



Ecological effects of winter road grooming on bison in Yellowstone National Park
by Daniel David Bjornlie

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University
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Abstract:

The effects of winter recreation on wildlife in Yellowstone National Park (YNP) have become high-profile issues. Snowmobiling is perhaps the most contentious of these issues. The road grooming needed to support snowmobile travel in YNP has also come under examination for its effects on bison (*Bison bison*) ecology. Data were collected from November 1997 through May 1998 and again from December 1998 through May 1999 on the effects of road grooming on bison in Madison-Gibbon-Firehole (MGF) area of YNP. Synoptic bison surveys of the entire study area were conducted 33 times during the study. Peak bison numbers in the study area occurred in late March/early April and were correlated with snow water equivalent measurements in the Hayden Valley area (1997-98: $r_2 = 0.62$, $P < 0.001$; 1998-99: $r_2 = 0.64$, $P < 0.001$). Data from an infrared trail monitor set up on the Mary Mountain trail between the Hayden Valley and the Firehole Valley suggest that this trail is the sole corridor for major bison distributional shifts between these locations. Of the 28,293 individual bison observations made during the study, 8% of the activities were traveling, while 69% were foraging. These percentages were nearly identical during the period of winter road grooming (7% and 68%, respectively). The majority of foraging activities during this period (77%) involved displacing snow, while 12% of the traveling activities involved displacing snow. The majority of travel took place off roads ($P < 0.001$). Bison utilized geothermal features, stream and riverbanks, and a network of established trails to travel in the study area.

Peak road use by bison occurred in April, with the lowest values during the road-grooming period. Groomed road use by bison in the MGF area of YNP seems to be an activity that is neither sought out nor avoided. The minimal use of roads compared to off-road areas, the short distances traveled on the roads, the decreased use of roads during the road grooming period, and the increased costs of negative interactions with over-snow vehicles suggest that roads are not the major influence on bison ecology that has been proposed.

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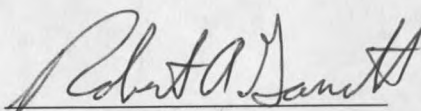
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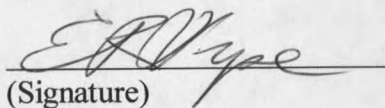
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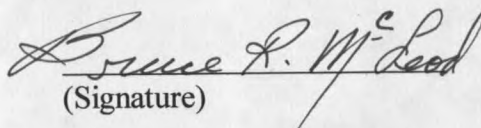
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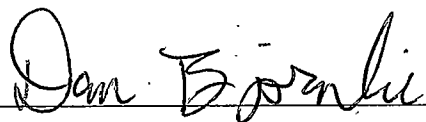
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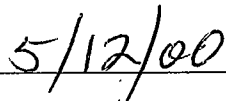
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ABSTRACT

The effects of winter recreation on wildlife in Yellowstone National Park (YNP) have become high-profile issues. Snowmobiling is perhaps the most contentious of these issues. The road grooming needed to support snowmobile travel in YNP has also come under examination for its effects on bison (*Bison bison*) ecology. Data were collected from November 1997 through May 1998 and again from December 1998 through May 1999 on the effects of road grooming on bison in Madison-Gibbon-Firehole (MGF) area of YNP. Synoptic bison surveys of the entire study area were conducted 33 times during the study. Peak bison numbers in the study area occurred in late March/early April and were correlated with snow water equivalent measurements in the Hayden Valley area (1997-98: $r^2 = 0.62$, $P < 0.001$; 1998-99: $r^2 = 0.64$, $P < 0.001$). Data from an infrared trail monitor set up on the Mary Mountain trail between the Hayden Valley and the Firehole Valley suggest that this trail is the sole corridor for major bison distributional shifts between these locations. Of the 28,293 individual bison observations made during the study, 8% of the activities were traveling, while 69% were foraging. These percentages were nearly identical during the period of winter road grooming (7% and 68%, respectively). The majority of foraging activities during this period (77%) involved displacing snow, while 12% of the traveling activities involved displacing snow. The majority of travel took place off roads ($P < 0.001$). Bison utilized geothermal features, stream and riverbanks, and a network of established trails to travel in the study area. Peak road use by bison occurred in April, with the lowest values during the road-grooming period. Groomed road use by bison in the MGF area of YNP seems to be an activity that is neither sought out nor avoided. The minimal use of roads compared to off-road areas, the short distances traveled on the roads, the decreased use of roads during the road grooming period, and the increased costs of negative interactions with over-snow vehicles suggest that roads are not the major influence on bison ecology that has been proposed.

INTRODUCTION

Over the past several decades, there has been a change in the focus of human use of public lands. The number of outdoor recreationists has increased rapidly with the increase in human population, disposable income, and leisure time (Knight and Gutzwiller 1995). This emphasis on recreation creates a new form of effects on the resources of public lands. In areas that were once used mainly for extractive industries like mining and logging, the predominant activity is now shifting to outdoor recreation (Knight and Gutzwiller 1995). Instead of localized effects, resource managers must now deal with a much broader range of effects over much larger areas (Cole and Knight 1991). It has been assumed that because recreation effects are dispersed over a wider area, they are diluted and cause less damage than extractive uses (Youmans 1999). This dispersion, however, is a primary reason why recreation effects can be so extensive (Flather and Cordell 1995).

For many animals in high latitudes, the winter season is the most physiologically taxing. Therefore, the additional effects of winter recreation can have major effects. Goodrich and Berger (1994) found that "since the quiet approach of researchers sometimes caused black bears (*Ursus americanus*) to abandon their dens and cubs, skiing and other recreational activities could have the same or more heightened effects." Snowmobiling has received the vast majority of attention dealing with winter recreation effects (Canfield et al. 1999). The reports on the effects of snowmobile activity show a broad range of results. In Maine, Lavigne (1976) found that snowmobile trails enhanced white-tailed deer (*Odocoileus virginianus*) mobility during periods of deep snow.

Dorrance et al. (1975) reported that whereas some white-tailed deer avoided areas where snowmobiles were present, there were no significant changes in home range or daily movement patterns. Other research found more negative effects, such as using snowmobiles for illegal hunting (Malaher 1967) and reduced home ranges of white-tailed deer in high-use snowmobile areas forcing them into less preferred habitat (Huff and Savage 1972). Snowmobiles in Canada created well-used trails through ungulate winter ranges that wolves (*Canis lupus*) had not previously been able to access, thus increasing predation (Claar et al. 1999). There has also been concern about air, water, and noise pollution created by snowmobiles (Aune 1981, National Park Service 1999, Youmans 1999).

It has been reported in several other studies, however, that snowmobiles confined to designated trails or roads are less disturbing to wildlife than cross-country skiers or persons on foot. Average flight distances for elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) in Yellowstone National Park were less for disturbances attributed to snowmobiles than for those attributed to skier interactions (Aune 1981). Freddy et al. (1986) found that responses by mule deer to persons on foot were longer in duration, more often involved running, and involved greater energy costs than reactions to snowmobiles on trails. These examples support the observation made by Parker et al. (1984:484) stating, "Greater flight distances occur in response to skiers or individuals on foot than to snowmobiles, suggesting that the most detrimental disturbance to the wintering animals is that which is unanticipated."

Yellowstone National Park (YNP) is a microcosm of the effects felt by growing recreational activities (Aune 1981, Gunther 1991, Cassirer et al. 1992, National Park Service 1999). Annual visitation to YNP has increased from 2,404,862 people in 1982 to 3,131,381 in 1999 (Tammy Wert, YNP, unpubl. data). Total winter visitation has increased at an even greater rate, from 77,679 in 1984-85 to 124,275 in 1998-99 (National Park Service 1999). The first permits were granted for snowcoaches in 1955 to bring tourists into YNP, with snowmobile tourism beginning in 1963-64 when the first private snowmobiles entered the Park (Aune 1981). In order to restrict the use of snowmobiles to the roads and facilitate better access to the Park, the National Park Service (NPS) began road-grooming operations in 1970. The number of snowmobile and snowcoach (over-snow vehicle) visitors entering YNP increased from 12,239 in 1970-71 to 42,597 in 1977-78 (Tammy Wert, YNP, unpubl. data). This increase in winter visitation was large enough to warrant a study of the impacts of winter recreation on wildlife (Aune 1981). The conclusion was that although minor impacts occurred, recreation activity was not a major factor influencing wildlife distribution and cover use. Since that time, over-snow vehicle (OSV) visitation has increased to 86,977 in 1998-99 (National Park Service 1999).

Concurrent with increasing Park visitation was a steady increase in the YNP bison (*Bison bison*) population (National Park Service 1998). The winter of 1996-97 brought above-average snow depths and thick ice layers that impeded foraging (Cheville et al. 1998). In search of forage, bison left YNP and over 1,000 were subsequently shot in a controversial management action to protect livestock from potential exposure to

brucellosis (Keiter 1997, National Park Service 1998). Prior to the killing of bison in 1996-97, an internal unpublished Park Service report (Meagher 1993) suggested that road grooming facilitated bison migration out of the Park. The contention raised was that groomed roads permit bison to move more freely and efficiently about the Park in winter, thus allowing them to save energy by avoiding snow displacement and to access more and higher quality winter forage than would be possible without the road system. Enhanced nutrition and overall postwinter health are purported consequences, leading to excessive numbers, habitat deterioration, range expansion, and movements of animals outside the Park. Prompted by the assertions in this report and the killing of the bison in the winter of 1996-97, several advocacy groups filed suit against the National Park Service, leading to an out-of-court agreement to write an environmental impact statement (EIS) (Baskin 1998, National Park Service 1998). To provide information for this EIS, more research was needed on the effects of road grooming on bison movements, distribution, and behavior.

