Yellowstone Science

volume 19 • issue 1 • 2011

Yellowstone Bison

Carrying Capacity and Movement

Balancing Brucellosis Risk and Wildlife Conservation

Historical Wolf Population Numbers

Juvenile male bison spar during the rutting season in Hayden Valley. They struggle for dominance and the opportunity to secure their genetic legacy.

A Little Learning Can Be A Provocative Thing

Although *Yellowstone Science* is used as a means of conveying the depth and breadth of research that takes place in the park, acknowledging what we haven't figured out yet is also important. In or between its lines, *Yellowstone Science* offers many questions still in search of answers.

In this issue, we present new information on an old topic—why do bison leave the park? Well, yes, because the grass is greener there, at least in early spring, but there's a lot more to it than that. Authors P.J. White, John Treanor, Michael Coughenour, and Rick Wallen raise and attempt to answer questions such as why bison have left even in years when less than half of the forage in the park had been eaten. Seasonal timing is also a critical factor in another management challenge addressed in this issue, brucellosis transmission by elk and bison.

Ever since the idea of reintroducing wolves in the Yellowstone area caught on decades ago, people have wanted to know how many wolves resided here before their widespread slaughter began in the nineteenth century. Lee Whittlesey and Paul Schullery show how letters written by a member of the 1872 Hayden Survey add to the evidence on this enigmatic topic, but they also point out the limitations of such evidence. Can we be reasonably certain that the number of skins Joseph Savage reported were those of wolves and not coyotes?

By raising such questions, we hope to provoke readers' curiosity and inspire further efforts to fill the information gaps.

We hope you enjoy the issue.

Mary Ann Franke

Yellowstone Science

a periodical devoted to
natural and cultural resources

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Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address: Editor, *Yellowstone Science*, PO Box 168, Yellowstone National Park, WY 82190. You may also email: yell_science@nps.gov.

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Cover photo:
Bison and elk grazing on Yellowstone's northern range. NPS photo by Jim Peaco.

NPS

Each spring, Yellowstone staff work with Montana Department of Livestock personnel to conduct bison hazing operations along the park's west boundary.

FEATURES

DEPARTMENTS

News & Notes

NPS and UW Renew Research Center Agreement

An agreement signed at the AMK Ranch in Grand Teton National Park will continue the longest-standing and one of the most successful partnerships between a university and the National Park Service. On July 21, 2010, University of Wyoming President Tom Buchanan and Grand Teton Superintendent Mary Gibson Scott signed a 10-year agreement for continued use of the historic Grand Teton Ranch, the site of the University of Wyoming-National Park Service (UW-NPS) Research Center. Scientists from around the world conduct biological and physical science research and cultural and social studies at the facility in support of resources throughout the Greater Yellowstone Ecosystem.

The ceremony featured remarks from Superintendent Scott, President Buchanan, University of Wyoming Vice President for Research and Economic Development Bill Gern, and Zoology Professor and UW-NPS Research Center Director Hank Harlow. The UW-NPS Research Center traces its roots to 1946, when the first research station was launched with the help of the Jackson Hole Preserve, Inc., the New York Zoological Society, and the Wyoming Game and Fish Department. In 1953, the UW joined in operating and sponsoring the station and its research program at the Jackson Hole Biological Research Station near the old Moran town site. The UW-NPS Research Center was established in 1977 when the headquarters were moved to the AMK Ranch. At any given time during the summer, the AMK Ranch serves as a base for 50 to 60 scientists. The AMK Ranch is also used for many seminars, field trips, workshops, and symposia. "We're honored to be a part of this relationship—one that has produced significant scientific research and crucial information that helps inform our current and future management of park resources," said Scott during the signing ceremony.


NPS/PEACO 2011

A group of 25 brucellosis seronegative bison being released from the Stephens Creek holding facility within Yellowstone National Park.


NPS

The Berol Lodge at AMK Ranch, location of the University of Wyoming-National Park Service Research Center.

Tested Bison Allowed in Gardiner Basin

On January 19, 2011, a group of 25 bison bulls and cows that tested negative for exposure to brucellosis (seronegative) were released from the Yellowstone National Park Stephens Creek capture facility to a 2,500-acre grazing area in the adjacent Gallatin National Forest by Interagency Bison Management Plan (IBMP) members. The bison were trailed by riders on horseback as they moved north through the park and the Royal Teton Ranch along the Old Yellowstone Trail and onto the national forest, where, based on the IBMP, they may remain until April 15, 2011. Bison are permitted to access the national forest via the privately-owned Royal Teton Ranch under a 30-year agreement with the Church Universal and Triumphant signed in 2008. Each of the bison is marked and fitted with monitoring devices.

Thirteen of the 25 bison repeatedly left the authorized grazing area. They were captured by the Montana Department of Livestock and released back into the park. One bull from the test group was shot after it entered private

Interagency staff trail the small group of bison across the Royal Teton Ranch and into the Gallatin National Forest.

property and behaved aggressively. The cooperating agencies will monitor the movement of the remaining 11 bison to determine how they use this landscape and may agree to allow as many as 100 untested bison on the authorized grazing area in the future. Other bison management within Yellowstone and at the park boundary will continue as outlined in the IBMP and park management policies.

The IBMP, established in 2000, is part of an interagency effort to conserve a viable, wild bison population while preventing the transmission of brucellosis from bison to cattle. The agencies cooperating under the IBMP are the National Park Service, the US Forest Service, the USDA Animal and Plant Health Inspection Service, the Montana Department of Livestock, the Montana Department of Fish, Wildlife and Parks, the InterTribal Buffalo Council, the Confederated Salish Kootenai Tribes, and the Nez Perce Tribe.

Department of the Interior Bison Conservation Initiative

On October 28, 2008, Secretary of the Interior Dirk Kempthorne announced an initiative for the Department to work with state, tribal, and agricultural interests to strengthen bison conservation efforts. In his announcement, Kempthorne stated "One of the classic symbols of the American frontier is the image of vast herds of bison grazing on the western plains…Americans today still find inspiration in bison ranging freely on the landscape, as Yellowstone National Park demonstrates." Kempthorne further remarked that, while the days of millions of free-roaming bison are gone, the Department policy must acknowledge the important role of bison on the landscape, in tribal culture, and in our national heritage.

There are more than 500,000 plains bison in North America today, but most are privately owned, have a large extent of cattle genetic introgression, and are kept in herds of less than 1,000 that are fenced within relatively small areas. There are also 4,000 woods bison free-roaming in Canada. The Department of the Interior (DOI) manages almost 7,000 bison in national wildlife refuges and national parks.

The initiative proposes several actions to address the health and genetic composition of the bison populations on the DOI lands. To promote cooperative conservation in bison management, the DOI will strengthen existing partnerships and build new ones with state agencies, American Indian tribes, landowners, agricultural interests, conservationists and others interested in bison health and recovery. Where there is strong local support, partnerships could permit small bison herds to recreate their natural role in areas where they are not currently present. Such arrangements may help support the restoration or maintenance of other native species and habitats, and become important tourist attractions.

An interagency working group will coordinate management and science needs and activities related to the DOI's bison herds and carry out cooperative efforts with other parties. The group includes representatives from the Fish and Wildlife Service, the National Park Service, the Bureau of Land Management, the US Geological

Bison at the Stephens Creek facility are tested to determine the degree to which the population is infected (called seroprevalence) with the *Brucella abortus* bacteria.

Survey, and a tribal liaison from the Bureau of Indian Affairs, as well as representatives of states in which bison are located. The Animal and Plant Health Inspection Service of the US Department of Agriculture, which plays a major role in bison disease issues, and the US Forest Service and Department of Defense, which are major public land managing agencies, have been invited to participate as well.

Additional information on the Bison Conservation Initiative can be accessed at *www.nature.nps.gov/biology*.

White Receives 2010 Intermountain Region Natural Resource Stewardship Award

NPS

Dr. P.J. White.

P.J. White, Branch Chief of Aquatic and Wildlife Resources at Yellowstone National Park, is one of six employees in the Intermountain Region (IMR) to have received Natural Resource Stewardship Awards for 2010. The awards, in categories ranging from management to maintenance to research, recognize outstanding contributions to the care, protection, and appreciation of the landscapes, wildlife, and other natural attributes of National Park Service sites. White received the Director's Award for Natural Resource Management.

"In their everyday duties, these six colleagues give us daily lessons in how to accomplish better a key part of our National Park Service mission: the protection and preservation of park resources," IMR Director John Wessels said. "With diligence and creativity, they represent the best of NPS efforts to safeguard some of the most precious qualities and natural resources of our park landscapes."

As noted in the nomination submitted by then Yellowstone Superintendent Suzanne Lewis, P.J. White has been a champion of producing objective science to support decisions regarding the conservation of natural resources and the processes that sustain them in Yellowstone National Park. He excels at building relationships between groups of scientists to conduct mission-critical research, making science accessible to managers and visitors by creating understandable products, and formulating and negotiating effective plans to conserve and restore species and processes across jurisdictions. P.J.'s commitment to the science-informed management of park resources contributed to four significant accomplishments in 2010:

- Completion of an adaptive management plan that significantly increased tolerance for Yellowstone bison migrating to essential winter ranges in Montana and reduced the capture and culling of bison due to concerns about disease transmission to cattle;
- Completion of an environmental impact statement analyzing the impacts of remote vaccination of bison (i.e., without capture) for brucellosis;
- Preparation of convincing legal responses to a federal lawsuit against the US Forest Service and Department of the Interior alleging impairment of Yellowstone bison and other complaints due to management actions; and
- Completion of an assessment of ecological process management in Yellowstone, with recommendations for improved approaches and practices to mitigate future uncertainties such as climate warming, invasive species, and land use changes.

Each of these accomplishments reflects the culmination of years of effort and required significant long-term vision, perseverance, patience, and diligence.

The other 2010 recipients are:

- *Superintendent of the Year for Natural Resource Stewardship*—Alexa Roberts, superintendent, Bent's Old Fort National Historic Site
- *Natural Resource Research*—William G. Parker, physical scientist, Petrified Forest National Park
- *Natural Resource Management in a Small Park*—Chris Ford, chief of Integrated Resources, Grant-Kohrs Ranch National Historic Site
- *Natural Resource Professional*—Gregory Mark Anderson, aquatic ecologist, Glen Canyon National Recreation Area

NPS/PEACO 1999

An elk herd searches for winter forage in Lamar Valley.

- *Natural Resource Stewardship through Maintenance*—Jackie Messer, facility manager, Chickasaw National Recreation Area

As regional winners, the six employees are eligible for the national 2010 NPS Director's Awards for Natural Resources, which will be presented during the biennial George Wright Society Conference on Parks, Protected Areas, and Cultural Sites, March 14–18, 2011 in New Orleans.

Winter Elk Count

The annual aerial survey of the northern Yellowstone elk herd conducted in December 2010 counted 4,635 elk, 24% less than the 6,070 reported in January 2010.

Park and university biologists say increased predation, ongoing drought, hunting pressure, and other factors have contributed to an apparent 70% decline in the herd population in the last fifteen years. The elk count in 1995, when wolf restoration began in Yellowstone National Park, was 16,791.

Predation by wolves and grizzly bears is cited as a major reason for the decline. Both prey primarily on elk, and predation on newborn elk calves may limit the population's ability to recover.

Drought during the early 2000s appears to have impacted the quality and abundance of forage, possibly lowering reproduction rates in some elk.

The number of permits issued for the antler-less Gardiner Late Elk Hunt was reduced from 1,102 in 2005 to 100 during the 2006–2010 seasons and has been eliminated for 2011.

Biologists suspect predator numbers may be responding somewhat to the decline in the elk population. The number of grizzly bears seen on the northern range during elk calving season has decreased slightly in recent years. Also, the wolf population on the northern range inside Yellowstone National Park has dropped from 94 wolves in 2007 to 39 wolves in 2010.

Biologists expect the reduction in the number of wolves and the elimination of the late season hunt will result in some increase in the elk population.

The Northern Yellowstone Cooperative Wildlife Working Group will continue to monitor trends of the northern Yellowstone elk population and evaluate the relative contribution of various components of mortality.

