Evaluating key uncertainties regarding road grooming and bison movements[1]

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Executive summary: In 1997, several plaintiffs filed suit against the Department of Interior to end grooming (i.e., snow packing) of roads and snowmobiling in Yellowstone National Park, alleging the Department failed to adequately consider the effects of these activities on the behavior, distribution, and demography of bison (*Bison bison*) and other wildlife. To settle this litigation, the National Park Service agreed to consider closing road segments to evaluate if there was a link between the groomed roads and bison movements. However, these closures were never implemented, in part because national parks are generally not suited for experimentation due to the lack of suitable controls and replicates, disruption of operations, visitor expectations regarding access, contracts with concessionaires, and economic concerns by gateway communities.

There has been much debate about whether groomed roads initially enabled or facilitated movements and redistribution of bison in Yellowstone. However, it is impossible to retrospectively answer this question because detailed information on bison travel patterns was not collected prior to road grooming or before bison extended their migratory range and gained knowledge of new foraging areas. Bison now use travel corridors along portions of roads that connect these foraging areas and, as a result, these travel corridors may persist whether or not roads are groomed. Instead, we focused our efforts on gaining insights into how road grooming and other factors currently affect bison travel. We considered various types of study designs and statistical approaches to evaluate three overriding uncertainties: 1) what is the influence of snow and terrain on bison movements; 2) what are the drivers of bison migration, re-distribution, and demography; and 3) what are the effects of road grooming on bison use of travel corridors? We developed testable predictions, proposed study designs and statistical analyses, and identified strengths of inference and potential pitfalls.

To evaluate the influence of snow and terrain on bison movements, we recommend using data from Global Positioning System (GPS) collars deployed on >30 bison during 2003-2007 to evaluate their odds of occupancy or

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[1] This information was distributed for expert peer review under applicable information quality guidelines. However, it has not been formally disseminated by the National Park Service and does not represent or should not be construed to represent any agency determination or policy.

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movement given certain snow pack levels. The data would be partitioned into traveling and non-traveling locations and a set of corresponding random points drawn from the winter range. Snow water equivalent and heterogeneity would be sampled at actual and random locations using a validated snow model, and log odds ratios would be calculated to estimate the likelihood of bison occurring at a particular location depending upon local- and landscape-scale snow conditions. These GPS data and snow metrics could also be used with matched case-control logistic regression and model comparison techniques to evaluate how the probability of bison travel and spatial distribution of travel and non-travel locations are affected by multiple topographic and habitat type attributes including slope, landscape roughness, habitat type, snow pack, and distances to streams, foraging areas, forested habitats, and roads. These approaches would provide quantitative comparisons of the magnitude of snow effects and potential for threshold snow levels to deter bison travel.

To determine the drivers of bison spatial dynamics and population vital rates, we recommend continuing the integration of data sets collected by biologists from the National Park Service and Montana State University. These data sets consist of animal distributions and movement patterns based on aerial and ground surveys and GPS-collared bison, winter foraging behavior from intensive observational studies, and adult and calf survival derived from individually radio-collared bison and various age composition surveys. Analyses would evaluate the general hypothesis that bison movements at all spatial and temporal scales are driven by per capita forage quantity, quality, and availability (i.e., individuals obtaining adequate forage at an acceptable energetic cost). The ability of a bison to obtain adequate forage, in turn, determines its probability of surviving and successfully reproducing. The available datasets would be used to formulate response variables describing variation in bison migration, foraging movements, adult survival, and calf survival with potential drivers of the variation evaluated within a multiple regression framework. The relative support for a suite of *a priori* models incorporating covariates representing forage biomass, snow pack influence on forage availability and energetic costs, and intra-specific competition could be assessed using information-theoretic techniques.

The consequences of closing a major road artery in the park for an extended period would be expensive, inconvenient to visitors, and disrupt the activities of concessionaires and park staff. Given these considerable impacts, we believe a tiered approach is warranted to gain reliable knowledge regarding the effects of road grooming on bison movements. This knowledge would contribute to the development of winter use policy. Under this approach, a progression of increasingly intrusive studies to park operations and visitors would be implemented during a succession of winters: 1) maintain a sample of 50-60 bison with GPS collars distributed between the central and northern breeding herds for at least 5 years to gain insights into the spatial and temporal factors influencing bison movements across the landscape; 2) deploy camera systems along the Firehole Canyon, Gibbon Canyon, and Mary Mountain trail to collect baseline data on the direction, frequency, magnitude, and timing of movement through major travel corridors; 3) experimental manipulations of bison movements through the Firehole Canyon by using metal gates or temporary cattle-guard bridges and fencing to deny bison access to the main groomed road and evaluate their use of alternate ungroomed routes; 4) manipulate bison movements through the Gibbon Canyon using gates/bridges and fencing to deny bison access to the new bridge and road (once construction completed), while evaluating their use of an alternate ungroomed route; and 5) close the road between Madison and Norris junctions with no grooming of the roadway.

Background

Managers in the National Park Service (Service) must conserve resources, while providing for their use and enjoyment by people (Organic Act of 1916; 16 USC 1, 2-4). Public interest in national parks stems largely from people being able to view awe-inspiring natural features and wildlife species with relatively little effort. However, the desires of people to see these features and wildlife at close range may conflict with the Service's mandate to conserve resources (Wright 1998). Also, recreation may disrupt ecological processes by disturbing wildlife and resulting in altered behavior and distributions, increased energetic costs, and changes in demography (Boyle and Sampson 1985, Knight and Cole 1995). Thus, management policies must address the effects of recreation on wildlife to ensure the integrity of these resources, and must ensure that the ecosystem processes on which they depend, are not harmed (National Park Service 2006).

The debate regarding snowmobile recreation in Yellowstone National Park exemplifies the dilemma posed to managers by this dual mandate. Snow coaches and snowmobiles were first used in the park during 1955 and 1963, respectively, and park staff began grooming (i.e., packing) snow-covered roads in 1971 to facilitate their safe passage (Yochim 1998). Snowmobile use increased dramatically in the following decades to more than 100,000 riders per year during the early 1990s (Gates et al. 2005). During this same period, numbers of bison increased from 700 to >4,000 and animals began migrating outside the park during winter and spring (National Park Service 2000a). Many Yellowstone bison carry the pathogenic bacterium *Brucella abortus*, which produces abortions in bison, cattle, and elk (*Cervus elaphus*) and can be transmitted among these species (Thorne et al. 1978, Rhyan et al. 1994). This disease (brucellosis) has been the subject of a national eradication program for more than 70 years and has cost approximately $3.5 billion in public and private funds (Gates et al. 2005). Thus, starting in the mid-1980s, federal and state agencies negotiated a series of management agreements for bison moving outside the park that included hazing bison back into the park, the capture and slaughter of bison that repeatedly left the park, culling of bison by agency personnel, and hunting of bison outside the park (National Park Service 2000a). These actions have been controversial and expensive because removals of bison from the population can exceed 500 animals when large population sizes and severe winter conditions combine to induce substantial migrations of bison outside the park (National Park Service 2000a, Gates et al. 2005).

In 1997, one of the three harshest winters of the 1990s drove a large number of bison out of the park, where 1,084 were captured and removed from the population as part of the continuing boundary control efforts. This record removal compelled several plaintiffs to file suit against the Department of Interior to end road grooming and snowmobiling, alleging the Department failed to adequately consider the effects of these activities on the behavior, distribution, and demography of bison and other wildlife (District of Columbia 2003). The plaintiffs contended the increased abundance, distribution, and culling of bison were direct consequences of energy savings provided by bison traveling on the groomed road system that led to better access to foraging habitat, increased survival, and enhanced movements outside the park (Meagher 1993, Cheville et al. 1998). Thus, they sought an injunction prohibiting road grooming and snowmobiling to reduce the number and rate of bison leaving the park and to induce bison to revert to their traditional, pre-road grooming distributions (District of Columbia 2003, Meagher 2003).

To settle this litigation, the Service agreed to prepare an Environmental Assessment that proposed closing road segments to grooming during the winters of 1998-2000, noting that experimental closures would provide useful information to researchers attempting to understand if a link existed between the groomed roads and wildlife movement (District of Columbia 2003). In January 1998, however, the Service issued a Finding of No Significant Impact on the grounds that current information did not "significantly demonstrate that an immediate closure [of trails] for study would provide the context or range of conditions necessary to make a closure productive" (District of Columbia 2003:9-10). The Fund for Animals filed new litigation alleging that the refusal to close any trails to obtain comparative data was a violation of the 1997 settlement agreement, as well as an impediment to completing a comprehensive Environmental Impact Statement. The U.S. District Court for the District of Columbia found these claims were premature because the Environmental Impact Statement was not yet complete (District of Columbia 2003).

The Service issued a final Environmental Impact Statement and Record of Decision in autumn 2000 that allowed snowmobile use during the 2000-01 winter, but completely phased-out snowmobile use in favor of snow coaches by the winter of 2002-03 (National Park Service 2000b). The International Snowmobile Manufacturer's Association contested this decision as an unsupported ban on snowmobiling. In June of 2001, the Service reached a settlement agreement with these parties that required the preparation of a Supplemental Environmental Impact Statement to consider data on new snowmobile technologies and incorporate additional public input on winter plans. In 2003, the Service issued a Final Supplemental Environmental Impact Statement that allowed continued snowmobile recreation in the park each winter, provided that all snowmobilers use "best available technology," that 80% use a commercial guide, and that no more than 950 snowmobiles enter Yellowstone daily (National Park Service 2003). The Record of Decision did not provide for any road closures to facilitate monitoring of potential road-grooming effects on wildlife.

The Fund for Animals challenged this decision to continue snowmobiling and road grooming and, in December 2003, the U.S. District Court for the District of Columbia ordered the Service to implement the 2000 Record of Decision that phased-out snowmobiles. The Court found it was "particularly damning that the NPS [National Park Service] has failed to close a single road to trail grooming, and consequently has never been able to engage in any true comparative analysis, and gather the resultant necessary data, of the effects of trail grooming on bison and other wildlife" (District of Columbia 2003:37-38). Despite this rebuke, the Court allowed road grooming to continue unabated.

