Mechanisms Influencing the Spatial Dynamics of the Central Yellowstone Bison Herd

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SUMMARY

This dissertation will be built upon a framework of four primary topics that consider the ecology of Yellowstone National Park's central bison herd across a range of spatial and temporal scales. On the broadest of these scales is the range expansion of the central herd that has occurred from east central to west central Yellowstone over the last forty years. Across a comparable spatial range, but of interest on an annual basis, is the central herd's migration from the summer range in the Hayden and Pelican Valleys to the winter range in the Madison, Gibbon, and Firehole drainages. This migration usually occurs relatively gradually over a span of months from November to April each year.

Once bison have migrated to the Madison-Gibbon-Firehole (MGF) winter range a new array of scales become important in their winter ecology. Bison use of the MGF is not spatially uniform as groups prefer certain regions over others as the winter progresses and the perceived value of these areas change to bison. Spatially this selection for different areas may be noticeable on a scale as large as one of the three river drainages. On a temporal basis these changes may manifest themselves as often as a daily basis. Comparing the attributes of the principal foraging areas within the MGF is imperative to understanding why bison discriminate between them. In order to conduct these analyses it is necessary to examine individual foraging areas and their attributes that affect bison decisions on a temporal scale that is as small as seconds.

Just as important as comprehending why bison differentiate between foraging areas is learning how they use the MGF landscape to travel between them. Bison preferences for developing and using trails along natural travel corridors is evident in the MGF as bison have established a travel network over the past few decades. The entire MGF landscape is not traveled equally by bison as certain regions do receive higher use than others. In addition, the magnitude of use of certain portions of their travel network varies temporally based upon biotic and abiotic factors. Owing partially to the fact that portions of the bison travel network overlap with segments of the road network used by visitors throughout the winter, a debate over winter recreation in Yellowstone has intensified over the last decade.

The purpose of this project is to integrate long-term data available from past research initiatives that have identified patterns of spatial distribution exhibited by bison. In addition, this study will examine specific movements between winter range foraging areas to identify the impetuses governing bison foraging decisions. Also, it is anticipated that significant differences in nutritional status can be detected between bison that migrate to the winter range compared to those that remain in the Hayden and Pelican Valleys throughout the entire winter. Finally, this study is exploring in more detail how bison move across the landscape between areas of high and low occupancy of habitats and identifying the ecological drivers of these spatial dynamics.

INTRODUCTION

The spatial dynamics of the central Yellowstone National Park (YNP) bison herd are complex and operate at several spatial and temporal scales. Historically, the population occupied the Pelican and Hayden grassland-sagebrush valleys of central Yellowstone and was essentially sedentary, living within these valleys year-round. As the population recovered from near extirpation, per capita resources within these valleys became limited, forcing the population to expand its range westward and down the natural elevation gradient presented by the Nez Perce drainage (Bjornlie and Garrott 2001). This range expansion reestablished what appear to be traditional migratory behaviors that existed prior to the severe human exploitation that occurred in the second half of the 19th century. The timing and extent of the annual migration to the Madison-Gibbon-Firehole (MGF) winter range is quite variable from year to year and is believed to be driven by a combination of population size and the stochastic annual climate (Bjornlie and Garrott 2001). Climate affects plant productivity during the growing season (Frank and McNaughton 1992) in the central Yellowstone valleys and snowpack dynamics during the winter period (Farnes et al. 1999). Understanding these interactions is essential to sound management of the bison population, as it is these mechanisms that are hypothesized to influence the propensity for animals to cross the western boundary of the Park into the Hebgen Lake Basin. It is beyond Park boundaries where bison are subjected to highly political and controversial control actions to protect livestock from the potential of Brucellosis transmission (Baskin 1998).

The impetus for bison movements between foraging areas within the Madison-Firehole winter range is not well understood. Considering the foraging ecology and nutritional requirements of herbivores lends some insight into the complex spatial dynamics of the central herd. The mobile, nomadic lifestyle of bison suggests an inherent ability to effectively exploit an ephemeral resource base throughout both space and time. The theory behind acceptance or refusal of a foraging area is rooted in the principles of marginal value by comparing the immediate gain expected from one area versus another, factoring in the travel time required between locations in the process (Owen-Smith 2002). Likewise, food in feeding patches—contained within foraging areas—should be accepted if the benefit from consuming it outweighs the opportunity cost of searching for and eating a more profitable item within the time entailed (Stephens and Krebs 1986). Departure from a patch is predicated upon a situation of diminishing returns as the benefits of continuing to feed in the present patch become outweighed by those offered in seeking a new patch.

Movements between winter range foraging areas by bison are intricate and highly variable on multiple temporal scales. Transient changes in plant phenology and snowpack quality throughout the winter and early spring are two factors that likely influence bison spatial dynamics. Fryxell (1991) suggests that aggregation patterns of large herbivores are influenced both by maturational changes in forage quality as well as spatial variations in primary productivity. In the former, vegetation is maintained in a "grazing lawn" state—being immature, nutritional, and of low biomass (but high biomass concentration)—by a large number of herbivores (McNaughton 1984, Hobbs and Swift 1988). The latter factor, seen in some African ecosystems by McNaughton (1985) and Western (1975), can become of increasing importance outside of the main growing season as populations become fragmented and herbivores concentrated in areas of higher quality vegetation.

Detailed studies of snowpack influences on fine scale ungulate spatial dynamics are limited, especially in a severe winter climate such as that in Yellowstone. On a broad, general spatial scale Sweeney and Sweeney (1984) documented that elk in southwestern Colorado are sensitive to snow depths greater than 40 cm. This cognizance manifests itself in an alteration of habitat usage and winter range area. Coupled to this is the regulation of the initiation and pattern of elk migration by snow cover. In an examination of snowpack characteristics Pruitt (1959) observed that a primary area of caribou concentration shifted as much as 65 km in response to an increase in density and hardness of the snowpack. In addition, he found that caribou winter movements occurred along a gradient from areas containing snow with high density and hardness to those with lighter weight, softer snow. At a finer scale, Turner et al. (1993) present a winter foraging simulation model for elk and bison in Yellowstone's northern range that predicted when resources are scarce the ability of ungulates to discern forage abundance and move in response resulted in lower mortality. In contrast, in a situation of abundant resources the search-and-move strategy was relatively inconsequential for survival.