Cougar Skulls Acquired by Heritage and Research Center

The museum at Yellowstone National Park's Heritage and Research Center recently received cougar skulls collected during Phase One of the Cougar Project in the park. Researchers studied predation and the reproductive success of cougars in northern Yellowstone and the surrounding area from 1987 to 1996. Conclusions from the project helped inform the park's management about cougar numbers and population dynamics, this carnivore's food requirements, and interactions with other predators.

YELL-134142/COLLECTED 12/18/1989

The skull of a six month-old male cougar (*pictured at two angles*) shows the two large puncture wounds where it was killed by adult male cougar.

YELL-134140/COLLECTED 8/18/1994

Skull of a male cougar that died from starvation at 6.5 years of age.

Cougars were essentially eliminated from their native habitat in the Yellowstone region in the early 1900s as part of a predator control program. The last known cougar was killed in 1925. Occasional sightings of cougars that might have dispersed from other areas were reported in the following years and increased after the 1950s. The project studied this population.

Researchers collared 80 of the 88 cougars captured during the project. They concluded the population's prey was primarily comprised of elk and mule deer, with elk calves being the most important prey and adult elk being the least important relative to their availability. Researchers also concluded that resident males (as opposed to roaming males) sired nearly all cougar litters. The number of breeding-age females present within a male's territory and the male's age were correlated with the number of litters the male sired each year.

Interviews with project lead Kerry Murphy appear in early issues of *Yellowstone Science*, 2(3) and 2(4), and can be accessed at *www.greateryellowstonescience.org/ys.*

The Heritage and Research Center is home to Yellowstone National Park's museum collections and holds more than 13,000 natural specimens, including 10,000 herbarium specimens. To access the collections, contact the museum staff at (307)344-2662 for an appointment or go to *www.nps.gov/yell/historyculture/collections.htm* for more information.

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NPS/OBSIDIAN CREEK THROUGH WILLOW FLATS

Shorts

Surface and Groundwater Flow in Yellowstone

Gardner, W.P., D.D. Susong, D.K. Solomon, and H. Heasler. 2010. Snowmelt hydrograph interpretation: Revealing watershed-scale hydrologic characteristics of the Yellowstone volcanic plateau. *Journal of Hydrology,* 383:209–222.

In this study, Gardner and others gained insights about surface and groundwater flow in the Yellowstone volcanic plateau by examining annual hydrographs from US Geological Survey stream gauges and dating groundwater samples from cool water springs. Analyses of annual streamflow hydrographs indicate that groundwater inflows—rather than direct runoff from precipitation—are the dominant influence on streamflow within the Yellowstone caldera and rhyolite volcanic plateaus. Rivers with headwaters in the Yellowstone caldera and associated rhyolitic plateaus have smaller spring runoff peaks, carry less sediment, and have larger base flows in the fall than rivers outside the caldera. This is because the extensive and young rhyolitic volcanic rocks in Yellowstone form large, fractured groundwater aquifers. Much of the spring snowmelt infiltrates these aquifers and is discharged to rivers throughout the year rather than primarily during spring runoff. Geochemical dating of water discharged from cool springs in the rhyolitic volcanic rocks indicates groundwater ages of less than 50 years. This short residence time for the groundwater implies a rapid circulation of groundwater within the rhyolitic volcanic aquifers. The results presented in this paper are part of a larger study investigating the shallow, groundwater-flow system in Yellowstone and its connection to the Yellowstone hydrothermal system.

—David D. Susong, Supervisory Hydrologist, US Geological Survey

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Nutrient Cycling: Transitioning from an Elk to Bison Dominated Grassland System

Based on data and fieldwork from Yellowstone National Park ungulate monitoring projects.

Plant production in grassland ecosystems is generally limited by moisture and nutrient availability, and may decrease or increase depending on how the plants are grazed. Although intensive grazing by ungulates may reduce nutrient cycling and plant production, more moderate grazing can maximize forage quality and quantity. The high densities of elk (12–17/km^2) on Yellowstone's northern range during the 1980s and 1990s deposited large quantities of nitrogen, phosphorus, and other nutrients, stimulating plant production. The reduction of elk numbers to 10–11/km^2 as a result of hunter harvest, predation by a growing wolf population, severe winterkill in 1997, and drought during 1999 and 2000 resulted in conditions less conducive to plant growth. Studies of the northern range suggest that nutrient dynamics and the system as a whole are within long-term variations. Migratory ungulates concentrate foraging for shorter intervals and transfer nutrients via feces and urine from other areas, while predators keep ungulate densities below carrying capacity.

However, there is some indication that the northern range grassland is in a state of flux. The decline in elk density to approximately 3–5/km^2 during 2006 to 2010 reduced forage consumption and nutrient deposition. Also, warmer temperatures in northern Yellowstone during the past 50 years have brought an earlier peak in the growing season followed by earlier curing of vegetation and more frequent periods of drought. Though early green-up provides high nutrition for ungulates during the latter stages of gestation and lactation, contributing to increased calf survival, an early decrease in forage could leave females with marginal fat reserves for pregnancy and survival the following winter.

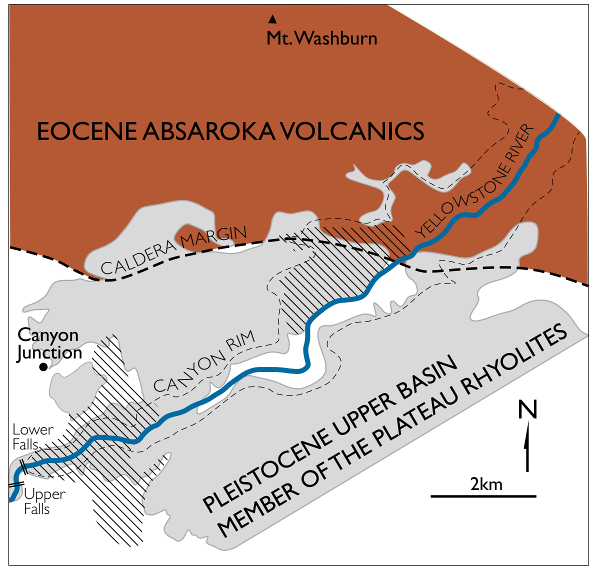
Relatively low elk body condition and pregnancy rates have been detected during recent years in the eastern portion of the northern grassland. The reduction in wintering elk numbers by more than one-half may have contributed to the more than doubling of bison numbers from 1996 to 2008. Elk and bison have dietary overlap, but elk feed more on isolated plants and most migrate to higher elevations after early spring. Bison, which comprise less than 5% of wolf kills, tend to create distinct grazing patches and remain on the northern range through the summer, resulting in different effects on nutrient cycling. Bison grazing and wallowing convert grass-dominated sites to sites of greater plant diversity and spatial heterogeneity. Depending on future bison density, the bison's larger biomass, strong herding tendencies, and selective consumption of dominant grasses and sedges could contribute to extensive areas of grazing-tolerant plants that are repeatedly grazed throughout the season, but shift across the landscape from year to year, as well as possible long-term changes in rates of nitrogen cycling and nutrient redistribution. Research on how recent changes in elk and bison distributions have affected ecosystem processes such as nutrient cycling is planned to begin in summer 2011 with Dr. Douglas Frank of Syracuse University.

—P. J. White and Rick L. Wallen, Yellowstone National Park

Older Hot Spring Alteration in the Grand Canyon of the Yellowstone River

Larson, P.B., A. Phillips, D. John, M. Cosca, C. Pritchard, A. Andersen, J. Manion. 2009. A preliminary study of older hot spring alteration in Sevenmile Hole, Grand Canyon of the Yellowstone River, Yellowstone Caldera, Wyoming. *Journal of Volcanology and Geothermal Research* 188: 225–236.

Erosion in the Grand Canyon of the Yellowstone River has exposed a cross-section of more than 300 vertical meters of rhyolites left by the most recent caldera collapse (640 ka) that have been altered by hydrothermal activity for about 150,000 years. Research on the canyon walls in the Sevenmile Hole area found minerals (quartz, opal, kaolinite, dickite, alunite, illite, adularia, and pyrite) that formed two alteration zones characteristic of shallow hydrothermal systems in volcanic environments. The advanced argillic zone, located in the first 100 meters below the canyon rim, has an intermediate argillic zone directly beneath it. This transition in clay mineralogy is also found in active alkali-chloride hydrothermal springs elsewhere in Yellowstone, at temperatures of 150°C to 170°C. The Sevenmile Hole area lies at the eastern end of a band of hydrothermal features that may be aligned with a ring fault across the northern part of the caldera. There it is concealed by the younger tuff of Sulphur Creek (480 ka).



Sevenmile Hole area (Modified from Christiansen and Blank 1975; Prostka et al. 1975; and Christiansen 2001).

—Peter Larson, Washington State University

Migration and Dispersal: Key Processes for Conserving National Parks

Based on data and fieldwork from Yellowstone National Park ungulate monitoring projects.

The seasonal round-trips undertaken by migrating wildlife can increase their access to food and mates, and release areas from intensive use for part of the year. Dispersal, in which one or more members of a population make a one-way movement to another area, can keep population density within the food-limited capacity of the environment. In Yellowstone National Park, the presence of species such as the bald eagle and trumpeter swan, for which the park has little suitable year-round habitat, depends on migration and dispersal from more productive areas. Elk, bison, deer, and pronghorn need to migrate beyond the park's boundaries to access some of their traditional winter range.

However, migration and dispersal have undergone a world-wide demise as wildlife has been compressed into disconnected areas. The proportion of pronghorn migrating from their truncated winter range near the park's northern boundary during summer increased in recent decades, possibly in response to extended droughts. Also, the first significant presence of pronghorn in the southern Paradise Valley in many decades apparently occurred when a group of Yellowstone pronghorn dispersed approximately 30 kilometers north of the park in 2000 and grew to 82 animals by 2009. Immigration and gene flow between pronghorn in Yellowstone and the Paradise Valley could improve the long-term viability of both populations.

Although more than half of the Greater Yellowstone ecosystem is on public land, livestock grazing is extensive on the national forests, and valley bottoms and flood plains with higher plant productivity and more moderate winter conditions are primarily on private land. Culling to prevent bison migration and expansion of winter range outside the park has perpetuated irruptive population dynamics and reduced female cohorts. Forcing bison to stay in the park would create artificially high densities that would have negative effects on vegetation, soils, and other ungulates.

Thus, initiatives are needed to maintain and restore ecological processes across management jurisdictions and prevent conflicts with species such as bison, bears, and wolves outside the park. Ideally, partnerships of government agencies, American Indian tribes, non-governmental organizations, and private landowners would develop a consensus on objectives and management actions. However, management of wildlife outside the park is the prerogative of the surrounding states, where many officials and citizens remain unconvinced that ecological integrity is in their best interests. Over time, however, ecosystem process management can enhance the lives of all of Greater Yellowstone's residents by sustaining its natural resources and making it possible to address other challenges such as climate change, forest die-offs, and emerging diseases that can be transmitted between wildlife, livestock, and humans.

—P. J. White, Glenn E. Plumb, and Rick L. Wallen,
Yellowstone National Park

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Carrying Capacity and Movements of Yellowstone Bison

P. J. White, Glenn E. Plumb, Michael B. Coughenour, and Rick L. Wallen

NPS

Postcard #157: "The Buffalo Herd", by Frank Jay Haynes. Date unknown. Haynes began issuing postcards out of his studio in 1897 and he retired in 1921.

The successful conservation of the bison of Yellowstone National Park from a low of about two dozen animals in 1902 to more than 5,000 animals in 2005 has led to enduring conflicts among various publics and management agencies regarding issues of perceived overabundance and the risk of brucellosis transmission to cattle (Plumb et al. 2009). Bison historically occupied approximately 20,000 square kilometers in the headwaters of the Yellowstone and Madison rivers in the northern portion of what is now referred to as the Greater Yellowstone area (fig. 1). However, by the early twentieth century, Yellowstone National Park (YNP) provided sanctuary to the only wild and free-ranging plains bison remaining in the United States (Plumb and Sucec 2006). These animals were spatially segregated into two herds occupying the central plateau and northern portions of the park, respectively (Meagher 1973). Also, these bison were exposed to *Brucella abortus* bacteria before 1917, likely from infected cattle (Meagher and Meyer 1994) and, since then, up to 60% of the population has tested positive for anti-bodies indicating exposure to this nonnative pathogen (Cheville et al. 1998). Brucellosis may induce abortions or the birth of non-viable calves in bison, cattle, and elk (Rhyan et al. 2009).

