EFFECTS OF WINTER ROAD GROOMING ON BISON IN YELLOWSTONE NATIONAL PARK

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Abstract: The effects of winter recreation—specifically snowmobiling—on wildlife in Yellowstone National Park (YNP) have become high-profile management issues. The road grooming needed to support oversnow travel in YNP is also being examined for its effects on bison (*Bison bison*) ecology. Data were collected from November 1997 through May 1998 and from December 1998 through May 1999 on the effects of road grooming on bison in Madison–Gibbon–Firehole (MGF) area of YNP. Peak bison numbers occurred during late March–early April and were strongly correlated with the snow water equivalent measurements in the Hayden Valley area (1997–1998: $r^2 = 0.62$, $P < 0.001$; 1998–1999: $r^2 = 0.64$, $P < 0.001$). Data from an infrared trail monitor on the Mary Mountain trail between the Hayden and Firehole valleys suggest that this trail is the sole corridor for major bison distributional shifts between these locations. Of the 28,293 observations of individual bison made during the study, 8% were traveling and 69% were foraging. These percentages were nearly identical during the period of winter road grooming (7% and 68%, respectively). During this period, 77% of bison foraging activity and 12% of bison traveling activity involved displacing snow. Most travel took place off roads ($P < 0.001$). Bison utilized geothermal features, a network of trails they established, and river and stream banks for travel. Bison road use was negatively correlated with road grooming, with peak use in April and lowest use during the road-grooming period. Bison in the MGF area of YNP neither seek out nor avoid groomed roads. The minimal use of roads compared to off-road areas, the short distances traveled on the roads, the decreased use of roads during the over-snow vehicle (OSV) season, and the increased costs of negative interactions with OSVs suggest that grooming roads during winter does not have a major influence on bison ecology.

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During the past several decades, the focus of human use of public lands has changed. The number of outdoor recreationists has expanded rapidly with the increase in human population, disposable income, and leisure time (Knight and Gutzwiller 1995). This emphasis on recreation creates new resource management issues on public lands. In areas that were once used mainly for extractive industries such as mining and logging, the predominant activity is now outdoor recreation (Knight and Gutzwiller 1995). Instead of localized effects, resource managers must now handle 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 recreation effects can be so extensive (Flather and Cordell 1995).

Yellowstone National Park is a microcosm of the effects of growing recreational activities (Aune 1981, Gunther 1991, Cassirer et al. 1992, National Park Service 1999). Annual visitation to YNP increased 30% from 2,404,862 people in 1982 to 3,131,381 in 1999 (T. Wert, National Park Service, unpublished data). Total winter visitation increased even more (60%), from 77,679 in 1984–1985 to 124,275 in 1998–1999 (National Park Service 1999). The first permits for snowcoaches to bring tourists into YNP were granted in 1955. Snowmobile tourism began during 1963–1964 when the first private snowmobiles entered the park (Aune 1981). To restrict the use of snowmobiles to the roads and facilitate better access to the park, the National Park Service (NPS) began road grooming in 1970. The number of snowmobile and snowcoach (over-snow vehicle) visitors entering YNP increased from 12,239 in 1970–1971 to 42,597 in 1977–1978 (T. Wert, National Park Service, unpublished 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

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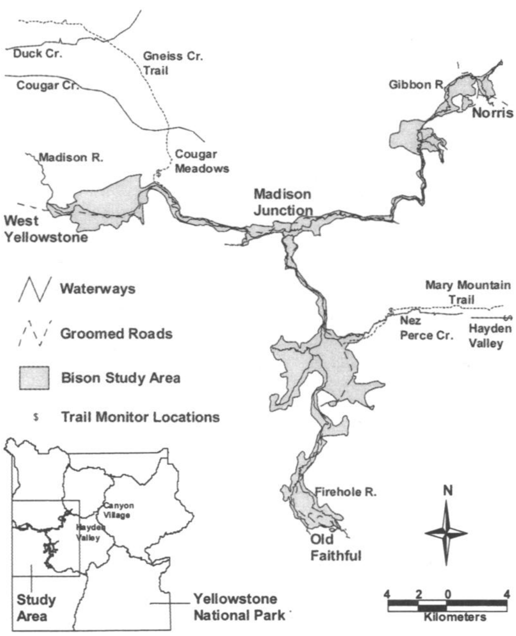

Fig. 1. Madison–Gibbon–Firehole study area in Yellowstone National Park. The shaded area represents the bison range, as delineated by Ferrari (1999).

influencing wildlife distribution and habitat use. Since 1978, OSV visitation has doubled to 86,977 in 1998–1999 (National Park Service 1999).