Within the MGF is the added complexity of a polarity in snowpack characteristics—geothermally influenced areas contain little to no snow while some surrounding regions retain prohibitively deep snow, with a high snow water equivalent (SWE), for ungulate foraging. Perhaps the most apropos novel research for this study is that by Messer (2003) with a focus on elk winter habitat usage within the MGF. Using the non-migratory Madison-Firehole elk herd, Messer considered the impacts of SWE on how elk distribute themselves using both landscape-scale snow conditions and local snow patterns. As we strive for analysis of bison movements in relation to SWE at fine spatial scales this work will undoubtedly prove valuable.

In addition, bison are at the center of Yellowstone's winter recreation debate as the population has grown from 1,800 in 1979 (National Park Service 2000a) to over 4,000 at present (Wallen personal communication). Meagher (1993) stated that road grooming, done to facilitate winter visitor access, was the major influence in both dramatic increases in the bison population and range expansion both within and beyond YNP boundaries. She purports that the roads provide a means of energy-efficient travel between foraging areas as bison seek out the groomed roads as an alternative to traveling through deep snow. The overall energy savings result in reduced bison winter kill and improved calf survival (Meagher 1993). Recommendations from Meagher (1993) included either fully or partially closing interior YNP roads to winter travel—an action that would negatively impact the economies of gateway towns (National Park Service 2000b) and deny the public to enjoy winter in Yellowstone. The debate intensified after the harsh winter of 1996-97 when hundreds of bison left YNP in search of more accessible forage. Acting under an interim management plan, the National Park Service (NPS) killed nearly 1,100 bison that left the Park to protect livestock in surrounding areas from the possibility of contracting the disease brucellosis, carried by some bison (Baskin 1998, Cheville et al. 1998, NPS 2000a). Litigation by environmental groups followed, leading the NPS to write Environmental Impact Statements (EIS) to provide YNP with both bison management and winter use plans (NPS 2000a, NPS 2000b).

To evaluate the effect of road grooming on bison for the EIS, Bjornlie and Garrott (2001) conducted a two-year study on the distribution, movements, and activities of YNP's central bison herd, which is at the middle of the controversy as its entire range is located within the Park's interior. They concluded that groomed road use by bison on the Madison-Firehole winter range is neither sought out nor avoided as the lowest magnitude of bison road travel occurred during the road grooming period. Locations where the roads received the most bison use were in areas of topographic constriction or high bison concentration. In addition, the majority of travel occurred off roads as bison, to avoid unnecessary energy expenditure displacing snow, established a network of trails that incorporated geothermal features as well as stream corridors (Bjornlie and Garrott 2001). This work has drawn criticism from environmental groups as being conducted over a short time period, during mild winters, in a small study area, and using irrelevant data (Fund for Animals Public Communication). At present, the debate and litigation over winter recreation in YNP continues. In the winter of 2003-04 YNP remained open to OSVs, but at reduced daily numbers of guided snowmobiles.

The purpose of this project is to integrate data available from past research initiatives that have identified patterns of spatial distribution exhibited by bison (Bjornlie and Garrott 2001, Hardy 2001, Ferrari and Garrott 2002). Furthermore, this study is exploring in more detail how bison move across the landscape between areas of high and low occupancy of habitats and identifying the ecological drivers of these spatial dynamics. The implications of addressing these issues are of utmost importance for managers at Yellowstone National Park, who need to understand these patterns of movement relative to bison ecology for implementing the Joint Bison Management Plan (National Park Service 2000a). An insight into how and when bison are apt to move across the landscape may help predict when animals are likely to move towards, and outside of, Park boundaries where they may be subject to control actions. In addition, understanding movement patterns will provide a mechanism for choosing locations to implement a remote vaccination program that delivers vaccines to a higher proportion of eligible individuals (National Park Service 2000a). Finally, the Park needs to understand the physical distribution of the bison travel network to objectively compare how it interfaces with human travel networks—primarily the road network used by motor vehicles. Overall, this project will provide the Park with a robust data set to educate the staff and visiting public about the ecological dynamics of bison population movements across the landscape of central Yellowstone National Park. In addition, this study will detail the relationship between snowpack dynamics, plant phenology, and the propensity for bison to travel between foraging areas and habitats across the landscape.

STUDY AREA

The Madison-Gibbon-Firehole (MGF) study area (Figure 1) in west central YNP consists of the drainages of the Firehole River upstream from Madison Junction to Old Faithful; the upper Madison River east from the Park boundary at West Yellowstone to Madison Junction, and the Gibbon River upstream to Norris Geyser Basin. Also included as part of an extended study area is the segment of the Mary Mountain trail extending from the Firehole drainage east to Mary Lake, the bison summer range in the Hayden Valley, and the meadows along Cougar Creek and Duck Creek along the western boundary of the Park. Elevations within the primary 8,000 ha study area range from 2,000 m to 2,250 m. The Hayden Valley and Mary Lake are at considerably higher elevation (2,440-2,500 m) while the Cougar Creek area is around 2,070 m.

The meadow complexes and geothermal regions within the primary study area are considered the principal winter range for the central YNP bison herd, which has increased from several hundred in the 1960s to around 2,800 at present (Meagher 1973, Bjornlie and Garrott 2001, Hess 2002, Wallen personal communication). Bison share this habitat with wildlife such as elk, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), a variety of waterfowl and raptors, coyotes (*Canis latrans*), and wolves—whose presence provides some predation pressure on the bison population. Sedges (*Carex* spp.) and grasses (*Calamagrostis* spp.) characterize wet meadows while dry meadows are dominated by grasses (*Poa* spp., *Festuca idahoensis*) and, in lower elevations in the Madison River valley, sagebrush (*Artemesia* spp.). During the summer of

1988 more than 50% of forested regions burned (Despain 1990) with these areas now characterized by downed trees, snags, regenerating lodgepole pine, Ross' sedge (*Carex rosii*), elk sedge (*Carex geyeri*), and leafy aster (*Aster foliaceus*). Unburned forested areas are predominantly lodgepole pine (*Pinus contortus*) with understories consisting of elk sedge, grouse whortleberry (*Vaccinium scoparium*), and pinegrass (*Calamagrostis rubescens*). At lower elevations scattered Douglas fir (*Pseudotsuga mensiesii*) exist with Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) found at higher elevations.

