sage	0.000	0.000	-0.005	0.013	-0.011	0.023
Oldest spruce-fir	0.170	0.254	0.024	0.086	0.041	0.175

Table 89. Chi-square values from pre-fire winter encounters with elk tracks along fixed transects in 10 cover categories.

	Early winter	Mid-winter	Late winter
Willow	0.32	64.63	6.39
Young lodgepole pine	1.20	290.87	28.93
Oldest lodgepole/sage	0.58	116.26	11.75
Oldest lodgepole pine	1.19	240.73	23.87
Oldest lodgepole/meadow	0.27	101.76	10.04
Conifer/willow	1.38	277.92	27.58
Oldest lodgepole/young conifer	1.06	213.29	20.95
Oldest spruce-fir/young conifer	0.18	35.55	3.48
Douglas fir/sage	0.78	158.29	14.60
Oldest spruce-fir	0.53	106.64	10.63

Table 90. Bonferonni Z-statistic intervals for pre-fire chi-square values from winter encounters with elk tracks along fixed transects in 10 cover categories.

	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
Willow	0.000	0.000	0.000	0.008	-0.010	0.060
Young lodgepole pine	-0.204	0.454	0.000	0.008	-0.010	0.060
Oldest lodgepole/sage	0.000	0.000	0.835	0.883	0.000	0.000
Oldest lodgepole pine	0.000	0.000	0.016	0.038	0.009	0.115
Oldest lodgepole/meadow	0.546	1.204	0.015	0.037	0.002	0.098
Conifer/willow	0.000	0.000	0.007	0.023	0.005	0.107
Oldest lodgepole/young conifer	0.000	0.000	0.005	0.021	0.071	0.229
Oldest spruce-fir/young conifer	0.000	0.000	-0.001	0.005	-0.007	0.069
Douglas fir/sage	0.000	0.000	0.027	0.055	0.494	0.710
Oldest spruce-fir	0.000	0.000	0.002	0.016	0.000	0.000

Table 91. Chi-square values from post-fire winter encounters with elk tracks along fixed transects in 10 cover categories.

	Early winter	Mid-winter	Late winter
Willow	86.84	51.42	4.91
Young lodgepole pine	391.08	231.46	22.31
Oldest lodgepole/sage	158.12	93.41	9.05
Oldest lodgepole pine	323.55	191.35	18.35
Oldest lodgepole/meadow	136.84	80.87	7.70
Conifer/willow	373.57	220.95	21.13
Oldest lodgepole/young conifer	286.77	169.62	15.95
Oldest spruce-fir/young conifer	47.74	28.27	2.71
Douglas fir/sage	212.26	125.47	11.63
Oldest spruce-fir	143.36	84.75	7.72

Table 92. Bonferonni Z-statistic intervals for post-fire chi-square values from winter encounters with elk tracks along fixed transects in 10 cover categories.

	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
Willow	0.027	0.051	0.001	0.015	-0.015	0.063
Young lodgepole pine	0.020	0.040	0.002	0.018	-0.012	0.020
Oldest lodgepole/sage	0.227	0.279	0.203	0.269	0.000	0.000
Oldest lodgepole pine	0.096	0.134	0.104	0.156	0.003	0.127
Oldest lodgepole/meadow	0.019	0.039	0.055	0.097	-0.002	0.114
Conifer/willow	0.076	0.112	0.096	0.148	0.022	0.1717
Oldest lodgepole/young conifer	0.021	0.041	0.048	0.088	0.107	0.313
Oldest spruce-fir/young conifer	0.024	0.046	0.003	0.019	-0.014	0.030
Douglas fir/sage	0.316	0.374	0.242	0.312	0.154	0.378
Oldest spruce-fir	0.019	0.039	0.044	0.082	0.127	0.341

Table 93. Chi-square values and Bonferroni Z-statistic intervals from winter encounters with mule deer tracks along fixed transects in 8 cover categories in the BS study unit.

	% Area	Chi-Square Value	All Winter	
			Lower	Upper
Willow/conifer	7.0	25.8	0.058	0.146
Young lodgepole	34.8	129.2	0.063	0.153
Oldest lodgepole/meadow	18.7	69.6	-0.005	0.013
Oldest conifer/young conifer	22.5	83.7	-0.004	0.026
Douglas fir/sage	3.8	13.6	0.219	0.351
Oldest spruce-fir/meadow	3.9	14.4	0.011	0.067
Douglas fir/meadow	9.4	34.3	0.258	0.394

APPENDIX R

CHI-SQUARE ANALYSIS DETERMINING IF MOOSE, ELK, AND MULE DEER TRACKS APPEAR
IN SNOW DEPTH CATEGORIES ALONG FIXED TRANSECT
IN PROPORTION TO THEIR AVAILABILITY

Table 94. Chi-square values for percentages of moose tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available.

Snow Depth (cm)	Early winter	Mid-winter	Late winter
0-20	93.09	0.65	6.08
20-40	297.31	17.96	6.05
40-60	356.22	65.55	22.24
60-80	131.20	199.94	46.60
80-100	34.48	179.62	58.96
100-120	5.59	107.04	51.96
120-140	5.59	39.34	34.47
140-160	0.00	20.00	11.26
160-180	0.00	8.39	10.50
180-200	0.00	2.58	0.51

Table 95. Bonferroni Z-statistics intervals for moose tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available.

Snow Depth (cm)	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
0-20	0.033	0.075	0.000	0.000	0.001	0.063
20-40	0.419	0.511	0.025	0.073	0.009	0.083
40-60	0.326	0.414	0.085	0.157	0.195	0.351
60-80	0.079	0.135	0.596	0.702	0.178	0.330
80-100	-0.002	0.008	0.125	0.207	0.143	0.287
100-120	0.000	0.000	0.002	0.030	0.073	0.193
120-140	0.000	0.000	-0.003	0.007	0.010	0.084
140-160	0.000	0.000	0.000	0.000	0.000	0.000
160-180	0.000	0.000	0.000	0.000	0.000	0.000
180-200	0.000	0.000	0.000	0.000	0.000	0.000

Table 96. Chi-square values for percentages of elk tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available.

Snow Depth (cm)	Early winter	Mid-winter	Late winter
0-20	218.09	2.90	6.91
20-40	697.22	81.20	6.91
40-60	834.05	295.80	25.63
60-80	307.52	904.80	52.99
80-100	80.70	809.10	66.82
100-120	13.09	481.40	58.75
120-140	13.09	176.90	38.88
140-160	0.00	89.90	12.67
160-180	0.00	37.70	11.81
180-200	0.00	11.60	0.54

Table 97. Bonferroni Z-statistics intervals for elk tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available.

Snow Depth (cm)	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
0-20	0.002	0.012	-0.001	0.003	-0.001	0.049
20-40	0.323	0.381	0.019	0.037	-0.001	0.049
40-60	0.610	0.668	0.086	0.118	0.042	0.136
60-80	-0.001	0.003	0.288	0.336	0.120	0.248
80-100	0.000	0.000	0.256	0.302	0.162	0.302
100-120	0.000	0.000	0.147	0.185	0.138	0.270
120-140	0.000	0.000	0.049	0.073	0.079	0.191
140-160	0.000	0.000	0.022	0.040	0.010	0.078
160-180	0.000	0.000	0.007	0.019	0.008	0.074
180-200	0.000	0.000	0.001	0.007	-0.003	0.043

Table 98. Chi-square values for percentages of mule deer tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available. Blank cells indicate no tracks found.

Snow Depth (cm)	Early winter	Mid-winter	Late winter
0-20	14.11	0.18	
20-40	136.72	1.23	
40-60	138.27	5.25	
60-80	22.22	17.11	
80-100		18.88	
100-120		11.62	
120-140		2.54	
140-160		2.95	
160-180			
180-200			

Table 99. Bonferroni Z-statistic intervals for mule deer tracks (use) found at various snow depths in the BC, SC, and SB study units compared to percent of the transect with various snow depths available. Blanks indicate no tracks found.

Snow Depth (cm)	Early winter		Mid-winter		Late winter	
	Lower	Upper	Lower	Upper	Lower	Upper
0-20	-0.129	0.129	0.000	0.000		
20-40	-1.242	1.242	0.527	0.863		
40-60	-1.242	1.242	0.137	0.473		
60-80	-0.200	0.200	0.000	0.000		
80-100						
100-120						
120-140						
140-160						
160-180						
180-200						

APPENDIX S

RESTULTS OF TESTS FOR SIGNIFICANT DIFFERENCES IN THE NUMBER OF 5 TREE SPECIES
BY SIZE CLASS FOUND AMONG 7 FOREST TYPES AT MOOSE FEEDING SITES