Concurrent with increasing park visitation has been a steady increase in the YNP bison population (National Park Service 1998). The winter of 1996–1997 brought above-average snow depths and thick ice layers in the snowpack that impeded foraging (Cheville et al. 1998). In search of forage, bison left YNP, and over 1,000 bison 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 1996–1997, Meagher (1993) suggested that road grooming facilitated bison migration out of the park. The contention 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 bison out of YNP. Prompted by these assertions and the killing of bison in the 1996–1997 winter, several advocacy groups filed suit against the NPS. This led 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 was to quantify bison distribution, movement, and activity patterns and evaluate the ecological consequences of winter road grooming on these aspects of bison ecology. Four testable hypotheses were formulated to address the purported effects of road grooming on bison: (1) road grooming facilitates major bison distributional shifts; (2) displacing snow while traveling is the major energetic cost to bison in the winter; (3) most bison travel in winter would be on groomed roads within the Madison–Gibbon–Firehole study area, thus facilitating long-distance movements by bison seeking to escape the costs of traveling in snowpack; and (4) traveling on groomed roads results in less energy expenditure by bison than traveling off-roads.

STUDY AREA

The MGF study area consisted 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 were considered the primary winter range for the Mary Mountain bison subpopulation, the largest in YNP and 60% to 75% of the entire YNP bison population (Thorne et al. 1991, Meagher 1993). The study area encompassed approximately 7,200 ha, with elevations ranging from 2,000 m to 2,250 m. Winter visitation in this area was 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 MGF study area, the Hayden Valley in the central region of YNP east of the study area, and the meadows above and along Cougar and Duck Creeks northwest of the study area, were also important to bison movements within the study area. Bison moved from the higher-elevation Hayden Valley (2,466 m) into the MGF area in winter (Meagher 1993). The Cougar and Duck Creek area and the Madison River were utilized as egress corridors for bison in the study area (National Park Service 1998). These egress points were of major concern due to the threat of bison transmitting brucellosis to cattle outside the park (Cheville et al. 1998).

The study area consisted of several extensive, flat meadows associated with the major river systems. Forested regions and canyons of the major rivers separate these areas. There is also considerable geothermal activity in the study area. Warm sites near these areas have less snow cover, become snow-free earlier in spring, and have a longer growing season than surrounding areas (Meagher 1973, Despain 1990). During 1988, several major fires burned through the area (Despain 1990). Prior to these fires, approximately 61% of the area was dominated by climax lodgepole pine (*Pinus contorta*) or seral stages (Aune 1981). The 1988 fires created 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 area has long, cold winters and short, cool summers. At nearby West Yellowstone, Montana, the mean monthly temperature ranged from 15.3 °C in July to –10.6°C in January (Aune 1981). Mean annual snowfall was 418 cm, and mean snow depth exceeded 46 cm for an average of 126 days per year. The beginning of snow accumulation at 2,100 m occurred in late October, and the end of the snowpack at this elevation is normally in late May (Despain 1990).

Paved, 2-lane roads along the major rivers extended throughout the area (Fig. 1). From West Yellowstone, the road extended 22 km to Madison Junction, 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 passed through the Gibbon Canyon and Gibbon Meadows and on to Norris for 22 km. The road from Madison Junction to Old Faithful followed the Firehole River for 26 km through Firehole Canyon, Lower and Midway geyser basins. The roads were open to visitors in wheeled vehicles (WV) from 15 April until 31 October. From 1 November until the third week in December, the roads were closed to all but travel by YNP personnel. However, the roads were not plowed, and snow was allowed to accumulate on the roads. Road grooming began the evening prior to the opening date of the OSV season—approximately the third week of December. Roads were groomed nightly until the end of the OSV season in early to mid-March. The roads were then closed to all visitor vehicles and were plowed to pavement. Travel was restricted to YNP personnel until approximately 15 April.