There are four major geothermal areas in the primary study area—the Upper, Midway, Lower, and Norris Geyser Basins—along with smaller pockets of geothermal activity (Watson et al. 2002). In addition, along Nez Perce Creek and the Mary Mountain trail there are a number of locations that have some geothermal influence. Within these regions are areas of reduced snow accumulation where the growing season is longer relative to surrounding regions that lack any geothermal influence. Owing to the thermal effluent from these areas the Firehole, Gibbon, and Madison Rivers remain ice-free throughout the winter.

Severe winters typify the MGF climate as the mean peak snow water equivalent (SWE) at the West Yellowstone Natural Resources Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) site (elevation 2,042 m) was 34.3 cm from 1966-2004 with 189 average number of days of snow cover (NRCS National Water and Climate Center 2004). Snowpack begins accumulating in late October in the valleys and continues to build until April, at which point ablation begins in average years. At higher elevations, such as that represented by the Madison Plateau SNOTEL site (elevation 2,362 m), snow begins accumulating in mid-October with snow cover remaining until the end of May. At this elevation the average peak SWE was 68.1 cm with average number of days with snow cover being 236 from 1968-2004 (NRCS National Water and Climate Center 2004).

Within the study area the road network consists of paved, two-lane roads that parallel the Madison, Gibbon, and Firehole Rivers. The 21.4 km section of road from West Yellowstone to Madison Junction passes through forest, along major meadow complexes, and through the Madison Canyon. From Madison Junction to Norris Junction and north to Nymph Lake the 25 km road section travels through the Gibbon Canyon and large meadow complexes in Gibbon Meadows and Elk Park. The Firehole River valley road system consists of the 28.8 km segment extending from Madison Junction south to Kepler Cascades, passing through Firehole Canyon as well as large meadow complexes and major geothermal areas. The roads within the study area are open to visitor travel in wheeled vehicles (WV) from mid-April until early November. From early November until mid-December the roads are closed to visitors, but open to WV travel by Park personnel as snow is allowed to accumulate and plowing is minimal. The OSV season lasts from mid-December until early March, during which time the roads are groomed daily for snowmobile and snowcoach travel by visitors. From the end of the OSV season until mid-April the study area is again closed to visitor travel, but the roads are plowed and open to WV travel by YNP personnel.

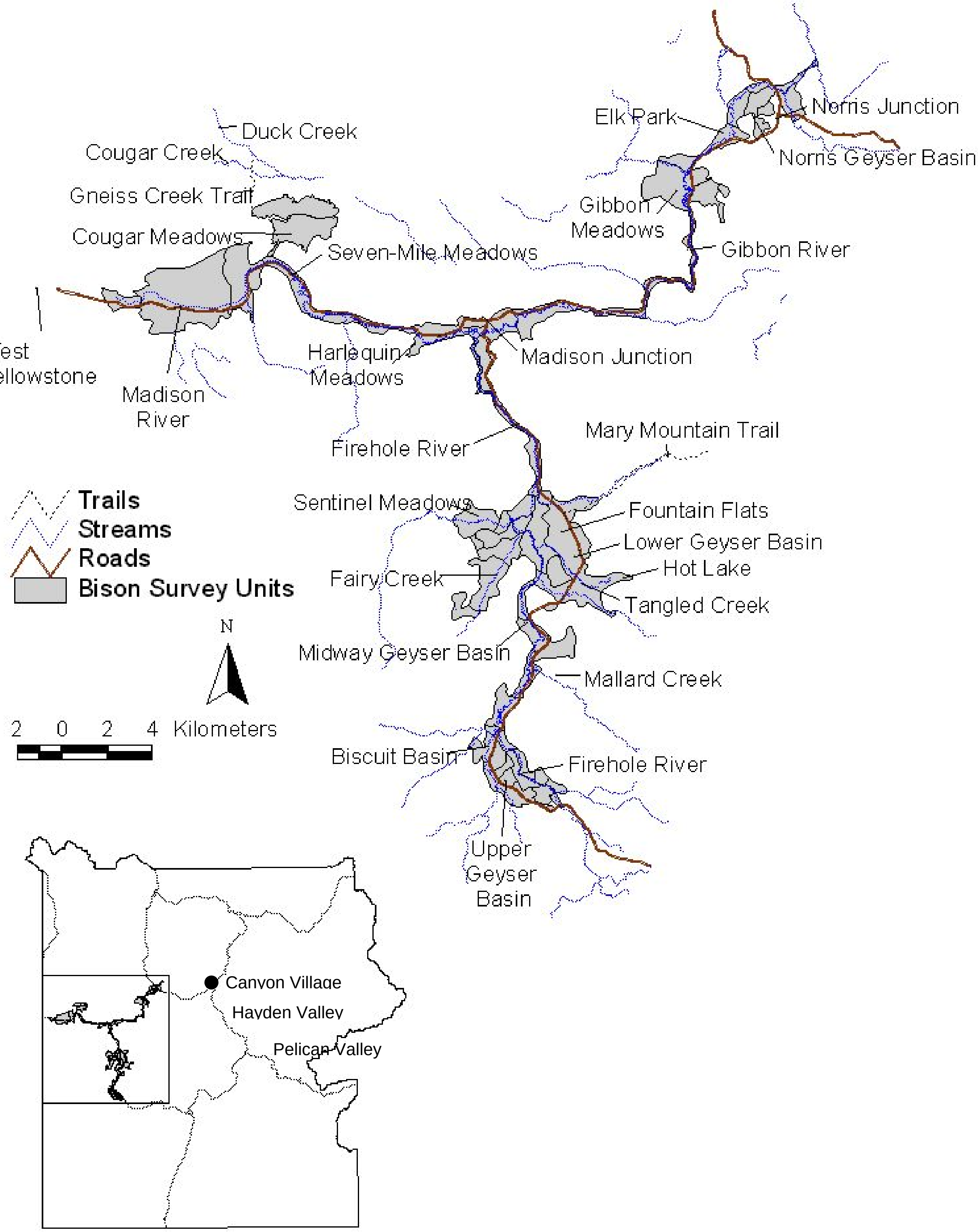

Figure 1. The study area in the Madison, Gibbon, and Firehole River Valleys with reference locations noted.