Table 100. Average number of subalpine fir per 0.02-ha plot by size class at moose feeding sites in 7 forest types: young (DF0), mid-age (DF2), and oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and oldest lodgepole (LP3) and oldest spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	LP1	LP2	LP3	SF	H	P<
Browsed <1m	0.3	0.0	2.8	0.0	2.0	2.9	2.2	12.89	0.045
Unbrowsed <1m	1.4	2.0	74.0	0.7	143.0	102.8	39.1	38.95	0.001
% Browsed <1m	15.4	0.0	5.4	0.0	9.9	5.0	2.4	7.29	0.294
All trees <1m	1.6	2.0	76.8	0.7	145.0	105.7	41.3	39.58	0.001
Browsed 1-5m	1.0	1.0	47.6	0.3	23.1	46.8	7.6	40.4	0.001
Unbrowsed 1-5m	0.9	2.0	73.8	0.3	88.9	138.9	16.5	45.76	0.001
% Browsed 1-5m	0.5	0.3	0.5	0.5	0.3	0.3	0.2	6.038	0.419
All trees 1-5m	1.9	3.0	121.0	0.7	112.0	185.7	24.1	48.67	0.001
Browsed <5m	1.3	1.0	50.0	0.3	25.1	49.7	9.7	39.77	0.001
Unbrowsed <5m	2.3	4.0	147.8	1.0	231.9	241.7	55.6	43.7	0.001
% Browsed <5m	35.7	20.0	34.3	50.0	22.8	19.8	7.2	12.22	0.057
All trees <5m	3.5	5.0	197.8	1.3	257.0	291.3	65.4	46.02	0.001
Trees >5	0.1	0.0	32.0	0.0	27.2	43.2	6.2	46.18	0.001
All trees	3.6	5.0	229.8	1.3	284.2	334.5	71.6	46.19	0.001

Table 101. Average number of subalpine fir per 0.02-ha plot by size class at moose feeding sites in Douglas fir forests of different ages: young (DF0), mid-age (DF2), and oldest Douglas fir (DF3) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	H	P<
Browsed <1m	0.3	0.0	2.8	6.73	0.034
Unbrowsed <1m	1.4	2.0	74.0	15.01	0.001
% Browsed <1m	15.4	0.0	5.4	2.47	0.291
All trees <1m	1.6	2.0	76.8	14.69	0.001
Browsed 1-5m	1.0	1.0	47.3	16.56	0.001
Unbrowsed 1-5m	0.9	2.0	73.8	15.35	0.001
% Browsed 1-5m	53.3	33.3	46.2	0.49	0.782
All trees 1-5m	1.9	3.0	121.0	15.34	0.001
Browsed <5m	1.25	1.0	50.0	16.26	0.001
Unbrowsed <5m	2.3	4.0	147.8	43.7	0.001
% Browsed <5m	35.7	20.0	34.3	0.49	0.782
All trees <5m	3.5	5.0	197.8	15.31	0.001
Trees >5	0.1	0.0	32.0	17.48	0.001
All trees	3.6	5.0	229.8	15.31	0.001

Table 102. Average number of subalpine fir per 0.02-ha plot by size class at moose feeding sites in lodgepole forests of different ages: young (LP1), mid-age (LP2), and oldest lodgepole (LP3) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

Size class	LP1	LP2	LP3	H	P<
Browsed <1m	0.0	2.0	2.9	4.8	0.096
Unbrowsed <1m	0.7	143.0	102.8	13.37	0.001
% Browsed <1m	0.0	9.9	5.0	1.68	0.431
All trees <1m	0.7	145.0	105.7	14.13	0.001
Browsed 1-5m	0.3	23.1	46.8	14.59	0.001
Unbrowsed 1-5m	0.3	88.9	138.9	17.08	0.001
% Browsed 1-5m	50.0	34.8	26.5	0.25	0.881
All trees 1-5m	0.7	112.0	185.7	19.57	0.001
Browsed <5m	0.3	25.1	49.7	14.66	0.001
Unbrowsed <5m	1.0	231.9	241.7	13.61	0.001
% Browsed <5m	50.0	22.7	19.8	0.1	0.949
All trees <5m	1.3	257.0	291.0	15.14	0.001
Trees >5	0.0	27.2	43.2	15.51	0.001
All trees	1.3	284.2	334.5	15.05	0.001

Table 103. Average number of subalpine fir per 0.02-ha plot at moose feeding sites in late successional Douglas fir (DF3), lodgepole pine (LP3), and spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

Size class	DF3	LP3	SF	H	P<
Browsed <1m	2.8	2.9	2.2	2.63	0.268
Unbrowsed <1m	74.0	102.8	39.1	5.95	0.051
% Browsed <1m	5.4	5.0	2.4	3.09	0.214
All trees <1m	76.8	105.7	41.3	5.86	0.053
Browsed 1-5m	47.3	46.8	7.5	13.02	0.002
Unbrowsed 1-5m	73.8	138.9	16.5	17.23	0.001
% Browsed 1-5m	46.2	26.5	23.2	4.99	0.082
All trees 1-5m	121.0	185.7	24.1	18.83	0.001
Browsed <5m	50.0	49.7	9.7	12.21	0.002
Unbrowsed <5m	147.8	241.7	55.6	13.69	0.001
% Browsed <5m	34.3	19.8	7.2	11.04	0.004
All trees <5m	197.8	291.3	65.4	14.92	0.001
Trees >5	32.0	43.2	6.2	14.71	0.001
All trees	229.8	334.5	71.5	15.2	0.001

Table 104. Average number of subalpine fir per 0.02-ha plot by size class at moose feeding sites in early successional Douglas fir (DF0) and lodgepole pine (LP1) forests. Significance is $P < 0.05$. Student's t-test was used to compare averages. Blank spaces indicate insufficient data. T and P values of tests are given in the table.

Size class	DF0	LP1	T	P<
Browsed <1m	0.25	0.0	0.86	0.408
Unbrowsed <1m	1.4	0.7	0.43	0.674
% Browsed <1m	15.3	0.0		
All trees <1m	1.6	0.7	0.49	0.628
Browsed 1-5m	1.0	0.3	0.56	0.583
Unbrowsed 1-5m	0.9	0.3	0.52	0.611
% Browsed 1-5m	53.3	50.0	0.5	0.962
All trees 1-5m	1.9	0.7	0.55	0.592
Browsed <5m	1.3	0.3	0.62	0.544
Unbrowsed <5m	2.3	1.0	0.47	0.649
% Browsed <5m	35.7	50.0	-0.22	0.839
All trees <5m	3.5	1.3	0.53	0.608
Trees >5	0.1	0.0	0.86	0.408
All trees	3.6	1.3	0.54	0.6

Table 105. Average number of lodgepole pine per 0.02-ha plot by size class at moose feeding sites in 7 forest types: young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blank spaces indicate insufficient data. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	LP1	LP2	LP3	SF	H	P<
Browsed <1m	0.0	0.0	0.0	0.7	0.2	0.0	0.0	13.73	0.033
Unbrowsed <1m	0.3	0.0	0.0	5.0	4.6	1.9	0.0	26.58	0.001
% Browsed <1m	0.0	0.0	0.0	6.3	3.8	0.0	0.0		
All trees <1m	0.3	0.0	0.0	5.7	4.8	1.9	0.0	26.76	0.001
Browsed 1-5m	0.5	0.0	0.0	19.0	1.1	0.3	0.0	24.43	0.001
Unbrowsed 1-5m	0.0	0.8	0.0	3.0	4.8	3.7	0.1	23.8	0.001
% Browsed 1-5m	100	0.0	0.0	86.4	33.6	6.2	0.0		
All trees 1-5m	0.5	0.8	0.0	22.0	5.9	4.1	0.1	23.55	0.001
Browsed <5m	0.5	0.0	0.0	19.7	1.3	0.3	0.0	24.46	0.001
Unbrowsed <5m	0.3	0.8	0.0	8.0	6.4	5.3	0.1	29.17	0.001
% Browsed <5m	75.0	0.0	0.0	74.6	16.7	3.3	0.0		
All trees <5m	0.8	0.8	0.0	27.7	7.7	5.7	0.1	27.94	0.001
Trees >5	0.0	0.2	1.5	40.0	20.9	5.9	0.4	50.28	0.001
All trees	0.8	1.0	1.5	67.7	28.6	11.6	0.5	47.65	0.001

Table 106. Average number of spruce per 0.02-ha plot by size class at moose feeding sites in 7 forest types young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blanks spaces indicate insufficient data. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	LP1	LP2	LP3	SF	H	P<
Browsed <1m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Unbrowsed <1m	1.5	0.0	6.9	0.0	26.1	12.1	7.8	30.67	0.001
% Browsed <1m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
All trees <1m	1.5	0.0	6.9	0.0	26.1	12.1	7.8	30.67	0.001
Browsed 1-5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Unbrowsed 1-5m	5.0	0.0	14.5	0.0	29.9	23.9	29.5	33.54	0.001
% Browsed 1-5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
All trees 1-5m	5.0	0.0	14.5	0.0	30.2	24.0	30.2	33.66	0.001
Browsed <5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Unbrowsed <5m	6.5	0.0	21.4	0.0	56.0	36.0	37.4	37.93	0.001
% Browsed <5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
All trees <5m	6.5	0.0	21.4	0.0	56.3	36.1	38.0	37.89	0.001
Trees >5	1.1	0.0	5.8	0.0	10.0	11.5	16.5	36.37	0.001
All trees	7.6	0.0	27.1	0.0	66.3	47.6	54.5	38.08	0.001

Table 107. Average number of Douglas fir per 0.02-ha plot by size class at moose feeding sites in 7 forest types young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blanks spaces indicate insufficient data. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	LP1	LP2	LP3	SF	H	P<
Browsed <1m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Unbrowsed <1m	11.0	6.0	49.5	0.0	17.1	4.2	0.5	26.55	0.001
% Browsed <1m	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
All trees <1m	11.0	6.0	49.5	0.0	17.1	4.2	0.5	26.55	0.001
Browsed 1-5m	2.0	3.8	0.1	0.7	0.6	0.3	0.0	22.04	0.001
Unbrowsed 1-5m	17.5	18.4	12.4	0.0	16.4	4.0	0.8	34.31	0.001
% Browsed 1-5m	9.3	17.5	0.3	100.0	5.6	1.0	0.0	17.75	0.007
All trees 1-5m	19.5	22.2	12.5	0.7	17.0	4.3	0.8	30.5	0.001
Browsed <5m	2.0	4.0	0.1	0.7	0.6	0.3	0.0	22.04	0.001
Unbrowsed <5m	28.5	24.4	61.9	0.0	33.5	8.2	1.4	35.2	0.001
% Browsed <5m	6.0	14.6	0.0	100.0	1.7	0.8	0.0	19.22	0.004
All trees <5m	30.5	28.4	62.0	0.7	34.1	8.5	1.4	32.89	0.001
Trees >5	12.5	10.6	3.6	1.3	3.9	2.0	0.3	36.93	0.001
All trees	43.0	39.0	65.6	2.0	38.0	10.5	1.6	37.25	0.001

Table 108. Average number of whitebark pine per 0.02-ha plot by size class at moose feeding sites in 7 forest types: young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests. Significance is $P < 0.05$. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blank spaces indicate insufficient data. H and P values of tests are given in the table.