METHODS

We collected data from mid-November 1997 through May 1998, and from early December 1998 through May 1999. The OSV season extended from 19 December to 9 March during 1997–1998, and from 16 December to 14 March during 1998–1999.

Spatial and Temporal Snowpack Variation

We used snow water equivalent (SWE) as an index of snowpack (Farnes 1996). Data were gathered from remotely operated Natural Resources Conservation Service (NRCS) Snowpack Telemetry (SNOTEL) sites near West Yellowstone and Canyon Village (Fig. 1). The West Yellowstone site—at an elevation of 2,042 m—indexed SWE in the lower-elevation valley bottoms of the study area, while the Canyon SNOTEL site—at 2,466 m—indexed SWE in the Hayden Valley (Fig. 1, inset), which is the major summer range for bison in YNP (Meagher 1973).

Synoptic Bison Surveys

The bison population, its 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 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. A 3-person crew could survey the entire study area in 2 days. Surveys were conducted to minimize 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. These complete synoptic bison surveys were conducted 33 times during this study: 17 during 1997–1998 and 16 during 1998–1999.

We recorded the location of each bison group detected in Universal Transverse Mercator (UTM) coordinates (using USGS 7.5-min maps) and the age and sex composition of the group as cows, bulls, calves of the year, and unknown adults. 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 excluded animals that were slowly wandering and stopping frequently to forage. Bison travel was categorized as either on or off roads, or on trails established by regular bison use. Foraging bison 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), placing depth 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, we 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, we randomly selected a stratum and 1 of the 2 travel routes within that stratum to survey that day. We conducted 3 partial surveys 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 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. 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 considered a census of the bison population in the study area. We used linear regression (Minitab Inc. 1998) to examine correlations between changes in the number of bison detected within the study area each winter and the 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. We also used linear regression to examine correlations between changes in the distribution of bison in the Madison and Firehole River valleys. We aggregated bison activity data from all complete and partial synoptic surveys from both years to evaluate monthly bison activity patterns. We used ArcView GIS software (ESRI 1998) to plot the locations of all traveling bison groups observed during complete and partial synoptic surveys to determine the spatial extent of traveling bison. We tested the differences in the mean number of bison groups observed traveling per 2-week time interval on and off roads, and trails (1-way analysis of variance, and orthogonal linear contrasts; PROC GLM; SAS Institute 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. Most of the road system was covered daily. Each crew member recorded the sections of road traveled daily and the attributes of any bison group observed using the road. We determined daily survey effort by summing the number of km traveled by crew members excluding road sections that were traveled by more than 1 crew member within 1 half hour of each other. Bison traveling less than 50 m on the roads were not recorded as road use. If possible, we recorded the direction of travel, location of the group where it was first observed, and where the group accessed and exited the road. 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 for diurnal road use.

We used regression models (Minitab Inc. 1998) to examine factors that may have contributed to the propensity for bison to travel on the road system. The time intervals for the models were centered on the date of each complete synoptic survey. The response variable 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 during the synoptic survey (Bison), the mean SWE at West Yellowstone for that time interval (SWE), whether the roads were groomed (Groom; 0 = ungroomed, 1 = groomed), and the year (Year; 0 = 1997–1998, 1 = 1998–1999). Because of limited sample sizes, we calculated a corrected Akaike's Information Criterion (AIC_c) value 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. Plots of the residuals revealed an outlier, which corresponded to a time interval when crew members could not travel the roads due to road-plowing operations. The outlier was discarded due to less than 50% normal survey effort, providing 32 observations per model and 8 observations per parameter for the most complex (4 parameter) models. The recommended minimum number of observations per parameter in a model has been suggested as 6 to 10 (Neter et al. 1996). Inference from models at or below this range should be viewed with caution. We used residual plots and Durbin-Watson test statistics 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 24.