METHODS—GENERAL BISON FIELD TECHNIQUES

Bison Ground Distribution Surveys

The distribution and activities of the MGF bison population have been recorded over eight winter seasons (1996-97 through 2003-04) using a total of 99 comprehensive ground-based surveys conducted every 10-14 days from late fall until late spring. Using methodology developed by Ferrari (1999) and refined by Bjornlie (2000) these surveys afford a nearly complete enumeration of the central bison herd on its 79.6 km^2 winter range as 74 units are surveyed using six distinct survey routes. Surveys last two days with the first involving an examination of the Firehole drainage using three routes and the second encompassing both the Gibbon (two routes) and Madison River valleys (one route). On both days each member of a three-person crew survey one route using snowmobiles and/or snowshoes. In an effort to minimize double counting or missing bison, crew members start each route simultaneously (Bjornlie and Garrott 2001).

For each bison group detected a Universal Transverse Mercator (UTM) location is recorded along with the age and sex composition of the group as cows, bulls, calves of the year, newborn calves, and unknown adults. The activity of each bison is classified using scan sampling (Altmann 1974) as foraging, resting, or traveling. Foraging bison are considered as any animal actively feeding or searching for forage. Resting bison are defined as those either bedded or standing and not involved in foraging or traveling. Traveling bison are those engaged in sustained and purposeful travel and not in search of forage. For each traveling bison group a record is made of where the animals are moving—on the road, on an established bison trail, or off trail and off road. Within both the foraging and traveling activities the number of bison displacing or not displacing snow is quantified along with an approximate snow depth (Bjornlie and Garrott 2001).

Bison Road Use Surveys

Bison road travel data has been collected over seven winter seasons (1997-98 through 2003-04) with a four-person field crew traveling independently on the road system using snowmobiles or trucks on a daily basis. The 87.3 km road network was divided into 61 segments based primarily upon topographical similarities and common travel destinations. Each crew member keeps a daily travel log in order to determine survey effort (in km) within each road segment. If one segment is traveled multiple times within one-half hour, only one traverse of the segment is considered as survey effort and the rest discarded. When a bison group is encountered traveling on the road it is recorded. Road use observations consist of bison groups traveling on the road for at least 50 m as well as fresh tracks and signs of road travel. Data collected with each sighting includes the direction of travel and the nearest access and exit locations to and from the road based upon the defined road segments. In addition, the group age and sex classification is recorded using the same categories as in the ground surveys (Bjornlie and Garrott 2001).

Travel Network Monitoring

Bison use of major migratory and travel routes has been remotely monitored using Trailmaster 1500 infrared trail monitors connected to 35 mm cameras that were placed along the

Mary Mountain and Gneiss Creek trails in the 1997-98, 1998-99, 2002-03, and 2003-04 seasons. The Mary Mountain trail is believed to provide the primary bison migratory route between the Hayden Valley summer range and the MGF winter range (Meagher 1973, 1993; Bjornlie and Garrott 2001) while the Gneiss Creek trail provides an important connection between the Madison River Valley and Cougar Meadows area (Bjornlie and Garrott 2001). Monitor locations were chosen in spots along the trail in which bison were coerced to travel primarily single file and where the topography and habitat favored a route in front of the monitor. As bison pass through the infrared beam the date, time, and event number are recorded. When bison trigger a photograph the picture is stamped with the date and time affording comparisons with the Trailmaster event data. A 10-minute camera delay was programmed so that once the beam was broken and a photograph taken the camera would not take another picture until this time had elapsed. A photograph, combined with a monitor event at a given time, provided species and travel direction data for the lead animal in a group. If the lead animal in the photograph is a bison the subsequent events clustered shortly thereafter the time of the first event inform of how many bison were in the group. Several mechanical failures with the monitor have resulted in missing data during 1997-99 (Bjornlie and Garrott 2001) as well as during 2002-04.

Snowpack Variation and Landscape Covariates

A snowpack simulation model, developed by Dr. Fred Watson from California State University—Monterey Bay (Watson et al. in review), is being used to obtain fine-scale spatial and temporal prediction of SWE and landscape metrics across the MGF bison range for the 1996-97 through 2003-04 seasons. The model, using a water and energy balance on the snowpack, simulates SWE estimates for each 28.5 m^2 pixel in the landscape on a daily basis. Temporal data sources for the model include NRCS SNOTEL and climate stations surrounding the study area while spatial data for terrain, precipitation, and vegetation are derived from a digital elevation model (DEM), mean annual precipitation historic site statistics, and Landsat Enhanced Thematic Mapper (ETM) imagery, respectively (Watson et al. in review). Spatial data on areas of geothermal influence are mapped using Landsat ETM thermal imagery as described in Watson et al. (2002). To examine larger-scale trends in snowpack, data from remote NRCS SNOTEL sites located near Canyon Village and West Yellowstone (Figure 1) are being used. The Canyon site (elevation 2,466 m) provides an estimate of SWE for the Hayden Valley bison summer range while the West Yellowstone location (2,042 m) approximates SWE trends for lower-elevation valley bottoms in the MGF. Snow water equivalent is being used to characterize the snowpack throughout these analyses as it represents the mean water content of the snow and is more biologically relevant to affecting bison activity than snow depth (Farnes et al. 1996).