Size class	DF0	DF2	DF3	LP1	LP2	LP3	SF	H	P<
Browsed <1m	0.0	0.0	0.0	0.0	0.3	0.1	0.0	6.93	0.327
Unbrowsed <1m	0.0	0.0	1.62	0.0	11.3	6.4	0.0	26.9	0.001
% Browsed <1m	0.0	0.0	0.0	0.0	2.4	1.3	0.0		
All trees <1m	0.0	0.0	1.6	0.0	11.6	6.5	0.0	26.87	0.001
Browsed 1-5m	0.0	0.0	0.0	0.2	1.1	0.6	0.0	15.79	0.015
Unbrowsed 1-5m	0.0	0.2	0.4	0.8	8.0	7.7	0.4	29.21	0.001
% Browsed 1-5m	0.0	0.0	0.0	0.2	0.4	0.1	0.0		
All trees 1-5m	0.0	0.2	0.4	1.0	9.1	8.3	0.4	32.6	0.001
Browsed <5m	0.0	0.0	0.0	0.2	1.4	0.7	0.0	20.27	0.003
Unbrowsed <5m	0.0	0.2	2.0	0.8	21.4	14.1	0.4	33.07	0.001
% Browsed <5m	0.0	0.0	0.0	16.7	32.9	36.4	0.0		
All trees <5m	0.0	0.2	2.0	1.0	20.7	14.87	0.4	35.32	0.001
Trees >5	0.0	0.0	2.5	1.7	1.9	2.9	0.0	20.75	0.002
All trees	0.0	0.2	4.5	2.7	22.6	17.7	0.4	37.08	0.001

Table 109. Average number of trees per plot 0.02-ha of the 5 tree species found in the study area for each of the 7 cover types where moose browsing occurred: young (DF0), mid-age (DF2), and the oldest Douglas fir (DF3), young (LP1), mid-age (LP2), and the oldest lodgepole (LP3) and the oldest spruce-fir (SF) forests.

Tree species	DF0	DF2	DF3	LP1	LP2	LP3	SF
Subalpine fir	3.6	5.0	229.8	1.3	284.2	334.5	71.6
Lodgepole pine	0.8	1.0	1.5	67.7	28.6	11.6	0.5
Spruce	7.6	0.0	27.1	0.0	66.3	47.6	54.5
Douglas fir	43.0	39.0	65.6	2.0	38.0	10.5	1.6
Whitebark pine	0.0	0.2	4.5	2.7	22.6	17.7	0.4

APPENDIX T

POST HOC TESTS DETERMINING SIGNIFICANT DIFFERENCES IN THE AVERAGE
PERCENT COVER AND HEIGHT OF SHRUB SPECIES AT MOOSE FEEDING SITES
AMONG DIFFERENT AGES AND TYPES OF FORESTS

Table 110. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of ninebark among moose feeding sites in 5 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.	4.
1.Young Douglas fir	37.6				
2.Mid-age Douglas fir	1.8	0.001*			
3.Oldest Douglas fir	0.1	0.001*	0.178		
4.Young lodgepole	0.1	0.001*	0.353	0.976	
5. Oldest lodgepole	0.0	0.001*	0.482	0.996	0.959

Table 111. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of gooseberry among moose feeding sites in 7 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.	4.	5.	6.
1.Young Douglas fir	2.2						
2.Mid-age Douglas fir	1.08	0.135					
3.Oldest Douglas fir	1.86	0.526	0.201				
4.Young lodgepole	0.1	0.006*	0.37	0.031*			
5.Mid-age lodgepole	0.3	0.009*	0.358	0.041*	0.805		
6.Oldest lodgepole	0.6	0.031*	0.405	0.087	0.715	0.593	
7. Oldest spruce-fir	10.0	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*

Table 112. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average height (cm) of gooseberry among moose feeding sites in 7 forest types (* indicates significance).

Forest type	height	1.	2.	3.	4.	5.	6.
1. Young Douglas fir	38.5						
2. Mid-age Douglas fir	52.7	0.005*					
3. Oldest Douglas fir	35.3	0.448	0.001*				
4. Young lodgepole	25.5	0.006*	0.001*	0.021*			
5. Mid-age lodgepole	63.5	0.001*	0.01*	0.001*	0.001*		
6. Oldest lodgepole	44.9	0.122	0.159	0.055	0.001*	0.001*	
7. Oldest spruce-fir	49.6	0.022*	0.469	0.004*	0.001*	0.003*	0.269

Table 113. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of grouse whortleberry among moose feeding sites in 4 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.
1.Oldest Douglas fir	0.3			
2. Mid-age lodgepole	2.4	0.947		
3.Oldest lodgepole	9.2	0.547	0.312	
4.Oldest spruce-fir	2.1	0.791	0.962	0.539

Table 114. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average height (cm) of grouse whortleberry among moose feeding sites in 4 forest types (* indicates significance).

Forest Type	Height	1	2	3
1. Oldest Douglas fir	9.7			
2. Mid-age lodgepole	13.5	0.016*		
3. Oldest lodgepole	15.2	0.001*	0.205	
4. Oldest spruce-fir	13.1	0.015*	0.739	0.246

Table 115. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of buffaloberry among moose feeding sites in 7 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.	4.	5.	6.
1. Young Douglas fir	5.7						
2. Mid-age Douglas fir	1.2	0.001*					
3. Oldest Douglas fir	1.2	0.001*	0.979				
4. Young lodgepole	0.4	0.001*	0.299	0.537			
5. Mid-age lodgepole	7.5	0.012*	0.001*	0.001*	0.001*		
6. Oldest lodgepole	2.1	0.001*	0.441	0.232	0.108	0.001*	
7. Oldest spruce-fir	0.2	0.001*	0.369	0.517	0.757	0.001*	0.077

Table 116. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average height (cm) of buffaloberry among moose feeding sites in 7 forest types (* indicates significance).

Forest type	height	1.	2.	3.	4.	5.	6.
1. Young Douglas fir	66.5						
2. Mid-age Douglas fir	71.4	0.322					
3. Oldest Douglas fir	76.1	0.125	0.337				
4. Young lodgepole	57.8	0.079	0.017*	0.001*			
5. Mid-age lodgepole	93.2	0.001*	0.001*	0.002*	0.001*		
6. Oldest lodgepole	86.3	0.001*	0.007*	0.039*	0.001*	0.162	
7. Oldest spruce-fir	93.5	0.001*	0.001*	0.003*	0.001*	0.98	0.329

Table 117. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of snowberry among moose feeding sites in 6 forest types (* indicates significance).

Forest type	%cover	1	2	3	4	5
1. Young Douglas fir	6.5					
2. Mid-age Douglas fir	5.13	0.012*				
3. Oldest Douglas fir	5.1	0.027*	0.957			
4. Young lodgepole	0.1	0.001*	0.001*	0.001*		
5. Oldest lodgepole	0.4	0.001*	0.001*	0.001*	0.783	
6. Oldest spruce-fir	0.1	0.001*	0.001*	0.001*	0.912	0.578

Table 118. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of Rocky Mountain maple among moose feeding sites in 3 forest types (* indicates significance).

Forest type	% cover	1.	2.
1. Young Douglas fir	3.18		
2. Oldest Douglas fir	0.4	0.001*	
3. Mid-age lodgepole	0.1	0.001*	0.488

Table 119. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of serviceberry among moose feeding sites in 4 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.
1. Young Douglas fir	1.1			
2. Mid-age Douglas fir	0.2	0.001*		
3. Mid-age lodgepole	0.1	0.001*	0.341	
4. Oldest spruce-fir	0.0	0.001*	0.336	0.647

Table 120. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average percent canopy cover of honeysuckle among moose feeding sites in 5 forest types (* indicates significance).

Forest type	% cover	1.	2.	3.	4.
1. Young Douglas fir	0.1				
2. Oldest Douglas fir	2.3	0.001*			
3. Mid-age lodgepole	2.9	0.001*	0.103		
4. Oldest lodgepole	1.4	0.001*	0.023*	0.001*	
5. Oldest spruce-fir	0.9	0.001*	0.001*	0.001*	0.18

Table 121. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average height (cm) of honeysuckle among moose feeding sites in 5 forest types (* indicates significance).

Forest type	height	1	2	3	4
1. Young Douglas fir	59.3				
2. Oldest Douglas fir	49.2	0.046*			
3. Mid-lodgepole	60.48	0.75	0.029*		
4. Oldest lodgepole	53.9	0.351	0.223	0.324	
5. Oldest spruce-fir	58.5	0.852	0.042*	0.869	0.232

Table 122. Results of Newman-Keuls *post hoc* tests for significant differences ($P < 0.05$) in average height (cm) of huckleberry among moose feeding sites in 4 forest types (* indicates significance).