In February 2004, however, the U.S. District Court for the District of Wyoming restrained the Service from enforcing the 2000 snowmobile ban and required them to develop a temporary rule for winter recreation that would be fair and equitable to snowmobile owners and users, the business community, and environmental interests (District of Wyoming 2004). In response, the Service developed a temporary winter recreation plan for winters during 2005-2007 that was consistent with, and addressed the concerns delineated in, these court opinions (National Park Service, U.S. Department of the Interior 2004). Also, the Service began rigorous analyses of the environmental effects of motorized winter recreation in Yellowstone and Grand Teton national parks. They contracted an independent assessment of the state of knowledge of the ecology of bison movements and distribution that concluded the "road segment through the Gibbon Canyon is the single area in the park where snow cover in combination with steep terrain may deter bison movements in the absence of grooming and snow compaction by over snow vehicles" (Gates et al. 2005:253). However, this assertion was subject to several key uncertainties and the authors recommended "[a]n adaptive management experiment should be designed to test permeability of the Firehole-to-Mammoth corridor under variable [*sic*] snow conditions, with a specific focus on the road section between the Madison Administrative Area and Norris Junction." More specifically, the experiment should "… test the hypothesis that the Central population's movement to the Northern Range is possible only with grooming of the snow pack on the road, in particularly in the Gibbon Canyon." Such an experiment should be designed to "test the effectiveness of unaltered snow pack as a barrier to winter movements between the Central and Northern Ranges in relation to varying environmental conditions including forage production, winter severity, and population size" (Gates et al. 2005:253).

A stakeholder workshop was convened by the Service and the Big Sky Institute of Montana State University during January 2006 to discuss the uncertainties and experiment proposed by Gates et al. (2005). The majority report recommended a "passive adaptive management experiment" to evaluate the effectiveness of unaltered snow as a barrier to winter movements between the central and northern ranges in relation to known and varying environmental conditions including forage production, winter severity, and population size. The majority report also recommended a set of "controlled" experiments to determine the maximum snow threshold for bison movements—that depth and density of snow that turns bison away from a desired path. This information could then be used to evaluate how often the Madison-Norris corridor receives such snow thresholds (Big Sky Institute 2006:14-16).

Objectives and Approach

There has been much debate about whether groomed roads initially enabled or facilitated movements and redistribution of bison in Yellowstone National Park. However, it is impossible to retrospectively answer this question because detailed information on bison travel patterns was not collected prior to road grooming or before bison extended their migratory range and gained knowledge of new foraging areas. Bison now use travel corridors along portions of roads that connect these foraging areas and, as a result, these travel corridors may persist whether or not roads are groomed (Gates et al. 2005, Bruggeman et al. 2007). Instead, we focused our efforts on gaining insights into how road grooming and other factors <u>currently</u> affect bison travel. Specifically, our task was to develop feasible plans for addressing the following key uncertainties identified by Gates et al. (2005) and attendees of the January 2006 workshop (Big Sky Institute 2006):

a. What is the threshold depth and density of snow at which bison cannot move through corridors in search of better foraging conditions?

b. How often, if at all, does the Madison to Norris road segment reach such snow thresholds?

c. Will bison movement rates be proportional to snow conditions in the absence of road grooming?

d. What terrain characteristics (e.g., slope, ruggedness) affect the snow depth/density threshold preventing bison movements?

e. What is the relationship between winter forage availability and probability of bison movement?

f. What is the relationship between winter forage availability, bison density, and bison over-winter mortality?

g. If road grooming stopped on the Madison to Norris road in Yellowstone, would bison continue to use the snow-covered roadway, maintaining trails at their own energetic expense, or would they shift to alternate but parallel routes along the Gibbon River or the power line corridor?

h. Would alternative forms of road grooming (e.g., grooming only one lane) or physical barriers to bison movement (e.g., fence, gate) alter bison use of the Madison to Norris road corridor?

Previous attempts to address the effects of road grooming on travel by bison have been criticized for making strong inferences in the absence of experimental designs (Gates et al. 2005, Bruggeman et al. 2006). True experimentation, with the use of replication and randomized controls and treatments, provides strong inference (i.e., deduction; Platt 1964) and partially controlled field manipulations have been conducted at the landscape-scale for wildlife research in some areas (e.g., Boutin 1992, Krebs et al. 1995). However, such endeavors are often problematic for assessing ecological issues at the system level where true controls are rare, replicates are difficult to obtain, and experiments take years to complete (Hobbs and Hilborn 2006). This is especially true in national parks which are managed to minimize human intervention (National Park Service 2006) and generally not suited for randomized treatments or manipulations due to disruptions of park operations, visitor expectations regarding access, contracts with concessionaires, and economic concerns by gateway communities. Furthermore, ecological experiments often produce partial support for competing views, rather than the unambiguous rejection of one over another, because interactions are complex and composite effects are common at the landscape scale (Hobbs and Hilborn 2006).

When true experiments are not feasible or produce ambiguous results, the issue then becomes how to gain useful and sensible results from field studies using non-experimental approaches such as observational studies with a sampling framework, modeling, and population analyses (Eberhardt 2003). Observational studies, whereby biologists sample nature using various techniques, are widely used in wildlife research (Cochran 1983, Eberhardt and Thomas 1991). These studies do not provide the strong inference derived from experimentation because they are not based on randomized selection of controls and treatments and, as a result, are more vulnerable to the effects of unconsidered confounding factors (Eberhardt 2003). However, well-planned studies with random sampling and respectable sample sizes can provide sound inferences about the degree of any differences detected and useful confidence intervals for stated probabilities (Cochran 1983, Eberhardt and Thomas 1991). Thus, biologists often use this approach to evaluate working hypotheses sequentially as more data are gathered and information gained, resulting in a sequence of studies to gain understanding of important issues (Eberhardt 2003).

Population analyses and simulation models are commonly used to explore and understand ecological systems by attempting to explain the past and project into the future. However, these approaches lack inferential strength and often contain uncertainties introduced by parameters not well supported by actual data (Eberhardt 2003). Thus, they are most useful when combined with experimentation or partially controlled field manipulations designed to falsify the model. Based on these results, new models can then be constructed and tested. The same general approach is useful with observational studies when natural systems can be perturbed (Eberhardt 2003).

Biologists and ecologists rely heavily on statistics to infer pattern and causation from data collected from complex systems characterized by high natural variability. Traditionally, hypothesis significance tests were used to compare null (i.e., no effect) and alternate hypotheses and determine the probability with which an effect would be observed if the true effect was zero. This approach is appropriate in many experimental settings, but not for studies where variance in the data is generated by unconsidered confounding factors rather than controlled, randomized manipulations (Burnham and Anderson 2002, Stephens et al. 2007). Also, the emphasis on falsification with this approach leads to a binary decision to reject or accept the null hypothesis that can obscure uncertainty about the best explanation for an observed phenomenon (Stephens et al. 2007).

To deal with these shortcomings, ecologists began using alternatives such as effect size statistics, model selection approaches based on information criterion, and Bayesian statistics (Anderson et al. 2000, Hobbs and Hilborn 2006, Stephens et al. 2007). Effect statistics measure the practical significance of an observed effect between two or more treatment groups, while the acceptance or rejection of hypotheses in Bayesian approaches is linked to previous beliefs and assumptions (Stephens et al. 2007). Information-theoretic model selection approaches evaluate the relative strength of evidence in data for alternate hypotheses represented as multiple competing models (Burnham and Anderson 2002). These approaches are especially useful for questions that use unreplicated or unconventionally replicated data involving multiple interactions (Hobbs and Hilborn 2006).

We propose to use a pluralistic approach to consider various types of study designs and inferential (statistical) approaches for the key uncertainties identified by Gates et al. (2005) and attendees of the January 2006 workshop (Big Sky Institute 2006). We grouped these uncertainties into three broad research themes: 1) what is the influence of snow and terrain on bison movements (uncertainties a-d); 2) what are the drivers of bison migration, re-distribution, and demographic characteristics (uncertainties e-f); and 3) what are the effects of road grooming on bison use of travel corridors (uncertainties g-h)? We developed testable predictions for each category and proposed general study designs and statistical analyses that could be used to gain knowledge and reduce uncertainty.

Research Theme 1:
Influence of Snow and Terrain on Bison Movements

The overriding premise of the uncertainties identified by Gates et al. (2005) and attendees of the January 2006 workshop (Big Sky Institute 2006) was that bison use of roads for travel during winter would significantly decrease or cease if grooming was terminated. Central to this premise is the hypothesis that there is some threshold of snow through which bison will not travel due to the cumulative energetic costs of movement, regardless of learned travel routes and destination foraging areas. No accurate or validated models exist for predicting bison energy expenditures in snow, but the cost of locomotion generally increases curvilinearly for ungulates as snow depth and density increase (Robbins 1993). However, travel is only a small percentage (11%) of all bison activity and only 7% of observations of traveling bison involved animals displacing snow (Bruggeman et al. 2006). While this observation may appear incongruous for animals that are wintering in Yellowstone National Park where snow packs can be extreme, bison have evolved a number of behavioral strategies that minimize the energetics costs of movement in snow. Bison begin moving back and forth along trails before the onset of deep snows and frequent, repeated use maintains them in a compacted, self-groomed state—thereby limiting snow depths and densities, saving energy, and enabling travel through areas with otherwise deep snows (Telfer and Kelsall 1984, Bjornlie and Garrott 2001, Bruggeman et al. 2006). Further, bison are social animals that trail each other through snow, with followers only experiencing a fraction of the cost experienced by the leader (Robbins 1993). Thus, an alternative hypothesis is that a snow threshold may not exist or be biologically meaningful for travel corridors between feeding areas because repeated use of trails by bison maintains them in a compacted, self-groomed state (Bjornlie and Garrott 2001, Bruggeman et al. 2007). Conversely, foraging is a major energetic cost to bison during winter because it comprised 67% of behavioral observations and 30% of foraging bison displaced snow (Bruggeman et al. 2006). Snow had no effect on bison foraging in snow pack <40 cm, but foraging essentially ceased when snow pack exceeded 75 cm (Carbyn et al. 1993, Coughenour 2005). Thus, bison likely vacate foraging areas (i.e., meadows) once snow pack reaches a threshold depth or density that severely restricts forage acquisition (Bruggeman 2006).

We expect snow covariates (e.g., depth, water content, heterogeneity) will influence both traveling and non-traveling (e.g., feeding) behavior, but that the magnitude of effects will be lower for traveling. We predict that:

a. There is a threshold (or pseudo-threshold) of snow depth and density that will deter bison foraging and cause them to vacate meadows due to the cumulative energetic costs of moving snow.

b. The threshold depth and density of snow that precludes foraging by bison will be exceeded in travel corridors, but not deter bison movements because they will maintain compacted trails.

c. The odds of bison occurrence in foraging areas and travel corridors will decrease as snow depth and density increases because bison will be less likely to occupy energetically demanding areas of high snow pack. There will be stronger avoidance of deeper snow pack (i.e., steeper curves) for foraging areas, with shallower curves for traveling corridors.

d. The odds of bison occurrence in foraging areas and travel corridors will increase as snow heterogeneity increases because a greater range of snow conditions will provide bison with more opportunities to locate areas of low snow pack.

e. Landscape characteristics will influence bison responses to snow pack conditions, with the odds of bison occurrence in areas with low snow pack and high heterogeneity becoming more pronounced as surrounding landscape-scale snow levels increase.

f. The numbers of bison migrating into the Madison headwaters drainages will increase as peak snow depth and density increases in the Hayden Valley and along the Mary Mountain trail.