The goal of this study, therefore, was to quantify bison distribution, movement, and activity patterns and evaluate the ecological consequences of winter road grooming. Four testable hypotheses were formulated to address the purported effects of road grooming on bison. The first hypothesis was that road grooming facilitates major bison distributional shifts. Second was that displacing snow while traveling is the major energetic cost to bison in the winter. The third hypothesis was that the majority of bison travel in winter would take place on groomed roads within the Madison-Gibbon-Firehole study area, facilitating long distance movements by bison seeking to escape the costs of

traveling in snowpack. The fourth hypothesis stated that traveling on groomed roads results in less energy expenditure than traveling off-roads.

STUDY AREA

The study area consists of the drainages of the upper Madison River east from the Park boundary at West Yellowstone to Madison Junction, the Gibbon River upstream to Norris Geyser Basin, and the Firehole River upstream from Madison Junction to Old Faithful (Fig. 1). The meadows and geothermal features in this area are considered the primary winter range for the Mary Mountain bison subpopulation, which is the largest in YNP and comprises 60% to 75% of the entire YNP bison population (Thorne et al. 1991, Meagher 1993). The study area is approximately 7,200 hectares with elevations ranging from 2,000 m to 2,250 m. Winter visitation in this area is the heaviest in the Park, with 60% of winter visitors to YNP stopping at Old Faithful (National Park Service 1998).

Although not within the formal study area, the Hayden Valley in the central region of the Park to the east of the study area and the meadows above and along Cougar and Duck creeks to the northwest of the study area are also important to bison movements within the study area. The Hayden Valley is higher in elevation (2,466 m) than the Madison-Gibbon-Firehole (MGF) study area. Bison move into the study area from this region in winter (Meagher 1993). The Cougar and Duck Creek area is lower in elevation (2,042 m) than most of the study area, and along with the Madison River, is utilized as an egress corridor for bison in the study area (National Park Service 1998). These egress points are of major concern due to the threat of brucellosis transmission to cattle outside of the Park (Cheville et al. 1998).

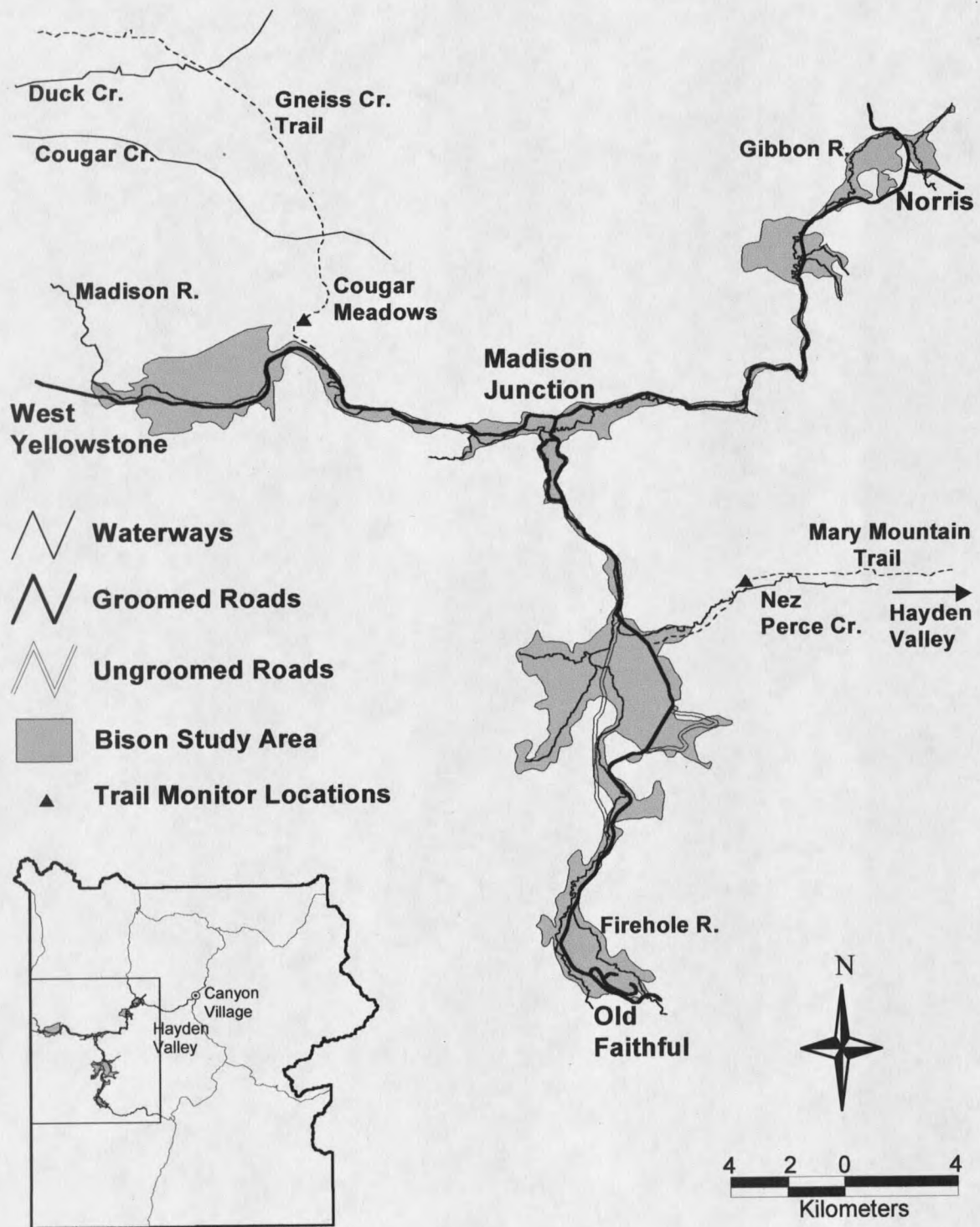


Figure 1. Madison-Gibbon-Firehole study area of Yellowstone National Park. The shaded area represents the bison range, as delineated by Ferrari (1999). Groomed and ungroomed roads within the study area are denoted. The locations of infrared trail monitors on bison off-road trails are identified.

The study area consists of extensive, flat meadows associated with the major river systems. Forested regions and the canyons of the major rivers break up these areas.

There is also significant geothermal activity in the study area. Warm sites near these and other geothermal areas are snow-free earlier in spring and have a longer growing season than surrounding areas. They also produce areas of reduced snow cover or bare ground in the winter (Meagher 1973, Despain 1990). In 1988 several major fires burned through the study area (Despain 1990). Prior to these fires, approximately 61% of the study area was dominated by climax lodgepole pine (*Pinus contorta*) or seral stages (Aune 1981). The 1988 fires resulted in large areas of open canopy with charred snags and downed wood. Many of these areas have been rapidly recolonized by lodgepole pine (Knight 1996).

The climate in the study area is characterized by long, cold winters and short, cool summers. Records from the National Oceanic and Atmospheric Administration (NOAA) for West Yellowstone, Montana, indicate the mean monthly temperature ranges from 15.3°C in July to -10.6°C in January (Aune 1981). Mean annual snowfall is 418 cm and mean snow depth exceeds 46 cm for an average of 126 days per year. The beginning of snow accumulation at 2,100 m occurs in late October and the end of the snowpack at this elevation is normally in late May (Despain 1990).

The road system within the study area consists of paved, 2-lane roads along the major rivers (Fig. 1). From West Yellowstone the road extends 22 km to Madison Junction, passing through meadows, forests and the Madison Canyon to the junction of the Firehole and Gibbon Rivers. From Madison Junction the road along the Gibbon

River passes through the Gibbon Canyon and Gibbon Meadows and on to Norris for a distance of 22 kilometers. The road from Madison Junction to Old Faithful follows the Firehole River for 26 kilometers through Firehole Canyon, Lower and Midway geyser basins. The roads in the study area are open to visitors in wheeled vehicles (WV) from April 15 until October 31. From November 1 until the third week in December the roads in the study area are closed to all vehicles driven by visitors. During this time, WV traffic is restricted to YNP personnel only. However, the roads are not plowed and snow is allowed to accumulate on the roads. Road grooming begins the evening prior to the opening date of the OSV season, which is approximately the third week of December. Roads are groomed nightly until the end of the OSV season, in early to mid March. The study area roads are then closed to all visitor vehicles and the roads are plowed to pavement. Travel is restricted to YNP personnel until approximately April 15.

METHODS

I began data collection for the first field season of this study in mid November 1997 and continued through May 1998. Data collection began again in early December 1998 and continued through May 1999. The OSV season extended from December 19 to March 9 during the winter of 1997-98, and from December 16 to March 14 during the winter of 1998-99.

Spatial and Temporal Snowpack Variation

Snow water equivalent (SWE) was used as an index of snowpack in the study area. This index calculates the equivalent amount of water contained in a column of snow (Farnes 1996). These data were gathered from remotely operated Natural Resources Conservation Service (NRCS) SNOTEL sites near West Yellowstone and Canyon Village (Fig. 1). The West Yellowstone site, at an elevation of 2,042m, reflects SWE in the lower-elevation valley bottoms of the study area, while the Canyon SNOTEL site, at 2,466m, reflects SWE in the Hayden Valley (Fig. 1, inset), which is the major summer range for bison in YNP (Meagher 1973).

Synoptic Bison Surveys

The spatial and temporal patterns of bison population, distribution, and activities were characterized by conducting synoptic surveys of the entire study area at 10-day intervals using methodology developed by Ferrari (1999). The study area was divided into 72 units ranging in size from 6 to 716 ha, with 6 survey routes designated through the units. Each member of a 3-person crew traversed 1 of these routes using

snowmobiles and/or snowshoes each day, attempting to locate all bison within each unit. Therefore, using a 3-person crew, it was possible to survey the entire study area in 2 days. Surveys were conducted in a manner that minimized the possibility of missing or double counting bison. This was accomplished by crew members starting each of the survey routes simultaneously and by surveying the 3 Madison and Gibbon routes on 1 day and the 3 Firehole routes on the other. The long distance between these 2 areas decreased the probability of bison moving from 1 area to another between survey days.