Forest Type	height	1	2	3
1. Oldest Douglas fir	29.7			
2. Mid-age lodgepole	40.8	0.001*		
3. Oldest lodgepole	39.5	0.001*	0.582	
4. Oldest spruce-fir	41.1	0.001*	0.872	0.757

APPENDIX U

POST HOC TESTS DETERMINING SIGNIFICANT DIFFERENCES IN FOREST STAND
CHARACTERISTICS AND AVERAGE NUMBER OF UNGULATE PELLET GROUPS
AMONG 4 SUCCESSIONAL STAGES OF LODGEPOLE FORESTS

Table 123. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average age of 10 largest trees in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	8.4			
LP1	92.9	0.001*		
LP2	185.4	0.001*	0.0018	
LP3	226.4	0.001*	0.001*	0.001*

Table 124. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of moose pellet groups in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.2			
LP1	0.4	0.765		
LP2	0.7	0.759	0.684	
LP3	8.1	0.001*	0.001*	0.001*

Table 125. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of elk pellet groups in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.7			
LP1	4.2	0.001*		
LP2	0.7	0.941	0.001*	
LP3	0.7	0.971	0.001*	0.993

Table 126. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of mule deer pellet groups in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	1.0			
LP1	0.5	0.3304		
LP2	0.2	0.377	0.833	
LP3	0.3	0.342	0.711	0.837

Table 127. Average number of browsed and unbrowsed subalpine fir per 0.02-ha plot by size class in lodgepole forests of different ages: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance. Differences among means were determined using ANOVA. F and P values of tests are given in the table.

	LP0	LP1	LP2	LP3	F	P <
Browsed <1m	0.2	2.5	37.6	84.9	53.05	0.001
Unbrowsed <1m	5.8	0.0	121.1	153.3	51.07	0.001
% Browsed <1m	1.8	50.0	20.3	38.5	25.83	0.001
All trees <1m	5.9	2.5	158.7	238.3	83.94	0.001
Browsed 1 – 5m	0.5	0.0	25.8	77.1	98.67	0.001
Unbrowsed 1 – 5m	6.6	0.0	14.9	6.1	9.02	0.001
% Browsed 1 – 5m	2.6	3.3	63.8	92.3	208.07	0.001
All trees 1 – 5m	7.2	0.0	40.8	83.2	74.29	0.001
Browsed <5m	0.7	2.5	63.4	162.1	91.5	0.001
Unbrowsed <5m	12.4	0.0	136.0	159.4	50.4	0.001
% Browsed <5m	5.5	100.0	28.6	51.8	111.54	0.001
All trees <5m	13.1	2.5	199.4	321.4	114.81	0.001
Trees >5m	0.8	0.4	3.4	12.9	62.85	0.001
All trees	13.9	2.9	202.9	334.4	121.99	0.001

Table 128. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed subalpine fir <1 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years-post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.2			
LP1	2.5	0.769		
LP2	37.6	0.001*	0.001*	
LP3	84.6	0.001*	0.001*	0.001*

Table 129. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of unbrowsed subalpine fir <1 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	5.8			
LP1	0.0	0.713		
LP2	121.1	0.001*	0.001*	
LP3	153.3	0.001*	0.001*	0.041*

Table 130. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average percent browsed subalpine fir <1 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	1.8			
LP1	50.0	0.001		
LP2	20.0	0.001	0.001	
LP3	38.5	0.001	0.047	0.002

Table 131. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed and unbrowsed subalpine fir <1 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	5.9			
LP1	2.5	0.849		
LP2	158.7	0.001*	0.001*	
LP3	238.3	0.001*	0.001*	0.001*

Table 132. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed subalpine fir 1-5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.5			
LP1	0.0	0.925		
LP2	25.8	0.001*	0.001*	
LP3	77.1	0.001*	0.001*	0.001*

Table 133. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of unbrowsed subalpine fir 1-5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.5			
LP1	0.0	0.049*		
LP2	25.8	0.003*	0.001*	
LP3	77.1	0.844	0.031*	0.005*

Table 134. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average percent browsed subalpine fir 1-5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	2.6			
LP1	3.3	0.866		
LP2	63.8	0.001*	0.001*	
LP3	92.3	0.001*	0.001*	0.001*

Table 135. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed and unbrowsed subalpine fir 1-5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	7.2			
LP1	0.0	0.259		
LP2	40.8	0.001*	0.001*	
LP3	83.2	0.001*	0.001*	0.001*

Table 136. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed subalpine fir <5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	7.2			
LP1	0.0	0.874		
LP2	40.8	0.001*	0.001*	
LP3	83.2	0.001*	0.001*	0.001*

Table 137. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of unbrowsed subalpine fir <5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	12.4			
LP1	0.0	0.451		
LP2	136.0	0.001*	0.001*	
LP3	159.0	0.0018	0.001*	0.156

Table 138. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average percent browsed subalpine fir <5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	5.5			
LP1	100.0	0.001*		
LP2	28.6	0.001*	0.001*	
LP3	51.8	0.001*	0.001*	0.001*

Table 139. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of browsed and unbrowsed subalpine fir <5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	13.1			
LP1	2.5	0.608		
LP2	199.4	0.001*	0.001*	
LP3	321.4	0.001*	0.001*	0.001*

Table 140. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of subalpine fir >5 meter tall in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.8			
LP1	0.4	0.702		
LP2	3.4	0.016	0.015	
LP3	13.0	0.001	0.001	0.001

Table 141. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of subalpine fir in 0.02-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	14.0			
LP1	3.0	0.596		
LP2	202.9	0.001	0.001	
LP3	334.4	0.001	0.001	0.001

Table 142. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average age of subalpine fir trees $>5\text{m}$ in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	15.6			
LP1	44.8	0.037*		
LP2	56.9	0.009*	0.384	
LP3	70.7	0.001*	0.152	0.325

Table 143. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average DBH of subalpine fir trees $>5\text{m}$ in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	1.5			
LP1	3.2	0.144		
LP2	3.9	0.086	0.509	
LP3	4.8	0.019*	0.323	0.438

Table 144. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of subalpine fir trees $>5\text{m}$ in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	1.2			
LP1	1.5	0.987		
LP2	21.8	0.517	0.281	
LP3	64.0	0.005*	0.003*	0.025*

Table 145. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average height of subalpine fir trees $>5\text{m}$ in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	5.1			
LP1	5.9	0.269		
LP2	8.7	0.053	0.225	
LP3	10.4	0.013*	0.13	0.473

Table 146. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average number of patches of subalpine fir trees in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.0			
LP1	0.8	0.953		
LP2	3.1	0.850	0.639	
LP3	81.2	0.009*	0.005*	0.004*

Table 147. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average size of patches (m^2) of subalpine fir trees in 0.25-ha plots among 4 successional stages of lodgepole forests: LP0- 0 to 40, LP1- 40 to 100, LP2- 100 to 300, and LP3- 300+ years post-disturbance (* indicates significance).

Successional stage	Average	LP0	LP1	LP2
LP0	0.0			
LP1	3.3	0.707		
LP2	4.4	0.869	0.899	
LP3	13.1	0.448	0.51	0.328

APPENDIX V

RESULTS OF TESTS FOR SIGNIFICANT DIFFERENCES IN PELLET GROUP COUNTS AND TREE
AND SHRUB CHARACTERISTICS AMONG 6 DISTANCES FROM THE BOUNDARY BETWEEN
CLEARCUTS AND MATURE FORESTS

Table 148. Average number of moose, elk, and deer pellet groups per 0.02-ha plot at different distances from a clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

Species	100	50	4-clearcut	4-forest	50	100	H	P <
Moose	0.4	0.5	0.8	3.3	3.1	2.1	23.01	0.001
Elk	0.9	0.8	0.9	2.3	3.5	2.3	18.1	0.003
Deer	0.6	0.5	0.4	1.5	1.1	1.0	7.47	0.188

Table 149. Average percent canopy cover per 0.02-ha plot of shrub species browsed by moose in clearcut and forest locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blanks indicate insufficient data. H and P values of tests are given in the table.

Species	100	50	4-clearcut	4-forest	50	100	H	P <
Alder	1.2	3.2	2.1	7.4	3.5	3.4	2.63	0.757
Honeysuckle	2.3	1.9	1.2	1.9	2.1	1.9	1.63	0.898
Gooseberry	0.5	1.0	1.3	0.3	0.5	0.5	16.61	0.005
Willow	3.0	3.1	9.6	0			15.11	0.009
Buffaloberry	3.0	1.5	1.4	4.1	1.8	3.4	7.15	0.209
Huckleberry	2.3	3.1	1.3	7.8	4.6	5.8	19.24	0.002
Whortleberry	8.6	7.6	9.3	19.6	14.4	17.5	5.22	0.39

Table 150. Results of tests for significant differences in percent canopy cover per 0.02-ha plot of shrub species browsed by moose among clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the edge. Results were compared among clearcut sites and among forest sites. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blanks indicate insufficient data. H and P values of tests are given in the table.