We propose four research initiatives to evaluate these predictions.

<u>Terrain Characteristics Affecting Snow Depth and Density</u>: This uncertainty has largely been addressed by extensive snow sampling and modeling efforts during 2001-2006. The Langur snow pack model provides daily, high-resolution, spatial and temporal predictions of snow depth, water content, and heterogeneity in the bison winter range (Watson et al. 2006a, b). The model simulates total water and energy balance, taking into account the propagation of water and energy through the atmosphere, vegetation, snow, and soil. Key inputs that affect snow depth and density include daily time series of precipitation, maximum and minimum temperature, elevation, slope, aspect, land cover type, canopy cover, mean annual precipitation, and ground heat flux (Watson et al. 2006a). The

model was validated by randomly sampling >3,500 cores of snow pack aggregated into 40 different stratum representing a range of dates, vegetation, topography, and elevation (Watson et al. 2006b).

The Langur snow pack model could be used to retrospectively estimate the frequency and duration that various travel corridors (e.g., Madison to Norris, Firehole Canyon) likely exceeded threshold snow depths and water equivalents (SWE) that preclude foraging or travel by bison without road grooming. The model could also be used to relate changes between consecutive aerial or ground counts of bison in the Madison headwaters drainages to snow depths and SWE along the Mary Mountain travel corridor from the Hayden Valley.

Log-Odds of Bison Occurrence in Foraging Areas and Travel Corridors: Data recorded by GPS collars deployed on >30 bison during the winters of 2003-2007, or aerial and ground survey locations of bison groups during all winters, could be used to evaluate the odds of occupancy or movement by bison given certain snow pack levels and approximate threshold snow levels that deter foraging or travel. The data could be partitioned into traveling and non-traveling locations based on the results of Bruggeman et al. (2007), after censoring data when bison were on roads to eliminate potential road-grooming effects. We will initially define the available universe for drawing a random sample of points to be matched with each bison location. A set of $\geq$10 random points would be drawn for each bison location using a fixed kernel estimate with an appropriate band width of the bison winter range based on groups of bison observed during winter aerial surveys between 1998-2007. Alternatively, a finer-scale definition of the available universe could be defined by selecting a circle with a biologically appropriate radius around each location.

SWE and heterogeneity would be sampled at actual and random locations using the Langur snow model (Watson et al. 2006a, b). SWE would be the average of all pixels at the scale of interest and represent the mean water content of the snow pack. Snow heterogeneity would be the standard deviation of all pixels at the scale of interest and represent the spatial variability of the snow pack. Each snow metric would be calculated at a local-scale using pixels within a 100-meter radius of each bison and random location. Each snow metric would also be calculated at a landscape-scale using all pixels within the defined boundary of the winter range, which bison were capable of moving through during a single winter. The mean SWE or heterogeneity in the 100-meter radius around each observed bison location would be compared to the mean SWE available within the winter range (Figure 1).

Log odds ratios could be used to determine the likelihood of bison occurring at a particular location depending upon local- and landscape-scale snow pack conditions. Actual and random locations would be sorted into one of three categories depending upon the landscape SWE estimate on their date of collection. We would designate categories so that approximately the same numbers of actual locations were in each category. Locations would then be sorted into local SWE levels, designated at every 0.05 meters. Thus, each location would be assigned to one local SWE level within one landscape SWE category. Odds ratios would then calculated for each local SWE within each landscape SWE category (Figure 2). The odds of a bison location occurring in a particular local SWE level would be calculated by dividing the probability of a bison location occurring in that level by the probability of a bison location not occurring in that level. After calculating the odds of a random location in the same manner, an odds ratio would be obtained by dividing the odds of a bison location by the odds of a random location occurring in that level. Odds ratios have an asymmetrical distribution ranging from 0 to infinity with values >1 indicating increased odds of occurrence, values <1 indicating decreased odds and values of 1 indicating equal odds of occurrence. Log odds ratios, the natural log of odds ratios, are symmetrical about 0 and allow comparison of the strength of positive and negative relationships. Confidence intervals would be calculated when the proportion of locations occurring in a particular local SWE level exceeded 0.01. Using this approach, we could also calculate log odds ratios at 0.02-meter levels of local snow heterogeneity within the same three landscape SWE categories. In addition, we could calculate log odds ratios for local SWE and heterogeneity levels across three categories of landscape snow heterogeneity.

<u>Covariates Affecting Spatial Variability in Bison Travel Behavior</u>: Bruggeman et al. (2007) collected 121,380 locations from 14 female bison with GPS collars in central Yellowstone (2003-2004) to examine how topography, habitat type, roads, and elevation affected the probability of bison travel year round. They also conducted daily winter bison road use surveys (2003-2005) to quantify how topography and habitat type influenced spatial variability in the amount of bison road travel. Using multiple logistic regression models and model comparison techniques, they found the probability of bison travel and spatial distribution of travel locations were affected by multiple topographic and habitat type attributes including slope, landscape roughness, habitat type, elevation, and distances to streams, foraging areas, forested habitats, and roads. Streams were the most influential natural landscape feature affecting bison travel and results suggested the bison travel network throughout central Yellowstone was spatially defined largely by the presence of streams that connect foraging areas. Also, the probability of bison travel was higher in regions of variable topography that constrained movements, such as in canyons. Pronounced travel corridors existed both in close association with roads and distant from any roads, and results indicated roads may facilitate bison travel in certain areas (e.g., Firehole Canyon). However, their findings

suggested that many road segments used as travel corridors were overlaid upon natural travel pathways because road segments receiving high amounts of bison travel had similar landscape features as natural travel corridors.

This analysis could be improved by incorporating snow metrics into the models and including data recorded by GPS collars deployed on >14 bison during the winters of 2005-2006 to evaluate if there is a threshold of snow depth or SWE that will deter bison occupancy or traveling. The available winter range for bison would be estimated using a fixed kernel estimator with an appropriate band width based on groups of bison observed in winter aerial surveys during 1998-2007. Alternative methods for defining available areas at a finer spatial scale could be based on defining circles around individual locations with the radius of the circle determined by the maximum distance a bison could be expected to travel in some time interval. The data would be partitioned into traveling and non-traveling locations, after censoring data when bison were on roads to eliminate potential road-grooming effects. A comparison of covariate coefficients and functional relationships between the two suites of models (i.e., traveling, non-traveling) could then be conducted to evaluate the magnitude of snow effects and potential for threshold snow levels during foraging and travel. To assess the contribution of SWE in explaining variation in winter bison distribution, we may use matched case-control logistic regression in which each bison location (a case) is matched temporally with 20 random locations (controls). Matched case-control logistic regression is typically used to control for potential confounding variables, temporal variables in this analysis. Further details on matched case-control logistic regression can be found in Collett (2003).

Hypotheses for both traveling and non-traveling locations would be expressed as the same candidate models in the form of regression equations consisting of covariate main effects and interactions. We expect that snow covariates will be larger negative values for non-traveling than traveling locations. Because of uncertainty in the true functional relationship between bison travel or non-travel activities and each covariate, we would hypothesize four functional structures for each continuous covariate: linear, pseudo-threshold, exponential, and moderated. The linear form predicts a fixed rate of increase or decrease per unit increase in the covariate. The pseudo-threshold form approximates an approach to an asymptotic value of the response variable with increasing covariate effects. The exponential form allows for unbounded growth in the response variable with increasing covariate levels. The moderated form (i.e., square root) allows for faster increases in the response than the pseudo-threshold function, but would be attenuated at larger covariate levels unlike the linear form.

We would use the sequential model fitting technique proposed by Borkowski et al. (2006) that incorporates the *a priori* candidate model list and four hypothesized covariate functional forms. The sequential approach begins by separately fitting all candidate models containing the most appropriate functional form for each covariate based on the initial analyses conducted by Bruggeman et al. (2007). A corrected Akaike Information Criterion (AICc) value is calculated for each model and the best approximating models are retained based on ΔAICc values $\leq$10 (Burnham and Anderson 2002). Next, the initial functional form of one covariate is replaced with an alternate functional form in each model, while preserving the model structure. New AICc values are calculated for each model and compared to the previous value for each model. If the new AICc value is less than the AICc value for the previous model and all variance inflation factors are <6, then the new form of the covariate for the model is retained. Otherwise, the previous form is retained. This sequential procedure is repeated for each form of each covariate in each model structure to obtain the most appropriate covariate forms with respect to the data. We would also calculate Akaike weights based on the final models combined with the originally discarded linear models as a measure of model selection uncertainty. To estimate the relative importance of each predictor variable, Akaike weights could be summed for all models containing the predictor (in any form) to calculate the predictor weight (Burnham and Anderson 2002).

Influence of Snow on Bison Migration: All bison migrating from the Hayden Valley to the Madison headwaters drainages do so over the ungroomed Mary Mountain trail, after which they distribute along the Firehole River or move through the Firehole Canyon and then either west along the Madison River or north along the Gibbon River (Bjornlie and Garrott 2001). Thus, bison do not encounter the Firehole Canyon or Madison to Norris travel corridors until after they have crossed the ungroomed Mary Mountain corridor. This initial migration through an ungroomed corridor provides an opportunity to assess if bison movement rates are proportional to snow conditions in the absence of road grooming. We could use the Langur snow pack model (Watson et al. 2006a, b) to predict the deepest snow locations along the Mary Mountain trail used by bison and then measure snow depth and SWE at these locations through several winters, including inside and nearby the trail. We could also use data from bison with GPS collars, aerial or ground data of bison numbers and distribution, or cameras/trail monitors to determine if bison movement is relatively continuous (starting in autumn and early winter) along this corridor through winter, thereby enabling bison to maintain self-groomed trails. In addition, we could use the Langur snow model to relate changes between consecutive aerial or ground counts of bison in the Madison headwaters drainages to snow depth or SWE along the Mary Mountain corridor between the Hayden Valley and Madison headwaters drainages, after accounting for variations in bison density and estimates of primary productivity. This would enable an assessment of how the timing and extent of bison migration over the Mary Mountain trail varies with changing snow conditions in the Hayden Valley and along the Mary Mountain trail.