In 1969, managers in Yellowstone stopped removing bison to limit their population size and allowed numbers to fluctuate in response to weather, predators, and resource limitations (Cole 1971). Bison abundance increased rapidly under this management regime (fig. 2) and, since the 1980s, increasing numbers have moved during winter outside the park where some have been culled or hunted by state, tribal, and federal agencies (Fuller et al. 2007a, b). Bison movements beyond the Yellowstone boundary led to claims that they were over-abundant and had degraded the range inside the park (e.g., Kay 1998). These claims, in turn, led to calls for intensive management to limit the abundance and distribution of bison inside YNP, including fencing, fertility control, hunting, and brucellosis test-and-slaughter programs (US Department of the Interior and US Department of Agriculture 2000a). Since 2000, the risk of brucellosis transmission from Yellowstone bison to livestock has been managed by the federal government and the state of Montana pursuant to the court-negotiated Interagency Bison Management Plan, which allows for the culling of bison in park boundary areas if hazing (i.e., forcing bison to move back into designated conservation areas) becomes ineffective at maintaining separation between bison and cattle (US Department of the Interior and US Department of Agriculture 2000b). These actions are highly contentious and polarizing, and the repeated culling of large numbers of bison could potentially affect the age structure, reproduction, recruitment, or genetics of Yellowstone bison in unintended ways over the long term (White et al. 2009).

We used the best available scientific information to evaluate a central question in this debate, which is whether bison move outside the park because their abundance has surpassed levels that can be supported by the forage base in the park. We also considered other potential explanations for bison movements outside the park during winter and spring, and appraised the implications of perceived overabundance and brucellosis transmission risk for long-term bison conservation.

Have Bison Exceeded their Carrying Capacity?

Ecological carrying capacity has been defined as the natural limit of a population set by resources in a particular environment (Caughley and Sinclair 1994). It is one of the equilibrium points that populations tend toward as animal density increases and the amount of food, space, cover, or other

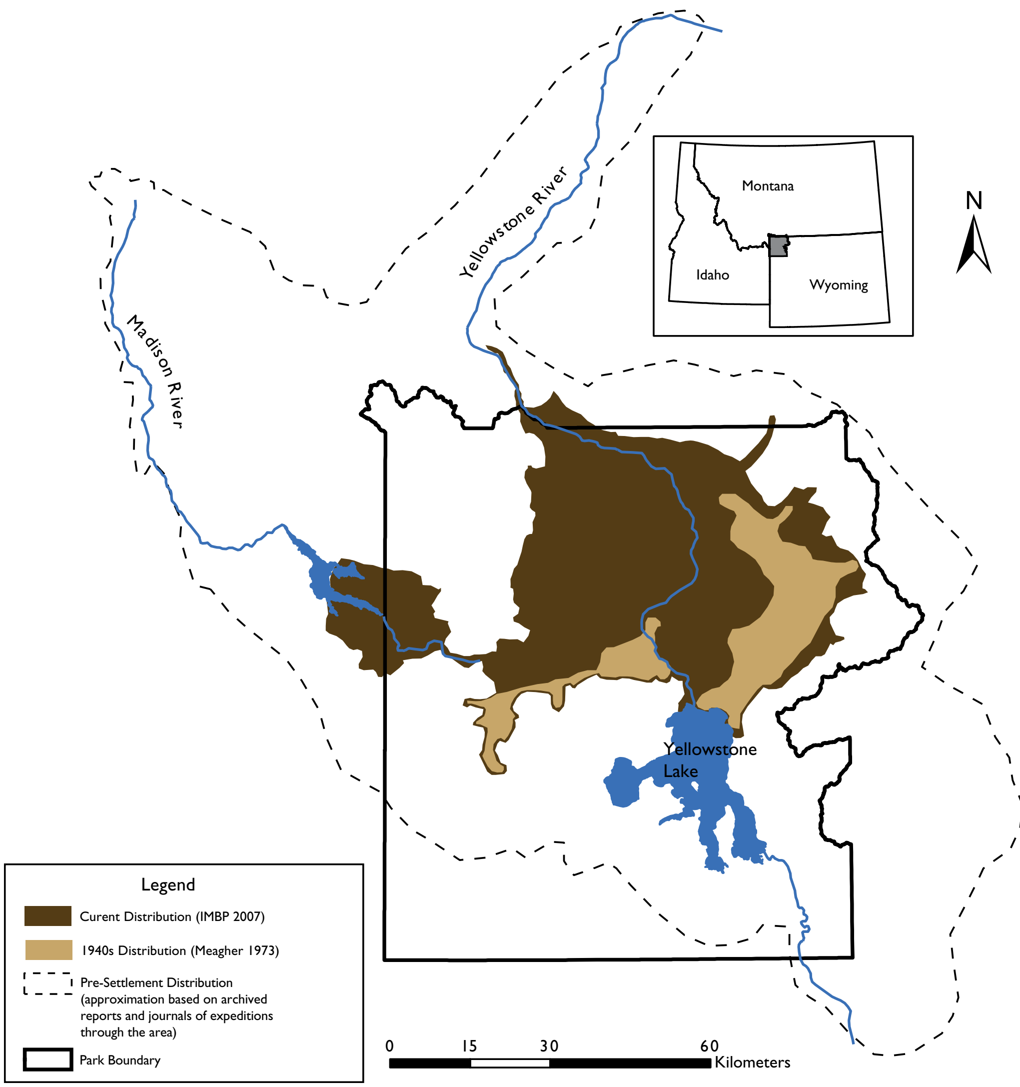

Figure 1. Pre-settlement, mid-twentieth century, and current distribution of Yellowstone bison (Meagher 1973; Plumb and Sucec 2006; Schullery and Whittlesey 2006; Plumb et al. 2009).

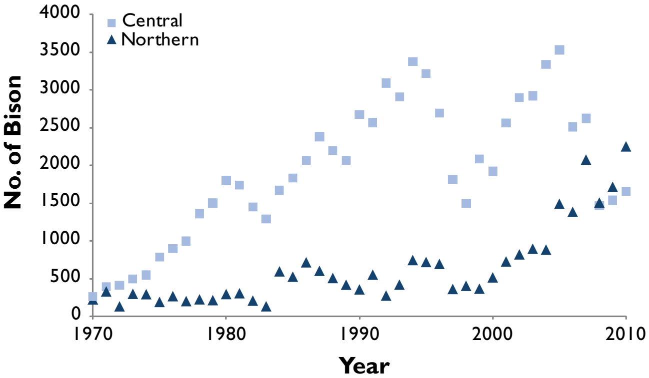

Figure 2. Number of Yellowstone bison observed during aerial surveys of the central (square) and northern (triangle) herds in July–August, 1970–2010.

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Yellowstone bison observed in the upper reaches of Alum Creek in Hayden Valley during summer aerial surveys.

resources diminishes. Coughenour (2005) evaluated whether Yellowstone bison had reached a food-limited carrying capacity inside YNP by developing and testing a spatially-explicit ecosystem model (SAVANNA) that integrated data on site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, ungulate population dynamics, predation, and predator population dynamics (fig. 3). The model simulated the central and northern herds of Yellowstone bison, as well as the two resident wintering elk herds (northern and Madison) and summer immigrant elk. Nine functional groups of plants were simulated, including fine- and coarse-leaved graminoids, forbs, sagebrush, deciduous shrubs, *Vaccinium* shrubs, and coniferous trees. The model used Geographic Information System (GIS) data for soils, vegetation, topography, and other variables, and was driven by weather data from 29 climate and snow telemetry sites located in and near the park. Precipitation and temperature maps were generated and a validated snow model simulated the accumulation and melting of snow.

YELL-15805/ G. BAGGLEY

Three mounted rangers separate bison for slaughter at the Lamar Buffalo Ranch in December 1930.

Simulated bison population dynamics agreed well with observed data (Coughenour 2005). When the model was run for eight simulations for the northern and central herds simultaneously over 50 years, with random weather variations and allowing no range expansion by bison outside the park, the northern herd increased to a mean of 2,417 bison (range=1,820–3,530, median=2,670) and the central herd increased to a mean of 3,776 bison (range=2,430–5,630, median=4,030). For comparison, the actual maximum total count of Yellowstone bison during summer 2005 was 1,484 bison in the northern herd and 3,531 bison in the central herd. Thus, neither the central nor the northern bison herd has exceeded its estimated mean food-limited carrying capacity in the park, though there are extensive inter-annual variations in carrying capacity due to variations in weather, forage availability, competition, and other factors (Plumb et al. 2009). Also, the model predicted that the bison population would be under nutritional stress well below food-limited carrying capacity during winters with deep snowpacks that restricted bison access to forage. As a result, there would be considerable calf mortality and increased adult mortality due to starvation (Coughenour 2005).

Why Do Bison Move Outside the Park?

As Yellowstone bison numbers increased, seasonal migrations along altitudinal gradients within YNP became the norm, with some bison in both herds moving from higher-elevation summer ranges to lower elevations from autumn through winter, returning to summer ranges in June (Meagher 1989; Bjornlie and Garrott 2001; Bruggeman et al. 2009). These seasonal, round-trip movements were initially detected in central YNP during the 1970s, when bison abundance was low (<500) and the summer range should have provided ample resources for bison year-round (Meagher 1993, 1998; Bruggeman 2006). Thus, Yellowstone bison were partially migratory well before their abundance began to approach the

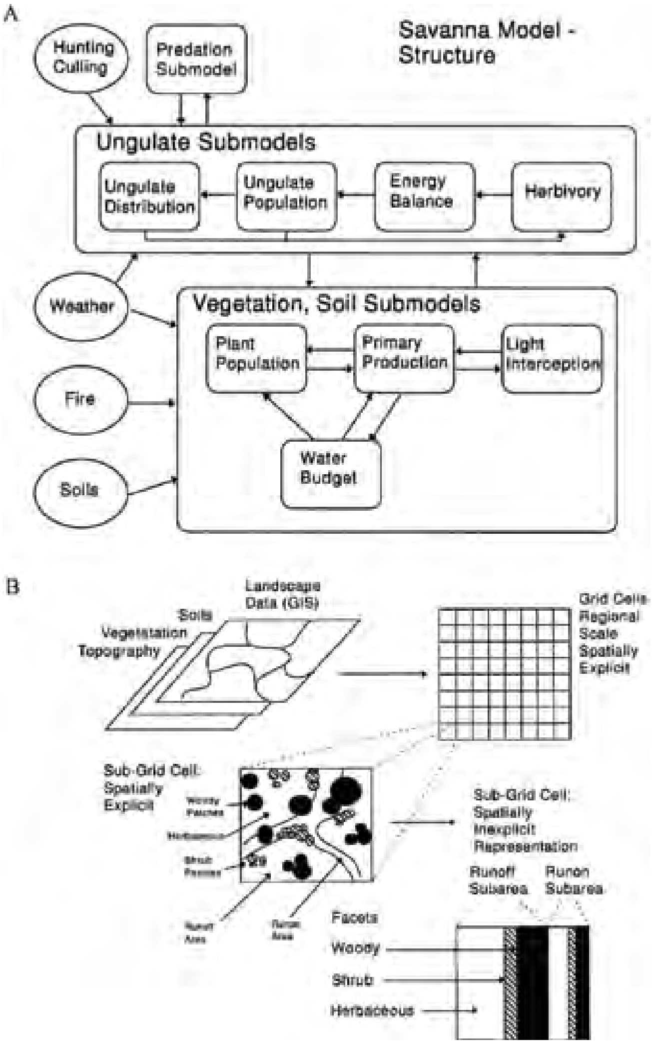

Figure 3. Primary components (*A*) and spatial structure (*B*) of the SAVANNA model (Coughenour 2005).

NPS/PEACO

In the winter, Yellowstone bison spend nearly one-third of their foraging time displacing snow.

estimated food-limited carrying capacity of their range inside YNP (Bruggeman et al. 2009). However, more bison began migrating earlier to lower-elevation winter ranges, including outside the park, as density increased, suggesting migration provided greater access to food supplies and allowed more efficient use of resources year-round (Meagher 1998, Bruggeman et al. 2009).