GPS Collars on Cow Bison

The initial deployment of global positioning system (GPS) collars on 15 cow bison occurred in fall of 2003 by Rick Wallen's National Park Service (NPS) Bison Management team. Collars, which were also equipped with radio-transmitters, were distributed on animals located throughout the summer range in the Hayden and Pelican Valleys as well as early migrants to the MGF winter range. Bison were immobilized using ground-based darting procedures that have been successful in recent epidemiology studies in the Park. The collars are collecting the locations of the animals for 12 months with seasonal variation in the frequency of location collection. During winter, locations were recorded every 30 minutes diurnally and three to four times at night. In the summer the collars were set to take location fixes five times during a 24-hour period. In December 2004 the bison whose collars have not blown off will be immobilized to remove the collar. After downloading data the collars will be reprogrammed, refurbished, and then redeployed by Wallen's NPS bison crew.

METHODS—WINTER RANGE BISON GROUP TRACKING

Bison Group Selection and Location

Collar surveys are conducted at least every two weeks throughout the winter to determine which of the 15 GPS collared cow bison are located in the MGF study area. Since bison move quite often, including into and out of the study area, searches consist of driving through each of the Madison, Gibbon, and Firehole drainages and checking for every possible frequency at multiple locations. Once the list of available study area collars is determined, a randomized order of the frequencies is generated to provide an unbiased selection technique and order in which to locate the bison. Each bison frequency is sampled without replacement until all of the available study area collars are located. A new random order is then generated and the procedure repeated. Diurnal locations are obtained using hand-held telemetry equipment and homing methods (White and Garrott 1990). Once the animal is found its UTM location is recorded along with the composition (cows, bulls, calves, newborn calves, unknown adults) of any other bison in the group. Locating the instrumented bison provides a means for selecting a group on which to record observations and a foraging area from which to record attributes.

Bison Behavioral Observations

Upon selecting the group, five-minute observations are conducted on five different foraging adult cow bison selected at random from the group. A voice recorder is used to document bison behavior as foraging, searching for forage, displacing snow, walking, standing/resting, standing/ruminating, bedded/resting, or bedded/ruminating. The time and type of each activity is later transcribed. At the beginning and between each of the individual observations a group herd activity scan is conducted using scan sampling (Altmann 1974) resulting in six scans over a 25 minute period. The number of bison doing each of the following activities is recorded: foraging/searching for forage, standing/resting, bedded/resting, and walking.

Foraging Area Attribute Sampling

As soon as possible after the group observations are finished the foraging area is sampled to obtain attribute measurements on the snowpack and vegetation. This is usually done within 24 hours of the time of the initial location, but depends upon bison presence in the area owing to safety concerns. Three measurements are taken on the snowpack: snow depth, snow water equivalent (SWE), and snow hardness. Only snow that has not been disturbed by bison foraging or traveling is sampled. Snow depth and SWE are measured using an aluminum snow corer by inserting the corer into the snow surface at a 90º angle and pushing it to the bottom of the snowpack. The depth is then recorded in inches marked on the side of the corer. The corer is then twisted to attach some ground material to its end and then carefully removed from the snowpack to ensure no loss of snow. After removing the ground material the corer is weighed using a hand-held spring balance calibrated to read the SWE in inches. An empty corer weight is recorded before beginning to sample the snowpack. Snowpack hardness is measured using a federal ram penetrometer—a stainless steel rod with a hardened 45º cone at its tip. The rod is vertically placed on the snow surface with the cone pointing down. Sliding weights are then dropped down the upper part of the rod from a known height to impart a force to the snowpack. The amount of weight dropped and the distance the rod penetrates the snowpack is recorded for each drop. This is continued until the rod has penetrated to the bottom of the snowpack.

A nested sampling design is used for all three of the snowpack measurements such that nine overall measurements of each are taken in three equilateral triangular clusters of three. The vertices of the triangular cluster are located 1 m apart to provide a means of sampling small-scale snowpack variability. Each of the clusters is spread throughout the foraging area to obtain a larger-scale representation of snowpack variability. These clusters are located immediately next to bison foraging craters in an attempt to measure the same snowpack characteristics that bison encountered during foraging bouts.

Three vegetation samples are clipped from randomly selected 0.25 m^2 square quadrats to provide a representative sample of the vegetation present throughout the foraging area. When snow is present in the foraging area, the vegetation samples are taken from locations of undisturbed snow located immediately next to bison foraging craters denoted by disturbed snow. When the foraging area is snow-free the clipped sample locations are taken from near the location where bison were observed foraging.

Bison Snow-Urine Sampling

Snow-urine samples are collected from individuals from each bison group observed provided there is enough snow in the area. Samples are collected after each group observation, if possible, or as soon after the group has left the foraging area. In collecting the sample the most urine-saturated snow is gathered and put into a plastic whirl-pak container for storage. After collection, samples are frozen and stored until they are assayed as described by DelGiudice et al. (1989).

DISSERTATION COMPONENTS

1. Mechanisms affecting the range expansion and migration of a bison herd

Objectives

The purpose of this study is to examine the large-scale annual migratory movements of the central herd from its summer to winter range as well as its range expansion from east central to west central Yellowstone that has occurred over the last forty years. In the analyses a suite of abiotic and biotic factors will be considered as hypothesized ecological driving forces that are believed to influence the timing and extent of the migration as well as how the historic range expansion has occurred. The abiotic factors that will be considered across the central herd's range include snowpack dynamics as well as the role that geothermally influenced areas play on the MGF winter range. The biotic factors to be analyzed include the effects of summer plant phenology and density dependence.

Snowpack dynamics will be examined both in the higher elevation Hayden and Pelican Valleys as well as on the Madison-Firehole winter range. Snowpack is important, as deeper snows on the summer range are believed to provide an impetus—in part—for bison to migrate to the relatively milder winter range climate. Geothermally influenced areas, located primarily on the winter range, may provide a more hospitable habitat for bison in the middle of winter owing in part to reduced snowpack and easier access to forage. The availability of forage to bison (i.e. lack of snowpack) is an important factor throughout winter that is dependent upon both the temporal and spatial patterns of snowpack accumulation and ablation.

Plant phenology is another possible factor influencing both the fall/winter migration as well as the return trip in late spring. The duration and extent of the growing season in the spring and early summer—affected by the amount of precipitation—may influence resource availability in the late summer and fall once the vegetation becomes senescent. In addition, the timing of snowmelt and subsequent green-up of vegetation both on the winter and summer ranges may affect the timing of the return migration as bison are likely to follow the green-up in an effort to obtain the most nutrient-rich forage.