Another approach would be to map bison trails throughout their winter range during aerial surveys each month from mid- to late-winter and estimate snow depths at each location using the Langur model (Watson et al. 2006a, b). We could also conduct concurrent counts to index movements between areas of this circulation network or monitor the frequency of movements along various arteries (e.g., Mary Mountain, Firehole Canyon, Gibbon Canyon) with trail counters or cameras. A simpler and more insightful approach would be to continue fitting bison with GPS collars and analyzing their travel vectors circa Bruggeman et al. (2007).

Research Theme 2:

Determining Drivers of Migration, Re-distribution, and Demographic Characteristics

We have made considerable progress in understanding the interactions between bison density, forage production, and forage availability (as influenced by snow pack) on bison spatial dynamics (Bjornlie and Garrott 2001, Bruggeman 2006, Bruggeman et al. 2006, 2007) and population vital rates (Fuller et al. 2007a, b). Thus, we propose to continue the integration and analyses of data sets collected by biologists from the Service and Montana State University. These data sets include animal distributions and movement patterns based on aerial and ground surveys and GPS-collared bison, and adult and calf survival derived from individually radio-collared bison and various age composition surveys. Our general hypothesis is that bison movements at all spatial and temporal scales are driven by individuals obtaining adequate forage at an acceptable energetic cost and that the ability of a bison to obtain adequate forage, in turn, determines its probability of surviving and successfully reproducing. Thus, we propose that there are three primary drivers of nutritional constraints for bison that influence their spatial dynamics and vital rates:

a. *Variation in Forage Quantity and Quality* – Timing of snowmelt, combined with warm season temperature and precipitation regimes, influence annual production of forage (monocot biomass) and the duration of the period when high quality forage (green) is available to bison.

b. *Variation in Forage Availability* – During the cold season, snow pack covers monocot communities and increases energetic costs of bison foraging due to the need to displace snow to access the forage and to move from one foraging patch to the next. Bison respond to these constraints of decreasing forage availability and increasing energetic costs as snow pack accumulates each winter by redistributing to areas with lower snow pack.

c. *Bison Abundance* – Forage resources are finite and the higher the bison density the lower the per capita availability of forage and the higher the intra-specific competition for forage. Thus, the higher the bison density the higher the propensity for bison to move in search of adequate forage.

We describe three research initiatives to evaluate these specific hypotheses. For each initiative, we identify response variables that will be used in a multiple regression framework where the relative support for a suite of *a priori* models with covariates representing the three hypothesized drivers of bison spatial dynamics and population vital rates will be evaluated using information-theoretic techniques (Burnham and Anderson 2002).

Bison Migration Dynamics (Spatial Dynamics at the Range Scale): There are three distinct areas occupied by the central bison herd—the high-elevation interior Hayden and Pelican Valleys are the primary summer range for the entire herd, while the headwaters of the Madison River drainages (i.e., Firehole, Gibbon, Madison) along the western border of the park serve as a primary winter range. The herd is partially migratory (Lundberg 1988), with a portion remaining in the Pelican and Hayden Valleys through the winter and a portion migrating to the Madison headwater drainages each winter. The number of animals migrating to the Madison headwater drainages each winter is highly variable. We have used a 10-year dataset on the number and distribution of bison wintering in the Madison headwater drainages, which was determined by conducting ground surveys every 10-14 days during November-May, 1996-97 through 2005-06 (Bjornlie and Garrott 2001, Ferrari and Garrott 2002, Bruggeman et al. 2007), to evaluate the relative contribution of the three hypothesized drivers of bison spatial dynamics at explaining variation in the winter distribution of the central bison herd. During 109 ground distribution surveys, counts ranged from 205-1,538 bison (775 ± 30). The response variable for this analysis was the maximum number of bison counted in the Madison headwaters range each winter, which varied between 888-1,538 bison (1,174 ± 64).

We considered the potential influence of both density-dependent and independent factors at explaining annual variation in the response variable by considering three covariates: an index of annual variation in forage biomass production, an index of snow pack severity, and an index of bison density. Direct measures of annual variation of forage biomass production require intensive plant sampling and are not available. However, remotely sensed data from satellites can be used to calculate a variety of normalized differential vegetative index (NDVI) metrics that are strongly correlated with green biomass (Reed et al. 1994, Goward and Prince 1995). We used NDVI metrics derived from satellite data and identified, *a priori*, the most likely metrics for indexing forage production on the summer range (Hayden and Pelican Valleys). An initial review of the literature suggests that the length of the growing season and the scaled integral metrics are the most promising (Pettorelli et al. 2007, Wittemyer et al. 2007). Alternative NDVI metrics were evaluated in exploratory analyses. We predicted the number of bison migrating to the Madison headwaters winter range would be negatively correlated with the NDVI metric because fewer animals would migrate to the winter range when growing season conditions resulted in higher forage biomass on the summer ranges.

The Langur snow pack model (Watson et al. 2006a, b) was used to compute mean daily estimates of SWE on the bison summer range, encompassing all pixels within the Hayden and Pelican Valleys. We added daily SWE values from October 1-April 30 to calculate a covariate, SWE_{acc}, that indexes snow pack severity and has been found to be an excellent metric for explaining annual variation in vital rates of other large herbivores in Yellowstone (Garrott et al. 2003). We predicted a positive correlation between SWE_{acc} and the number of bison migrating to the Madison headwaters winter range because more severe snow pack conditions on the summer range should result in more bison migrating.

The most accurate and precise estimates of bison abundance in the central herd are obtained from aerial surveys conducted during middle to late July when the herd is concentrated in the Hayden Valley for mating (Hess 2002). We used these annual estimates as a covariate for bison density, and predicted that more bison would migrate to the Madison headwaters winter range each winter as density increased.

We found that population size had a significant, positive effect on the magnitude and timing of migration, with more bison migrating earlier to winter in the Madison headwaters area as density increased. Some of the annual variability in the proportion of bison migrating each winter was also explained by density-independent climate covariates. Snow accumulation in the Hayden and Pelican valleys had a positive effect on the timing of migration with more bison moving to the lower-elevation Madison headwaters area as winter progressed and snow pack deepened. Also, the magnitude of migration analysis included a positive annual winter severity (SWE_{acc}) effect, though its coefficient had confidence intervals slightly spanning zero.

Bison Foraging Dynamics (Spatial Dynamics at the Patch Scale): The same potential drivers of landscape-scale movement dynamics of bison are also likely influencing local-scale movement dynamics. We recently completed analyses of bison foraging behavior using data from a sample of bison equipped with GPS telemetry collars during the past 4 years. Winter movement and foraging data were collected from 16 adult female bison during winter 2003-04 and another 14 adult females during winter 2004-05. Data from these bison were used to develop two response variables that provided an index of the perceived quality of foraging patches and evaluated the relative contribution of the three hypothesized drivers of bison spatial dynamics to explain observed variation in these patch-scale foraging metrics. Collars recorded location data at 30-45 minutes intervals each winter. Also, from January-March during 2004 and 2005, we used a random sampling scheme (without replacement) and VHF telemetry to visually locate instrumented bison found within the Madison headwaters winter range. We recorded foraging area location and conducted five consecutive 5-minute focal animal behavioral observations (Altmann 1974) on randomly selected foraging adult female bison within the group, classifying behavior into six categories: foraging (e.g., biting, chewing), searching for forage (e.g., walking with head lowered in between biting or chewing actions), displacing snow (e.g., pawing, head sweeping), walking, and resting (bedded or standing). We obtained approximately 140 telemetry locations and recorded the foraging behavior of 735 individual bison for five minutes each and 882 herd scans. From these data, we generated two response variables; foraging area residence time and foraging ratio.

Foraging area residence time was determined for each collared bison in each foraging area by matching observed locations to their corresponding GPS locations and identifying the arrival and departure dates and times for the bison in that foraging area. The extent of a foraging area was determined by identifying a concentration of consecutive GPS locations in an area around the observed location, with arrival to and departure from the area defined as one significant movement (>200 m) away from the concentration of locations. Foraging area residence time was calculated by subtracting the date/time the bison arrived in the foraging patch from the departure date/time. The intensive focal animal behavioral observations were used to determine foraging ratios for each habitat patch for each bison observation, where the foraging ratio was defined as the sum of the time the focal animal spent searching for forage and displacing snow, divided by the total time during the observation bout the focal animal was feeding. The foraging ratio can be interpreted as the proportion of time spent finding forage relative to the proportion of time actually foraging, and offers an index of patch quality and foraging efficiency using animal behavior.

Following an observation session, we sampled forage biomass and SWE within three local areas, each situated as close as possible to where the focal bison were observed foraging. When bison foraging craters were distinctly defined in the snow, we sampled snow and forage immediately next to the craters in areas of undisturbed snow. We clipped forage within 0.25 square meter quadrats at each of the three areas and vegetation samples (n = 390) were later dried for 60 hours at 65ºC and weighed to the nearest 0.1 gram. We defined a covariate for forage quantity as the average of the three biomass measurements (g/m^2), with the covariate evaluated in both the residence time and foraging ratio model suites. We predicted that forage biomass would be positively correlated with residence time as bison would remain in foraging patches with relatively abundant forage longer than in patches where forage biomass was less abundant. Conversely, we predicted that the foraging ratio would be negatively correlated with plant biomass since increasing biomass would result in bison spending more time foraging in one crater and less time searching or displacing snow. At each of the three local sampling areas we also made three measurements of SWE, each located 1-meter apart in an equilateral triangular design (n = 1170), using a standard snow corer and spring balance. We defined a SWE covariate for each bison foraging location using averages of the nine individual patch measurements, with the covariate evaluated in both the residence time and foraging ratio model suites. We predicted that residence time would be negatively correlated with SWE as bison would not remain in a foraging patch as long where deep and/or dense snow pack (higher SWE) made movement and displacing snow from forage energetically costly. We predicted the foraging ratio would be positively correlated with SWE as bison would require more time to displace snow to reach forage if the snow was deep, wet, or had a crust (i.e., higher density), resulting in decreased foraging time. The total number of bison in the group was used as a covariate to index local intra-specific foraging competition and we predicted a negative correlation in the residence time models as bison would tend to leave a foraging patch. Finally, we predicted that increasing numbers of bison would lead to an increased foraging ratio (positive correlation) since more intra-specific competition for forage would result in bison spending more time searching for forage and being displaced from patches by conspecifics

We found that residence times within foraging patches were affected by the ratio of local to landscape scale snow pack SWE, previous foraging experiences, and both local- and landscape-scale intra-specific competition (Bruggeman 2006). These results indicate the amount of time bison spend in one foraging area is dependent on a suite of abiotic and biotic factors that affect resource availability, and the perceived value of the area relative to other recently visited areas. The complimentary analyses of patch scale foraging efficiency revealed that foraging behavior in winter was predominantly affected by snow pack, with forage biomass and intraspecific competition having minimal influence (Bruggeman 2006). Combined, these studies indicate that snow is the primary factor reducing foraging efficiency and patch quality for bison, supporting other studies that found snow to influence the use of foraging areas, foraging behavior, and diet selection by large herbivores (Gross et al. 1995, Wallace et al. 1995, Bailey et al. 1996, Johnson et al. 2001, Fortin et al. 2002, Johnson et al. 2002). The results reinforce the idea that foraging by large herbivores and movements among foraging patches may be simultaneously affected by mechanisms operating across multiple spatial and temporal scales and reinforce the role of heterogeneity in affecting large herbivore behavior. The research of Watson et al. (2006a, b) demonstrates that snow pack distribution in Yellowstone is highly variable and the behavioral studies demonstrate that this heterogeneity is influential in affecting bison foraging behavior on multiple scales, which has implications for both small and medium-scale movement as well as large-scale movements and distribution patterns. There is certainly more to be learned from foraging studies that would enhance our understanding of bison movements at small to moderate spatial scales. The deployment of additional GPS radio collars would provide an opportunity for additional work if the Service determined such studies were required to inform management.