We obtained data on bison use of major established trails from 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 and from a second monitor on the Gneiss Creek trail leading from the Madison River at Seven Mile Bridge to the Cougar Meadows area (Fig. 1). We chose the Mary Mountain trail because it is considered 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 on observations in previous winters of heavy bison travel on the trail. Once bison had established well-defined trails in the snowpack, the monitors were placed on the trails where bison were restricted to traveling in single file. The monitors recorded the number of bison using the trails, and time and date of use. The monitors recorded 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 monitor. The monitors were programmed so that once the beam was broken and a photograph was taken, the camera did not take another picture for 10 minutes. The photographs identified the species of the lead animals of each group that broke the beam as well as the direction of travel. By analyzing the timing of the events immediately following the photographs, the species of the entire group could be determined. For instance, 25 events occurring from 12:42 to 12:47 were considered a single group. A photograph of the lead animal identified as a bison was interpreted to mean that the remaining 24 events were also bison. The monitor on the Mary Mountain trail operated from early December 1997 until early July 1998 and from mid-September 1998 until early July 1999. Bison moving into the study area before December 1997 were not recorded. Also, several mechanical failures with the trail monitor occurred in December 1997 and November 1998 causing missing data. The monitor on the Gneiss Creek trail operated from late November 1997 until late May 1998 and from mid-October 1998 until early June 1999.

Behavioral Observations

We recorded behavior of traveling bison groups throughout each field season to obtain information on the influence of groomed roads and human interactions. We used 2 sampling regimes. During the partial synoptic surveys, we recorded the behavior of the first bison group traveling on the road and the first group traveling off the road. In addition, between each complete synoptic survey we set aside a day solely for intensive behavioral observations of all traveling bison groups detected. One of the 3 river drainages 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.

The behavior of a traveling bison group was recorded from when it was first seen until the group was out of sight or until it stopped traveling for >5 minutes. The route traveled by the group was recorded on 7.5-minute USGS topographical maps. Data included distance traveled on and off roads, travel time, whether snow was being displaced, and the number and type (snowmobile or snowcoach) of interactions with park visitors. Interactions were defined as any snowmobile or snowcoach approaching within 100 m of any traveling bison. Bison reactions to these interactions were categorized as either ran, pushed off road, changed direction of travel, or none. If a reaction included more than 1 of these

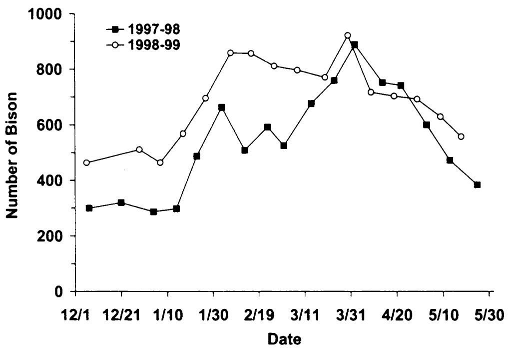

Fig. 2. Temporal trends in the number of bison enumerated in the Madison–Gibbon–Firehole study area in Yellowstone National Park. Data are from complete synoptic surveys of the study area at approximate 10-day intervals during 1997–1998 (n = 17) and 1998–1999 (n = 16).

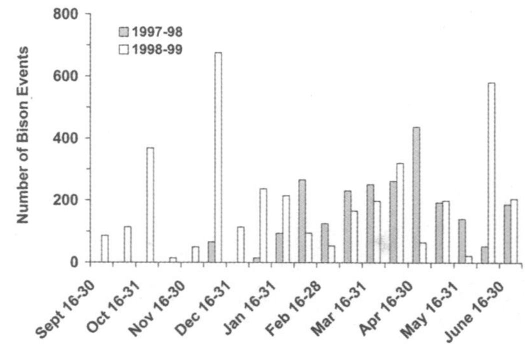

Fig. 3. Number of events recorded as bison by an infrared trail monitor on the Mary Mountain trail between the Hayden Valley and Firehole River Valley in Yellowstone National Park. n = 2,473 in 1997–1998 and 3,783 in 1998–1999. Missing data due to monitor failures occurred in December 1997 and November 1998.

categories (i.e., changed direction and ran), the reaction was recorded as the one assumed to cost the bison the most energy. We assumed that running cost more energy than being pushed off the road, and that changing direction cost the least of the 3 negative reactions.