Species	Clearcut H	P <	Forested H	P <
Alder	0.99	0.607	1.47	0.479
Honeysuckle	1.25	0.537	0.23	0.891
Gooseberry	5.24	0.073	1.09	0.578
Willow	0.06	0.97		
Buffaloberry	1.23	0.54	4.07	0.131
Huckleberry	0.68	0.71	1.35	0.509
Whortleberry	0.00	0.999	0.65	0.724

Table 151. Average percent canopy cover per 0.02-ha plot of shrub species browsed by moose in clearcuts and forests ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Student's t-test was used to compare averages. H and P values of tests are given in the table.

Species	Clearcut	Forest	T	P <
Alder	2.18	4.78	1.37	0.173
Honeysuckle	1.81	1.97	0.38	0.703
Gooseberry	0.93	0.45	-2.27	0.026
Willow	0.35	0.00	-2.26	0.026
Buffaloberry	1.99	3.09	1.44	0.155
Huckleberry	2.22	6.08	3.97	0.001
Whortleberry	8.49	17.16	2.81	0.006

Table 152. Average height per 0.02-ha plot of shrub species browsed by moose in clearcut and forest locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicate insufficient data. H and P values of tests are given in the table..

Species	100	50	4-clearcut	4-forest	50	100	H	P <
Alder	108.0	118.1	110.0	158.5	141.7	178.7	F0.99	0.442
Honeysuckle	42.6	43.8	45.2	49.4	43.7	40.8	H6.69	0.245
Gooseberry	28.9	33.4	34.7	35.6	32.7	33.1	F1.07	0.38
Willow	51.9	58.2	38.8				F1.07	0.379
Buffaloberry	76.6	71.9	75.5	75.0	70.2	69.7	F0.25	0.936
Huckleberry	18.5	20.5	25.7	26.6	29.3	28.0	H26.1	0.001
Whortleberry	11.1	10.8	10.9	13.2	12.1	11.8	F1.23	0.305

Table 153. Results of tests for significant differences in average height per 0.02-ha plot of shrub species browsed by moose among clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25 year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Results were compared among clearcut sites and among forest sites. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicate insufficient data. F, H, and P values of tests are given in the table.

Species	Clearcut F/H	P <	Forested F/H	P <
Alder	F0.11	0.896	F0.24	0.791
Honeysuckle	F0.348	0.708	H4.72	0.094
Gooseberry	F2.45	0.102	F0.31	0.742
Willow	F1.07	0.379		
Buffaloberry	F0.19	0.831	F0.27	0.769
Huckleberry	H7.01	0.03	F0.49	0.613
Whortleberry	F0.34	0.967	F0.79	0.459

Table 154. Differences in average shrub height per 0.02-ha plot of shrub species browsed by moose between forests and clearcuts ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Student's t-test was used to compare averages. Blanks indicate insufficient data. T and P values of tests are given in the table.

Species	Clearcut	Forest	T	P <
Alder	112.1	156.8	2.17	0.039
Honeysuckle	43.7	44.6	0.43	0.669
Gooseberry	32.6	34.1	0.74	0.464
Willow	49.6	0.0		
Buffaloberry	74.7	71.9	-0.61	0.542
Huckleberry	21.4	27.9	4.27	0.001
Whortleberry	10.9	12.38	2.13	0.037

Table 155. Average number of browsed and unbrowsed subalpine fir per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

	100	50	4-clearcut	4-forest	50	100	H	P <
Browsed <1m	0.3	0.7	1.0	12.1	12.3	10.3	41.16	0.001
Unbrowsed <1m	14.3	30.7	28.7	149.3	117.3	91.7	38.54	0.001
% Browsed <1m	2.5	12.8	2.8	12.4	8.0	17.0	20.34	0.001
All trees <1m	14.6	31.4	29.7	161.4	129.7	101.9	42.54	0.001
Browsed 1-5m	0.9	1.1	3.8	10.6	15.7	12.7	37.12	0.001
Unbrowsed 1-5m	20.7	40.1	22.3	36.0	15.9	16.4	9.14	0.104
% Browsed 1-5m	4.4	7.2	20.8	32.7	57.8	62.5	38.38	0.001
All trees 1-5m	21.6	41.3	26.1	46.6	31.6	29.1	10.09	0.073
Browsed <5m	1.3	1.8	4.8	22.7	28.1	23.0	48.43	0.001
Unbrowsed <5m	34.9	70.8	51.1	185.3	133.2	108.1	26.33	0.001
% Browsed <5m	4.1	7.8	9.6	16.9	16.2	25.2	24.18	0.001
All trees <5m	36.2	72.7	55.9	208.0	161.3	131.1	30.75	0.001
Trees >5m	1.7	1.9	2.7	7.0	5.5	4.9	16.05	0.007
All trees	37.9	74.6	58.5	215.0	166.8	135.9	30.59	0.001

Table 156. Results of tests for significant differences in average number of browsed and unbrowsed subalpine fir per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Results were compared among clearcut sites and among forest sites. Data are summarized by size class. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F and P values of tests are given in the table.

	Clearcut H	P <	Forested F	P <
Browsed <1m	1.34	0.513	0.43	0.647
Unbrowsed <1m	2.35	0.309	2.11	0.134
% Browsed <1m	1.44	0.486	2.3	0.112
All trees <1m	2.4	0.301	2.14	0.13
Browsed 1-5m	0.95	0.621	0.34	0.712
Unbrowsed 1-5m	0.36	0.836	0.12	0.886
% Browsed 1-5m	2.23	0.328	1.18	0.316
All trees 1-5m	0.19	0.907	0.07	0.932
Browsed <5m	1.13	0.568	0.29	0.751
Unbrowsed <5m	0.2	0.903	1.88	0.165
% Browsed <5m	1.79	0.408	1.88	0.391
All trees <5m	0.26	0.88	1.65	0.204
Trees >5m	0.45	0.797	0.17	0.843
All trees	0.35	0.841	1.78	0.181

Table 157. Differences in average number of browsed and unbrowsed subalpine fir per 0.02-ha plot in clearcut and forested locations ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Data are summarized by size class. Student's t-test was used to compare averages. T and P values of tests are given in the table.

	Clearcut	Forest	T	P <
Browsed <1m	0.7	11.6	-4.64	0.001
Unbrowsed <1m	24.6	119.4	-5.25	0.001
% browsed <1m	5.9	12.5	-1.87	0.065
All trees <1m	25.2	131.0	-5.74	0.001
Browsed 1-5m	1.9	13.0	-4.57	0.001
Unbrowsed 1-5m	27.7	22.8	.54	0.589
% Browsed 1-5m	10.9	50.8	-6.78	0.001
All trees 1-5m	29.7	35.8	-.63	0.528
Browsed <5m	2.6	24.6	-4.96	0.001
Unbrowsed <5m	52.3	142.2	-3.89	0.001
% Browsed <5m	7.2	19.4	-3.81	0.001
All trees <5m	54.9	166.8	-4.69	0.001
Trees >5m	2.1	5.8	-2.73	0.008
All trees	57	172.6	-4.81	0.001

Table 158. Average number of browsed and unbrowsed lodgepole per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

	100	50	4-clearcut	4-forest	50	100	H	P <
Browsed <1m	0.1	0.1	0.7	0.3	0.3	0.1	4.16	0.526
Unbrowsed <1m	8.1	8.3	26.3	4.7	3.9	3.7	26.94	0.001
% Browsed <1m	0.5	1.0	4.5	2.1	3.1	1.0	5.24	0.387
All trees <1m	8.1	8.4	26.9	5.0	4.2	3.7	27.34	0.001
Browsed 1-5m	1.6	0.5	2.5	0.5	1.1	0.3	2.07	0.839
Unbrowsed 1-5m	33.7	31.7	35.7	2.4	2.3	1.5	60.27	0.001
% Browsed 1-5m	2.8	2.1	5.1	10.5	16.1	22.9	9.42	0.093
All trees 1-5m	35.3	32.2	38.3	2.9	3.4	1.8	57.17	0.001
Browsed <5m	1.7	0.6	3.2	0.7	1.4	0.3	1.02	0.961
Unbrowsed <5m	41.7	40.0	62.0	7.1	6.1	5.1	52.89	0.001
% Browsed <5m	2.7	1.8	4.9	4.6	7.6	5.1	1.78	0.882
All trees <5m	43.4	40.6	65.2	7.9	7.6	5.5	50.97	0.001
Trees >5m	4.4	3.9	1.5	12.1	11.1	9.3	31.68	0.001
All trees	47.8	44.5	66.7	19.9	18.7	14.9	31.55	0.001

Table 159. Results of tests for significant differences in average number of browsed and unbrowsed lodgepole per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Results were compared among clearcut sites and among forest sites. Data are summarized by size class. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F, and P values of tests are given in the table.

	Clearcut H	P <	Forested F/H	P <
Browsed <1m	2.79	0.248	H1.14	0.566
Unbrowsed <1m	8.51	0.014	F0.14	0.872
% Browsed <1m	2.64	0.267	F0.56	0.578
All trees <1m	9.62	0.008	F0.16	0.853
Browsed 1-5m	0.82	0.665	H0.79	0.671
Unbrowsed 1-5m	0.07	0.968	F0.26	0.769
% Browsed 1-5m	0.79	0.673	F0.32	0.727
All trees 1-5m	0.02	0.992	F0.41	0.664
Browsed <5m	0.43	0.809	H0.07	0.963
Unbrowsed <5m	2.8	0.247	F0.21	0.812
% Browsed <5m	0.42	0.809	H0.64	0.726
All trees <5m	3.22	0.2	F0.23	0.795
Trees >5m	2.27	0.322	F0.62	0.545
All trees	1.86	0.395	F0.62	0.545

Table 160. Differences in average number of browsed and unbrowsed lodgepole per 0.02-ha plot in clearcut and forested locations ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Data are summarized by size class. Student's t-test was used to compare averages. T and P values of tests are given in the table.