Bison Population Dynamics: Understanding the role of density-independent (climate variation) and density-dependent factors (bison population size) and their interactions on bison population dynamics can be addressed by direct analyses of the time-series of bison population counts. There have been several such analyses performed and presented in reports (Taper et al. 2000, Coughenour 2005, Gates et al. 2005) and a recent analyses has been published in a peer-reviewed scientific journal (Fuller et al. 2007a). Additional work with the time-series data could apply relatively new state-space analytical tools to the data to compliment and extend the analyses of Fuller et al. (2007a). While these efforts are important and insightful, studies of specific vital rates provide an opportunity to understand the underlying mechanisms influencing bison population dynamics (Gaillard et al. 2000). Thus, we propose to investigate the influence of forage production, snow pack, and bison numbers on annual variation in adult female survival and calf recruitment. We recently completed and published preliminary analyses (Fuller et al. 2007b). However, a substantial quantity of additional data have been accrued since this study was completed, providing an opportunity to extend and refine our understanding of variation in bison vital rates.

We recommend combining data on the fate of radio collared adult female bison from a multi-agency brucellosis epidemiology study conducted during 1995-2001 (Aune et al. 1998, Roffe et al. 1999, Rhyan et al. 2001, Fuller et al. 2007b) with similar data collected by the park biologists during 2002-2007 to obtain annual survival estimates. A total of 101 bison were instrumented and monitored for periods of time varying from 6 months to 6 years, providing 11 years of annual survival estimates. We would also use a time series of calf:adult ratios collected during aerial surveys of bison on the central and northern ranges during May-June, 1970-2006 (Dobson and Meagher 1996; National Park Service, unpublished data). The ratio of calves to adults (C:A) from these data represents a response variable that incorporates pregnancy, fetal loss, and neonatal mortality during the first 1-2 months of life which is hypothesized to be influenced by the severity of over-winter nutritional stress driven by snow pack conditions when calves were in utero. The most pronounced influence of snow pack on calf survival, however, is likely manifested when calves are 6-12 months old and experience their first winter (DelGuidice et al. 1994). Thus, we would also develop another calf:adult ratio response variable using a shorter time series of calf:adult ratios derived from the bison ground surveys conducted over the last 10 years on the Madison headwaters winter range as described earlier (Bjornlie and Garrott 2001, Ferrari and Garrott 2002, Bruggeman et al. 2007). These surveys were carried out each winter until early May. Thus, we can combine the mid-April to early May surveys to obtain a spring calf:adult ratio immediately after the winter mortality period and capture annual variation in calf mortality due to snow pack severity.

The same covariates proposed for use in analyses of bison distribution dynamics (described above) could be evaluated as drivers of annual variation in adult female survival and calf:adult ratios. We would consider NDVI metrics as an index of forage production and predict a positive correlation with all three demographic response variables because adult female and calf survival should be higher in years when growing season conditions result in higher forage biomass on the summer ranges. We would also use the Langur snow pack model (Watson et al. 2006a, b) to compute snow pack metrics. We predict a negative correlation between snow pack and adult female and calf survival because more severe snow pack conditions should result in higher over-winter mortality of both adults and calves. Further, the influence of density-dependent competition should be evaluated using the summer population estimates for the central herd derived from aerial surveys (Hess 2002) as a covariate for bison density. We predict a negative correlation with adult female survival and calf:adult ratios.

Research Theme 3:

Effects of Road Grooming on Bison Use of Travel Corridors

Partially controlled field manipulations involving road closure, a cessation of grooming, or denial of access to one or more road segments by bison could be implemented to evaluate the premise that bison use of roads for travel during winter would significantly decrease or cease if grooming was terminated (District of Columbia 2003, Meagher 2003). The consequences of closing major road arteries in the park for an extended period, however, would be high and includes financial expenses, inconvenience to visitors, and disruptions of activities by concessionaires and park staff. Given these considerable impacts, we believe a tiered approach is warranted to gain reliable knowledge and contribute to the development of winter use policy. Under this approach, the following progression of increasingly intrusive studies to park visitors and operations could be implemented during a succession of winters (November through March):

1. Maintain a sample of 50-60 bison with GPS collars distributed between the central and northern breeding herds for at least 5 years. This has been the primarily methodology used to obtain bison movement data that have been employed in many of the detailed studies described under the previous two research themes.
2. Deploy automated video camera systems triggered by sensors along the Firehole Canyon, Gibbon Canyon, and Mary Mountain trail to collect baseline data on the direction, frequency, magnitude, and timing of movement through major travel corridors;
3. Experimental manipulations of bison movements through the Firehole Canyon by using metal gates or temporary cattle-guard bridges and fencing to deny bison access to the main groomed road and evaluate their use of alternate ungroomed routes;
4. Manipulate bison movements through the Gibbon Canyon using gates/bridges and fencing to deny bison access to the new bridge and road (once construction is completed), while evaluating their use of an alternate ungroomed route; and
5. Close the road between Madison and Norris junctions with no grooming of the roadway.

Continuing deployment of GPS collars on bison and deployment of camera systems along known important travel corridors (activities 1-2), both associated with road systems and important corridors where no roads exist, will allow continued data collection on bison spatial dynamics under variable bison densities and winter severities, enhancing the range of variation captured and our ability to understand that variation as described in the analyses outlined under the first two research themes. We do not think these activities alone will be sufficient to resolve the policy dispute about road grooming and its effects on bison movements. However, these data are necessary to identify travel corridors and the extent they are used under varying snow pack conditions and bison population levels. Data from the video camera monitoring systems also are needed to provide baseline information on bison travel on important movement corridors to aid in interpretation of the alternate route experimental manipulations (activities 3-4). The alternate route experiments are designed to gain insight on the propensity of bison to travel on ungroomed roads with a minimal disruption to winter visitation by the public and essential administrative and concessionaire travel to maintain public safety and maintenance of essential services and infrastructure in the park’s interior. If bison responded to the barriers to their travel on the groomed road by either traveling the alternate ungroomed road system or by refusing to travel the ungroomed road and returning to their previous foraging areas, then these experiments may be definitive enough to provide a clear indication of the likely influence of road grooming on bison movements without the need to perform the more-disruptive experiment of closing down all winter travel on the Madison to Norris road segment (activity 5). A mixed response of bison, where some animals are turned back by the barriers and ungroomed alternate route while others continue their travel by using the alternate route, would be less conclusive and may require the complete road closure experiment to gain addition insight.

Deployment of GPS Telemetry Collars: Maintaining a sample of 50-60 bison with GPS collars distributed between the central and northern breeding herds would be the most efficient and cost-effective method to continue to gain insights into the spatial and temporal factors influencing bison movements across the landscape, including the use and potential influence of groomed roads. A 30-60 minute relocation frequency during the rut to calving period (August-June) provides essential insights regarding the actual timing and pathways of movement both on and off roadways and from central to northern range before and during winter. Continuing the GPS-collaring program and expanding the sampling to include northern range animals would also enable us to assess the fidelity of movements and use areas, behavioral flexibility in movements of individuals within and among years, and the demographic rates of animals using different strategies (i.e., partial migration theory). Additional GPS data would enable more rigorous evaluations of the odds of occupancy or movement by bison given certain snow pack levels and examinations of how topography, habitat type, roads, snow conditions, and elevation affect the probability of bison travel or foraging activities.

Deployment of Camera Systems to Collect Baseline Data: Previous still-frame camera systems used to monitor bison movements in Yellowstone experienced problems with data storage capacity limitations, power supply failures in severe cold temperatures (e.g., -30^{o} F), animals chewing through wires connecting sensor units to the cameras, and heavy snows or strong winds activating the system. Thus, there is a need to develop and test a reliable camera system for collecting baseline data on the direction, frequency, and timing of bison movements prior to implementing any landscape-scale manipulations such as road closures, cessation of grooming, or impediments to movement (e.g., gates, fences). The prototype camera system currently under development includes a (1) standard, bullet-type video camera, (2) infrared light source for night operations, (3) digital video recorder capable of capturing video or still images with a user-defined rate, (4) storage medium with adequate memory and easy exchange capability, (5) adjustable activation system, (6) solar, fuel cell, or battery power system, (7) enclosure to provide protection from the elements, and (8) data retrieval and image processing system (Appendix B).

Integrated camera and counting systems that emitted an infrared light sensor beam and activated when this beam was broken by animals traveling along a trail have worked quite well in Yellowstone (Bjornlie and Garrott 2001). Each time the beam was broken an "event" was recorded with a date and time stamp and a photo was taken of the animal that broke the beam, thereby providing information on the direction, number, species, and timing of animals traveling along the trail. However, these systems required frequent visits by research personnel to replace batteries and film and were quite constrained with respect to acquiring photographs due to their reliance on film. Similar systems are available that use digital cameras, but both triggering devices (passive infrared) and power systems (standard batteries) have not proven reliable for our applications. A more flexible, reliable, and informative camera system is needed that has the capability of providing video images to interpret bison behavior, as well as enumerate the number of bison in a group and the direction of travel. More reliable and sophisticated sensor systems are needed for activating the monitoring system as cameras will often be deployed along roads where there will be a lot of snowmobile and coach traffic. Thus, an ideal sensor system should be able to discriminate between relative fast-moving snowmobile and coach traffic and the slower moving bison, minimizing camera activation for non-bison targets. Alternate power sources are needed, as well as large capacity information storage devices, so that camera systems can be deployed for extended periods of time along remote trails as well as ungroomed roads where maintenance visits to service the systems would be time intensive (remote trails) or undesirable (ungroomed roads).