RESULTS

Spatial and Temporal Snowpack Variation

Snowpack began to accumulate during late October–early November and continued to increase throughout the winter (Bjornlie 2000). Peak snowpack occurred in early April and was followed by a rapid meltoff lasting about 6 weeks. Canyon SWE was about twice that of West Yellowstone. Peak SWE during the winter of 1998–1999 was 44% higher than 1997–1998 at Canyon and 71% higher at West Yellowstone. West Yellowstone peak SWE during the winter of 1997–1998 was 37% lower than the historic average SWE (1967–1997), whereas 1998–1999 peak SWE was 24% higher than the historic average. Peak SWE at Canyon was only 2% lower than the historic average (1981–1997) during 1997–1998, whereas it was 43% above the historic average during 1998–1999.

Bison Population and Distribution Dynamics

The bison population in the study area ranged from 299 to 888 in 1997–1998 and 464 to 921 in 1998–1999, with peaks near 1 April for both years (Fig. 2). SWE at the Canyon SNOTEL site and the number of bison counted were positively correlated for both 1997–1998 and 1998–1999 (1997–1998: r^2 = 0.62, $P < 0.001$; 1998–1999: r^2 = 0.64, $P < 0.001$; Bjornlie 2000). This evidence suggests that snowpack in the Hayden Valley influences the number of bison in the study area.

The infrared trail monitor on the Mary Mountain trail recorded 6,256 events identified as bison during the study, 2,473 in 1997–1998 and 3,783 in 1998–1999. These events included travel in both directions. Most (74%) were diurnal travel, between 0600 and 1759 hours. During the OSV season, 81% of the bison events were diurnal. The number of bison events in a 2-week period ranged from 0 to 437 in 1997–1998, and 4 to 676 in 1998–1999 (Fig. 3).

Bison were not evenly distributed throughout the 3 major river valleys (Bjornlie 2000). The Gibbon River Valley contained the lowest percentage of bison observed during complete synoptic surveys during both field seasons with an overall average of 8%. The Madison River Valley contained an average of 19% of the bison, 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 were in the Madison and Firehole valleys. Exchange of bison between these areas was indicated by a strong inverse relationship between the percentages of bison in these 2 valleys during both seasons (1997–1998: coefficient = –1.00, r^2 = 0.94, P = 0.001; 1998–1999: coefficient = –0.99, r^2 = 0.85, $P < 0.009$). The percentage of bison was lowest in the Madison River Valley in February and March in both seasons.

Data from the infrared trail monitor on the Gneiss Creek trail indicated that bison leaving the Madison River area in midwinter did not

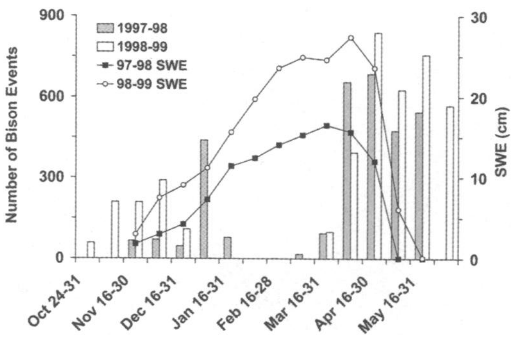

Fig. 4. Number of events recorded as bison by an infrared trail monitor on the Gneiss Creek trail between the Madison River and Cougar Meadows in Yellowstone National Park. n = 3,168 in 1997–1998 and 4,157 in 1998–1999. Mean snow water equivalent (SWE) values recorded at the Natural Resources Conservation Service automated SNOTEL site near West Yellowstone are also plotted.