For all groups of bison detected during surveys we recorded the location of each group in Universal Transverse Mercator (UTM) coordinates (using USGS 7.5 minute maps) and the age and sex composition of the group divided into cows, bulls, calves of the year, and unknown adults. In addition, the activity of each observed bison was classified as traveling, foraging, or resting. Traveling bison were defined as any individual that was engaged in directed, sustained travel. This would exclude animals slowly wandering and stopping frequently to forage. Bison travel was categorized as either on roads, on established trails, or off of roads and established trails. Foraging animals were defined as any individual that was feeding or slowly moving around in search of forage. Resting animals were defined as stationary individuals, either lying down or standing, that were obviously not engaged in either foraging or traveling. If bison were displacing snow in any of these activities, we noted snow depth in relation to bison anatomy using a reference diagram from Carbyn et al. (1993) and placed it into 1 of 6 categories (1-20 cm, 21-40 cm, 41-60 cm, 61-80 cm, 81-100 cm, >100 cm).

To augment data collected during the complete synoptic surveys, I also performed

partial surveys of randomly selected blocks of survey units during the 8-day interval between each complete survey. For these partial surveys, the 6 routes were combined into 3 geographic strata consisting of 2 adjacent travel routes. These were the Madison River/lower Firehole River, the Gibbon River drainage, and the middle/upper Firehole drainage. Each morning of a partial survey, a stratum was randomly selected. Then 1 of the 2 travel routes within that stratum was randomly selected and followed that day. The survey schedule was tailored so that 3 partial surveys were conducted between each complete survey, with 1 route in each of the 3 strata. Approximately half of the survey units in each of the 3 strata were then covered once in the 10-day rotation, and the other half of the units were covered in the next rotation. No units were resurveyed until all units in the study area had been surveyed once. These partial surveys employed the same data collection techniques used in the complete synoptic surveys.

The total number of bison enumerated during each complete synoptic survey was calculated and considered a census of the bison population in the study area. Linear regression (Minitab Inc. 1998) was used to examine correlations between changes in the number of bison detected within the study area each winter and snowpack in the Hayden Valley, as indexed by the mean SWE measurements at the Canyon SNOTEL site for the 10-day period centered on the date of each bison population estimate. Linear regression was also used to examine the correlations between changes in the distribution of bison in the Madison and Firehole River valleys of the study area. Bison activity budget data from all complete and partial synoptic surveys from both years were aggregated to obtain information on bison activity patterns by month through the winter/spring field season.

The locations of all traveling bison groups observed during complete and partial synoptic surveys were plotted to determine the spatial extent of traveling bison in the study area using ArcView GIS software (ESRI 1998). The differences in the mean number of bison groups observed traveling per 2-week time interval on roads, trails, and off-roads and off-trails were tested using 1-way analysis of variance, and orthogonal linear contrasts (PROC GLM; SAS 1998).

Bison Travel Monitoring

Data on bison road use were collected opportunistically by a 4-person field crew traveling independently on the road system daily in trucks and on snowmobiles. This extensive travel resulted in coverage of a majority of the study area road system on a daily basis. Each crew member recorded the sections of the road system traveled daily and attributes of any bison group observed using the road. Daily survey effort was determined by summing the total number of kilometers traveled by crew members excluding road sections that were traveled by more than 1 crew member within one half hour of each other. Bison traveling less than 50 meters on the roads were not recorded as road use. If possible, the direction of travel, location of the group at the point where they were first observed, and the locations of where the group accessed and exited the road were identified. The group age and sex composition were recorded using the same categories employed in the synoptic surveys. In some instances, access and exit points could not be determined.

To acquire data on nocturnal road use by bison, bison tracks on the road were recorded in the early morning prior to the onset of daily travel by Park visitors, as crew

members were traveling to their respective survey areas. Because the road system was groomed every evening, any bison tracks on the roads in the early morning were made by bison traveling the roads the previous night. The number of bison and the age and sex composition of bison groups could not be determined from tracks. However, all other data collected were the same as those collected for diurnal road use.

Regression models were constructed in an effort to examine potential factors that may have contributed to the propensity for bison to travel on the groomed road system. The time intervals for the models were centered on the date of each complete synoptic survey. The response variable in these models was the number of bison groups observed traveling on the roads per 100 km traveled by observers in each interval. Potential explanatory variables included the number of bison counted in the study area during the synoptic survey (Bison), the mean SWE at West Yellowstone for that time interval (SWE), an indicator variable specifying whether the roads were groomed (Groom; 0 - ungroomed, 1 - groomed), and an indicator variable for year (Year; 0 - 1997-98, 1 - 1998-99). The statistical software package Minitab (Minitab Inc. 1998) was utilized in conducting these regression analyses. Because of limited sample sizes, a corrected Akaike's information criterion (AIC_c) value was calculated for each of the models (Burnham and Anderson 1998). Models were then ranked based on ΔAIC_c values, with the most parsimonious model having the lowest value. After inspecting the plots of the residuals, an outlier was noticed. This outlier corresponded to a time interval during which crew members could not travel the study area roads for much of the time due to road plowing operations. Thus, it was discarded due to less than 50% normal survey

effort, providing one less observation for the models. The recommended number of observations per each parameter in a model has been suggested as 6 to 10 (Neter et al. 1996). Therefore, inference from models at or below this range should be viewed with some caution. Residual plots and Durbin-Watson test statistics were utilized to test for the presence of autocorrelation (Neter et al 1996). Models were run using all possible combinations of the 4 parameters. In addition, terms addressing the possible 2-way interactions between Year and Bison, and Year and SWE were included with each model that contained those parameters. The total candidate list of models was then 24.

The road system in the study area was divided into 10 sections (3 from West Yellowstone to Madison Junction, 4 from Madison Junction to Old Faithful, and 3 from Madison Junction to Norris) based upon topography of the study area. A chi-squared goodness-of-fit test was used to illustrate spatial and temporal trends in road use. The chi-squared expected values for each road section were weighted based upon the proportion of km traveled by observers in that section of the total km traveled in that time interval.

To obtain data on bison use of established trails for distributional shifts, I placed a Trailmaster 1500 infrared trail monitor on the 35-km-long Mary Mountain trail between the Hayden Valley and the Lower Geyser Basin of the Firehole Valley (Fig. 1). A second monitor was placed on the Gneiss Creek trail leading from the Madison River at Seven Mile Bridge to the Cougar Meadows area (Fig. 1). The Mary Mountain trail was chosen because it is considered to be the major migration route for bison moving between the Hayden Valley summer range and the Madison-Firehole winter range (Meagher 1973,

1993). The Gneiss Creek trail was chosen based upon observations of heavy bison travel on the trail made by researchers in previous winters. Once well-defined trails were established in the snowpack by traveling bison early in the season, the monitors were placed on the trails to quantify the number of bison using the trails and the times, dates, and direction of use.

Monitors were set up with infrared beams crossing the trail in areas where bison were restricted to traveling in single file. The monitors recorded the date and time of any "events" that broke the infrared beam. The sensitivity of the monitors was set to ensure that only large animals were recorded. Cameras were set up in conjunction with each of the monitors. In order to reduce the possibility of exposing the entire roll of film on 1 bison group, the monitors were programmed with a 10-minute camera delay so that once the beam was broken and a picture was taken, the camera did not take another picture for 10 minutes. The photographs provided the species identity of the lead animals of each group that broke the beam as well as recording the direction in which they were traveling. By analyzing the timing of the events immediately following the photographs, the species identity of the entire group could then be determined. For instance, 25 events taking place from 12:42 to 12:47 was considered a single group. A photograph of the lead animal identifying it as a bison was then interpreted to mean that the remaining 24 events were also bison. Data were then downloaded and film was replaced at 7-10 day intervals. The monitor on the Gneiss Creek trail was initially set up in late November of 1997 and was taken down in late May of 1998. It was placed back on the trail in mid October of 1998 and maintained until early June of 1999. The monitor on the Mary Mountain trail

was initially set up in early December of 1997 and taken down in early July of 1998. It was set up again in mid September of 1998 and left in place until early July of 1999.

Behavioral Observations

Behavioral observations of traveling bison groups were conducted regularly through each field season to gain additional insights into this activity and the potential influence of groomed roads and human interactions. Two sampling regimes were used to collect these behavioral observations. During the partial synoptic surveys, the first bison group observed traveling on the road system and the first group observed traveling off of the road were each chosen for an intensive behavioral observation. In addition, between each complete synoptic survey I set aside a day solely for intensive behavioral observations of all traveling bison groups detected. One of the 3 river drainages in the study area was randomly chosen as the starting point for each of the daylong surveys. Each subsequent intensive behavioral survey day started with a different randomly chosen river drainage until all 3 had been used as a starting point.

Once a traveling bison group was detected on these surveys, continuous observations were conducted until the group could no longer be seen or until it stopped traveling for a period of over 5 minutes. The path traveled by the group during the observation period was recorded on 7.5-minute USGS topographical maps in the field. Data collected included distance traveled on and off roads, travel time, mode of travel (single file vs. multiple animals abreast), whether snow was being displaced, and interactions with Park visitors. The data recorded for interactions with Park visitors included the number of bison/visitor interactions during the observation time and the type

of visitor interaction, categorized as snowmobile, snowcoach, or skier. Interactions were defined as any snowmobile, snowcoach, or individual approaching within 100 meters of any traveling bison. Bison reactions to these interactions were recorded and categorized as either ran, pushed off road, changed direction of travel, or none. If a reaction included more than 1 of these categories (i.e. changed direction and ran), then the reaction was classified in the category assumed to cost the bison the most energy. It was assumed that running cost more energy than being pushed off of the road and that changing direction cost the least of the 3 negative reactions.