There is substantial variability in the proportion of bison migrating outside the park each winter due to random variations in climate that affect the abundance and accessibility of food (Gates et al. 2005). Yellowstone bison spend the majority of their time finding and eating forage during winter, with nearly one-third of that time spent displacing snow to reach forage (Bruggeman 2006; Bruggeman et al. 2009). Thus, snow is the primary factor that reduces foraging efficiency and bison prefer patches with minimal snowpack compared to the surrounding landscape (Bruggeman 2006). As snow depth increases, the available foraging area for Yellowstone bison is reduced to increasingly limited areas at lower elevations and on thermally warmed ground (Meagher 1989; Bruggeman 2006; Bruggeman et al. 2009). Also, snow melts earlier at lower elevations outside the park (e.g., Gardiner basin, Horse Butte peninsula) resulting in earlier green-up and more energy-efficient foraging opportunities than on the higher-elevation summer ranges in the park (Thein et al. 2009). Thus, the numbers and timing of bison migrating from their summer range to their winter range in or outside the park is positively related to snow build-up on the higher-elevation summer range in the park. The return migration from lower-elevation winter ranges typically begins in mid-May and June, following the wave of growing vegetation from lower to higher elevations, similar to other ungulates (e.g., bighorn sheep, deer, elk, pronghorn) in this ecosystem (Gates et al. 2005; White et al. 2007, 2010; Thein et al. 2009).

Bison also move out of the park in an attempt to expand their range. This dispersal, or movement from one spatial unit to another without return, is essentially a continuum of migration. Increasing bison density decreases the resources available for each animal, which can negatively influence their nutrition, body condition, reproduction, and survival (Sinclair 1975; Caughley 1976). Range expansion can delay these responses to food limitation since new ranges provide additional forage and limitations will become apparent primarily when new ranges can no longer be colonized (Messier et al. 1988). Indeed, increases in Yellowstone bison winter range areas from 1983 onwards contributed to sustained population growth in both herds, and ecological carrying capacity increased once new ranges were found (Taper et al. 2000; Coughenour 2005; Gates et al. 2005).

Decreased foraging efficiency can induce dispersal movements at population levels well below ecological carrying capacity and the large-scale starvation of animals. Increases in the winter range areas used by Yellowstone bison were detected in the 1980s and continued as bison numbers increased, eventually including movements to areas outside

Even if the risk of brucellosis transmission could be eliminated from Yellowstone bison, it is unlikely these massive animals would be tolerated in most areas outside Yellowstone National Park due to social and political barriers…

the park (Taper et al. 2000; Gates et al. 2005). There were also pulses of dispersal from the central herd to the northern range during this period (Coughenour 2005; Fuller et al. 2007a; Bruggeman et al. 2009). These dispersal movements began when population size increased above 1,500 bison for the central herd and 550 for the northern herd (Gates et al. 2005), which is well below the mean estimates of food-limited carrying capacity for Yellowstone bison (Coughenour 2005). These findings suggest there was increased competition for food supplies, even though less than one-half of the total forage was eaten. Higher-quality foraging areas for bison in YNP are limited in overall area, patchily-distributed, and likely depleted first (Cheville et al. 1998; Bruggeman 2006). Also, severe winter snow conditions have prompted dispersal movements of bison to low-elevation meadows beyond their historical winter range, as well as pulses of dispersal from the central herd to the range of the northern herd, where there is less snowpack and more energy efficient foraging (Meagher 1989; Gates et al. 2005; Fuller et al. 2007; Bruggeman et al. 2009).

Implications for Bison Conservation

Plains bison evolved in the variable climatic environments of the North American central grasslands (McHugh 1972) and adapted to this variability through large-scale movements (Moodie and Ray 1976; Hanson 1984). Bison occupying the Yellowstone and Madison river watersheds historically operated at a scale larger than YNP and recent migration and dispersal movements by Yellowstone bison represent an attempt to operate at this larger scale (Gates et al. 2005; Plumb et al. 2009). These movements are a natural process resulting from successful conservation and population increases inside the park. However, for much of the past 100 years as Yellowstone bison recovered from near extirpation, they were constrained to two herds that migrated to discrete wintering areas and did not regularly and extensively venture outside the park. This led to the widespread belief that Yellowstone bison should remain in YNP, which is reflected in the status and authority for management afforded to bison in states adjacent to the park. Idaho's Comprehensive Wildlife Conservation Strategy mentions bison as a species of concern that is critically imperiled, but the state's agricultural regulations do not recognize wild bison and consider them livestock. The State of Montana considers the Yellowstone bison population to be wildlife, but authorizes the Department of Livestock to remove or destroy Yellowstone bison that enter Montana due to the risk of disease transmission to cattle. The State of Wyoming has designated specific areas adjacent to Grand Teton National Park and YNP where bison are considered wildlife, but elsewhere they are considered livestock. Even if the risk of brucellosis transmission could be eliminated from Yellowstone bison, it is unlikely these massive animals would be tolerated in most areas outside YNP due to social and political barriers such

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Bison moving west along the roadway in the upper Madison Valley. Each spring a pulse of migrating bison moves out of the interior ranges of the park to seek low-elevation areas where spring green up occurs earlier.

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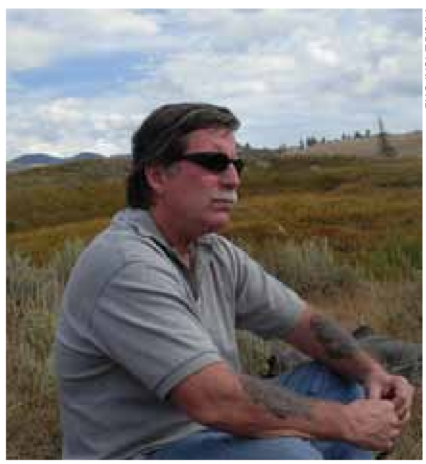
Bison select the most productive habitats within the valleys they occupy. This group of bison have migrated to a lower elevation and found an irrigated meadow on private land to graze during the early spring.

as human safety concerns (e.g., motorists), conflicts with private landowners (e.g., property damage), depredation of agricultural crops, competition with livestock grazing, lack of local public support, and lack of funds for state management (Boyd 2003). Since the evolution of a substantially larger bison conservation area outside of YNP is the prerogative of the states in the Greater Yellowstone area, the prevailing social carrying capacity of Yellowstone bison is perhaps most limiting (Plumb et al. 2009).

With the exception of Yellowstone bison, the plains bison is considered ecologically extinct across North America (Freese et al. 2007). Thus, conservation of the migratory and nomadic tendencies of Yellowstone bison, as well as their genetic integrity and ecological role, is paramount for the perpetuation of the species (Sanderson et al. 2008). Approximately 1,000–2,000 Yellowstone bison likely are needed in each of the central and northern herds to retain enough genetic diversity to enable adaptation to a changing environment through natural selection, drift, and mutation (Gross et al. 2006; Freese et al. 2007). Also, many thousands of bison are likely necessary to fully express their ecological role through the creation of landscape heterozygosity, nutrient redistribution, competition with other ungulates, prey for carnivores, habitat creation for grassland birds and other species, provision of carcasses for scavengers, stimulation of primary production, and opened access to vegetation through snow cover (Freese et al. 2007; Sanderson et al. 2008). However, it appears that the interactive effects of severe winters with population levels greater than 4,700 bison could induce large-scale movements of bison to lower-elevation winter range outside YNP (Geremia et al. 2010). Such large movements jeopardize brucellosis risk management objectives by overwhelming land managers' abilities to maintain separation between bison and livestock. Thus, we propose that a Yellowstone bison population that varies on a decadal scale between 2,500 and 4,500 animals should satisfy the collective long-term interests of stakeholders, as a balance between the park's forage base, conservation of the genetic integrity of the bison population, protection of their migratory tendencies, brucellosis risk management, and other societal constraints (Plumb et al. 2009). YS

Acknowledgments

Portions of this article were taken with kind permission from Elsevier: Plumb, G.E., P.J. White, M.B. Coughenour, and R.L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation*, 14:2377–2387 ©2009, Elsevier. The SAVANNA model for the Yellowstone ecosystem was funded by the US Geological Survey Greater Yellowstone Bison Research Initiative at the Northern Rocky Mountain Science Center, Bozeman, Montana.



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COURTESY OF G. PLUMB

Glenn E. Plumb spent 12 years in Yellowstone National Park before stepping into his current role as the chief wildlife biologist for the NPS Biological Resource Management Division in Fort Collins, Colorado. Plumb has served as Chair of the US Animal Health Association committee on Brucellosis, a member of the DOI Strategic Science Working Group for the Deepwater Horizon oil spill, and a consulting brucellosis scientist with the US State Department Bureau of International Security and Nonproliferation/Cooperative Threat Reduction.

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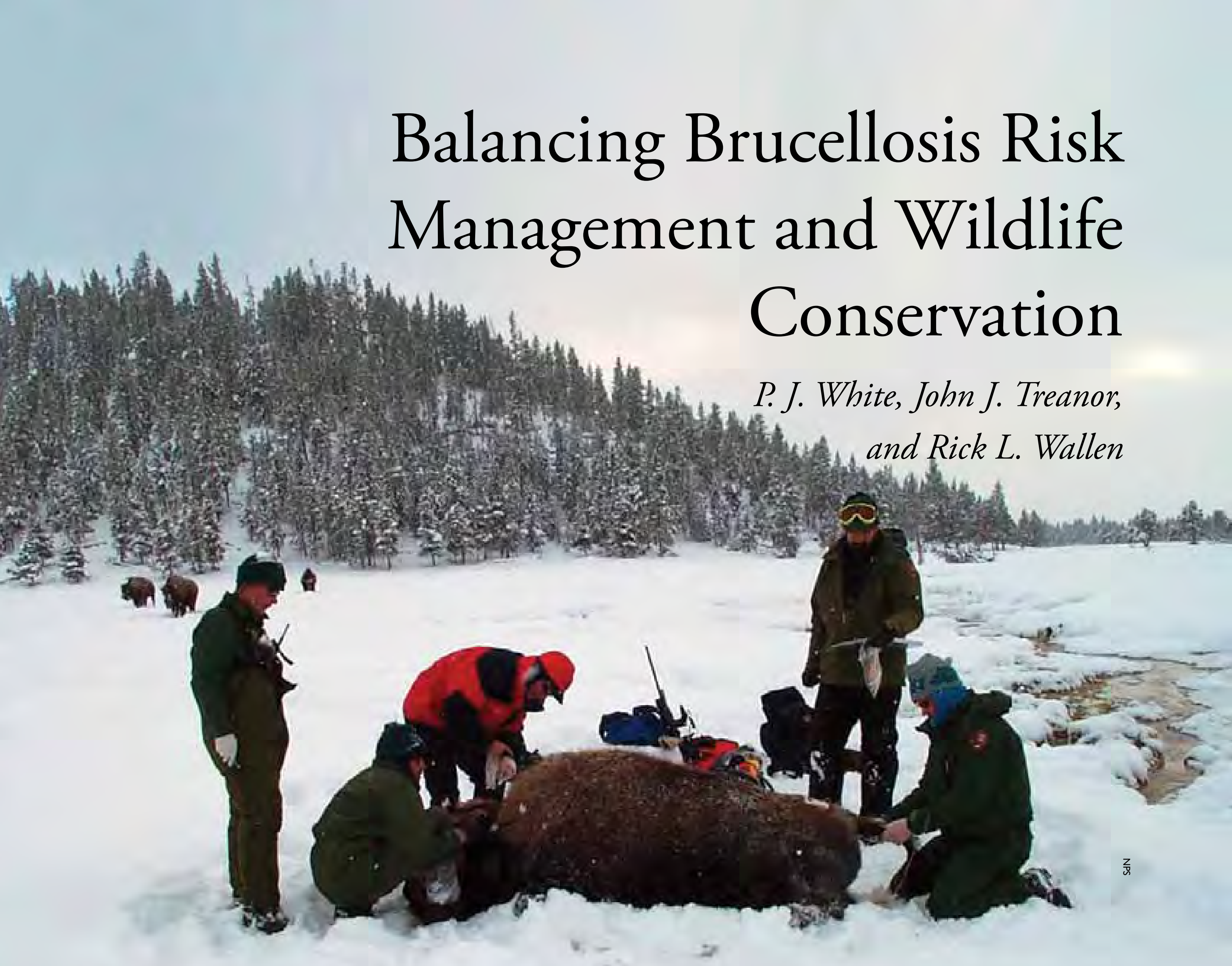
Balancing Brucellosis Risk Management and Wildlife Conservation

P. J. White, John J. Treanor, and Rick L. Wallen



Each fall Yellowstone National Park's Bison Ecology and Management Office monitors a group of about 30 bison cows to track pregnancy and calf rearing. They use temporary immobilization (as seen above) to assess body condition and brucellosis status. The team also follows their migration using radio telemetry.