	Clearcut	Forest	T	P <
Browsed <1m	0.3	0.2	0.58	0.563
Unbrowsed <1m	14.2	4.1	3.83	0.001
% Browsed <1m	2.1	1.9	0.07	0.946
All trees <1m	14.5	4.3	3.82	0.001
Browsed 1 - 5m	1.5	0.6	1.33	0.186
Unbrowsed 1 - 5m	33.7	2.0	5.73	0.001
% Browsed 1 - 5m	3.4	15.1	-2.67	0.009
All trees 1 - 5m	35.2	2.7	5.73	0.001
Browsed <5m	1.8	0.8	1.34	0.183
Unbrowsed <5m	47.9	6.1	6.41	0.001
% Browsed <5m	3.2	5.6	-1.19	0.237
All trees <5m	49.8	6.9	6.38	0.001
Trees >5m	3.3	10.8	-5.85	0.001
All trees	53.0	17.8	5.24	0.001

Table 161. Average number of browsed and unbrowsed spruce per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

	100	50	4-clearcut	4-forest	50	100	H	P <
Browsed <1m	0.0	0.0	0.1	0.0	0.1	0.0	4.05	0.543
Unbrowsed <1m	9.5	7.5	30.1	14.0	26.2	17.1	11.7	0.039
% Browsed <1m	0.0	0.0	0.1	0.0	0.3	0.0	3.6	0.606
All trees <1m	9.5	7.5	30.2	14.0	26.3	17.1	11.7	0.039
Browsed 1 - 5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Unbrowsed 1 - 5m	4.9	4.3	5.1	9.2	15.4	10.2	7.9	0.163
% Browsed 1 - 5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
All trees 1 - 5m	4.9	4.3	5.1	9.2	15.4	10.2	7.9	0.163
Browsed <5m	0.0	0.0	0.0	0.0	0.1	0.0	4.0	0.543
Unbrowsed <5m	14.4	11.8	35.3	23.2	41.6	27.1	10.0	0.75
% Browsed <5m	0.0	0.0	0.1	0.0	0.1	0.0	3.84	0.573
All trees <5m	14.4	11.8	35.3	23.2	41.7	27.3	10.1	0.072
Trees >5m	0.6	0.0	0.1	3.7	3.8	1.5	39.9	0.001
All trees	15.0	11.8	35.4	26.9	45.5	28.7	12.2	0.032

Table 162. Results of tests for significant differences in average number of browsed and unbrowsed spruce per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Results were compared among clearcut sites and among forest sites. Data are summarized by size class. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicated insufficient data. H, F, and P values of tests are given in the table.

	Clearcut H	P <	Forested F/H	P <
Browsed <1m	2.0	0.368	H2.0	0.368
Unbrowsed <1m	7.24	0.027	F1.3	0.289
% Browsed <1m	1.5	0.472	H2.1	0.354
All trees <1m	7.24	0.027	F1.3	0.283
Browsed 1-5m				
Unbrowsed 1-5m	2.02	0.363	F0.5	0.625
% Browsed 1-5m				
All trees 1-5m	2.02	0.363	F0.5	0.625
Browsed <5m	2.0	0.368	H2.0	0.368
Unbrowsed <5m	4.96	0.084	F0.9	0.378
% Browsed <5m	1.71	0.424	H2.08	0.354
All trees <5m	4.96	0.084	F1.0	0.375
Trees >5m	4.96	0.084	F1.6	0.212
All trees	4.8	0.091	F1.1	0.354

Table 163. Differences in average number of browsed and unbrowsed spruce per 0.02-ha plot in clearcut and forested locations ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Data are summarized by size class. Student's t-test was used to compare averages. Blanks indicate insufficient data. T and P values of tests are given in the table.

	Clearcut	Forest	T	P <
Browsed <1m	0.0	0.0	-0.45	0.656
Unbrowsed <1m	15.7	19.1	-0.59	0.556
% Browsed <1m	0.0	0.1	-0.45	0.656
All trees <1m	15.7	19.1	0.59	0.555
Browsed 1-5m	0.0	0.0		
Unbrowsed 1-5m	4.8	11.6	-2.29	0.024
% Browsed 1-5m	0.0	0.0		
All trees 1-5m	4.8	11.6	-2.29	0.024
Browsed <5m	0.0	0.0	-0.45	0.656
Unbrowsed <5m	20.5	30.6	-1.32	0.191
% Browsed <5m	0.0	0.06	-0.19	0.842
All trees <5m	20.5	30.7	-1.32	0.191
Trees >5m	0.2	2.9	-4.44	0.001
All trees	20.7	33.7	-1.65	0.102

Table 164. Average number of browsed and unbrowsed Douglas fir per 0.02-ha plot in clear cut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25 year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

	100	50	4-clearcut	4-forest	50	100	H	P <
Browsed <1m	0.0	0.0	0.0	0.2	0.2	0.1	5.9	0.31
Unbrowsed <1m	0.1	0.0	0.1	4.3	3.3	19.2	14.3	0.014
% Browsed <1m	0.0	0.0	0.0	17.2	1.3	4.6	0.0	1.0
All trees <1m	0.1	0.0	0.1	4.5	3.5	19.3	14.2	0.014
Browsed 1-5m	0.0	0.0	0.0	0.1	0.6	0.7	13.5	0.019
Unbrowsed 1-5m	0.1	0.0	0.1	0.1	1.1	9.7	19.6	0.002
% Browsed 1-5m	0.0	0.0	0.0	50.0	38.5	17.1	0.0	1.0
All trees 1-5m	0.1	0.0	0.1	0.1	1.7	10.3	20.7	0.001
Browsed <5m	0.0	0.0	0.0	0.3	0.8	0.8	11.6	0.041
Unbrowsed <5m	0.1	0.0	0.2	4.4	4.3	28.9	17.76	0.003
% Browsed <5m	0.0	0.0	0.0	13.3	21.6	9.7	0.00	1.0
All trees <5m	0.1	0.0	0.2	4.7	5.1	29.7	18.1	0.003
Trees >5m	0.0	0.0	0.0	1.1	1.1	1.0	25.2	0.001
All trees	0.1	0.0	0.2	5.8	6.2	30.7	27.02	0.001

Table 165. Results of tests for significant differences in average number of browsed and unbrowsed Douglas fir per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the edge. Results were compared among clearcut sites and among forest sites. Data are summarized by size class. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicate insufficient data. H, F, and P values of tests are given in the table.

	Clearcut H	P <	Forested F/H	P <
Browsed <1m			F0.37	0.695
Unbrowsed <1m	1.02	0.599	F3.18	0.052
% Browsed <1m			H1.57	0.455
All trees <1m	1.024	0.599	F3.11	0.548
Browsed 1-5m			H2.69	0.259
Unbrowsed 1-5m	1.023	0.56	H7.11	0.029
% Browsed 1-5m			H0.28	0.871
All trees 1-5m	1.023	0.56	H5.73	0.057
Browsed <5m			F2.53	0.092
Unbrowsed <5m	1.024	0.599	H2.21	0.331
% Browsed <5m			H0.19	0.905
All trees <5m	1.024	0.599	H2.14	0.343
Trees >5m			H0.31	0.736
All trees	1.024	0.599	H1.11	0.574

Table 166. Differences in average number of browsed and unbrowsed Douglas fir per 0.02-ha plot in clearcut and forested locations ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Data are summarized by size class. Student's t-test was used to compare averages. T and P values of tests are given in the table.

	Clearcut	Forest	T	P <
Browsed <1m	0.0	0.2	-2.07	0.041
Unbrowsed <1m	0.1	8.9	-1.77	0.079
% Browsed <1m	0.0	6.1	-0.59	0.567
All trees <1m	0.1	9.1	-1.8	0.075
Browsed 1-5m	0.0	0.5	-2.8	0.006
Unbrowsed 1-5m	0.0	3.6	-1.54	0.126
% Browsed 1-5m	0.0	30.1	-1.03	0.314
All trees 1-5m	0.0	4.0	-1.72	0.089
Browsed <5m	0.0	0.6	-2.76	0.007
Unbrowsed <5m	0.1	12.5	-1.71	0.089
% Browsed <5m	0.0	14.7	-0.92	0.368
All trees <5m	0.1	13.1	-1.79	0.077
Trees >5m	0.0	1.1	-4.12	0.001
All trees	0.1	14.2	-1.91	0.059

Table 167. Average number of browsed and unbrowsed whitebark pine per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the edge. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. H and P values of tests are given in the table.