The population size of the central herd is yet another potential driving force controlling both the timing and extent of the migration as per capita resource availability is directly affected by the number of bison within an area. It is believed that a combination of these abiotic and biotic factors act in concert to influence the bison migration. Also, it is likely that this same suite of conditions has also affected the range expansion of the central herd.

Methods Utilized

- Bison ground distribution surveys
- Snowpack simulation model
- National Park Service aerial bison surveys

Databases

- Bison ground distribution surveys
  - -Conducted biweekly from 1996-97 to 2003-04
  - -99 surveys conducted (average of 12 per season)
  - -7,522 bison groups mapped representing 74,226 individual bison
- National Park Service aerial bison surveys
  - -Meagher bison distribution data (1970-1997)—public data

Statistical Analyses

For the migration analysis the response variable is the number of bison located on the MGF winter range at two-week intervals. This will be determined from the population census from the biweekly bison ground distribution surveys. For the range expansion analysis one possible response variable is the number of bison located on the MGF winter range in late March, the month at which the MGF bison population usually reaches its peak. This response variable would be considered on an annual basis. Another possible response variable for the range expansion is the percent of the current central herd range (measured in area (km^2)) occupied each March. Both of these dependent variables would be obtained from National Park Service aerial surveys and the Meagher public database of bison distribution in Yellowstone.

Possible predictor variables for both analyses include the number of central herd bison, snowpack metrics, and an indicator of summer range plant phenology (i.e. summer precipitation, a drought index, etc.). Snowpack metrics will be calculated using the snowpack simulation model and will involve comparisons of SWE on the summer range relative to the MGF winter range. Likewise, forage availability (in the form of snow-free patches) can be determined for both ranges using the snowpack model. Hypotheses for both analyses will be expressed as a suite of multiple regression models. Models will be ranked using Akaike's Information Criterion (AIC) and the best approximating models supported by the data will be selected (Burnham and Anderson 2002) to identify the most influential covariates affecting migration and the range expansion.

2. Spatial dynamics of the central herd on the Madison-Firehole winter range

Objectives

The purpose of this study is to identify possible driving forces behind bison movements on the Madison-Firehole winter range. More specifically, the goal is to examine the relative importance of foraging area attributes on the amount of time (residence time, τ) bison spend in particular foraging areas on the Madison-Gibbon-Firehole winter range. The area attributes to be considered include snow depth, snow water equivalent (SWE), snowpack hardness, and plant biomass. Bison behavior may also be able to be considered as an area attribute using a combination of individual foraging cow observations as well as herd activity scans. A potential derived quantity of interest involves bison energetics for displacing snow that may be determined from snowpack hardness and depth measurements as well as individual bison observations. Another foraging area attribute of interest that will ideally be able to be considered is the phenology of vegetation during the spring green-up period.

The area residence time is of importance because it reflects the ability of an area to "hold" bison and satisfy nutritional needs. For this study I postulate that the amount of time bison spend in an area is a function of the quality or value of the foraging area. If costs exceed benefits over a given period of sampling time, bison will leave the foraging area in search of a more profitable area. Shorter residence times would indicate that bison are not finding what they require within a foraging area and, as a result, lead to a movement to a new area. This analysis will lend insight into the factors influencing the spatial dynamics on the winter range and provide a basis for comparing the "value" of foraging areas in the MGF across various spatial and temporal scales. Foraging area attributes can be considered important in terms of their perceived value to bison in a spatial and temporal manner as the same foraging areas can have a different value over time as the snowpack builds, possibly changes form (i.e. hardness), and—subsequently—melts. Likewise, although biomass will not change during the winter (save for the amount that bison remove from an area), the vegetation green-up that occurs in the spring undoubtedly influences the value of an area. By using what can be analyzed at a smaller scale—the foraging area in this study—it will be possible to understand and, possibly, predict bison foraging behavior across a hierarchy of spatial and temporal scales.

The examination of larger scales is imperative to comprehending why bison prefer to choose different foraging areas in the various drainages throughout the winter and spring. This will include an analysis as to why many bison move to and beyond Cougar Meadows in the spring and the factors that influence movements towards the western Park boundary.

Additionally, the role that geothermally influenced areas play in bison foraging area choice needs to be quantified. The possibility does exist that different seasons, or more specifically the presence or absence of different area attributes—snow versus no snow, high versus low biomass, and green versus senescent vegetation—govern winter range spatial dynamics differently.

Methods Utilized

- Winter range bison group tracking methods:
    - Bison group selection and location
    - Bison behavioral observations
    - Foraging area attribute sampling
    - Bison snow-urine sampling
- GPS collars on cow bison

Databases

- Bison group selection and location
  - -101 telemetry group locations; 117 individual locations
- Bison behavioral observations
  - -509 individual bison foraging observations (5 minutes each)
  - -101 group activity herd scans (25 minutes long with scans at 5 minute intervals)
- Foraging area attribute sampling
  - -Snowpack characterization
    - -Depth: 909 measurements from 101 locations
    - -SWE: 909 measurements from 101 locations
    - -Hardness: 288 measurements from 32 locations
  - -Forage biomass
    - -303 clippings from 101 locations
- Bison snow-urine sampling
  - -274 snow-urine samples from 40 group locations
- GPS collars on cow bison
  - -Location, date, and time GPS data on 13 different bison from 2003-04

Statistical Analysis

The response variable for this analysis is τ—the foraging area residence time. Using the actual time series data from the GPS collared cow bison will provide quantification of τ by comparing ground telemetry locations with the GPS data. Predictors include area attributes such as snowpack metrics—depth, SWE, and hardness—as well as forage biomass. The size of the bison group is also an important predictor as the number of bison may influence how long a group remains in a foraging area. Possible other derived quantities to use in the analysis include the individual behavioral observations and the group herd scans. Additionally, the proximity of the foraging area to other foraging areas may be important as would be an energetic cost of foraging metric that may be derived using observational and snow data. By building a candidate list of multiple regression models using foraging area attributes as the predictors, the best approximating models will be selected using AIC. After selecting the top model the predictor coefficients will be examined for their significance. This top model, containing the most relevant covariates to influencing bison foraging behavior, will be used in additional analyses, comparisons, and predictions across the MGF winter range.