The increasing emergence or resurgence of infectious diseases that move between livestock, wildlife, and humans has raised interest in disease ecology and wildlife health. Wildlife and diseases do not recognize jurisdictional or political boundaries, and wildlife conservation can become challenging when risks to human health arise. Bovine brucellosis is a contagious bacterial disease caused by *Brucella abortus* that may induce abortions or the birth of non-viable calves in livestock and wildlife (Rhyan et al. 2009). The bacterium was likely introduced from European livestock to Yellowstone bison and elk before 1930 (Meagher and Meyer 1994). Infection of bison, cattle, or elk typically occurs through contact with infectious reproductive tissues shed when a pregnancy is terminated during an abortion or live birth (Rhyan et al. 2009).

Human infection by *B. abortus* typically involves ingestion of the bacteria or exposure through the eyes, open wounds, or by direct contact with skin. Infected bison and elk pose a health risk for people that handle animal carcasses without proper protective equipment. Intensive efforts to eradicate *B. abortus* in livestock during the twentieth century decreased infections nationally from 6,500 cases in 1940 to 70 cases in 1994. There were five confirmed cases reported to the Wyoming Department of Health from 1995 to 2005, and 17 confirmed cases reported to the Idaho Department of Health and Welfare from 1980 to 2003, though none of these cases were attributed to wildlife (Snow 2005). However, there have been two confirmed cases of hunters contracting brucellosis from elk in Montana (Zanto 2005). Infection by *B. abortus* is rarely fatal in humans, but can cause severe, recurring, fever-like symptoms. Humans cannot pass the disease to animals or other humans.

Most livestock and natural resources personnel believe the primary sources for brucellosis transmission to other herds of elk and cattle are the supplemental feeding of elk in Wyoming and Yellowstone bison.

Most livestock and natural resources personnel believe the primary sources for brucellosis transmission to other herds of elk and cattle are the supplemental feeding of elk in Wyoming and Yellowstone bison (Bienen and Tabor 2006). Thus, brucellosis management focuses on elk in the southern Greater Yellowstone area and bison in the northern portion. Elk often mingle with cattle, and all recent brucellosis transmissions to cattle have been attributed to elk (Beja-Pereira et al. 2009). Conversely, resource agencies prevent bison from mingling with cattle through active management practices such as hazing, hunting, and culling (US Department of the Interior and US Department of Agriculture 2000), which may explain the lack of transmissions from bison to cattle. We review the state of the knowledge regarding brucellosis transmission risk and its control in bison and elk in the Greater Yellowstone area.

Brucellosis Transmission Risk

The risk of brucellosis transmission to livestock or wildlife is proportional to the amount of infectious material shed onto the landscape where it can be contacted. Environmental factors such as deep snow and the presence of predators may influence brucellosis transmission by increasing stress and concentrating animals, which increases exposure to shed infectious tissues. However, expelled tissues are quickly removed by scavengers, and the behavior of elk and bison during calving may limit the risk of transmission to cattle. The birthing period for Yellowstone bison is synchronous, with 80% of births occurring from late April to late May (Jones et al. 2010). Birthing females meticulously clean and leave birth sites within two hours after calving, thereby lowering the risk of brucellosis transmission to cattle and bison that later encounter the birth site. Although the potential for exposure is higher for bison within the social group where the birth occurred. From 2004 to 2007, at least one bison interacted with potentially infectious material in 30% of observed births. Thus, infectious live births could be an important transmission event for brucellosis among Yellowstone bison (Rhyan et al. 2009).


R. SCHOENHARD

A bison cow and newborn calf rest near the Firehole River. Eighty percent of bison births occur between late April and late May.

Yellowstone elk also exhibit a high degree of birth synchrony, with the majority calving between mid-May and mid-June. In Yellowstone, the potential for brucellosis transmission between elk is likely lower than between bison because females segregate themselves while giving birth and also clean the birth site. Thus, birth sites are dispersed and the likelihood of other elk encountering infected birth tissues is low. However, transmission risk may be higher during the potential abortion period from February through April when many elk aggregate in larger groups on lower-elevation winter ranges. Spontaneous abortions under these conditions could expose many susceptible elk to infectious material. During the past decade, elk abundance has increased substantially in some areas, with large groups congregating on winter ranges (Cross et al. 2010). Coincident with these changes in abundance and group sizes, brucellosis seroprevalence (i.e., presence of antibodies to *Brucella* circulating in blood) has increased 7%–20% on some non-feed ground areas (Cody and Buffalo Valley, Wyoming). Thus, elk populations far from both bison and feed grounds may be becoming viable reservoirs for perpetuating higher levels of brucellosis due to increased densities and group sizes on their winter ranges (Cross et al. 2010).

The high seroprevalence (40%–60%) of brucellosis in Yellowstone bison suggests they are a likely candidate for transmission to elk, recent data suggests such transmission is rare. The peak bison calving period occurs approximately one month earlier than for elk and, overall, there is little overlap in distribution during the period when *B. abortus* is expected to be shed from each species. In areas where elk do mingle with bison during winter and spring, such as the Madison headwaters area in Yellowstone, elk have much lower seroprevalence rates for brucellosis (3%) than do Yellowstone bison or elk associated with feeding programs in Wyoming. Proffitt et al. (2010b) found that brucellosis transmission risk from bison to elk was quite low in the Madison headwaters area, despite a high degree of spatial overlap when *B. abortus* is typically shed. Predation risk associated with wolves increased elk and bison spatial overlap

NPS/PEACO

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Most elk births occur between mid-May and mid-June (above, June 9, 2010). Female elk thoroughly clean the birthing site and then leave soon after when the calf (here, age 23 minutes) is ready to begin walking.

temporarily, but these behavioral responses by elk did not have important disease implications. Also, DNA genotyping indicates a relatively high genetic divergence between *B. abortus* isolates from bison and elk, which suggests that *B. abortus* is not extensively exchanged between bison and elk (Beja-Pereira et al. 2009). It appears that brucellosis in the Greater Yellowstone area is a disease sustained by multiple hosts and control measures aimed at managing the risk of transmission to cattle will require addressing both wildlife reservoirs and the factors maintaining infection.

Brucellosis Control

Elk—The best available scientific information suggests that elk-to-elk transmission is primarily responsible for the observed levels of *B. abortus* exposure within elk populations and the risk of their transmitting brucellosis to cattle. There is general agreement that as sustainable alternatives for maintaining elk numbers are developed, supplemental feeding should be phased out, which may lead to decreased brucellosis seroprevalence over time (Bienen and Tabor 2006). Wyoming has 22 state feed grounds and one federal feed ground (National Elk Refuge, US Fish and Wildlife Service) where feeding reduces elk foraging on cattle ranches, but consequently sustains higher numbers of elk than the remaining winter habitat could otherwise support (Cross et al. 2007). Additionally, supplemental feeding creates large elk aggregations that facilitate brucellosis transmission (Bienen and Tabor 2006; Cross et al. 2007). Wildlife and livestock managers remain concerned that reduced feeding of elk would lead to increased brucellosis transmission to cattle as a result of increased mingling of elk and cattle (Cross et al. 2007). In the interim, strategies that reduce the length of the feeding season and the duration of elk aggregation during the peak transmission period (February through May) may decrease brucellosis seroprevalence in elk on feed grounds in the southern Greater Yellowstone area (Cross et al. 2007).

Another factor that may influence the maintenance of brucellosis in elk in the Greater Yellowstone area is the increasing human population and land use practices that sustain it. Ranching and the development of rural homes have fragmented valley bottom and flood plain habitats crucial for elk migration and use during winter. The conversion of traditional winter habitat for human use has contributed to an increase of elk on cattle feed lines and refuges that results in large elk aggregations (Haggerty and Travis 2006; Cross et al. 2010). Studies of migratory elk near Yellowstone National Park suggest they tend to select areas during winter with a lower probability of wolf occupancy, lower road density, and higher forage abundance (Proffitt et al. 2010a). Many of these areas occur on lower-elevation private ranchlands and portions of public grazing allotments. Effective brucellosis control measures should recognize that elk aggregating on feed grounds, natural winter ranges, or refuges influence brucellosis transmission, especially near the calving period in late winter and early spring. Thus, wildlife agencies need to explore strategies for dispersing large aggregations of elk in late winter and spring, such as gaining enhanced cooperation from landowners to increase access for hunters, providing increased tolerance and protection of large predators such as wolves that may disperse elk, and assisting landowners with infrastructure to isolate cattle and their feed from wildlife.

Bison—After intensively managing bison numbers for 60 years through husbandry and regular culling, the National Park Service instituted a moratorium on culling in the park in 1969 and allowed bison numbers to fluctuate in response to weather, predators, and resource limitations. Abundance increased rapidly and large-scale bison migrations out of the park during winter began in the late 1980s. These migrations led to a series of conflicts with stock growers and the state of Montana, largely because of the possibility of brucellosis transmission to cattle. As a result, in 2000 the federal government and the state of Montana agreed to a court-negotiated

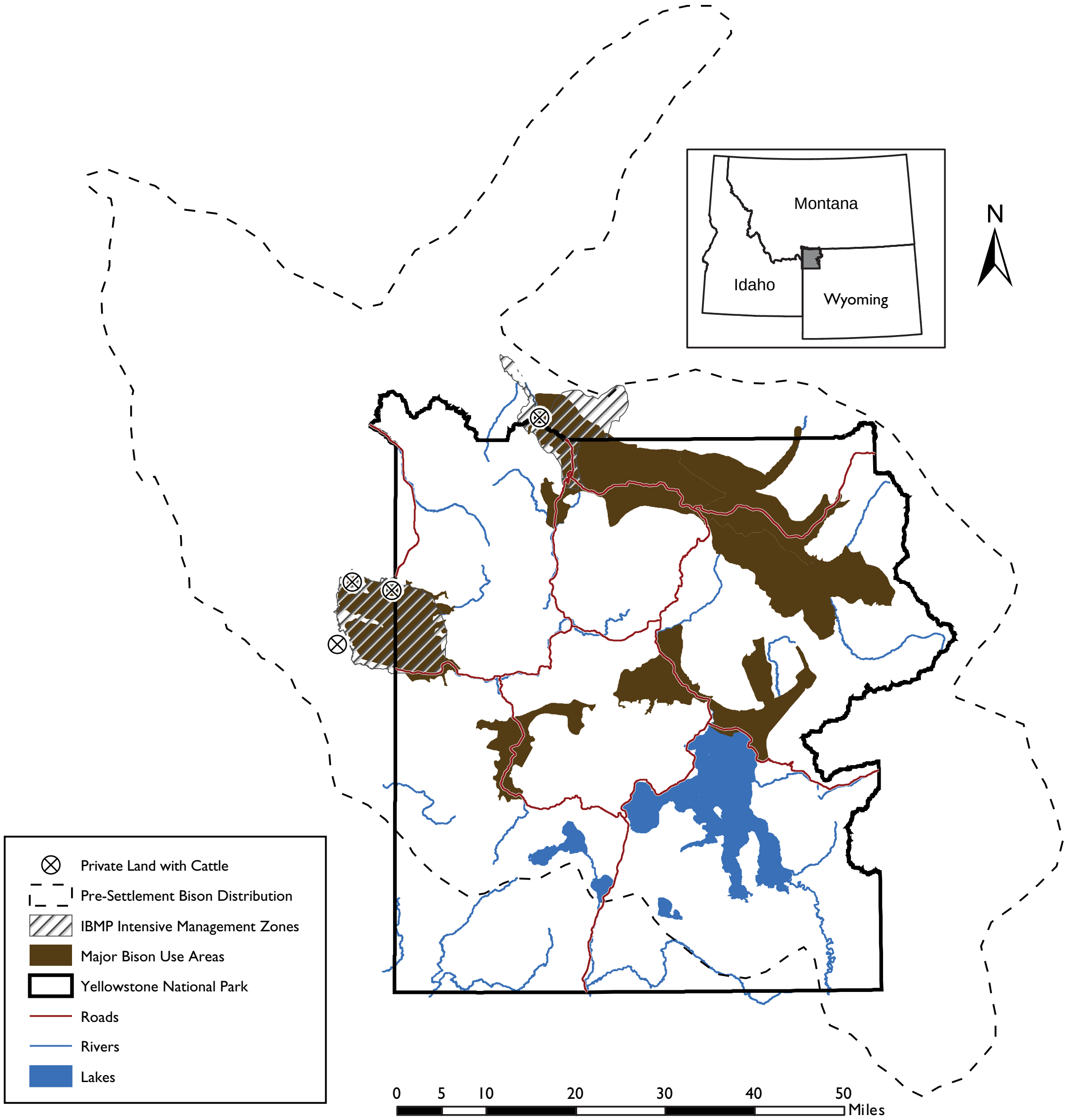

Figure 1. Bison management zones and major use areas in and near Yellowstone National Park.