move west into the Cougar Meadows–Duck Creek area because bison vacated that area in early winter. Overall, 7,325 events identified as bison were recorded by this trail monitor: 3,168 in 1997–1998 and 4,157 in 1998–1999. Over both years, and during the OSV seasons, 76% of the events were diurnal travel between 0600 and 1759 hours. The number of events peaked moderately in early January of the first season and early December of the second season (Fig. 4). 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. 4). This period corresponds with the maximum snowpack. Large peaks occurred during the spring in both years, corresponding with the start of snowpack melt at West Yellowstone (Fig. 4).

Bison Activity

Overall, bison spent 69% of time foraging, 23% resting, and 8% traveling (Table 1). During the OSV season, the time spent foraging (68%) and traveling (7%) were nearly the same. Overall, 42% of foraging bison and 6% of traveling bison were displacing snow. During the OSV season, 77% of foraging bison and 12% of traveling bison were observed displacing snow. Plotting the locations of all traveling bison groups observed during complete and partial synoptic surveys demonstrated that where bison were not constricted by topography to travel along road corridors, they traveled widely over the study area (Bjornlie 2000). This was also true of traveling bison during the OSV season only.

During complete and partial synoptic surveys, 383 traveling bison groups, representing 2,323 individual bison, were observed. The number of bison groups traveling off-road–off-trail (n = 206), on roads (n = 72), or on trails (n = 105) differed significantly (ANOVA; $P < 0.001$; Fig. 5). Overall, the mean number of bison groups traveling off-road and off-trail ($\bar{x}$ = 17.2) was higher than those traveling on roads ($\bar{x}$ = 6.0; $P < 0.001$) and trails ($\bar{x}$ = 8.8; P = 0.004). 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, 19% of all bison travel was on roads, 27%

Table 1. Activities of individual bison observed during 33 complete and 99 partial synoptic bison surveys in the Madison–Gibbon–Firehole study area of Yellowstone National Park[a].

Month	Total number of observations	Percent displacing snow		Percent not displacing snow		
		Traveling	Foraging	Traveling	Foraging	Resting
November[b]	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 observations	28,293	130.0	8,223.0	2,193.0	11,256.0	6,491.0
Percent		0.5	29.1	7.8	39.8	22.9

[a] n = 12,871 in 1997–1998 and 15,512 in 1998–1999.

[b] November data are from 1997–1998 partial synoptic surveys only.

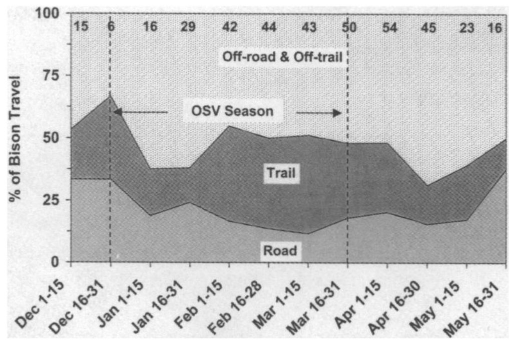

Fig. 5. The temporal trends in the proportion of all bison groups observed traveling on roads, established trails, and off roads and established trails in the Madison–Gibbon–Firehole area of Yellowstone National Park. Data are percentages of traveling bison groups observed during each 2-week period. The numbers of traveling groups observed during each period are at the top of the figure. The over-snow vehicle (OSV) season is the period when the roads are groomed.

was on established trails—which peaked during February, March, and April, and 54% was off-road and off-trail. During the OSV period, travel on roads remained low at 17%, travel off-road and off-trail was 52%, and travel on established trails increased to 31%.

Bison Road Use

Although the magnitude of road use by bison differed between years, the general seasonal pattern was similar both years (Fig. 6). During 42,576 km of travel on the study area roads, 812 bison groups were observed traveling on the roads: 277 in 1997–1998 and 535 in 1998–1999.