RESULTS

Spatial and Temporal Snowpack Variation

Snowpack began to accumulate in late October/early November and continued to build throughout the winter (Fig. 2). Peak snowpack occurred in early April and was followed by a rapid melt-off period lasting about 6 weeks. Canyon SWE was generally about twice that of West Yellowstone. Peak SWE during the winter of 1998-99 was 44% higher than 1997-98 at Canyon and 71% higher at West Yellowstone. West Yellowstone peak SWE during the winter of 1997-98 was 37% lower than the historic average SWE (1967 – 1997), whereas 1998-99 peak SWE was 24% higher than the historic average. Peak SWE at Canyon was only 2% lower than the historic average (1981 – 1997) during 1997-98; whereas it was 43% above the historic average during 1998-99.

Bison Population and Distribution Dynamics

Complete synoptic bison surveys were conducted 33 times during this study, 17 during 1997-98 and 16 during 1998-99. Three surveys were conducted each month except for December 1997 and 1998 and in May 1999, when only 2 were conducted due to logistic limitations. The bison population in the study area ranged from 299 to 888 in 1997-98 and 464 to 921 in 1998-99, with peaks near April 1 for both years (Fig. 3). There was a positive correlation between SWE at the Canyon SNOTEL site and the number of bison counted in the study area for both the 1997-98 and 1998-99 field seasons (1997-98: $r^2 = 0.62$, $P < 0.001$; 1998-99: $r^2 = 0.64$, $P < 0.001$) (Fig. 4), suggesting that snowpack in the Hayden Valley influences the number of bison in the study area.

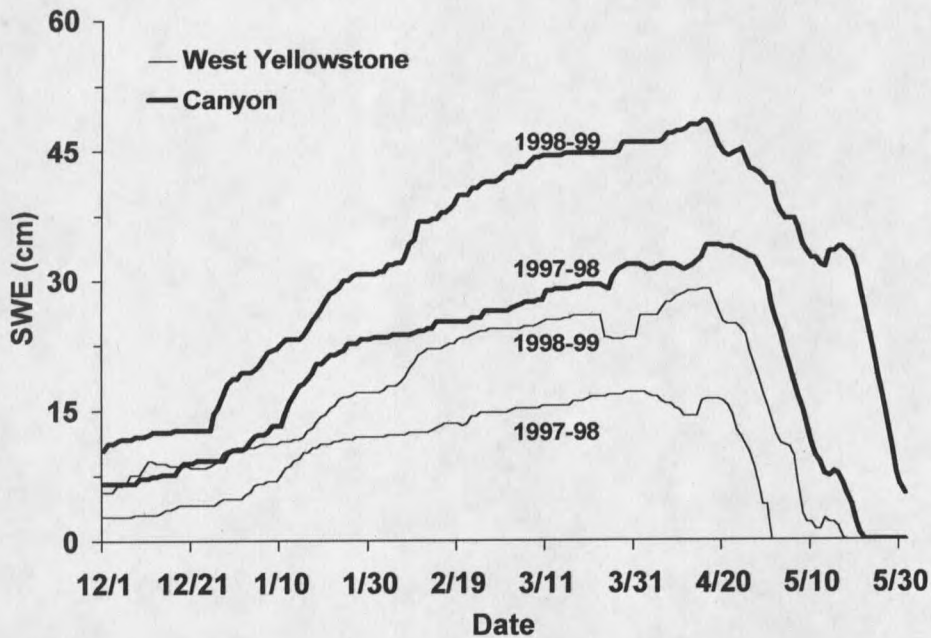


Figure 2. Temporal trends in snowpack as indexed by snow water equivalent (SWE) measurements recorded at the Natural Resources Conservation Service automated SNOTEL sites in the West Yellowstone (2,042 m) and Canyon (2,466 m) areas of Yellowstone National Park during the 1997-98 and 1998-99 field seasons.

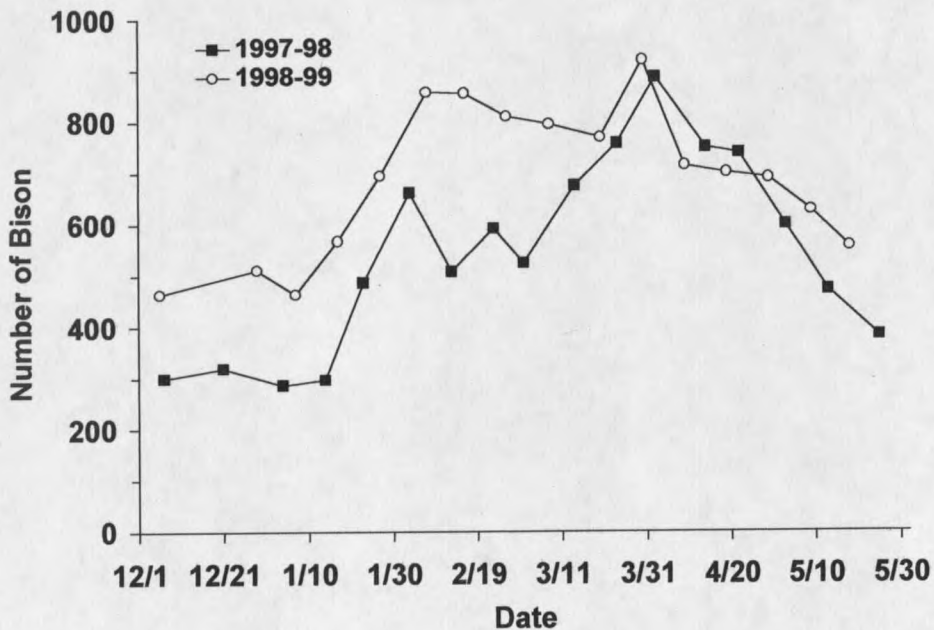


Figure 3. Temporal trends in the number of bison enumerated in the Madison-Gibbon-Firehole study area of Yellowstone National Park. Data are from complete synoptic surveys of the study area conducted at approximate 10-day intervals during the 1997-98 ($n = 17$) and 1998-99 ($n = 16$) field seasons.

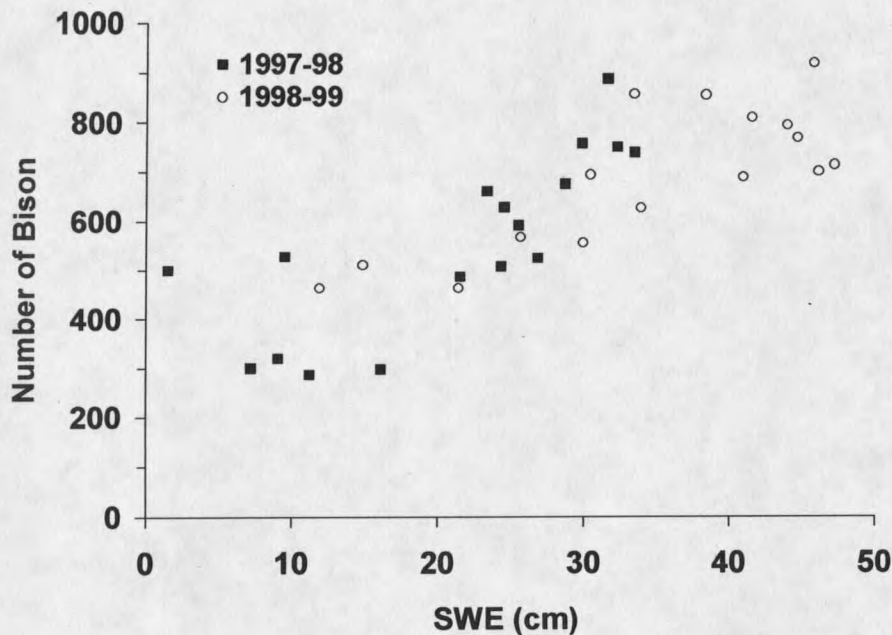


Figure 4. The correlation between snow water equivalent (SWE) measured at the Canyon SNOTEL site and the number of bison enumerated in the Madison-Gibbon-Firehole study area of Yellowstone National Park. Data are from the 1997-98 ($r^2 = 0.62$, $P < 0.001$, $n = 17$) and 1998-99 ($r^2 = 0.64$, $P < 0.001$, $n = 16$) field seasons.

The infrared trail monitor placed on the Mary Mountain trail between the Hayden Valley and the Firehole recorded 6,256 events identified as bison during the study, 2,473 in 1997-98 and 3,783 in 1998-99. These events included travel in both directions. The majority of these events (74%) were diurnal travel, occurring between 6:00 and 17:59. During the OSV season, 81% of the bison events were diurnal. The number of events in a 2-week period recorded as bison ranged from 0 to 437 in 1997-98, and 4 to 676 in 1998-99 (Fig. 5). Because the monitor was not set up until December 1997, bison moving into the study area earlier in that year were not recorded. There were several mechanical failures with the trail monitors during December 1997 and November 1998 causing missing data.