3. Bison use of a road system and travel network for aiding distribution shifts

Objectives

The primary goals of this study are to extend Bjornlie and Garrott's (2001) work for an additional five years, address limitations and recommendations from their initial study, and evaluate the influence of winter road grooming on bison in the Madison-Firehole winter range. This research provides insights into mechanisms influencing bison travel in multiple ways. Firstly, I will assess causes of temporal variation in bison travel—both on-and off-road—by evaluating competing hypotheses to determine the relative contributions of snowpack, road grooming, density-dependence, and forage accessibility on magnitudes of travel. Secondly, I will examine how topography and habitats influence the choice of bison travel routes. Bjornlie and Garrott (2001) proposed that portions of the road system receiving heavy bison use are natural travel corridors, much like stream courses and geothermal features, and that some road segments are actually a small part of a larger travel network used by bison all year. To test these claims I will evaluate *a priori* hypotheses to assess the relative contributions of topography, habitat type, and snowpack to explain spatial variation in on-and off-road bison travel. Using the resulting best-supported model from this analysis I will develop a predicted travel network spanning the entire bison winter range. Finally, I will compare the predicted travel network and actual regions of high bison road use to objectively identify factors that affect paths of bison travel. All of the analyses will be conducted using two distinct data sets to comprehend bison movements throughout the entire winter range, not just on roads. In addition, a spatially explicit snowpack model was utilized to help capture the fine-scale dynamic variations missing from Bjornlie and Garrott's (2001) study. Overall, I will analyze seven years of bison travel data—spanning a variety of winter severities—to quantify temporal and spatial travel trends and identify the ecological impetuses affecting bison movements.

Methods Utilized

- Bison road use surveys
- Bison ground distribution surveys
- Snowpack simulation model
- Travel network monitoring
- GPS collars on cow bison

Databases

- Bison road use surveys
  - -Conducted daily from 1997-98 to 2003-04
  - -2,162 bison groups mapped representing 33,120 individual bison
- Bison ground distribution surveys
  - -Conducted biweekly from 1996-97 to 2003-04
  - -99 surveys conducted (average of 12 per season)
  - -7,522 bison groups mapped representing 74,226 individual bison
  - -Activity budgets on 5,500 bison groups
- Snowpack simulation model
- Travel network monitoring

-Nez Perce and Gneiss Creek trail remotely monitored daily in 1997-99 and 2002-04
-Nez Perce trail has a database of 15,126 bison events
-Gneiss Creek trail has a database of 14,593 bison events

- GPS collars on cow bison

Statistical Analysis

Temporal Bison Travel Analyses:

Using data from the road use surveys I defined a response variable (BGR) for the magnitude of bison road travel using a combination of the number of bison groups observed traveling on the roads per 100 km traveled by observers for each time interval (i) within each year (j) multiplied by a road use weighting factor (WR_{ij}). The WR_{ij}, defined as the total number of individual bison in road traveling groups for the time interval of interest divided by the total number of individual bison in road traveling groups for the entire season, accounted for the temporally dynamic sizes of bison groups that generally increase as the season progresses. Two-week time intervals ($1 \leq i \leq 14$) were defined from November through May for each season ($1 \leq j \leq 7$) to account for the biweekly ground surveys that provided a census of the MGF bison population. Likewise, using travel data from our ground distribution surveys I defined a response variable (BGT) for general bison travel using the number of bison groups observed traveling per survey for each time interval within each season multiplied by a general travel weighting factor (WT_{ij}). Using ground survey travel data WT_{ij} was defined as the total number of individual bison in survey traveling groups for the time interval of interest divided by the total number of individual bison in survey traveling groups for the entire season.

Landscape covariates used in the temporal analysis of bison travel will be obtained from Geographic Information System (GIS) data layers generated using the snowpack model. In an effort to accurately depict the dynamic snow cover, daily estimates of covariates will be determined from November through May for each season. Using model output, covariates for both the snowpack and forage availability will be calculated. The snowpack will be characterized using two metrics—snow water equivalent (SWEL) and snow heterogeneity (SHGL)—determined at a MGF bison range scale. Snow water equivalent will be calculated as the mean of SWE for all pixels within the MGF bison range; SHGL will be calculated as the standard deviation of SWE and represented the spatial variability of the snowpack (Messer 2003). Forage availability will be characterized using five different metrics on an MGF bison range scale: percent of snow-free area (PLo); mean snow-free patch size (PSLo); snow-free patch heterogeneity (PHGLo); median snow-free patch size (PSMLo), and snow-free patch cohesion (COHo). Each forage availability covariate is to be determined using pixels where SWE was zero across the MGF bison range. Patch and cohesion covariates will be calculated as per McGarigal and Marks (1995) with the cohesion metric indexing the physical connectivity of snow-free patches. The MGF bison range scale will be used in this analysis as field observations indicate that bison move freely throughout their range and seem to respond to temporal variations in snowpack at large spatial scales. Landscape covariates for snowpack and forage availability will be averaged across each time interval for the final analyses. In addition to the landscape metrics already mentioned, two additional covariates will be used. A variable will be defined to denote whether the roads were groomed (GROOM: 0 = ungroomed; 1 = groomed) and, to obtain a measure of density-dependence, the number of bison enumerated from our ground surveys (BISON) will be considered. To estimate the relative contributions of snowpack, forage availability, road grooming, and bison density-dependence to the temporal variations of both on-road and general bison travel, *a priori* hypotheses will be developed and compared. Using the aforementioned response variables and covariates, hypotheses will be expressed as a set of candidate models in the form of multiple linear regression equations that could be fit to the data. Models will be ranked and selected using AIC and the best-supported model will be examined for its covariate coefficients.