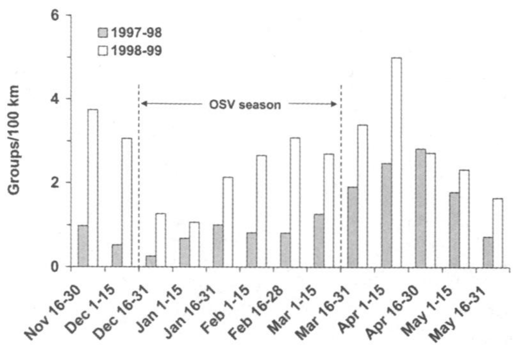

Fig. 6. Bison use of the Madison–Gibbon–Firehole road system in Yellowstone National Park. Data are the number of groups observed traveling on roads per 100 km of roads traveled by crew members during 1997–1998 (n = 277 groups, 22,113 km) and 1998–1999 (n = 535 groups, 20,463 km). The over-snow vehicle (OSV) season is the period when the roads are groomed.

The amount of bison travel on the road system declined during the OSV season and was lower than the peaks in fall and spring (Fig. 5). Road use decreased from a fall peak to a minimum in early winter, increased in midwinter, and peaked in April. This peak in road use coincided with the beginning of spring snow meltoff at the lower elevations of the study area (Bjornlie 2000) as well as with peak numbers of bison in the study area (Fig. 2). 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 of bison found in the morning that indicated nocturnal use. These data suggest that nocturnal use of the road system by bison was not a major factor in bison movements.

The regression model analyses we used 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 2). Models 1 and 2 differed by only 1 parameter. 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 a difference in road use between years that was not captured by the other parameters in the model. None of the models that included 2-way interaction terms fell within 3 ΔAIC_c values of the most parsimonious model, suggesting interactions between SWE and 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.

When bison were traveling on roads, 53% of the groups encountering over-snow or wheeled vehicles had negative reactions to them (Bjornlie 2000). During behavioral observations, 145 bison groups were 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 had negative reactions (22 ran, 9 pushed off road, 2 changed direction), and during the WV season, 17 of 39 (44%) groups had negative reactions (12

Table 2. Results of the regression model of the factors influencing bison road use in the Madison–Gibbon–Firehole area of Yellowstone National Park. The top 4 models are ranked by ΔAIC_c value with the lowest being the most parsimonious. $n = 32$ 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	Adjusted 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

[a] Groom = road not groomed (0) or groomed (1).

[b] SWE = snow water equivalent at West Yellowstone SNOTEL site.

[c] Year = 1997–1998 (0) or 1998–1999 (1) field season.

[d] Bison = number of bison in the study area.

ran, 5 pushed off road, 0 changed direction). 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 returned to the roads, while others remained off the roads and continued to travel.

Behavioral observations also indicate that long-distance travel by bison on the 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 (Bjornlie 2000). Bison traveled 5 km or farther on the roads in only 11 (12%) 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 farther. During the WV season, 25 of 46 (54%) distances were less than 1 km, while 8 (17%) were 5 km or farther.

DISCUSSION

For many species in high latitudes, snow cover is the most important environmental factor 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 interior 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 considerably 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 through 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 that links the western edge of the Hayden Valley with the nearly contiguous meadow–geothermal complex of upper Nez Perce Creek, which leads into the lower-elevation Firehole Valley (Fig. 1). 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 travel back and forth along this corridor during these seasonal migrations (Meagher 1973). Major shifts in bison distribution between the Hayden Valley and the MGF area via alternative routes have not been documented. Our study and those by Meagher (1973) and Aune (1981) indicate that this seasonal shift from the central part of YNP to the Firehole drainage is 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, which suggests 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 descriptions presented by Meagher (1993). Similar seasonal movements have been documented for 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 activity data indicate that the predominant energetic costs bison incurred were in foraging rather than traveling. Traveling accounted for only 8% of bison activities observed throughout the study and only 7% of all activities during the OSV season. Since most of this travel occurred on established trails, along streambanks, or through geothermal areas, only 6% (0.5% of all activities) and 12% (0.8% of all activities) of this travel involved displacing snow. In contrast, bison spent approximately 68% of their daylight activity foraging, with 42% of all foraging observations and 77% of those made during the OSV season involving displacement of snow. Bison spent approximately 30% of daylight hours displacing snow during the 1997–1998 and 1998–1999 winters. Although the energetics of snow displacement for bison are unknown, studies of other ungulate species indicate that the energetic costs of displacing snow during travel and foraging are higher than the energetic costs of these activities when snow is minimal or absent (Parker et al. 1984; Fancy and White 1985, 1987; Hobbs 1989). Likewise, the increased energetic costs of displacing snow to gain access to underlying forage greatly influences ungulate demographics (Formozov 1946, Hobbs 1989). Since only 1.6% of all instances of snow displacement were by traveling bison, the energetic costs of this activity would be minor compared to the costs of displacing snow while foraging and would have a minor effect on the rate at which bison body reserves are depleted over the winter.