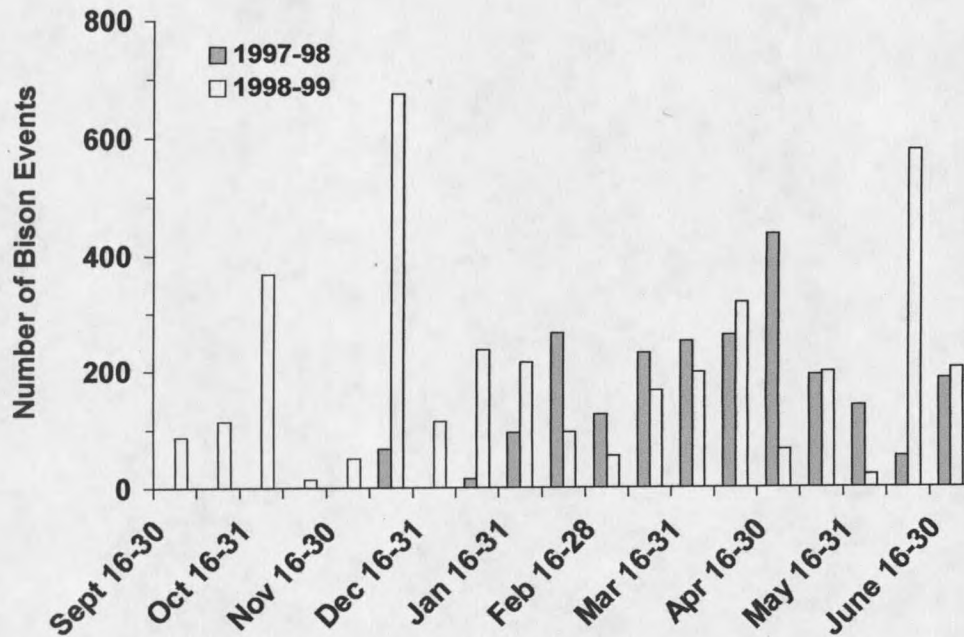


Figure 5. The number of events recorded as bison by an infrared trail monitor placed on the Mary Mountain trail between the Hayden Valley and the Firehole River Valley in Yellowstone National Park. Data are from the 1997-98 ($n = 2,473$) and 1998-99 ($n = 3,783$) field seasons. Problems with missing data due to monitor failures occurred in December 1997 and November 1998.

Bison were not evenly distributed throughout the 3 major river valleys of the study area (Table 1). The Gibbon River Valley contained the lowest percentage of bison observed during complete synoptic surveys in the study area during both field seasons with an overall average of 8%. The Madison River Valley contained an average of 19% of the bison during the study, while the Firehole River Valley consistently contained the largest percentage with an average of 73%. The largest fluctuations in bison distribution within the study area took place in the Madison and Firehole valleys. There was a strong inverse relationship between the percentages of bison in these 2 valleys in both seasons (1997-98: coefficient = -1.00, $r^2 = 0.94$, $P = 0.001$; 1998-99: coefficient = -0.99, $r^2 =$

0.85, $P < 0.009$). The percentage of bison was lowest in the Madison River Valley in the mid-winter months of February and March in both seasons (Table 1).

Table 1. The distribution of bison among the 3 major river valleys of the Madison-Gibbon-Firehole study area of Yellowstone National Park. Data are from complete synoptic bison surveys conducted at 10-day intervals over the entire study area during the 1997-98 and 1998-99 field seasons. Numbers for each area are reported as percents of the total number of bison detected for that month. The mean number of bison enumerated per survey and the total observations for each month are given by year.

Year	Area	Dec	Jan	Feb	Mar	Apr	May
1997-98	Gibbon	5	7	4	4	3	5
	Firehole	81	73	79	82	80	65
	Madison	14	20	17	14	18	31
	Mean/Surv	309	357	587	653	793	485
	Total	618	1,070	1,762	1,959	2,379	1,860
1998-99	Gibbon	16	13	13	12	10	4
	Firehole	49	65	76	79	67	67
	Madison	35	22	11	10	23	29
	Mean/Surv	488	576	842	829	703	593
	Total	975	1,727	2,525	2,487	2,136	1,353

Data from the infrared trail monitor placed on the Gneiss Creek trail between the Madison River and Cougar Meadows indicated that bison leaving the Madison River area in mid-winter did not move west into the Cougar Meadows/Duck Creek area. Overall,

7,325 events identified as bison were recorded by this trail monitor, 3,168 in 1997-98 and 4,157 in 1998-99. Over both years, and during the OSV seasons, 76% of the events recorded were diurnal travel, occurring between 6:00 and 17:59. The number of bison events recorded by this monitor peaked moderately in early January of the first season and early December of the second season (Fig. 6). The mean SWE values for these 2-week time intervals were 7.3 and 7.5 cm, respectively, suggesting a possible threshold effect causing bison to vacate the Cougar Meadows area. From late January through March, there was little or no bison use of this trail (Fig. 6). This period corresponds with the maximum snowpack in the study area. Large peaks occurred during the spring in both years, corresponding with the start of snowpack melt at West Yellowstone (Fig. 6).

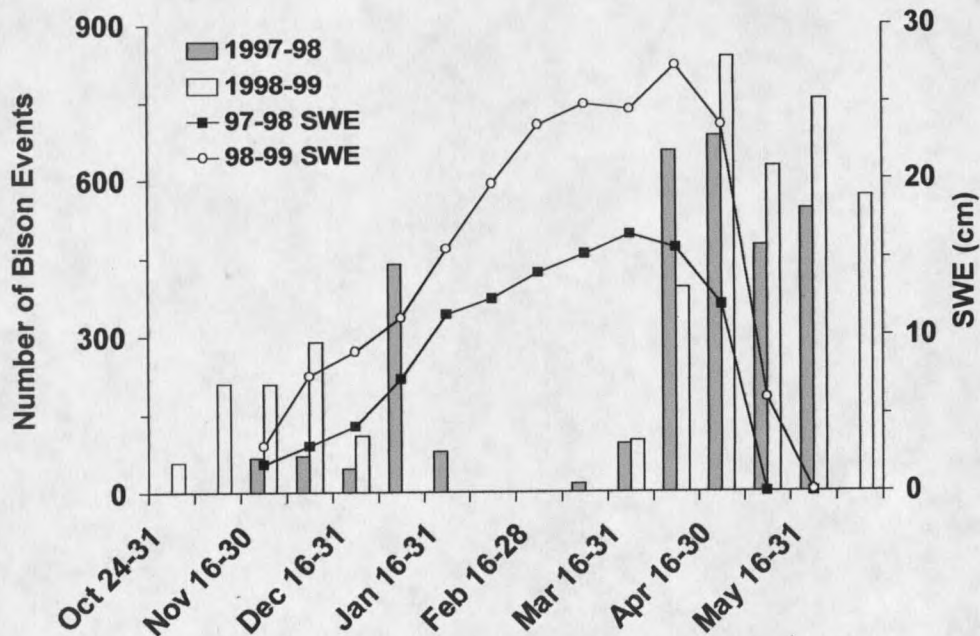


Figure 6. The number of events recorded as bison by an infrared trail monitor placed on the Gneiss Creek trail between the Madison River and Cougar Meadows in Yellowstone National Park. Data are from the 1997-98 ($n = 3,168$) and 1998-99 ($n = 4,157$). Mean snow water equivalent (SWE) values recorded at the Natural Resources Conservation Service automated SNOTEL site near West Yellowstone are also plotted.

Bison Activity Budgets

During the 33 complete and 99 partial synoptic bison surveys conducted over both field seasons, a total of 29,184 individual bison observations were recorded. Of these observations, bison activity data were obtained from 28,293 (1997-98: $n = 12,871$; 1998-99: $n = 15,512$) (Table 2). Bison spent 69% of their time foraging, 23% resting, and 8% traveling. During the OSV season, the percentage of foraging (68%) and traveling (7%) remained nearly the same. Bison were observed displacing snow in 42% of the foraging observations and 6% of the traveling observations. During the OSV season, 77% of the foraging observations and 12% of the traveling observations involved displacing snow.

Plotting the locations of all traveling bison groups observed during complete and partial synoptic surveys demonstrates that in areas where bison were not constricted by topography to travel along road corridors, they were found traveling widely over the study area (Fig. 7). The locations of traveling bison observed during the OSV season are also distributed widely over the study area, suggesting that groomed roads are not a major attractor for traveling bison.

During complete and partial synoptic surveys, 383 traveling bison groups, representing 2,323 individual bison, were observed. Travel was not equal among the 3 categories (ANOVA; $P < 0.001$). Overall, the number of bison groups observed traveling off-road and off-trail ($\bar{x} = 17.2$) was higher than road ($\bar{x} = 6.0$; $P < 0.001$) and trail ($\bar{x} = 8.8$; $P = 0.004$) travel. During the OSV season, the level of off-road and off-trail travel ($\bar{x} = 15.3$) was higher than travel on roads ($\bar{x} = 5.0$; $P = 0.012$). Overall, travel on roads accounted for 19% of all bison travel observed during these surveys (Fig. 8). The use of

established trails accounted for 27%, and peaked during February, March, and April. Off-road and off-trail travel was the most common category of travel throughout the study, accounting for 54% of all observed travel. During the OSV period, road use remained low, accounting for only 17% of bison travel observed during that period. Off-road and off-trail travel accounted for 52% of all travel, while use of established trails increased to 31% of observed travel during the OSV period.

Table 2. Percentage of activities of individual bison observed during complete and partial synoptic bison surveys in the Madison-Gibbon-Firehole study area of Yellowstone National Park. Data are reported as percentages of total observations for each month. Data are from the 1997-98 ($n = 12,871$) and 1998-99 ($n = 15,512$) field seasons.

Month	Total No. Obs.	Displacing Snow		Not Displacing Snow		
		Traveling	Foraging	Traveling	Foraging	Resting
^a November	326	0.0	26.4	0.0	48.2	25.5
December	2,089	0.5	61.3	4.5	6.9	26.8
January	4,568	0.9	63.3	4.0	3.7	28.1
February	5,805	0.6	44.3	7.9	22.6	24.7
March	6,224	0.6	19.3	8.7	51.4	20.0
April	5,825	0.1	3.3	12.0	69.4	15.2
May	3,456	0.0	0.0	6.2	64.8	29.0
Total Obs.	28,293	130	8,223	2,193	11,256	6,491
Percent		0.5	29.1	7.8	39.8	22.9

^aNovember data are from 1997-98 partial synoptic surveys only.