Ideally, the prototype camera system would be deployed in November 2007 for evaluation. If the system works satisfactorily, then 2-3 additional units could be purchased for delivery by December 2007 and deployment through March 2008. We recommend deploying one camera system on the road in Gibbon Canyon just north of the falls, another system on the road in Firehole Canyon near the Cascades of the Firehole River, and another system along Mary Mountain trail someplace near the watershed divide to monitor natural movements along this travel corridor. If available, a fourth camera system could be deployed on the Gneiss Creek trail that bison use to travel to the western boundary area near West Yellowstone, Montana. These camera systems would provide baseline data on bison movements along the most important groomed road segments and key ungroomed trails, prior to implementing any manipulations such as road closure, a cessation of grooming, or denial of access to one or more road segments by bison.

<u>Firehole Canyon Experimental Manipulation</u>: In our first-generation evaluation of bison travel movements using data from the first year's deployment of GPS radio collars, we found that landscape attributes were effective at predicting bison travel through the topographically constrained Gibbon Canyon, but failed to predict travel through

the less-constrained lower Firehole drainage; even though snow pack is similar in both areas (Bruggeman et al. 2007). Travel through the lower Firehole drainage was only predicted after distance to road was included in exploratory models, suggesting road grooming may facilitate movements by bison through this area. The Firehole Canyon is suitable for a partially-controlled field manipulation because the main groomed road through this area receives the highest amount of bison travel during winter and the Firehole Canyon Drive Road provides a 3.5-km alternate road that follows the Firehole River. Streams are the most influential natural landscape feature affecting bison travel in Yellowstone during winter, and results suggest the bison travel network is spatially defined largely by the presence of streams that guide bison movements between foraging areas (Bruggeman et al. 2007). Also, bison must traverse the Firehole Canyon before moving west along the Madison River towards the park boundary or north along the Gibbon River towards Norris and, eventually, the park's northern boundary.

Once the camera system deployed near the Cascades of the Firehole River has collected sufficient baseline data on the direction, frequency, and timing of bison movements through this area, we recommend constructing barriers at both ends of the Firehole Canyon Drive Road where it junctures with the main groomed road (Figure 3). The barriers would be placed to prohibit bison travel on the main groomed road during November through March and force them to either use an alternate parallel, ungroomed Firehole Canyon Drive Road to traverse this area or turn back because the ungroomed route is perceived as a barrier to movement. To our knowledge, the Firehole Canyon Drive Road has not been used by bison to move through this area during winter. Traffic would be prohibited on the Firehole Canyon Drive, which would not be groomed during the winter. Barriers would consist of sturdy gates that could raise with the snow level (Appendix C) or temporary cattle-guard bridges (Appendix D) and wing fences extending on each side for several hundred meters to deter bison from walking around the gate to access the groomed road (Figure 3). The gates or bridges would enable snowmobile and coach guides, concessionaires, park staff, and groomer operators to use the main groomed road throughout the winter, while blocking bison movements along this road segment.

Cameras would be positioned near each gate to monitor the area where bison movement along the groomed road is impeded and they must choose to use the alternate, ungroomed travel route or turn back. The camera system will document the number of bison groups encountering the barrier and the outcome of their choice. Ideally, we would also place another camera someplace along the ungroomed route to quantify the number of bison actually using this route for comparison with baseline data collected before the manipulation. Cameras will be mounted on solid wooden posts along the edge of roads or trails and oriented along the road in the direction bison are expected to be traveling from as they approach the gated section of road where they will have to make a choice. The triggering system could be some distance from the gate itself so that people stopping their vehicles to open and close the gate don't trigger the system. Data from previous research on bison use of the road system indicates that bison travel the road in groups that tend to respond to barriers, winter visitors, and choices of travel routes as a single unit (Bjornlie and Garrott 2001, Borkowski et al. 2006, Bruggeman et al. 2006). Therefore, we would consider a bison group encountering the barrier as the experimental unit and anticipate the entire group will either choose to take the alternate ungroomed route or turn around, providing a dichotomous response variable that can be modeled using logistic regression. Any group that circumvents the barrier in some way (Meagher 1989) and continues down the groomed road would be considered an experimental failure and would be censored from analysis. If we are incorrect in assuming a uniform group response we can treat groups that split, with part of the group turning around and part traveling the ungroomed road, as a third response category and analyze the data using multinomial logistic regression. Covariates that can be considered in the analysis include bison group size, snow pack metrics on the ungroomed road, mean snow pack SWE on the winter range, bison condition as indexed by SWE_{acc} (as described previously), direction of travel, and number of bison on the winter range or in the entire population. We can also compare the number of bison (or groups) that travel the ungroomed road each winter the experiment is performed against baseline data collected on the adjacent groomed road system. Such comparisons would also need to account for annual differences in bison population size and SWE.

This manipulative investigation would be less intrusive to park staff and visitors than closing an entire road segment to traffic, but the probability of success of such an experiment is uncertain due to a number of factors. While signage, training of guides and concessionaires at the start of the winter season, and the presence of the camera monitoring systems should discourage unauthorized use of the alternate road that needs to remain in an "ungroomed" state, there is a real possibility that a renegade snowmobile or coach driver could travel the ungroomed Firehole Canyon loop road and create a groomed trail for bison which would negate the experiment from that point forward. It is also possible that some bison could find a way around the barrier and wing fences and continue traveling down the groomed road, possibly becoming trapped between the barriers. Such behaviors have been described when fences and cattle guards were installed on the northern range in an attempt to keep bison from exiting the park in the Gardiner area (Meagher 1989). However, these barriers attempted to block all bison movements. In the experiments we propose, the bison encountering the barriers on the groomed road would have an alternative route readily apparent and immediately adjacent to the barrier. Thus, if bison are willing to travel through the ungroomed snow of the alternate route, there will be less of a chance that the barriers will be circumvented and allow bison to continue traveling on the groomed road between the barriers. If this were to occur, however, then we anticipate that the experimental road section would be closely monitored to allow quick detection of such an event and opening of the gate or a section of fence adjacent to the bridge barrier to allow bison to pass. The camera system and snow-tracking should provide insight on how the bison group circumvented the barrier which, in turn, may allow remedial actions to forestall other bison groups from taking the same route. If gates are used as barrier, then it is also possible that occasionally someone will fail to shut gate which would result in the loss of any data from bison traveling the experimental road section until the gate was again closed. Finally, it is possible that low snow pack could result in little bison migration through this area (e.g., winter 2006-07) and necessitate several winters of replication.

Gibbon Canyon Experimental Manipulation: Gates et al. (2005:253) suggested an experiment should "… test the hypothesis that the Central population's movement to the Northern Range is possible only with grooming of the snow pack on the road, in particularly in the Gibbon Canyon." Thus, the road through the Gibbon Canyon may provide a second site to perform a similar experiment as described for the Firehole Canyon once construction of the new road and bridge is completed. The main road is being rerouted along a 3.1-km stretch of the Gibbon Canyon that will move the road from the canyon bottom in one of the most constricted areas of the canyon to an adjacent bench above the river valley. The new road has been constructed, but a bridge over the Gibbon River to connect the new road to the existing road has not yet been built. While the complete rerouting plan calls for the removal of the existing road and restoring the right-a-way, delaying this work for one or more years after the new road is completed would provide parallel road segments that would facilitate an experimental manipulation. The manipulation would involve grooming the new road segment, but placing gates or bridge barriers as described for the Firehole Canyon experiment at both junctions of the new road segment with the old road (just above Gibbon Falls and at Tanker's Curve; Figure 4). The gates or bridges and wing fences would force bison to either use the alternate parallel, ungroomed route along the Gibbon River to traverse this area or turn back because the ungroomed route is perceived as a barrier to movement. Barrier construction, camera placement, and response variables would be similar to those described for the Firehole Canyon manipulation. Thus, snowmobile and coach guides, concessionaires, park staff, and groomer operators would be able to use the new, groomed road throughout the winter. If possible, after one winter we would recommend switching the treatment (i.e., gate and groom the old road, but not the new road) to see if bison make similar choices regardless of which road is gated. However, the practicality of this action would depend on an adequately gentle and safe grade transitioning from the new road juncture to the old road. The potential limitations and constraints of this manipulative experiment are the same as those described for the Firehole Canyon experiment. This manipulation also may not be feasible because it is dependent on modification of current construction plans for the new road system, which may not be practical.

Closure of Madison to Norris Road: The simplest but most disruptive and perhaps costliest experiment to evaluate bison responses to a cessation of road grooming involves closing the existing road gates near Madison and Norris junctions to prohibit vehicle traffic and not grooming this road segment during winter. Once sufficient baseline data has been collected on the road near Gibbon Falls, cameras would be positioned near each gate to monitor the area where bison movement along the groomed road is impeded and they must choose to go around the gate and use the ungroomed roadway or turn back. The camera systems would document the number of bison groups encountering the ungroomed road segment and the outcome of their choice. We would also place another camera along the road near Gibbon Falls to quantify the number of bison actually using this route for comparison with baseline data collected before the manipulation. The response variables and analyses would be the same as those described for the Firehole and Gibbon Canyon manipulative experiments.

Acknowledgments

Funding for this project was provided by the National Park Service. We are grateful to K. Aune and J. Millspaugh for expert peer review, J. Bruggeman for analyses; T. Bushey for gate design; K. Tonnessen and the Rocky Mountains Cooperative Ecosystem Studies Unit for facilitating funding agreements; T. Olliff, J. Sacklin, and G. Plumb for discussions and support; T. Davis for map development; and M. Yochim and D. Swanke for review of various documents.