	100	50	4-clearcut	4-forest	50	100	H	P <
Browsed <1m	0.1	0.2	0.1	0.3	1.6	1.1	10.81	0.055
Unbrowsed <1m	1.3	2.0	3.2	8.3	7.5	14.5	14.3	0.014
% Browsed <1m	15.0	4.9	3.6	4.2	7.7	12.6	5.49	0.358
All trees <1m	1.5	2.2	3.3	8.6	9.1	15.6	14.65	0.012
Browsed 1-5m	0.1	0.1	0.1	0.3	2.3	1.6	10.28	0.067
Unbrowsed 1-5m	2.1	2.3	1.8	3.3	1.5	3.7	4.09	0.535
% Browsed 1-5m	2.3	5.5	3.6	5.4	52.8	24.3	13.58	0.019
All trees 1-5m	2.2	2.4	1.9	3.6	3.7	5.3	4.0	0.548
Browsed <5m	0.3	0.0	0.1	0.6	3.9	2.7	18.97	0.002
Unbrowsed <5m	3.4	0.3	5.0	11.6	9.1	18.3	26.36	0.001
% Browsed <5m	5.6	0.0	2.5	5.6	13.5	14.5	13.98	0.015
All trees <5m	3.7	4.6	5.1	12.2	12.9	20.9	10.22	0.069
Trees >5m	0.0	0.0	0.0	1.3	1.1	1.5	27.81	0.001
All trees	3.7	4.6	5.1	13.5	14.0	22.4	15.8	0.007

Table 168. Results of tests for significant differences in average number of browsed and unbrowsed whitebark per 0.02-ha plot in clearcut and forested locations at different distances from the clearcut/forest boundary ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the boundary. Results were compared among clearcut sites and among forest sites. Data are summarized by size class. Kruskal-Wallis ANOVA by ranks was used to test for differences among averages. Blanks indicate insufficient data. H and P values of tests are given in the table.

	Clearcut H	P <	Forested H	P <
Browsed <1m	0.473	0.789	2.59	0.273
Unbrowsed <1m	0.82	0.664	0.88	0.642
% Browsed <1m	0.21	0.9	2.96	0.228
All trees <1m	0.614	0.736	0.99	0.608
Browsed 1-5m	0.003	0.999	2.2	0.332
Unbrowsed 1-5m	0.411	0.814	3.41	0.181
% Browsed 1-5m	0.029	0.986	5.35	0.069
All trees 1-5m	0.502	0.778	2.15	0.341
Browsed <5m	2.09	0.351	3.08	0.214
Unbrowsed <5m	12.35	0.002	1.53	0.466
% Browsed <5m	0.552	0.759	2.29	0.318
All trees <5m	12.35	0.002	1.35	0.509
Trees >5m			1.57	0.457
All trees	12.35	0.002	1.43	0.49

Table 169. Differences in average number of browsed and unbrowsed whitebark pine per 0.02-ha plot in clearcut and forested locations ($P < 0.05$). Sample plots were paired in 25-year-old clearcuts and mature lodgepole forests at 4, 50, and 100 meters from the clearcut/forest boundary. Results were compared between clearcut and forest sites combined. Data are summarized by size class. Student's t-test was used to compare averages. T and P values of tests are given in the table.

	Clearcut	Forest	T	P <
Browsed <1m	0.1	0.9	-2.54	0.013
Unbrowsed <1m	2.2	10.1	-4.03	0.001
% Browsed <1m	8.3	8.2	0.03	0.979
All trees <1m	2.3	11.1	-4.15	0.001
Browsed 1-5m	0.19	1.4	-2.5	0.14
Unbrowsed 1-5m	2.1	2.8	-0.94	0.349
% Browsed 1-5m	3.9	26.1	-2.94	0.005
All trees 1-5m	2.2	4.2	-1.9	0.061
Browsed <5m	0.1	2.4	-2.82	0.006
Unbrowsed <5m	2.9	12.9	-4.19	0.001
% Browsed <5m	3.9	11.3	-1.85	0.069
All trees <5m	3.0	15.4	-4.39	0.001
Trees >5m	0.0	1.3	-3.79	0.001
All trees	3.0	16.6	-4.8	0.001

APPENDIX W

RESULTS OF TESTS FOR SIGNIFICANT DIFFERENCES
IN AVERAGE NUMBER OF BROWSED TWIGS, AVERAGE ANNUAL HEIGHT
AND AVERAGE ANNUAL TWIGS PRODUCED AMONG 7 WILLOW COMMUNITIES,
7 WILLOW AND 1 BIRCH SPECIES, AND 7 YEARS (BETWEEN 1988 – 1997)

Table 170. Average annual height per plot of 7 willow, 1 birch, and all species combined in centimeters. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	P <
Wolf's	62.1	47.2	41.0	47.8	48.4	47.0	48.2	F0.55	0.768
Booth's	130.9	130.1	117.5	114.8	128.8	126.8	126.0	F0.12	0.993
Farr's	102.2	102.1	99.2	93.8	79.2	70.2	73.7	F2.97	0.009
Drummonds	127.0	126.2	111.9	108.4	106.9	96.8	116.6	F0.17	0.983
Barclay's	135.0	135.0	123.0	121.3	119.2	113.5	104.0	F0.95	0.472
Geyer's	125.3	125.7	101.1	115.6	162.3	160.9	196.8	H50.95	0.001
Eastwood's	108.6	112.4	125.1	116.8	88.2	94.2	85.3	F10.48	0.001
Dwarf birch	86.4	83.2	100.0	93.3	81.4	81.4	82.4	H2.82	0.831
All	110.9	107.2	96.4	95.5	99.9	95.8	100.8	F0.4	0.876

Table 171. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual height of Eastwood's willow per 1-m plot among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.568					
1990	0.063	0.136				
1991	0.440	0.515	0.209			
1995	0.006*	0.002*	0.001*	0.001*		
1996	0.030*	0.017*	0.001*	0.004*	0.370	
1997	0.003*	0.001	0.001*	0.001*	0.663	0.377

Table 172. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual height of Farr's willow per 1-m plot among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.992					
1990	0.961	0.796				
1991	0.881	0.745	0.637			
1995	0.254	0.182	0.184	0.199		
1996	0.073	0.057	0.081	0.162	0.712	
1997	0.124	0.092	0.114	0.183	0.634	0.757

Table 173. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average height of willow per 1-m plot among 7 willow communities (*indicates significance).

	1	2	3	4	5	6
1 Fisher Creek						
2 Soda Butte	0.001*					
3 Bannock	0.951	0.025*				
4 Warm Creek	0.001*	0.001*	0.001*			
5 Frenchy's	0.029	0.001*	0.014*	0.144		
6. Lost Creek	0.010*	0.001*	0.009*	0.165	0.621	
7. Slough Creek	0.861	0.019*	0.899	0.001*	0.026*	0.011*

Table 174. Average annual height of willow per 1-m plot in centimeters, all species combined, at each willow stand. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicate insufficient data. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	<P
Fisher Creek	108.6	112.4	125.1	116.7	88.2	94.2	85.3	F10.48	0.001
Soda Butte	154.8	159.8	148.7	145.5	132.9	124.4	106.5	H8.93	0.178
Bannock	119.3	115.1	114.2	106.8	92.9	85.7	84.5	F0.96	0.468
Warm Creek	67.7	56.9	41.7	46.4	35.1	30.1	33.7	H108.88	0.001
Frenchy's	96.7	80.0	53.2	48.8				F0.59	0.633
Lost Creek	75.2	69.0	42.9	52.3	59.9	57.9	84.4	F0.87	0.542
Slough Creek	91.7	88.7	82.4	89.3	118.6	120.7	139.0	F1.2	0.344

Table 175. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average height of willow per 1-m plot among the years 1988-1991 and 1995-1997 at the Fisher Creek willow stand (*indicates significance).

	1998	1989	1990	1991	1995	1996
1988						
1989	0.568					
1990	0.063	0.136				
1991	0.440	0.515	0.209			
1995	0.006*	0.002*	0.001*	0.001*		
1996	0.030*	0.017*	0.001*	0.004*	0.370	
1997	0.003*	0.001*	0.001*	0.001*	0.663	0.377

Table 176. Average annual utilization per 1-m plot for each species. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	P <
Wolf's	7.4	40.9	24.4	42.7	23.2	29.3	12.7	H13.36	0.038
Booth's	15.5	61.4	35.9	30.5	19.4	22.1	20.8	H20.56	0.002
Farr's	15.3	38.2	32.8	17.9	17.1	19.9	21.0	F9.94	0.001
Drummonds	20.1	56.5	33.3	34.1	26.1	20.2	18.6	F4.48	0.005
Barclay's	27.8	51.3	49.9	37.6	16.7	23.6	30.0	F4.03	0.003
Geyer's	24.5	64.9	30.5	36.3	10.8	6.5	1.2	H54.9	0.001
Eastwood's	0.0	0.9	0.4	0.1	0.7	2.2	0.3	H47.49	0.001
Dwarf birch	26.7	37.6	29.2	40.9	30.3	33.2	17.9	H9.23	0.161
All	16.2	49.7	30.9	32.3	20.5	21.7	17.9	F14.94	0.001

Table 177. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot of 7 willow and 1 birch species among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.010*	0.001*				
1991	0.003*	0.001*	0.999			
1995	0.965	0.001*	0.249	0.129		
1996	0.888	0.001*	0.404	0.235	0.999	
1997	0.999	0.001*	0.066	0.028*	0.998	0.982

Table 178. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot of Farr's willow among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.170				
1991	0.783	0.001*	0.001*			
1995	0.641	0.001*	0.001*	0.841		
1996	0.655	0.001*	0.003*	0.624	0.769	
1997	0.598	0.001*	0.003*	0.715	0.761	0.772

Table 179. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot of Drummond's willow among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.006*					
1990	0.465	0.042*				
1991	0.534	0.020*	0.934			
1995	0.782	0.013*	0.428	0.651		
1996	0.991	0.005*	0.325	0.424	0.515	
1997	0.868	0.006*	0.484	0.525	0.834	0.982

Table 180. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot of Barclay's willow among the years 1988-1991 and 1995-1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.104					
1990	0.097	0.884				
1991	0.543	0.312	0.191			
1995	0.454	0.010*	0.011*	0.177		
1996	0.647	0.051	0.052	0.434	0.458	
1997	0.812	0.117	0.093	0.416	0.477	0.764

Table 181. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot among 8 species. Eastwood's willow is included (* indicates significance).