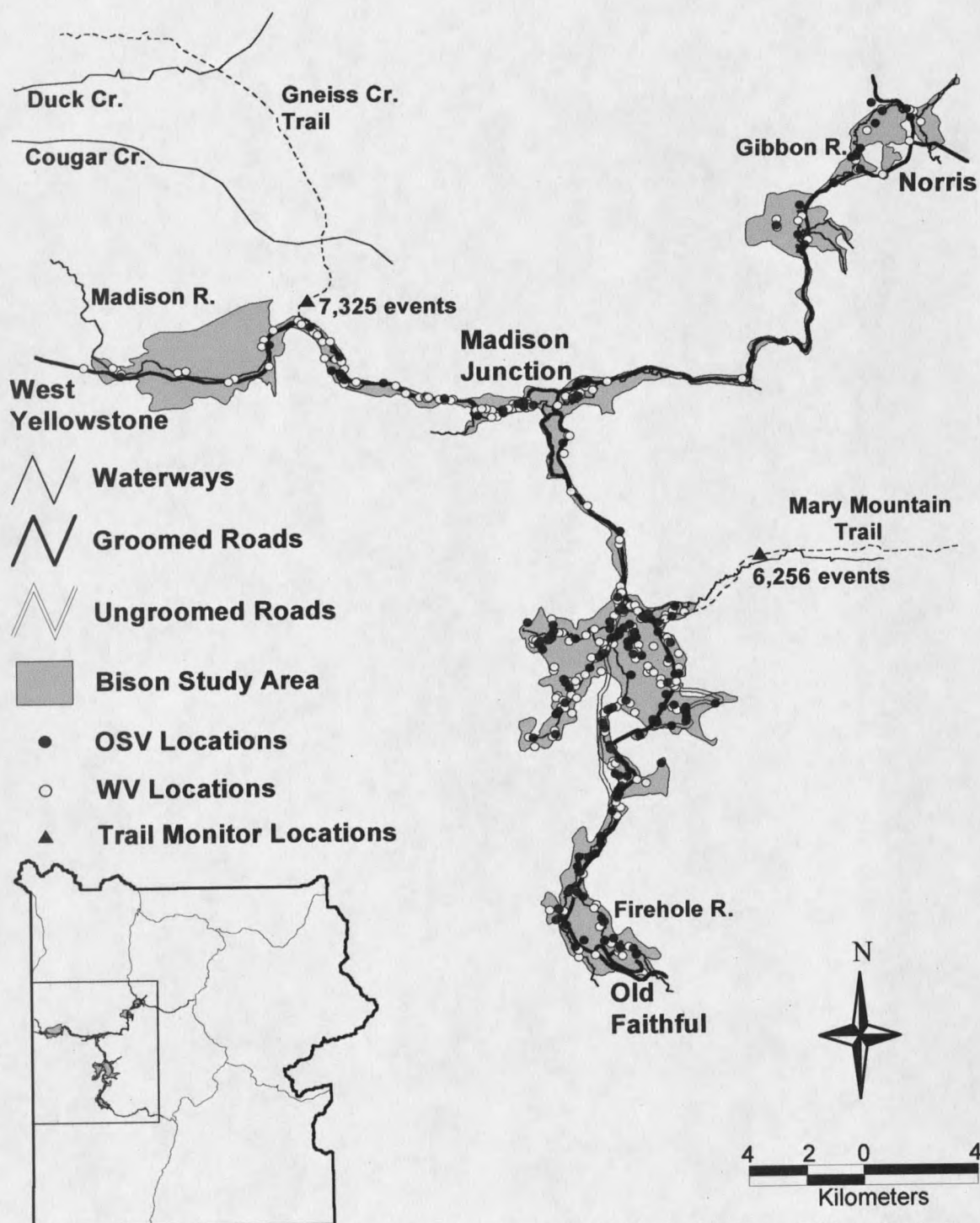


Figure 7. The locations of traveling bison groups ($n = 383$) in the Madison-Gibbon-Firehole study area of Yellowstone National Park. The shaded area denotes the bison range, as delineated by Ferrari (1999). Dark circles represent locations from the over-snow vehicle (OSV) season ($n = 166$), when roads are groomed. Open circles represent data from the wheeled vehicle (WV) season ($n = 217$). The number of traveling bison events recorded by the trail Mary Mountain and Gneiss Creek trial monitors are also given.

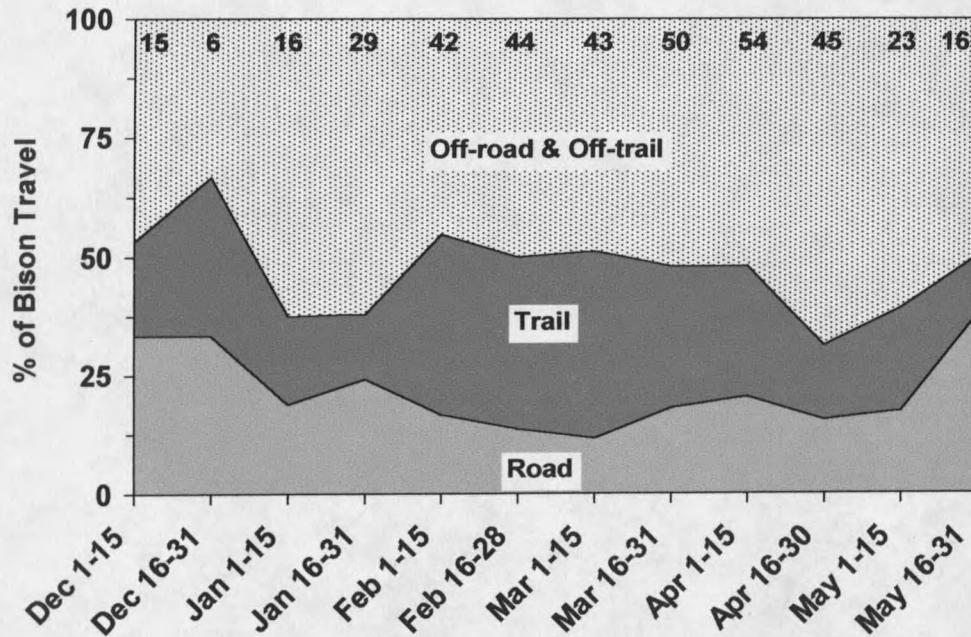


Figure 8. The temporal trends in the proportion of all bison groups observed traveling on roads, established trails, and off roads and established trails in the Madison-Gibbon-Firehole area of Yellowstone National Park. Data are percentages of total bison travel for each time period. Numbers at the top of the figure are the number of traveling groups observed during each 2-week period.

Bison Road Use

While there was a difference in the magnitude of road use by bison between years, the general seasonal pattern of bison road use was similar for both years (Fig. 9). During 42,576 km of travel on the study area roads (1997-98: $n = 22,113$ km; 1998-99: $n = 20,463$ km), 812 bison groups were observed traveling on the roads, 277 in 1997-98 and 535 in 1998-99. As seen in the data from synoptic bison surveys (Fig. 8), the rate of bison use of the road system during the OSV season declined and was lower than the peaks in fall and spring. Road use decreased from a fall peak to a minimum in early winter, increased and leveled off in mid-winter, and peaked in April. This peak in road use coincided with the beginning of spring snow melt-off at the lower elevations of the

study area (Fig. 2) as well as with peak numbers of bison in the study area (Fig. 3). Of all bison road use events that could be recorded as either nocturnal or diurnal during the OSV season, 51 of 335 (15%) were either bison groups observed traveling at night or tracks found in the morning indicating nocturnal use. These data suggest that nocturnal use of the road system by bison was not a major factor in bison travel.

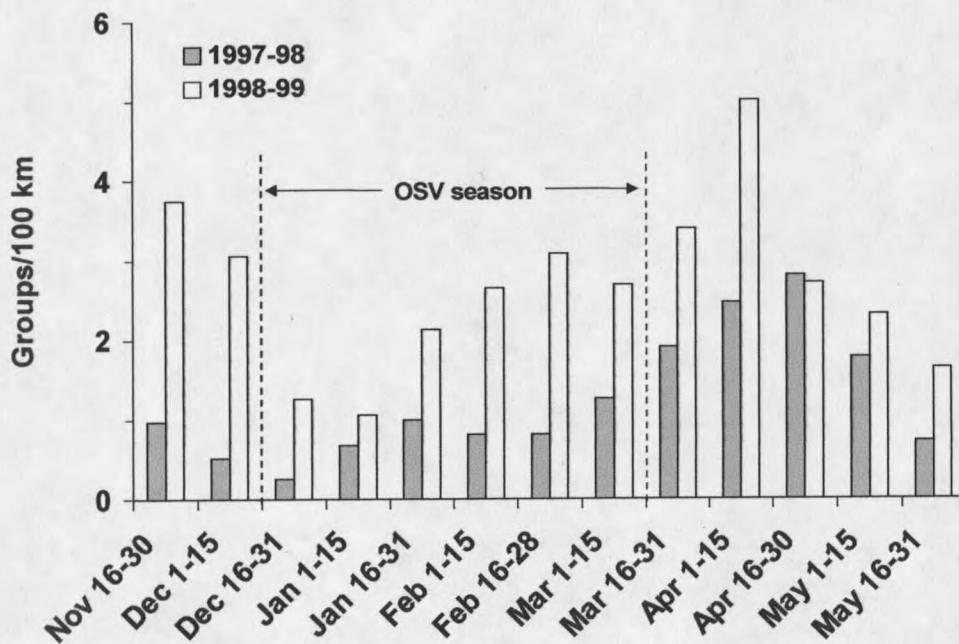


Figure 9. Bison use of the Madison-Gibbon-Firehole road system in Yellowstone National Park. Data are presented as the number of groups observed traveling on roads per 100 km of roads traveled by crew members during the 1997-98 ($n = 277$ groups, 22,113 km) and 1998-99 ($n = 535$ groups, 20,463 km) field seasons. The over-snow vehicle (OSV) season is delineated by dashed lines and is the period when the roads are groomed.