Interagency Bison Management Plan (IBMP) that established guidelines for (1) cooperatively managing the risk of brucellosis transmission from bison to cattle, and (2) preserving the bison population and allowing some bison to occupy winter ranges on public lands in Montana (fig. 1).

The IBMP is designed to adaptively progress through a series of management steps that initially tolerate only bison testing negative for brucellosis exposure on winter ranges outside Yellowstone National Park, but will eventually tolerate limited numbers of untested bison on key winter ranges adjacent to the park when cattle are not present (US Department of the Interior et al. 2000, 2008). The IBMP uses intensive management (e.g., hazing, hunting, and culls) of bison migrating outside the park to maintain separation between bison and cattle. The agencies have successfully maintained spatial and temporal separation between bison and cattle with no transmission of brucellosis (White et al. 2011). However, this intensive management is expensive, logistically taxing, and controversial due to culls of more than 1,000 bison which have occurred in some winters when large numbers of bison have migrated outside the park.

To reduce the risk of brucellosis transmission to cattle, recurrent, small (less than 100) to large (about 1,700) numbers of bison have been shipped to domestic slaughter facilities following capture near park boundaries since the late 1980s. Despite these actions, brucellosis seroprevalence in Yellowstone bison has not decreased (Kilpatrick et al. 2009). This non-random culling strategy serves more as a population reduction program than to reduce brucellosis (Bienen and Tabor 2006). Intensifying this strategy to a level that would be effective at reducing brucellosis transmission would be extremely expensive, unacceptable to the public, and questionable as a management practice given

Another factor that may influence the maintenance of brucellosis in elk in the Greater Yellowstone area is the increasing human population and land use practices that sustain it.

the National Park Service policy to maintain ecosystem integrity (Bienen and Tabor 2006; White et al. 2011).

A more effective and acceptable approach to brucellosis reduction might involve management actions on selected bison in combination with brucellosis vaccination. Approaches that target pre-reproductive females for vaccination, while removing reproductively active, seropositive females may be effective at reducing disease transmission (Ebinger et al. 2010). Consistent vaccination of female bison has the potential to reduce brucellosis prevalence by increasing herd immunity, especially if vaccine technology and methods for remote vaccine delivery to free-ranging wildlife are improved (Treanor et al. 2010). However, a vaccine with low or medium efficacy is unlikely to succeed in controlling brucellosis in the long term without the eventual inclusion of test and slaughter or fertility control (Ebinger et al. 2010; Treanor et al. 2010). Thus, the development of more effective vaccines, delivery methods, and diagnostic techniques is urgently needed. Until substantial improvement is made in these areas, proposed vaccination efforts will, at best, only result in a relatively slow decline in brucellosis seroprevalence over decades (Treanor et al. 2010).

Contraception has also been suggested as a method to reduce brucellosis transmission because the disease is known to only be transmitted by pregnant bison or elk. National Park Service policy allows for the use of reproductive intervention in wildlife if these techniques are appropriate for achieving management goals. Thus, if an effective, reliable, and safe contraceptive was developed, contraception of seropositive bison or elk might be considered for decreasing brucellosis transmission; especially when combined with the vaccination of seronegative animals (Ebinger et al. 2010). However, fertility control products may also cause negative long-term effects, such as permanent sterility, altered reproductive or social behaviors, and changes in the age and sex structure of a population. Thus, it is uncertain whether available fertility control products can effectively decrease brucellosis infection in free-ranging bison and elk over a reasonable time frame without unacceptable side effects.

Until effective brucellosis reducing methods are developed, the best approach to control the risk of brucellosis transmission from bison to cattle is to maintain spatial and temporal separation. Management agencies should continue to allow bison migration to essential winter range areas in and adjacent to Yellowstone National Park, but actively prevent dispersal and range expansion to outlying private lands until there is tolerance for bison in these areas (Plumb et al. 2009). Bison abundance and distribution on lands adjacent to Yellowstone can be adjusted based on evaluations of available habitat, new conservation easements or land management strategies, reduced brucellosis prevalence in bison, and new information or technology that reduces the risk of disease transmission (US Department of the Interior et al. 2008). However, the comprehensive wildlife conservation strategies of Idaho, Montana, and Wyoming express little support for resident, free-ranging wild bison (Plumb et al. 2009).

To increase tolerance for bison, Kilpatrick et al. (2009) recommended establishing a local brucellosis infection status zone for cattle in the Greater Yellowstone area and testing all cattle within this area for brucellosis (with a “split status” for

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Predator species influence the migration patterns and population density of native ungulates. These factors then affect transmission and prevalence rates of disease among herds.

[Bison] removals have differentially affected the central and northern breeding herds, altered gender structure, created reduced groups of females in some years, and temporarily dampened productivity…

the remaining portions of Idaho, Montana, and Wyoming). In 2010, the Animal and Plant Health Inspection Service published an interim rule that eliminated the automatic reclassification of any Class Free State or area to a lower status if two or more herds are found to have brucellosis within a two-year period (US Department of Agriculture, Animal and Plant Health Inspection Service 2010). Under this rule, detections of brucellosis in domestic livestock within the Greater Yellowstone surveillance area are dealt with on a case-by-case basis, which should eliminate many economic barriers created by the brucellosis class status system. As long as the outbreaks are investigated and contained, state brucellosis-free status for cattle does not change. In fact, brucellosis was detected in several domestic bison and cattle herds in Idaho, Montana, and Wyoming during 2009 and 2010, without any changes in state status.

Kilpatrick et al. (2009) also recommended the cessation of cattle grazing in areas where bison leave the park in winter and compensating ranchers for lost earnings and wages. Conservation groups and government agencies have successfully used, and are still pursuing, this strategy with willing landowners (US Department of the Interior et al. 2008). However, further efforts are needed to identify additional habitat and conservation areas for bison in Montana, develop fencing strategies in collaboration with private landowners that raise susceptible cattle, and identify opportunities for the enhancement or creation of bison habitat in Montana to sustain bison from April to early June and discourage bison movements onto private lands with cattle (US Department of the Interior et al. 2008).

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Some studies recommend the cessation of cattle grazing in areas where bison leave the park in winter and improved fencing strategies in collaboration with private landowners.

Conservation Implications

An essential first step for the conservation of both elk and bison is to develop acceptable brucellosis control methods that balance risk management with wildlife conservation. Over time, the strategies discussed herein could reduce the costs and need for brucellosis risk management activities, while maintaining low risk for the cattle industry. However, the potential for elk to serve as a brucellosis maintenance host in the absence of bison and away from feed grounds complicates brucellosis control. Brucellosis is present in elk populations throughout Greater Yellowstone area, where they number approximately 50,000. Eradication of brucellosis from these populations is likely not possible or practical with current technology without resorting to ethically and politically unacceptable techniques such as mass test and slaughter or depopulation (US Animal Health Association 2006). Thus, management of brucellosis in elk populations might best be achieved by curtailing practices that unnaturally increase elk densities and group sizes during the potential abortion period.

Chronic brucellosis infection does not adversely affect the long-term viability of Yellowstone bison (Geremia et al. 2009). Thus, the Yellowstone bison population will likely continue to grow and attempt to expand its range unless hunting, culling, and/or relocations are used to remove several hundred bison per year from the population (Hobbs et al. 2009). Thus far, Yellowstone bison have only been transported to domestic slaughter or research facilities due to the potential for infection with brucellosis. These removals have differentially affected the central and northern breeding herds, altered gender structure, created reduced groups of females in some years, and temporarily dampened productivity (White et al. 2011). If large-scale culls (more than 1,000 bison) are continued over time, these effects could diminish the ecological role of the largest remaining free-ranging plains bison population in the world which, in turn, would diminish the ecological processes within the park (White et al. 2011). Thus, there is a need to increase tolerance for bison on key winter ranges in Montana and reduce the frequency of large-scale culls of the population. The shipment of "surplus" Yellowstone bison to quarantine sites operated by American Indian tribes or other conservation organizations rather than to domestic slaughter facilities would be a transformational moment in the conservation of plains bison. This action would help preserve the culture of American Indians while promoting bison conservation by establishing wild populations or augmenting existing populations from the only existing pure source of wild plains bison. YS

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The Lamar Buffalo Ranch

Cori Knudten

AS THE VAST HERDS OF BISON disappeared from the American West in the nineteenth century, they became a symbol of the vanishing frontier. By 1885 the bison herd in Yellowstone National Park was the largest existing bison population south of Canada (Bartlett 1985).

In 1901 park officials attempted to increase bison numbers by starting a captive herd with bison purchased from ranchers. An enclosure was constructed near Fort Yellowstone at Mammoth Hot Springs, and 15 cows and 3 bulls were transported to the park (Haines 1977). By 1907 the herd was too large for the Mammoth enclosure and was moved to a site on Rose Creek in the Lamar Valley, which became known as the Lamar Buffalo Ranch. At Lamar, park employees used cattle ranching techniques to monitor and manage the bison herd. Bison roamed freely in the summer, but in the winter they were corralled and fed hay that was raised at the ranch on 600 acres of plowed, seeded, and irrigated land. The herd grew from fewer than 50 animals in 1902 to around 950 by 1929 (Haines 1977; Sellars 1997).

The Lamar Buffalo Ranch was a popular attraction with tourists because they could easily see the bison in the corrals. In the 1920s, under Superintendent Horace Albright, large round-ups and stampedes were held for the amusement of visitors. Although the program started over concerns that bison might become extinct in the park, managing the herd as a tourist attraction quickly became an important part of the ranch's operation. Other wild bison still roamed the park, but because they ranged in more remote areas they were subject to little or no interference by park managers (Haines 1977, Sellars 1997).

By the late 1920s, some worried that the population of the Lamar Valley herd was becoming too large. In order to reduce the population, the park shipped bison to preserves and zoos around the country and slaughtered "surplus" bison.

YELL-27615

The "show herd" in the Mammoth Hot Springs pen, 1924.


YELL-5517/ R. R. ROBINSON

Corralled bison, circa 1912–1920. Winter feeding of bison at the Lamar Buffalo Ranch was discontinued in 1952.

In 1933 a group of National Park Service biologists compiled *Fauna of the National Parks of the United States: A Preliminary Survey of Faunal Relations in National Parks*. The report was based on a multi-year survey of wildlife issues in national parks across the country. It was intended to be the "first comprehensive statement of natural resource management policies" in the National Park Service. The biologists argued for letting natural processes dominate when possible and for restoring parks and their wildlife populations to resemble their condition prior to the arrival of Europeans. The report stated explicitly that every wildlife species should be allowed to "carry on its struggle for existence unaided" unless a species was threatened with extinction (Sellars 1997).

This publication eventually contributed to a major shift in the operation of the Lamar Buffalo Ranch. As new attitudes took hold in the National Park Service and Yellowstone, the function of the Lamar Buffalo Ranch changed with them. Newton B. Drury, who became Director of the National Park Service in 1940, stated that Yellowstone was not a "zoological park or game farm" and that the bison should be allowed to become "self-sustaining" (Sellars 1997). The last winter feeding took place in 1952, and the operations at the ranch were discontinued.