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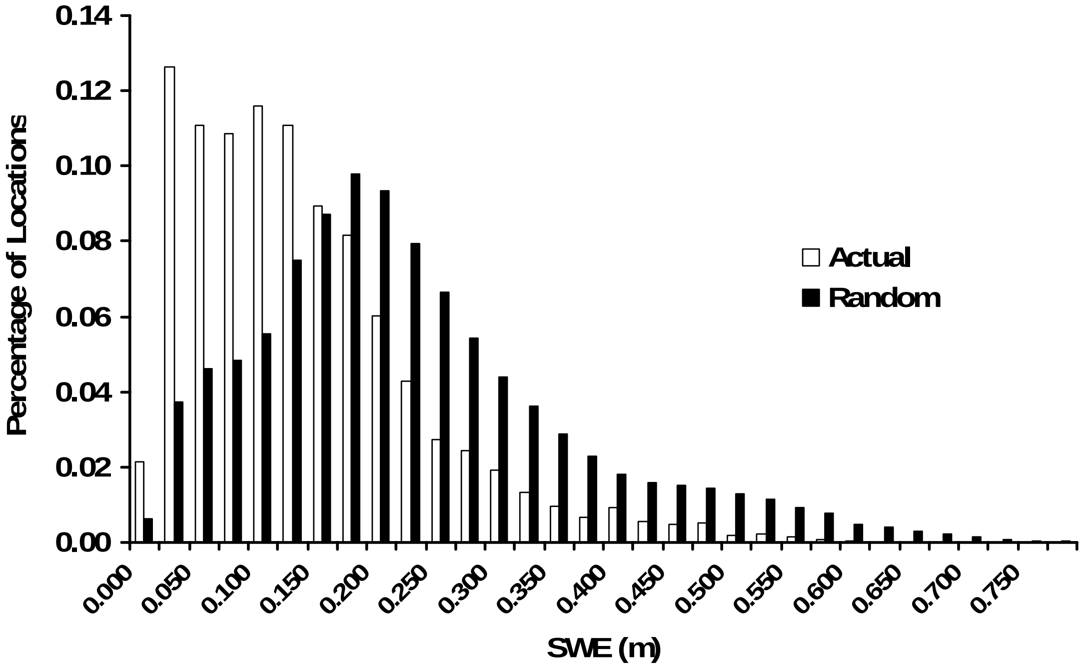


Figure 1. Fictitious histogram comparing mean snow density (SWE) available within the entire bison range (random) to the mean snow density in a 100-meter radius around observed each bison location (actual).

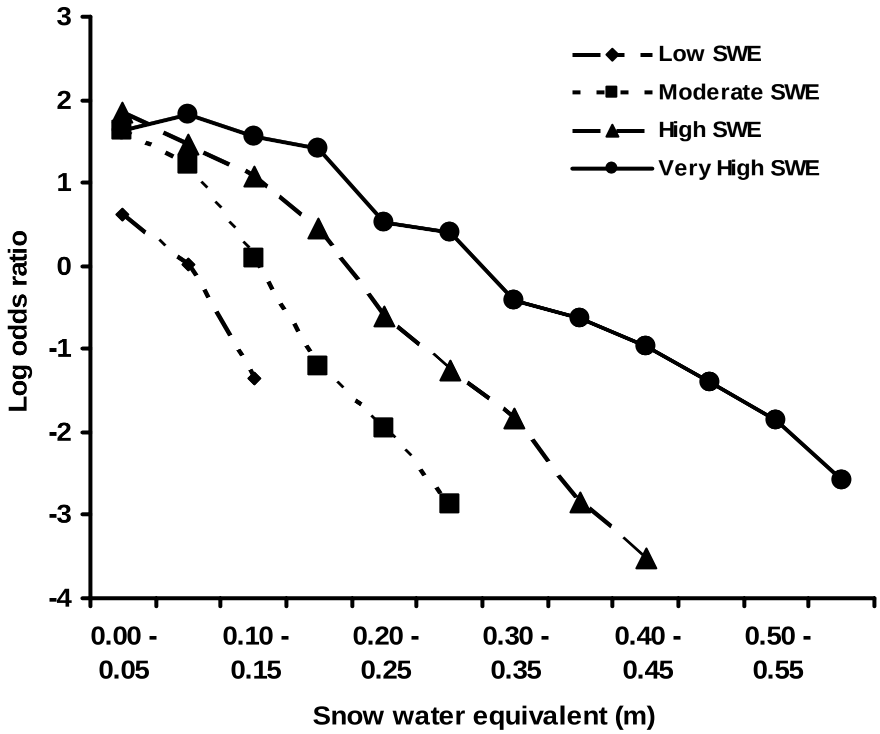


Figure 2. Fictitious plot illustrating the log odds of a bison occupying a local area (100-m radius around an observed location) with a particular mean snow density for four levels of overall snow pack severity, as characterized by mean snow density in the entire winter range.

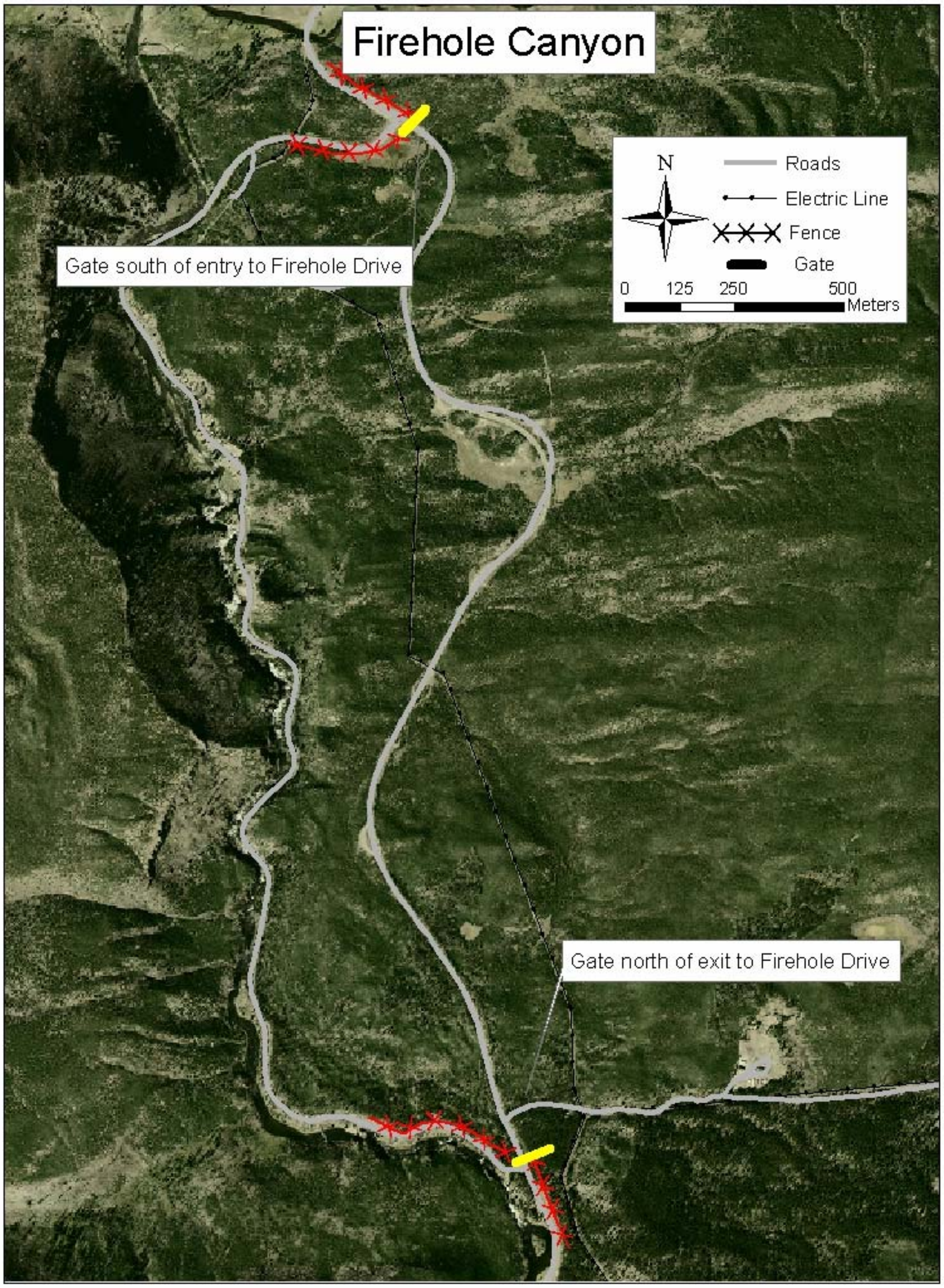


Figure 3. Area of the Firehole Canyon affected by the proposed partially-controlled field manipulation, including the main groomed road and the 3.5-km alternate Firehole Canyon Drive Road that follows the Firehole River.