Bison did not travel consistently on the same sections of the study area road system throughout the season (Table 3). Bison road use seemed to follow the distribution shifts of the bison population within the study area. The intensity of use was not in contiguous road sections, suggesting that road use events were not long distance

movements, but rather movements within certain sections. The 4-km-long Madison Canyon section had the highest level of road travel in the fall and spring when bison were more concentrated in the Madison area (Table 1). This road section, about 5 km west of Madison Junction, is constricted from the north by high canyon walls and from the south by the Madison River, necessitating travel on the road for that stretch. During midwinter, road use was highest in the Firehole sections from Fountain Flats to Old Faithful. Bison were concentrated in this area during this time interval (Table 1). The road sections in the Gibbon River Valley were excluded from the analysis due to the low percentage of bison and amount of movement between other portions of the study area.

The regression model analyses to explore potential mechanisms that influence bison road travel yielded 3 essentially equivalent models differing by a ΔAIC_c value of only 0.63 (Burnham and Anderson 1998) (Table 4). Models 1 and 2 differ by only 1 parameter and model 3 contains all 4 parameters, indicating that all 4 parameters influence bison road travel. The coefficients and 95% confidence intervals for the Groom parameter are negative, indicating that bison road use decreased during road grooming. The Bison and SWE parameters were positively correlated with road use indicating that as the snowpack and number of bison in the study area increased, road use also increased. The Year parameter was found in all of the top 4 models, indicating that there was a difference in road use between years that was not captured by the other parameters in the model. Of all 24 models, none that included the 2-way interaction terms fell within 3 ΔAIC_c values of the most parsimonious model, suggesting interactions between SWE and

Table 3. The amount of road use by bison for 7 road sections in the Madison and Firehole Valleys of Yellowstone National Park. Data are presented as the percentage of chi-squared value contributed by each road section for each 2-week time interval. Dashes represent time intervals with non-significant chi-squared values at $\alpha = 0.05$. Bold type in boxes indicates the road section or sections that contributed the largest percentage of chi-squared value for that time interval. The Upper Madison and Fountain Flats sections in the May 1-15 interval had lower than expected values of road use. The largest values in all other time intervals were higher than expected values. Data are from the 1997-98 and 1998-99 field seasons. Sections start with the lower Madison section at West Yellowstone and progress upstream up the Firehole to Old Faithful.

Time Interval	n	km	Road Sections						
			Lower Mad.	Mad Cany	Upper Mad	Firehole Cany	Ftn Flats	Midway	Old Faithful
Nov 16-30	17	664	-	-	-	-	-	-	-
Dec 1-15	34	1747	-	-	-	-	-	-	-
Dec 16-31	11	2780	<1	5	7	2	8	27	50
Jan 1-15	29	3955	11	60	<1	18	1	10	<1
Jan 16-31	49	3592	-	-	-	-	-	-	-
Feb 1-15	50	3429	17	3	2	5	<1	2	72
Feb 16-28	39	2254	16	3	10	13	23	27	8
Mar 1-15	45	2640	-	-	-	-	-	-	-
Mar 16-31	63	2577	-	-	-	-	-	-	-
Apr 1-15	122	3013	4	73	14	<1	6	2	<1
Apr 16-30	96	3138	2	61	21	1	7	<1	7
May 1-15	37	1768	2	19	30	11	32	5	<1
May 16-29	10	1001	9	70	13	1	<1	2	5

the year of the study, or the number of bison in the study area and the year of the study were not as influential to bison road travel as non-interaction parameters.

Table 4. Results of the regression model of the factors influencing bison road use in the Madison-Gibbon-Firehole study area of Yellowstone National Park. The top 4 models are ranked by ΔAIC_c value with the lowest being the most parsimonious. The sample size was 32 for all models. Confidence intervals for the estimated coefficients are 95%. Durbin-Watson statistics and residual plots for models 1-3 indicate no autocorrelation; the statistic and plot for model 4 indicate possible autocorrelation.

Model	Adj. R^2	ΔAIC_c	Parameters	Estimated Coefficients	Lower C.I	Upper C.I
1	0.78	0.00	Groom ^a	-1.161	-1.562	-0.759
			SWE ^b	0.087	0.059	0.115
			Year ^c	0.830	0.389	1.272
2	0.77	0.50	Groom	-0.729	-1.144	-0.313
			Bison ^d	0.004	0.003	0.005
			Year	0.871	0.426	1.315
3	0.82	0.63	Groom	-0.946	-1.353	-0.538
			Bison	0.002	0.0003	0.004
			SWE	0.052	0.013	0.090
			Year	0.766	0.359	1.174
4	0.68	2.42	Bison	0.004	0.003	0.006
			Year	0.758	0.235	1.280

^aGroom = road not groomed (0) or groomed (1)

^bSWE = snow water equivalent at West Yellowstone SNOTEL site

^cYear = 1997-98 (0) or 1998-99 (1) field season

^dBison = number of bison in the study area

When bison were traveling on roads, 53% of the groups encountering over-snow or wheeled vehicles had negative reactions to them (Table 5). During behavioral observations, a total of 145 bison groups were observed traveling, 77 during the OSV season and 68 during the WV season. Of these, 94 (65%) included bison-vehicle

interactions, 55 during the OSV season and 39 during the WV season. During the OSV season, 33 of 55 (60%) groups observed had negative reactions, and during the WV season 17 of 39 (44%) groups observed had negative reactions. Of all negative reactions, 34 of 50 (68%) involved running. The distance ran ranged from approximately 50 m to more than 4 km. Some bison groups that were pushed off the roads immediately got back onto the roads, while others remained off the roads and continued travel.

Table 5. The percentages of reactions of bison groups traveling on roads to interactions with over-snow and wheeled vehicles in the Madison-Gibbon-Firehole area of Yellowstone National Park. Data are reported as percentages of total vehicle encounters observed each month during the 1997-98 and 1998-99 field seasons. Total observations for each month and reaction are given.

Month	No. Bison Groups	No. Vehicle Encounters	Reactions			
			Pushed off road	Ran	Change direction	None
Dec	11	3	0	100	0	0
Jan	19	14	14	36	7	43
Feb	37	32	22	41	3	34
Mar	39	19	11	32	0	58
Apr	22	16	13	31	0	56
May	17	10	10	20	0	70
Total Obs.	145	94	14	34	2	44
Percent			15	36	2	47

Data from the behavioral observations also indicate that long distance travel by bison on the study area road system was not common. Of the 90 observations of bison groups traveling on roads where the distance was recorded, 55 (61%) traveled less than 1 km (Fig. 10). Bison traveled 5 km or further on the roads in only 11 (12%) of the observations. During the OSV season, 30 of 44 (68%) of the recorded distances were less than 1 km, while 3 (7%) were 5 km or further. During the WV season, 25 of 46 (54%) distances were less than 1 km, while 8 (17%) were 5 km or further.

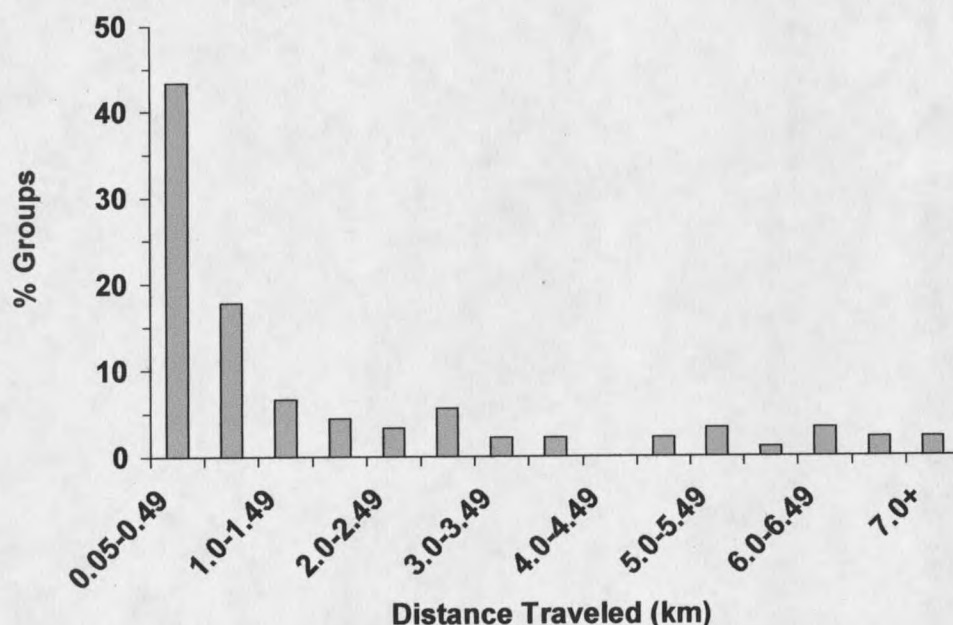


Figure 10. Frequency of distances traveled by 90 groups of bison observed during behavioral observations in the Madison-Gibbon-Firehole area of Yellowstone National Park. Data are from the 1997-98 and 1998-99 field seasons.

DISCUSSION

For many species in high latitudes, snow cover is the most important environmental factor in determining winter survival (Formozov 1946). The seasonal movements of bison in YNP are driven in large part by this factor. The topography and climate of the interior of YNP forces bison movement to the west in a natural flow to lower elevation. The Pelican Valley has the harshest winter environment of any of the bison wintering areas (Meagher 1993). The Hayden Valley also receives significantly more snow than the Madison-Firehole area. For bison to leave the Pelican or Hayden Valleys to the east, north, or south they would be forced to travel over a high mountain range or extensive stretches of unbroken forest with minimal forage. The only suitable direction for seasonal migration, therefore, is to the west over approximately 6 km of the Mary Mountain trail linking the western edge of the Hayden Valley with the nearly contiguous meadow/geothermal complex of upper Nez Perce Creek leading into the lower-elevation Firehole Valley. The Firehole River, in turn, flows into the Madison River, providing a relatively continuous series of meadows leading down the elevational gradient to the western boundary of the Park.