The historic buildings at the Lamar Buffalo Ranch currently serve as instruction and lodging space for the non-profit Yellowstone Association Institute.

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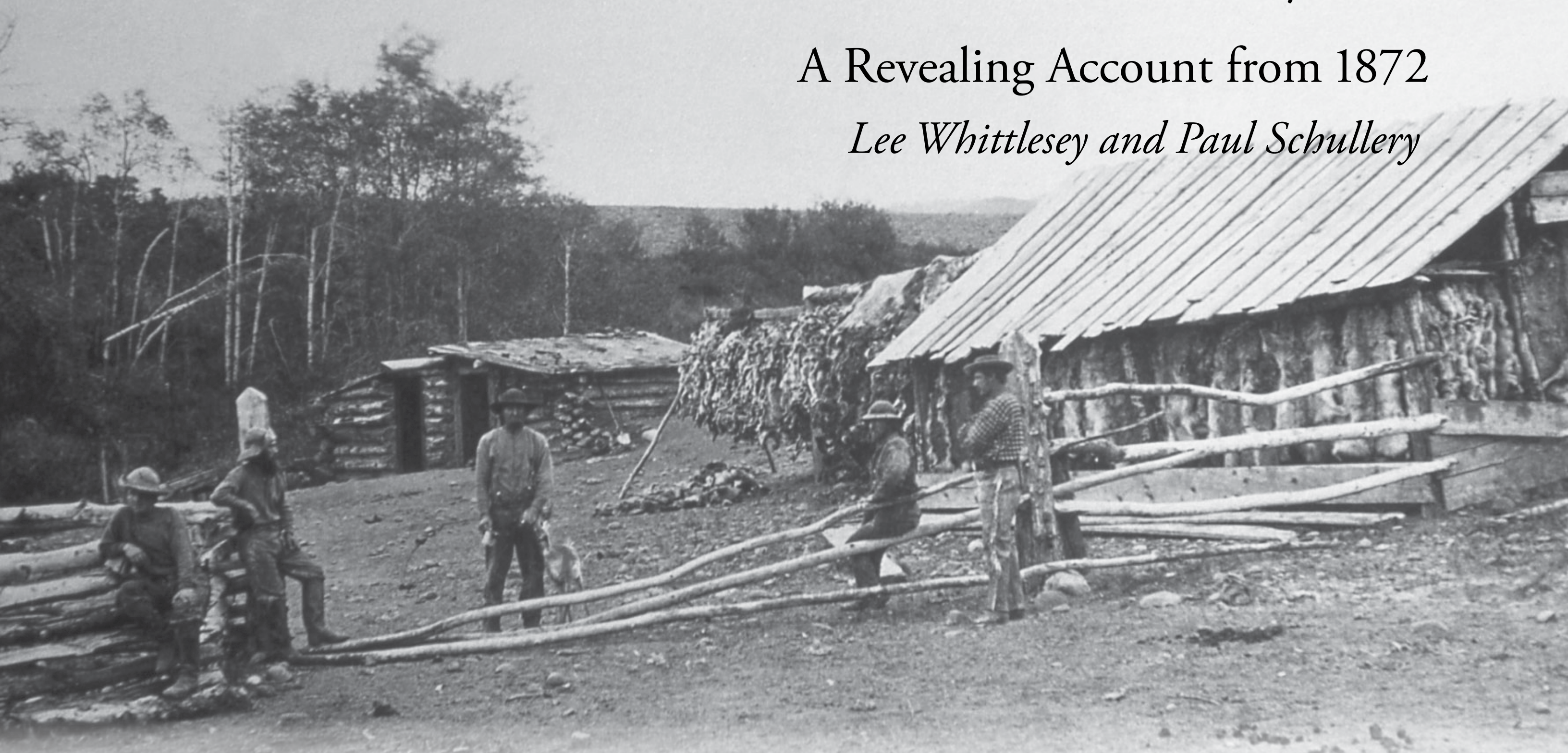
How Many Wolves Were in the Yellowstone Area in the 1870s?

A Revealing Account from 1872

Lee Whittlesey and Paul Schullery



This photo, taken by William Henry Jackson on July 17 or 18, 1871, while he was with the Hayden survey, reveals the substantial scale of the Bottlers' hide-hunting operations by that year.

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Prior to the 1995 restoration of wolves to Yellowstone National Park (YNP), we researched the historical record of large- and medium-sized wildlife species in the Greater Yellowstone Ecosystem (GYE). In our initial review of 168 distinct accounts of visits to the GYE from 1796 through 1881, we found numerous general statements indicating that wolves were present or common and more specific statements reporting individual sightings, howls, or other substantive evidence of wolf presence (Schullery and Whittlesey 1992, 1995). These sources of evidence were buttressed by the official administrative record, especially Yellowstone Superintendent Philetus Norris's statement in his annual report for 1880:

> *The large, ferocious gray or buffalo wolf, the sneaking, snarling coyote, and a species apparently between the two, of a dark-brown or black color, were once exceedingly numerous in all portions of the Park, but the value of their hides and their easy slaughter with strychnine-poisoned carcasses of animals have nearly led to their extermination* (Norris 1881).

Our initial publication (Schullery and Whittlesey 1992) analyzed eight times as many accounts as any previous review of the historical record of GYE wildlife, but it was clear to us that many hundreds of additional unanalyzed accounts awaited attention. Besides the customary trapper and prospector diaries, tourist accounts, official survey party reports, administrative documents, and other readily accessible material, Yellowstone was the subject of countless articles in newspapers, sporting periodicals, other narrowly distributed periodicals, and other sources that are still being discovered.

Since that initial publication, we have searched for additional information and, with the assistance of additional investigators, compiled a much larger volume of material and a database that further confirm Norris's assertion that wolves were widespread and abundant in the park prior to their extirpation by Euro-Americans (Schullery et al. forthcoming). However, until recently we had not found any documents that allowed us to resolve early Yellowstone-area wolf numbers any further than the general impressions we published in 1992. We have now located one such document, but it is necessary first to provide the context for its interpretation.

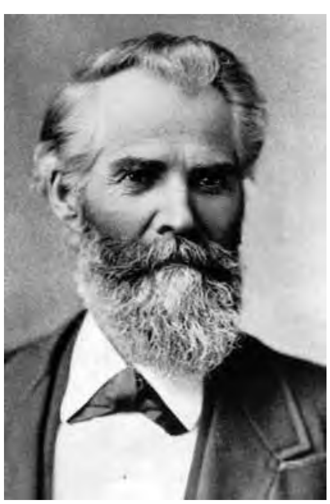
Coming to Terms with Historical Wolf Numbers

Determining historical wildlife numbers in a large geographical area has vexed generations of researchers. The abundance of wolves throughout much of the American West was a matter of historical record, but except for the most general of estimates it has been impossible to calculate that abundance with any precision. It is almost as difficult to calculate the number of wolves killed during the slaughter of western wildlife that became widespread starting in the 1860s. Record keeping was often casual, species were sometimes confused (Norris's description of the wild canids in the park is one of many examples of this taxonomic uncertainty), and the conditions under which the killing took place were not conducive to precise accounting or the durability of records (Hampton 1997).

It is certain, however, that wolves were proportionately abundant with the bison they preyed and scavenged upon in the American West at the beginning of the nineteenth century. Raymond Burroughs (1961) compiled numerous reports of wolves from the journals of Lewis and Clark, a few representative examples of which follow, all recorded in what is now Montana. In June 1805, near the mouth of the Marias River, Lewis said that the "innumerable herds of Buffalo were seen attended by their shepherds the wolves." In July 1806, Lewis reported that there were "vast assemblages of wolves" near the Sun River. In late July 1806, on the Yellowstone River near present Billings, Clark said that "for me to mention or give an estimate of the different species of wild animals on this river particularly Buffalow, Elk, Antelopes and Wolves would be incredible. I shall therefore be silent on the subject further."

Historians and naturalists have made occasional attempts to estimate the number of wolves inhabiting all or parts of the American West prior to the arrival of white settlers. The naturalist Ernest Thompson Seton estimated about 2 million wolves in all of North America and northern Mexico before the arrival of Europeans. (Seton 1953). More recently, Edward Curnow, whose "The History of the Eradication of the Wolf in Montana" (1969) served for some time as a primary scholarly source text, estimated that in the 1860s there were "several hundred thousand wolves" in the region that would become Montana. He said that the number of wolves killed during the 1860s and 1870s was unknown, but "a conservative estimate would be over 100,000 per year between 1870 and 1877." He illustrated the scale of the trade in wolf hides by quoting from an 1873 article in *The Daily Herald* of Helena, which reported that a group of "wolfers" using five or six teams of horse-drawn wagons accumulated "about 10,000 wolf skins among them" in one winter.

It is certain, however, that wolves were proportionately abundant with the bison they preyed and scavenged upon in the American West at the beginning of the nineteenth century.



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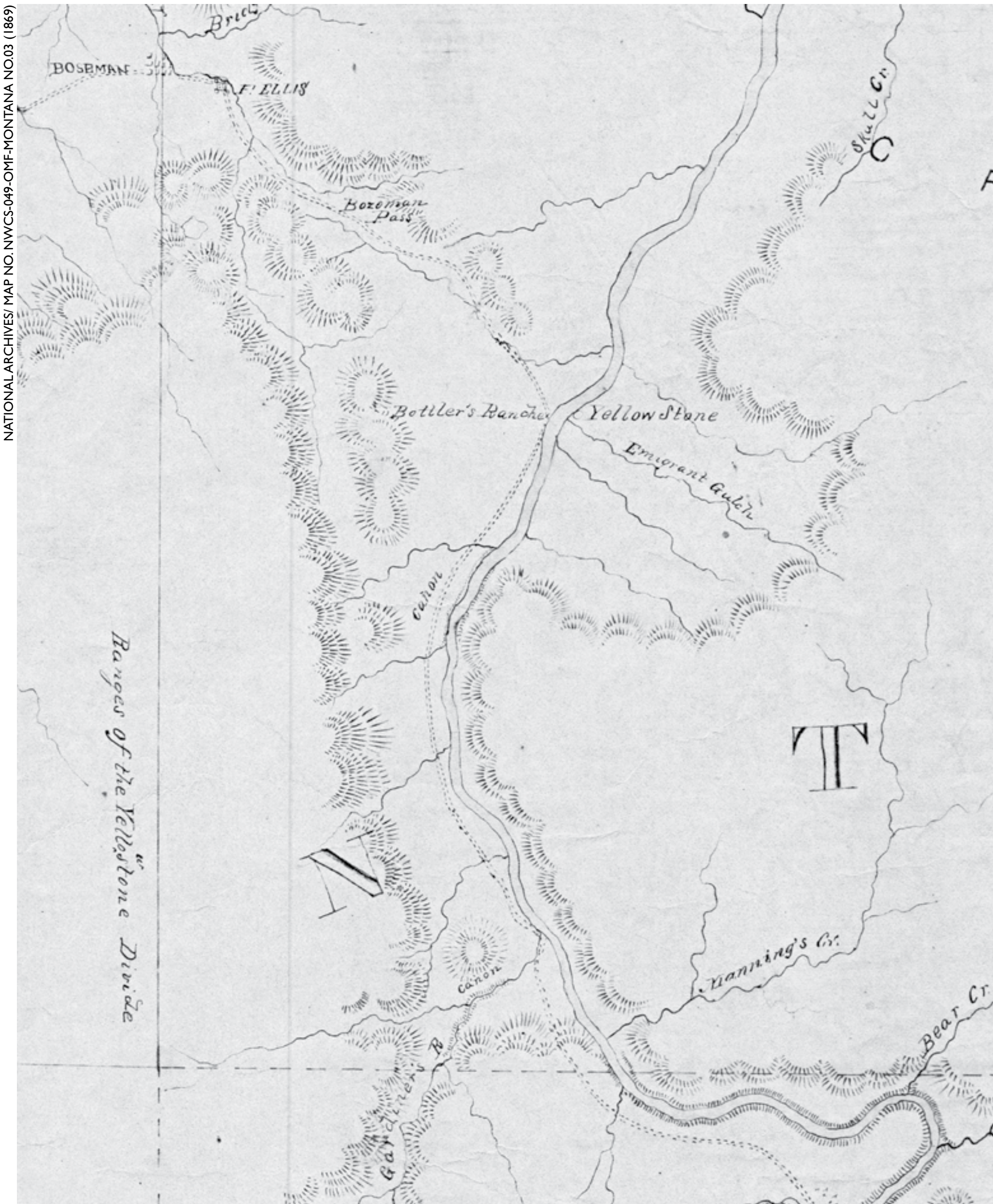
Yellowstone National Park's second superintendent, Philetus W. Norris, regularly chronicled the park's wildlife in his annual reports and other writings. His notes provide the first official record of hide-hunting and related killing of wildlife in the park. Norris was one of several commentators who spoke highly of the Bottlers despite their wholesale slaughter of park animals.