When bison were traveling, they traveled off-road more than on roads. This travel pattern was not restricted to areas near the groomed road system. Bison traveled over all portions of the study area during both the OSV and the WV seasons. As snowpack increased from fall into winter, bison established a network of trails throughout the area. Through repeated travel, this network was maintained in an effectively groomed state during the winter. Van Camp (1975) and Aune (1981) also 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 used stream corridors and geothermal features extensively in their travel, indicating that roads are a small segment of a much larger travel network that bison utilize during all seasons.

Peak periods of bison road use occurred before and after the OSV season, with road use negatively correlated with road grooming. The 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 deep snow cover in nearly all of the winter range. As the snowpack begins to diminish, newly melted foraging patches are small and scattered widely throughout the study area. Bison need to travel farther and more often to reach them. As meltoff progresses and more forage is made available to bison in larger and more numerous areas, bison do not have to travel as far for forage and overall travel and travel on roads decreases. Van Camp (1975) observed similar timing of movements. 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 through the extensive geothermal areas where snow was absent. In addition, more than half of bison groups 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. This suggests that traveling the groomed road system is no more energetically efficient than most off-road travel, and in some instances may be more energetically costly to bison than traveling off roads. However, most bison did not switch to nocturnal use of the groomed roads to avoid these interactions. Observations of nocturnal travel, tracks found on the road in the morning, and data from trail monitors all indicate that most bison road use occurs during daylight. 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 on roads during the 1997–1998 OSV season and 22 during 1998–1999.

Use of groomed roads by bison in the MGF area of YNP seems to be 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 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 by Meagher (1993). Indeed, the most controversial aspect of the changes in bison distribution and movement—the shift from the central part of YNP to the Firehole and Madison drainages—was 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 observations of the YNP bison population support the conclusion that recent changes in bison distribution are a natural occurrence. As early as the 1870s and 1880s, as many as 200–300 bison were known to inhabit the Madison and Firehole areas (Meagher 1973). After near extirpation, bison were intensively managed in a ranching-style operation until 1952 (Meagher 1973). Periodic reductions of the bison population continued until 1967, when YNP policy changed to natural regulation (National Park Service 1998). At this time, the park-wide bison count was 397, the lowest since ranching operations began (Meagher 1973). Once culling 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. The magnitude of expansion was strongly correlated with population size, and major shifts in distribution were in response to a density-driven dispersal (Gates and Larter 1990).

The change in bison distribution and movement patterns observed over the past 30 years in YNP suggests a natural process of range expansion as the population increased following termination of culling. Therefore, the increasing bison population, rather than road grooming (Meagher 1993), 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 YNP boundary. This pattern was effectively eliminated during periods of extremely low populations and intensive management. The premise that road grooming has significantly influenced this process, however, is not supported by this study.

MANAGEMENT IMPLICATIONS

If our interpretations are correct, they 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 its 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 snowpack. Unusually severe snowpack combined with a high bison population relative to the ecological carrying capacity of YNP will result in increased 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 1996–1997. These events are unpredictable as they depend upon winter severity and should be considered a natural dynamic of the system.

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