Meagher (1973) and Aune (1981) both observed that the most frequent and largest movements of bison occurred between the summer range in the Hayden and Pelican Valleys and the winter range in the Firehole Valley over Mary Mountain. As early as 1894, bison were known to utilize this corridor to travel back and forth during these seasonal migrations (Meagher 1973). Major shifts in bison distribution between the

Hayden Valley and the MGF area utilizing alternative corridors have not been documented. Based upon data from this study and observations made by Meagher (1973) and Aune (1981), this seasonal shift from the central part of the Park to the Firehole drainage appears to be driven by increasing snowpack in the higher elevation Hayden and Pelican Valleys. Movement of bison into the Firehole drainage begins in the fall, however, prior to significant snow accumulation, suggesting that the bison herd has developed a migratory pattern that is not entirely weather dependent. After entering the Firehole drainage, some bison dispersed down to the Madison River Valley and Cougar Meadows. This movement occurred in the fall, prior to road grooming. As snowpack increased in December and January, bison in these areas moved back into the Firehole Valley where geothermal activity creates accessible forage throughout the winter. These movements are consistent with Meagher (1993), who stated that bison utilized the Madison and Cougar Meadows area in fall/early winter and in spring, but vacated many west side foraging areas as winter progressed and foraging became difficult to impossible due to snow conditions. Similar seasonal movements have been documented in bison in Wood Buffalo National Park (Carbyn et al. 1993), elk on the National Elk Refuge (Smith and Robbins 1994), and mule deer in Colorado (Garrott et al. 1987).

The major shifts in bison distribution observed during the fall and spring periods in YNP suggest that significant energetic costs are incurred by bison due to the displacement of snow while traveling (Meagher 1993). The activity budget data collected during this study however, indicate that the predominant energetic costs bison incurred were in foraging and not traveling. Traveling accounted for only 8% of bison

activities observed throughout the study and only 7% of all activities during the OSV season. Since a large majority of this travel took place on established trails or along stream banks or geothermal features, only 6% (0.5% of all activities) and 12% (0.8% of all activities) of this travel involved displacing snow, respectively. In contrast, bison spent approximately 68% of their daylight activity budgets foraging, in which they displaced snow in 42% of all observations and 77% of observations made during the OSV season. Bison were estimated to have been engaged in snow displacement behavior approximately 30% of the daylight hours during the winters of 1997-98 and 1998-99. Although no snow displacement energetics studies have been conducted on bison, results of such studies on other ungulate species indicate that the energetic costs of displacing snow during travel and foraging activities are increased over base energetic costs of these activities when snow is minimal or absent (Parker 1984, Fancy and White 1985, 1987, Hobbs 1989). Likewise, the decreased availability of forage buried under the snow and the increased energetic costs of displacing that snow to gain access to the forage greatly influences ungulate demographics (Formozov 1946, Hobbs 1989). Since travel activity accounted for only 1.6% of all observations where snow displacement took place, the energetic costs of displacing snow due to traveling would have to be very minor compared to the costs of snow displacement while foraging, thus playing a minor role in the rate at which bison body reserves are depleted over the winter.

When bison were traveling, they traveled off-road more than they traveled on roads. This travel was not restricted to areas close to the groomed road system. Bison utilized all portions of the study area for travel during both the OSV and the WV seasons.

As snowpack increased from fall into winter, bison created a network of established trails throughout the study area. Through repeated travel, this network was maintained in an effectively "groomed" state during the winter. Similar observations were made by Van Camp (1975) and Aune (1981), who both observed that bison established a network of trails throughout their winter range and traveled them extensively until snowmelt. The largest proportion of bison travel during the OSV season, however, remained off of both roads and trails established by bison. Bison utilized stream corridors and geothermal features extensively in their travels. Thus, it seems that roads are a small segment of a much larger travel network that bison utilize during all seasons, and suggestions that groomed roads are an essential or exclusive travel corridor for winter movements, or that without them bison range expansion would entail energy costs that do not occur presently, seem unfounded.

Bison travel on the road system in the study area also varied spatially. The sections of heaviest road use were in areas of high bison concentration and/or topographic constriction. The section of road that passes through the Madison Canyon was utilized heavily in the fall and spring. At these times, bison numbers had increased in the Madison area. Because the Madison Canyon is tightly constricted on both sides by the Madison River and canyon walls, bison had little choice but to travel on the road for this segment. Once through this segment, the road use data from the road sections on either end of this canyon indicate that bison did not continue on the road into these sections. During the midwinter months, sections in the Firehole had the highest road use. These data, along with data on the frequency of distances traveled on roads suggest that

most road use events were short distance movements within localized areas and not long distance movements that would result in major changes in bison distribution.

The intensity of bison road use was variable temporally as well as spatially. Peak periods of bison road use occurred before and after the OSV season, with road use negatively correlated with road grooming. The larger spring peak coincided with the beginning of snowmelt and the peak number of bison in the study area. The peak in overall road and off-road travel also occurred at this time. This, along with bison travel data from synoptic surveys, suggests that during midwinter bison travel less frequently due to heavy snow cover in nearly all areas of the winter range. As the snowpack begins to diminish, newly melted foraging patches are small and scattered widely throughout the study area. This creates the need for bison to travel further and more often to reach them. As melt-off progresses and more forage is made available to bison in larger and more numerous areas, bison do not have to travel as far to reach these areas and thus overall travel and road use decreases. Similar timing of movements was observed by Van Camp (1975), who found that as soon as snow began to melt on south-facing slopes, bison utilized them for forage.

Although bison traveling on the groomed road system avoided all energy expenditures associated with displacing snow, most bison traveling off the road system also avoided these costs by traveling on previously established trails, along riverbanks and in geothermally-influenced streams, and by traveling in the extensive geothermal areas where snow was absent. In addition, more than half of bison groups observed traveling on roads came in close contact with vehicles on the roads and responded

negatively by either running, changing direction of travel, or exiting the road into the snowpack. These observations suggest that traveling the groomed road system is no more energetically efficient than most off-road travel, and in some instances may actually be more energetically costly to bison than traveling off roads. However, the large majority of bison did not switch to nocturnal use of the groomed roads to avoid these interactions. Data from both observations of nocturnal travel and tracks found on the road in the morning illustrate that the majority of bison road use occurs during daylight hours. This conclusion is supported by logs kept by road groomer operators at Madison Junction during both winters. In the 640 to 700 hours spent grooming the roads to West Yellowstone and Norris at night, only 9 bison groups were observed during the 1997-98 OSV season and 22 during 1998-99. These data, along with data from the infrared trail monitors suggest that bison travel occurs predominantly during daylight hours.

Groomed road use by bison in the MGF area of YNP seems to be an activity that is neither sought out nor avoided. Bison obviously use groomed roads within the study area for travel. However, use of natural off-road areas for travel is much more common. The minimal use of roads compared to off-road areas, the short distances traveled on the roads, the decreased use of roads during the OSV season, and the increased costs of negative interactions with OSVs suggest that roads are not the major influence on bison ecology that has been proposed. Indeed, the most controversial aspect of the changes in bison distribution and movement dynamics, the shift from the central part of YNP to the Firehole and Madison drainages to the west, is affected almost exclusively by the movement of bison along the Mary Mountain trail. Thus, it seems that the practice of

grooming YNP roads to facilitate visitor access in winter has had little effect on: 1) the shift in winter distribution of the Mary Mountain bison herd from the central portion of the Park, 2) bison movements within the MGF winter range, and 3) the periodic exodus of bison from YNP along the western boundary.

Historic changes in the YNP bison population support the conclusion that recent changes in bison distribution are a natural occurrence. As early as the 1870s and 1880s, bison were known to inhabit the Madison and Firehole areas in numbers as high as 200-300 individuals (Meagher 1973). After near-extirpation, bison were introduced from herds in Texas and Montana and were intensively managed in a ranching-style operation until 1952 (Meagher 1973). Periodic reductions of the bison population continued until 1967, when official Park policy changed to natural regulation (NPS 1998). At this time, the Park-wide bison population count was 397, the lowest since ranching operations began (Meagher 1973). Once population reductions ceased, the bison population began a steady increase (Meagher 1993), with the absolute population growth rate remaining essentially constant from 1972 to 1995 (Cheville et al. 1998). Gates and Larter (1990) described the expansion of bison range with an increasing population. They found that range size was strongly correlated with population size and that major range shifts were in response to a density-driven dispersal. Similar instances of range expansion of increasing ungulate populations have been documented in caribou (Messier et al. 1988), elk (Lemke et al. 1998), and muskox (Reynolds 1998).

The change in bison distribution and movement patterns over the past 30 years suggests a natural process of range expansion as the population increased from near

extirpation and was released from the intensive management and culling. Therefore, the increasing bison population, which has been the purported effect of road grooming, seems more likely to be the cause of the shifts in bison distribution to areas not commonly used in previous winters. Historically, it seems likely that bison migrated out of the MGF area to the west in winter, following the Madison River to the large, lower-elevation valley approximately 40 km downstream from the current Park boundary. This pattern was effectively eliminated during periods of extremely low populations and intensive management. Since population regulation has ceased, it seems this pattern is being re-established. The premise that road grooming has significantly influenced this, however, is not supported by this study.

If these interpretations are correct, it would suggest that the management problem associated with the movement of bison across the western boundary of YNP onto public and private lands would persist whether the Park roads were groomed for winter visitation or not. The bison population appears to have recovered from near extirpation and fully expanded their use of suitable habitat within YNP. Under these conditions, per capita resources become limiting and the population can be expected to become increasingly sensitive to the unpredictable annual variation in winter snowpack. Unusually severe winter snowpack combined with a high bison population relative to the ecological carrying capacity of YNP will result in accentuated winter mortality and dramatic shifts in distribution as bison seek to escape deep snow and find forage. These distributional shifts will occur down elevation gradients leading to variable numbers of bison leaving YNP along the western boundary as was experienced during the winter of

1996-97. These events will be unpredictable as they are dependent upon winter severity, and should be considered a natural dynamic of the system.

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