Spatial Bison Travel Analyses:

The response variable to be used in the analysis of the travel data from the ground distribution surveys is of logistic form with a 1 denoting a "used" traveling location and a 0 indicating an "available" traveling location. For each traveling location on a specific survey date, at least 20 random locations will be generated and considered as available. The spatial analysis of bison travel will utilize landscape covariates obtained both from static GIS data layers and from the snowpack model. A United States Geological Survey (USGS) DEM will be used to obtain estimates of slope while habitat categories will be assigned using vegetation cover type (Fred Watson unpublished data) and geothermal (Watson et al. 2002) data layers. Seven habitat categories will be defined: aquatic (AQ), burned forest (BF), unburned forest (UF), meadow (MD), road (RD), geothermal (TH), and talus/rock (TA). Proximity to these seven habitats will be measured using a GIS data layer. For each of the 61 road segments in the MGF a central UTM point location will be defined so that adjacent segments along the road were equidistant from the center point. Using these road segment point locations and those for traveling bison groups obtained from the bison ground surveys, a slope covariate (SLP) will be calculated as follows. A circle of 200 m radius around each point will be defined, the slopes each pixel within the circle are to be measured, and the average will be taken; a slope heterogeneity covariate (SLHG) will then be calculated by taking the standard deviation. Proximity to habitat covariates (dAQ, dBF, dUF, dMD, dTH, dTA) will be calculated for both the road segment and traveling bison group point locations by measuring the closest distance from the point to each of the six habitats. In addition, a proximity to road covariate (dRD) will be evaluated for bison ground survey traveling locations along with a habitat covariate (HBT) using the seven defined categorical habitat variables.

Covariates for small-scale snow water equivalent (SWES) and snow heterogeneity (SHGS) will be obtained from the snowpack model for both road segment and traveling bison group point locations on a daily basis as follows. The SWES will be calculated as the mean snow water equivalent for all pixels within a 200 m radius from the location while SHGS is the standard deviation about this mean. For each of the randomly generated locations representing available sites, these snow, habitat, and topographic metrics will also be determined. For all of the small-scale spatial calculations a 200 m radius was chosen as it is assumed bison would choose travel paths based on topography, habitat, and snow at a scale larger than one 28.5 m^2 pixel, but smaller than the large MGF meadow complexes. Finally, *a priori* hypotheses will be developed and compared. Using the response variable and suite of covariates, hypotheses will be expressed as a set of candidate models in the form of multiple logistic regression equations that could be fit to the data. The best approximating models will be selected via AIC.

4. Nutritional costs and benefits of large herbivore seasonal migration

Objectives

The purpose of this study is to present a new technique for understanding the spatial dynamics of bison. The basis for this work is using allantoin:creatinine (A:C) ratios from snow-urine samples to provide an index to quantify bison nutrition. Assays conducted on samples from the 2003-04 winter revealed promising preliminary results and full conceptualization of this study is just beginning with three preliminary goals. The first is a basic validation of the snow-urine technique for indexing bison nutrition using captive bison and controlled nutrition experiments in similar fashion to that already done with elk (Garrott et al. 1997). Secondly, sample collection on the winter range—done both in a "tracked group" and batch manner—can be used to look at changes in nutrition throughout the winter. Finally, extending batch sample collection to the summer range of the Hayden and Pelican Valleys will afford a look at the nutritional costs and benefits of migration and provide comparisons with the Madison-Firehole winter range. Given that migration serves to reduce the environmental heterogeneity experienced by an animal and place it under optimal conditions for survival, it is anticipated that significant differences will exist in A:C ratios for bison that migrate to the winter range compared to those that remain in the Hayden and Pelican Valleys throughout the entire winter. One portion of this study is dependent upon first obtaining some captive bison and conducting controlled nutrition experiments to validate the technique. Secondly, the comparison between the Madison-Firehole and Hayden and Pelican Valleys may be dependent upon coordinating with portions of Rick Wallen's staff and/or other Park personnel to gather samples across the summer range throughout the winter.

Allantoin:creatinine has been shown to be an effective index of nutritional status—specifically metabolizable energy intake—in elk (Vagnoni et al. 1996; Garrott et al. 1997; Pils et al. 1999). Allantoin excretion is positively correlated with dietary energy intake for both domestic ruminants (Chen et al. 1990, Verbic et al. 1990) and elk (Vagnoni et al. 1996; Garrott et al. 1997; Pils et al. 1999) as allantoin is the principal by-product of nucleic acid catabolism as ruminal microbial matter is digested in the small intestine. Additionally, it is purported that urinary allantoin excretion provides a measure for the overall availability of digestible nutrients and per capita resources. Of particular interest is the sensitivity of A:C ratios to changes in nutritional status and its ability to index the dietary intake of animals over the short time period of several days.

Although the use of A:C ratios has been primarily applied to nutrition in elk as well as domestic cattle and sheep, the technique has seen minimal use with regard to bison. DelGiudice et al. (1994, 2001) considered Urea Nitrogen:Creatinine (UN:C) ratios as a measure of nutritional stress in bison in Yellowstone National Park with some success in examining longer term, severe dietary restriction that reflected accelerated protein catabolism. Results of an unpublished report (Garrott personal communication) demonstrate that A:C ratios appear to follow similar trends in bison as they do in elk over a period of winter nutritional restriction. These results, coupled with our 2003-04 findings, lead us to believe that applications of this method to bison can be used in a similar fashion as that done with elk. Given the similarities in digestive processes across ruminant species it is reasonable to expect the A:C ratios to be a sufficient index of the short-term nutritional status of bison.

Methods Utilized

- Snow-urine sampling

Databases

- 274 urine samples in 2003-2004

Statistical Analysis

The methods of statistical analysis for these topics have yet to be determined. Preliminary ideas on the sampling protocol are as follows. For comparisons between the summer and winter range there will be two sampling strata: 1) the summer range in the Hayden and Pelican Valleys; 2) the MGF winter range. Within each stratum bison groups will be sampled randomly throughout the study area. The groups to be sampled should only be mixed groups of cows, yearlings, calves, and young bulls. Groups consisting primarily of old bulls should be avoided. The sampling period will be from mid-November until April (or earlier if the snow melts). This entire season will be divided into two-week intervals with a goal of 25 samples per interval for each strata. This sampling requirement is based upon recommendations from Pils et al. (1999).

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