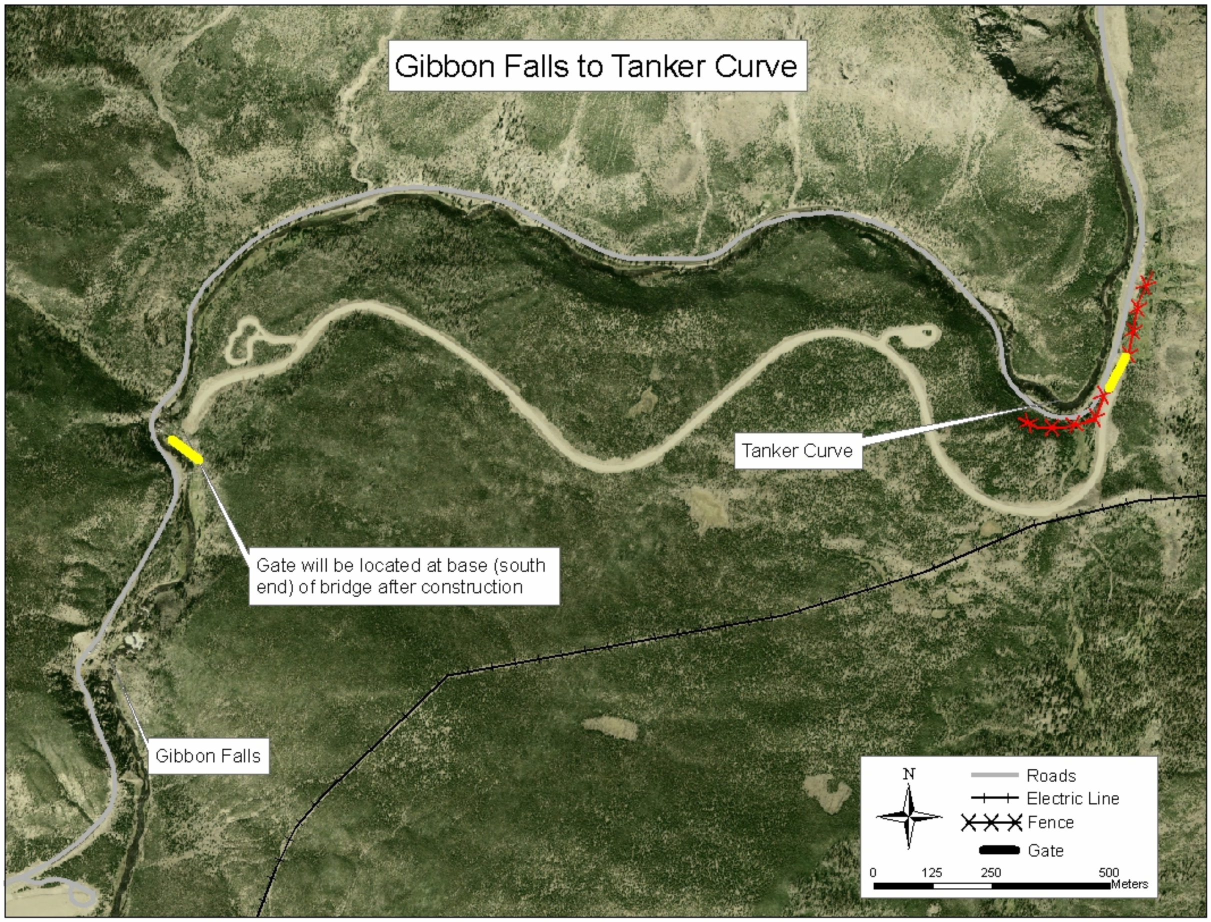


Figure 4. Area of the Gibbon Canyon affected by the proposed partially-controlled field manipulation, including the 3.1-km new groomed road and the alternate old road route that follows the Gibbon River.

Appendix A. Credentials of the authors of this report.

ROBERT A. GARROTT is both a Professor in the Ecology Department at Montana State University Bozeman and Director of the Fish and Wildlife Management Program. He has 30 years of experience as a research biologist and has specialized in carnivore and large mammal ecology and management and predator-prey dynamics. He has published 90 papers in a variety of scientific journals, coauthored an authoritative book on wildlife telemetry data analysis, and four chapters in other ecological books. He has served as an expert scientific advisor to managers and administrators of numerous of national parks, state natural resource management agencies, and served as a primary scientist evaluating the impacts of the Exxon Valdez oil spill on wildlife resources in Prince William Sound, Alaska. He has held several editorial positions with professional journals and routinely serves as a reviewer and panelist for the National Science Foundation. He received a doctorate in Wildlife Conservation from the University of Minnesota, a Master of Science degree in Wildlife Management from Pennsylvania State University, and a Bachelor of Science degree in Wildlife Biology from the University of Montana. Prior to assuming his current academic position, he held numerous other research positions including Staff Scientist with Los Alamos National Laboratory, and was an Assistant Professor in the Wildlife Ecology Department at the University of Wisconsin Madison.

Disclosure: Dr. Garrott has taken positions regarding the effects of road grooming on bison movements that are closely associated with the National Park Service, as evidenced by numerous contracts with the National Park Service regarding wildlife-related research in Yellowstone National Park during 1996-2007 and articles he has published in scientific journals on this issue.

P.J. WHITE is the Supervisory Wildlife Biologist and primary program manager for ungulates in Yellowstone National Park. He has 20 years of research, management, and regulatory experience and has designed and implemented numerous research programs that contributed essential information for the conservation of wildlife in complex ecosystems. As a Supervisory Biologist with the U.S. Fish and Wildlife Service, he was responsible for all decisions pertaining to the implementation of the Endangered Species Act in a region of high biological diversity in southern California with diverse stakeholders, including federal, state, tribal, mining, agricultural, flood control, ground water recharge, water diversion, recreation, and development interests. He has published 50 papers in a variety of scientific journals and prepared hundreds of environmental documents issued for compliance with the Endangered Species Act, National Environmental Policy Act, Clean Water Act, and other federal and state regulations. He also serves as an Adjunct Faculty member for the Ecology Department of Montana State University. He received a doctorate in Wildlife Ecology from the University of Wisconsin, a Master of Science degree in Wildlife Conservation from the University of Minnesota, and a Bachelor of Science degree in Wildlife Science from Cornell University.

Disclosure: Dr. White has taken positions regarding the effects of road grooming on bison movements that are closely associated with the National Park Service due to his current position as a Wildlife Biologist in Yellowstone National Park and as evidenced by articles he has published in scientific journals on this issue.

Appendix B. Proposal for a prototype bison trail monitor.

Ares Engineering, Lawrenceville, Georgia, proposes to design, develop, fabricate, and deploy a prototype bison trail monitor based on a digital imaging system coupled with multiple sensor systems. The digital imaging system will capture images of objects passing in front of its field of view, time and date stamp the images, and store the images for later retrieval and analysis. The sensor systems will be used to identify when an appropriate target (e.g., a bison instead of a snowmobile) has entered the field of view and initiate image capture. Multiple sensors will be deployed to reduce the number of false or inappropriate triggers.

Digital Imaging System.—The digital imaging system will consist of a camera, microcontroller, digital data storage, and infrared (IR) illuminator. The camera will be based on a commercial-off-the-shelf (COTS) CCD or CMOS imager that allows for the capture of both single frame and multiple frame (up to 24 frames per second) images. The microcontroller will be used to cross-correlate the trigger sensors, as well as time and date stamp the images. The microcontroller also provides flexibility to adapt to changing requirements after the system is deployed. The digital data storage will be based on an industry-standard hard disk solution. A plug-and-play solution is envisioned whereby the hard disk is hot-swapped periodically to allow researchers to access the captured data. The IR illuminator provides the capability to illuminate the target area at night without disturbing wildlife.

Sensor Systems.—Multiple sensor systems will be employed to reduce the number of false and inappropriate triggers. The goal is to reduce the amount of video that will be stored and subsequently reviewed to determine the number of bison transiting the field of view. The sensors will be placed to ensure that the target animal(s) are within the field of view when the images are captured. Sensors may include:

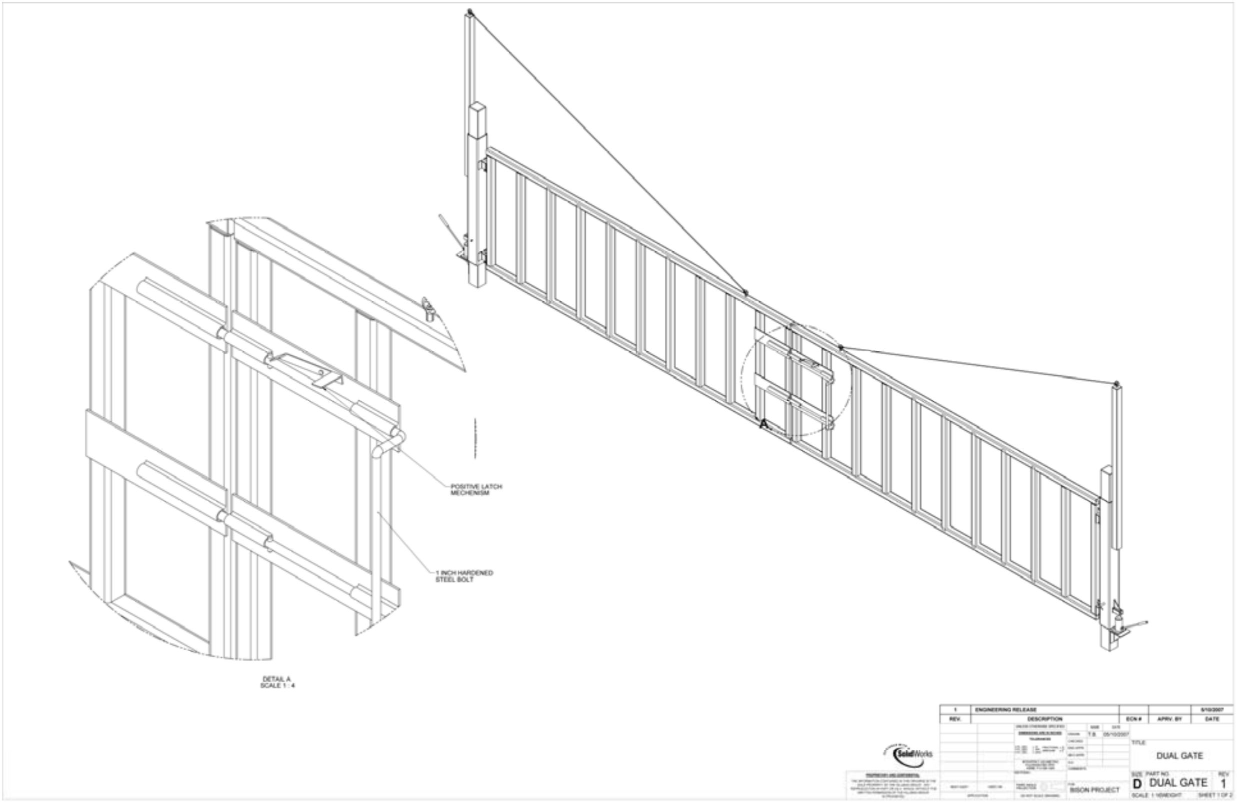
(a) Light beam: This consists of one or more visible or infrared light beams “shot” across the entrance to the target area. To ensure that the sensor is not affected by wind, it would be anchored to a post on each side. To eliminate the need to run a power source to the far side, the transmitter and receiver units would be located on the same post with a mirror on the far side.

(b) Motion Detector: This consists of an ultrasonic or infrared detector that senses a target by either the sonic beam bouncing off of an object or the heat radiating from an object. These detectors are not affected by wind and can cover a broader target area than a typical light beam.

(c) Image Discriminator: This consists of using images from the camera to discriminate objects as they appear and disappear from the field of view. An averaging routine is performed on the pixel information from the camera and the system is triggered when a sufficient change in the pixel information is detected. The system would automatically compensate for slow changes, such as light conditions and weather, but would react to an animal moving through.

Power System.—Ideally, the power system will be based around a propane-based fuel cell, though a methanol-based fuel cell would also be suitable. Methanol-based fuel cells offer the highest energy efficiency, though it is affected by humidity. Propane-based fuel cells are not as efficient, but are not dependant on outside humidity. A grill-sized propane tank can run a 50-watt fuel cell for 8 to 10 days. Unfortunately, fuel cells are not commercially available at this time. Thus, we may need to use deep-cycle batteries in the interim.

Appendix C. Preliminary Gate Design.



Appendix D. Preliminary Design of a Temporary Cattle-Guard Bridge.