	Wolf's	Booth's	Farr's	Drummond's	Barclay	Geyer's	Eastwood's
Wolf's							
Booth's	0.814						
Farr's	0.031*	0.058					
Drummonds	0.984	0.554	0.021*				
Barclay's	0.326	0.382	0.001*	0.576			
Geyer's	0.183	0.161	0.377	0.114	0.023*		
Eastwood's	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*	0.001*
Dwarf birch	0.420	0.335	0.001*	0.578	0.784	0.014*	0.001*

Table 182. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot among 7 species. Eastwood's willow is not included (* indicates significance).

	Wolf's	Booth's	Farr's	Drummond's	Barclay	Geyer's
Wolf's						
Booth's	0.849					
Farr's	0.502	0.456				
Drummonds	0.703	0.103	0.004*			
Barclay's	0.985	0.598	0.666	0.050		
Geyer's	0.381	0.486	0.807	0.007*	0.644	
Dwarf birch	0.275	0.211	0.041*	0.431	0.177	0.058

Table 183. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual percent of browsed willow twigs per 1-m plot among 7 willow communities (*indicates significance).

	1	2	3	4	5	6
1 Fisher Creek						
2 Soda Butte	0.001*					
3 Bannock	0.001*	0.841				
4 Warm Creek	0.001*	0.772	0.787			
5 Frenchy's	0.001*	0.550	0.654	0.648		
6. Lost Creek	0.001*	0.406	0.280	0.349	0.605	
7. Slough Creek	0.001*	0.581	0.527	0.573	0.692	0.576

Table 184. Average annual utilization at each location. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. Blanks indicate insufficient data. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	P <
Fisher Creek	0.0	0.9	0.4	0.1	0.7	2.2	0.3	H47.49	0.001
Soda Butte	20.2	50.6	44.5	25.2	17.7	24.4	31.1	H22.12	0.001
Bannock	22.9	49.5	45.2	39.4	29.9	30.9	20.8	H23.88	0.001
Warm Creek	1.9	43.8	50.4	33.7	20.8	42.3	19.3	H101.36	0.001
Frenchy's	13.0	41.0	11.7	41.4				F1.48	0.29
Lost Creek	10.3	46.9	19.0	32.5	19.6	11.0	5.9	H13.43	0.036
Slough Creek	15.3	66.5	18.4	31.4	15.5	12.4	10.4	H15.57	0.016

Table 185. Average number of twigs per plot without sites where willow did not persist. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	P <
Wolf's	347.4	129.2	141.5	198.9	255.5	243.9	157.8	F25.82	0.001
Booth's	252.1	159.1	179.7	203.5	262.5	283.3	216.4	F8.93	0.001
Farr's	300.4	138.5	170.1	276.8	264.1	278.7	263.9	F7.11	0.001
Drummond's	221.4	127.6	140.5	167.9	272.9	299.2	219.5	F9.93	0.001
Barclay's	234.3	172.8	205.3	170.3	221.0	257.7	167.5	F0.44	0.846
Geyer's	290.4	84.8	119.1	124.7	329.0	379.5	348.9	H55.56	0.001
Eastwood's	370.9	313.4	273.0	372.4	250.8	267.7	256.5	F5.16	0.001
Dwarf birch	76.6	49.4	45.9	48.3	126.6	74.3	74.3	H4.42	0.62
All	284.1	161.2	171.2	218.0	258.8	272.2	216.4	F30.9	0.001

Table 186. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of 7 willow and 1 birch species among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.413				
1991	0.001*	0.001*	0.001*			
1995	0.097	0.001*	0.001*	0.001*		
1996	0.333	0.001*	0.001*	0.001*	0.272	
1997	0.001*	0.001*	0.001*	0.893	0.002*	0.001*

Table 187. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Wolf's willow among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.569				
1991	0.001*	0.007	0.021			
1995	0.001*	0.001*	0.001*	0.024		
1996	0.001*	0.001*	0.001*	0.037	0.594	
1997	0.001*	0.381	0.449	0.057	0.001*	0.001*

Table 188. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Booth's willow among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.004*	0.339				
1991	0.062	0.098	0.269			
1995	0.630	0.001*	0.001*	0.031		
1996	0.317	0.001*	0.001*	0.001*	0.335	
1997	0.097	0.039*	0.203	0.548	0.082	0.010*

Table 189. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual average number of willow twigs per 1-m plot of Farr's willow among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.335				
1991	0.751	0.001*	0.006*			
1995	0.682	0.001*	0.011*	0.695		
1996	0.508	0.001*	0.008*	0.954	0.895	
1997	0.799	0.001*	0.004*	0.918	0.997	0.969

Table 190. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Drummond's willow among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.011*					
1990	0.029*	0.660				
1991	0.160	0.351	0.347			
1995	0.078	0.001*	0.001*	0.002*		
1996	0.021*	0.001*	0.001*	0.001*	0.368	
1997	0.949	0.009*	0.019*	0.078	0.161	0.033*

Table 191. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Eastwood's willow among the years 1988-1991 and 1995-1997. Data excludes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.079					
1990	0.008*	0.217				
1991	0.962	0.168	0.013*			
1995	0.003*	0.309	0.905	0.004*		
1996	0.009*	0.341	0.869	0.012*	0.864	
1997	0.004*	0.302	0.868	0.005*	0.862	0.733

Table 192. Average number of twigs per plot, including plots where willow did not persist. Differences among means were determined using ANOVA or Kruskal-Wallis ANOVA by ranks. H, F, and P values of tests are given in the table.

	1988	1989	1990	1991	1995	1996	1997	F/H	P <
Wolf's	322.9	126.2	116.6	165.9	237.2	212.6	141.1	F31.66	0.001
Booth's	234.3	172.8	205.3	170.3	221.0	257.7	167.5	F0.44	0.846
Farr's	293.9	135.8	170.1	276.8	264.1	278.7	245.3	F7.49	0.001
Drummonds	220.9	127.6	132.4	158.1	272.9	303.4	219.6	F11.07	0.001
Barclay's	243.5	154.5	163.6	172.1	273.8	278.9	223.6	F12.4	0.001
Geyer's	306.5	68.8	86.9	101.0	329.0	381.9	348.9	F38.8	0.001
Eastwood's	367.2	309.4	267.4	371.8	250.8	267.7	256.5	F5.18	0.001
Dwarf birch	59.7	37.5	42.3	45.9	97.9	62.7	69.2	F2.36	0.042
All	278.9	152.6	150.4	193.1	255.3	260.4	208.4	41.16	0.001

Table 193. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual average number of twigs per 1-m plot among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.849				
1991	0.001*	0.001*	0.001*			
1995	0.109	0.001*	0.001*	0.001*		
1996	0.116	0.001*	0.001*	0.001*	0.659	
1997	0.001*	0.001*	0.001*	0.196	0.001*	0.001*

Table 194. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual average number of willow twigs per 1-m plot of Wolf's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.633				
1991	0.001*	0.117	0.067			
1995	0.001*	0.001*	0.001*	0.001*		
1996	0.001*	0.001*	0.001*	0.020*	0.221	
1997	0.001*	0.458	0.441	0.216	0.001*	0.001*

Table 195. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Farr's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.281				
1991	0.853	0.001*	0.004*			
1995	0.783	0.001*	0.009*	0.687		
1996	0.633	0.001*	0.006*	0.952	0.889	
1997	0.542	0.002*	0.018*	0.580	0.554	0.717

Table 196. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Drummond's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.011*					
1990	0.012*	0.870				
1991	0.076	0.542	0.373			
1995	0.072	0.001*	0.001*	0.001*		
1996	0.012	0.001*	0.001*	0.001*	0.291	
1997	0.962	0.008*	0.007*	0.034*	0.155	0.020*

Table 197. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Barclay's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.847					
1990	0.922	0.669				
1991	0.913	0.974	0.888			
1995	0.861	0.800	0.837	0.907		
1996	0.759	0.792	0.899	0.853	0.878	
1997	0.947	0.997	0.958	0.970	0.953	0.891

Table 198. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Geyer's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.001*					
1990	0.001*	0.580				
1991	0.001*	0.586	0.665			
1995	0.493	0.001*	0.001*	0.001*		
1996	0.102	0.001*	0.001*	0.001*	0.241	
1997	0.399	0.001*	0.001*	0.001*	0.543	0.314

Table 199. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of willow twigs per 1-m plot of Eastwood's willow among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.074					
1990	0.011*	0.396				
1991	0.889	0.131	0.011*			
1995	0.004*	0.366	0.864	0.003*		
1996	0.006*	0.196	0.995	0.007*	0.953	
1997	0.006*	0.357	0.735	0.005*	0.860	0.936

Table 200. Results of Newman-Keuls *post hoc* test for significant differences ($P < 0.05$) in average annual number of twigs per 1-m plot of dwarf birch among the years 1988-1991 and 1995-1997. Data includes study plots where willow died and did not reestablish before 1997 (*indicates significance).

	1988	1989	1990	1991	1995	1996
1988						
1989	0.880					
1990	0.831	0.873				
1991	0.646	0.958	0.905			
1995	0.582	0.416	0.439	0.420		
1996	0.922	0.917	0.904	0.841	0.472	
1997	0.946	0.895	0.896	0.863	0.342	0.828

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