It is important to distinguish between the killing of wolves by early professional "wolfers" in Montana and YNP, and the later killing of wolves for a state-sponsored bounty. In the 1870s and early 1880s, wolfers killed wolves for, as Norris said, "the value of their hides." There was a booming market for wolf hides, just as there was for the hides of other wildlife species (Zmyj 1996; Hampton 1997). After 1883, when Montana's territorial legislature passed the territory's "first workable bounty law" (Curnow 1969), killing was still done for money, but the primary purpose was to protect livestock.

Thanks to the more consistent paperwork required by the bounty laws, we have a somewhat better grasp of the number of wolves killed during the bounty period. From 1883 to 1918, Montana recorded bounty claims on more than 80,000 wolves; between 1895 and 1917, Wyoming recorded almost 30,000 (Hampton 1997). However, it is thought that these official tallies may overstate the number of wolves killed because bounty hunters were creative and energetic in defrauding authorities (Zmyj 1996). Still, the historical records, including the one presented below for the Yellowstone area, are sobering evidence of a massive slaughter of Montana and Wyoming wolves after their numbers had already been significantly reduced by the hide-hunters.

Subsequent estimates of the Montana wolf population and the number of wolves killed in the 1870s were lower than Curnow's. Dave Walter (1986) thought that the annual kill of Montana wolves in the 1870s was on the order of 55,000. Bruce Hampton (1997) regarded Walter's number as still too large, pointing out many problems with early tallies,

NATIONAL ARCHIVES/ MAP NO. NWCS-049-OMF-MONTANA NO.03 (1869)



A section of Lieutenant Gustavus Doane's "Map of the Route of the Yellowstone Expedition," based on his 1870 visit to the area as commander of the military escort of the Washburn-Langford-Doane expedition, showed "Bottler's Ranche" on the Yellowstone River near the mouth of Emigrant Creek. From this base of operations, the Bottlers conducted hide- and meat-hunting operations in the region, killing thousands of animals in the present park area. Courtesy of the National Archives.

including the possible combining of wolf and coyote hides in some totals.

Recently, scientific methods unavailable to researchers only a generation ago have been applied to the question of the western wolf population. Leonard et al. (2005) extracted mitochondrial DNA from 34 wolf specimens in the collection of the National Museum of Natural History (Smithsonian Institution) in Washington, D.C., that were killed before 1916, some as early as 1856. Most of these wolves were killed within the historical ranges of *Canis lupus nubilus*, the wolf of the Great Plains and Interior West, and *C. l. baileyi*, the Mexican wolf, but a few were from as far north and east as Labrador. Based on the time required for the gray wolf to achieve the degree of genetic diversity displayed by this set of specimens, Leonard et al. arrived at a "rough estimate" of 380,000 wolves in the western United States and Mexico prior to the near destruction of both species south of Canada in the late 1800s and early 1900s.

Considering the recovery of Yellowstone wolves in this context, it is worth noting that Leonard et al. concluded that "modern wolves are a depauperate subset of the historic population," whose large size "provides a striking contrast to restoration goals in the western US," which are limited to a total of 400 wolves for *C. l. nubilis* and *C. l. baileyi*. Taking a position that makes current wolf recovery goals in the northern American Rockies seem modest in the extreme, Leonard et al. recommended a much more ambitious restoration effort in the West that "would restore wolves to past population sizes and enable them to significantly influence the dynamics of the Rocky Mountain ecosystem."

US GEOLOGICAL SURVEY PHOTOGRAPHIC LIBRARY WHJ-1257

The entire roster of the combined parties of the Hayden Survey, photographed by W. H. Jackson about August 15, 1872, in the Lower Geyser Basin. An enlargement of the lower right corner of the photograph (inset, right) provides a look at #21, Joseph Savage, the author of a historic and previously unknown account of wolf-hide trade in the Yellowstone area.

A Greater Yellowstone Wolf Harvest

The slaughter of YNP wildlife in the 1870s and early 1880s has been documented repeatedly (Hampton 1971; Reiger 1975; Haines 1977; Schullery and Whittlesey 1992; Schullery 1997). Among the published contemporary reports was Superintendent Norris's annual report for 1877, his first year in office. Norris estimated that an annual average of 1,000 elk, as well as "hundreds if not thousands" of each of the other species of large ungulates, had been killed and taken from the park since 1870 (Norris 1878).

Though hunting was legal in the park until 1883, the act creating the park in 1872 had placed limits on it. Visitors were allowed to hunt for their own subsistence and for sport but not for profit. The act directed the Secretary of the Interior to provide against the wanton destruction of the fish and game found within said park, and against their capture or destruction for the purposes of merchandise or profit (Schullery 1996). Until the arrival of the US Cavalry to protect the park in 1886, little or no notice was paid to this prohibition against commercial hunting.

The slaughter of thousands of the park's large mammals for their hides and for the regional meat trade was regarded as a great scandal among conservationists in the 1870s and early 1880s, but it was carried on with remarkable aplomb by local entrepreneurs. The Bottler family, who established their ranch in today's Paradise Valley in the late 1860s, were hard-working farmers and ranchers in addition to professional hunters. In the years just before and after 1872, the Bottlers routinely hosted parties on their way to and from the park, often serving as guides to important groups. They were among the best known and most trusted guides for early survey parties, and were apparently forthright in describing their hide-hunting activities. Despite their energetic hide-hunting in and near the park, the Bottlers were often on the best of terms with park managers; when Superintendent Norris's operating funds were lost in a local bank failure in 1878, the Bottlers provided him with money to meet his payroll (Haines 1977).

Among the evidence of the Bottlers' hunting is an account by Norris of an 1875 visit to the Yellowstone valley, when he was guided by "my old comrade Frederick Bottler" (Norris no date). According to Norris, "the Bottler Bros. assure me that they alone packed over 2,000 elk skins from the forks of the Yellowstone [the lower Lamar Valley area], besides vast numbers of other pelts, and other hunters at least as many more, in the spring of 1875." William Henry Jackson's 1871 photograph of the Bottler Ranch provides rare visual evidence of their work, showing a large shed overflowing with hides (and possibly unbutchered carcasses). An 1872 photograph of Bottler with Hayden Survey members and five elk freshly shot near the Grand Canyon of the Yellowstone is additional evidence of Bottler's hunting success.

The magnitude of the killing was rarely reported as specifically as the number of elk hides that Bottler described to Norris in 1875. An important exception to the mostly vague accounts has just come to light, identified by Whittlesey in a series of letters in the *Western Home Journal*, a newspaper published in Lawrence, Kansas, in 1872. As many small local newspapers have been scanned and made available online in the last decade, hundreds of previously uncollected Yellowstone items from the late nineteenth and early twentieth centuries have been added to the files of the park's Research Library. This item is one of those.

A series of five letters by Joseph Savage, a member of Ferdinand Hayden's US Geological Survey, was published

The Savage account of the Bottler collection of wolf "peltry" is thus uniquely important among known sources for its ability to clarify our understanding of the distribution and abundance of Yellowstone-area wolves.

in three issues of the *Western Home Journal*. Like some other early official travelers who published less formal accounts of their experiences and adventures, Savage wrote letters to what seems to have been his home-town newspaper. In his first letter, written from "Fort Ellis, Montana Territory, Camp of the US Geological Survey" on July 18, 1872, and published on August 1, Savage mentions the "younger Bottler," Frederick, and the "elder Bottler," Phillip. "The younger Bottler brother is employed as a hunter for our party, and the 'aching void' within us, which even the mountains cannot fill, is now supplied with tender, juicy elk steak, the fruit of two days' hunting." Only Frederick was listed on the official roll of members of the 1872 Hayden Survey (Haines 1977), but apparently Phillip was at Fort Ellis at the time and told Savage about his hide-hunting:

> *The elder Bottler gave us the number of his peltries, killed and traded for during the past year, which he sold in the New York market. It was this: three hundred and one elk skins, two hundred and fifty deer and antelope skins, and five hundred and fifty-five wolf skins; bringing in market two thousand nine hundred and ninety-one dollars and thirty-two cents—freight being three hundred and ninety-seven dollars.* (Savage 1872)

Interpretations of the Savage Account

As with so many tidbits of wildlife information gleaned from early accounts, this paragraph is both revealing and tantalizing. A few generalizations seem warranted. "The past year" mentioned by Savage as the time during which Bottler gathered the 555 wolf hides presumably refers to the period from July 1871 to July 1872. Considering that by 1872 the Bottlers were obviously very active in killing elk and other large mammals, they had regular opportunities to poison carcasses and collect the resulting dead wolves.

Phillip Bottler apparently did not kill all these animals himself. Savage said that Bottler "killed and traded for" the hides. The range of Bottler's killing and trading is therefore of interest. Operating from the present Emigrant area along the Yellowstone River approximately 30 miles north of the park, Bottler was placed well south of the main commerce centers of the Montana Territory hide trade. Hides were routinely gathered in Bozeman and along the Yellowstone River for transport down that river, or in Fort Benton for transport down the Missouri River. We infer from this that the people with whom Bottler traded for wolf hides were most likely in his neighborhood, because if they were farther north they could have more conveniently dealt with the big shippers in Bozeman or Fort Benton. For this reason, we assume that most or all of the skins Bottler obtained came from animals in Paradise Valley and adjoining areas.

As for the wolves that the Bottlers killed, it seems most likely that these were also from the region surrounding the ranch where they lived. Their hunting grounds during 1871 and 1872 may or may not have included the present park area, but would almost certainly have been confined to the northern portion of the Greater Yellowstone ecosystem.

The Savage account of the Bottler collection of wolf "peltry" is thus uniquely important among known sources for its ability to clarify our understanding of the distribution and abundance of Yellowstone-area wolves. That the Bottlers could accumulate several hundred wolf hides in the space of one year reinforces the reliability of reports of predator and prey abundance left by many other early observers. However, the question necessarily arises whether these 550 pelts all came from wolves or if some were from coyotes. In an assessment of the Savage account, wolf historian Rick McIntyre concluded:

> *There is the issue that many people during that period did not properly distinguish between the two species. I found in some of the historic documents I looked at that the words coyote and wolf were used interchangeably. In some cases, the same animal would be called a wolf in the first*

"The Successful Hunter" by W. H. Jackson shows Frederick Bottler and other Hayden Survey party members on August 6 or 7, 1872, near the Grand Canyon of the Yellowstone where Bottler has just killed five bull elk.

part of a sentence and a coyote later in the same sentence.

But the Bottlers would have been more experienced in buying and selling hides than most others in that period and their income depended on being somewhat accurate in tabulating hide types and numbers. As the elder Bottler told Savage that they sold 555 wolf skins, I would have to regard that statement as being reasonably accurate. The buyers in New York would certainly have given them a lower price if there were a significant number of smaller sized coyote pelts in the shipment. A wolf pelt would have brought a much higher price than a coyote hide (McIntyre, personal communication, January 13, 2011).

We agree with McIntyre's assessment. Established and locally respected shippers like the Bottlers were not in a position to perpetrate a wholesale fraud on dealers downstream. However, as is always the case when evaluating anecdotal material of this sort, we are left with other unresolved questions. From how far afield were the hides gathered by the Bottlers? Were any, or many, of the wolves killed in the present park area? For how many years did the Bottlers sustain their trade in wolf hides on this scale? Whatever answers we may eventually find to these and other questions, the Savage account does demonstrate what many other accounts have shown, that when Yellowstone National Park was established, the area supported large numbers of wolves as part of a robust community of wildlife species. YS

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NPS

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From the Archives

In this photo from 1964, a group of bison are being hazed into the Crystal Creek pen by helicopter.

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