



Review

Carrying capacity, migration, and dispersal in Yellowstone bison

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ARTICLE INFO

Article history:

Received 13 September 2008

Received in revised form 6 May 2009

Accepted 20 May 2009

Available online 21 June 2009

Keywords:

Bison

Brucellosis

Carrying capacity

Conservation

Dispersal

Migration

Yellowstone

ABSTRACT

The conservation of bison in Yellowstone National Park, from near extinction in the late 19th century to a recent high of 5000, has led to long-term societal conflict regarding perceived overabundance, trans-boundary movements, and potential transmission of brucellosis from bison to livestock. We synthesized available information to address two central questions in this debate: (1) has the Yellowstone bison population surpassed numbers that can be supported by the forage base in the park; and (2) why do some bison move outside the park during winter, even when numbers are below food-limited carrying capacity? A spatially-explicit model of the system that integrated abiotic variables with biotic processes indicated bison have not reached a theoretical food-limited carrying capacity of 6200 in Yellowstone National Park. However, more bison began to migrate earlier to lower-elevation winter ranges as numbers increased and climatic factors interacted with density to limit nutritional intake and foraging efficiency. A gradual expansion of the winter range as bison numbers increased enabled relatively constant population growth and increased food-limited carrying capacity. Current management actions attempt to preserve bison migration to essential winter range areas within and adjacent to the park, while actively preventing dispersal and range expansion to outlying areas via hazing and removals (i.e., dispersal sink). A population of 2500–4500 bison should satisfy collective interests concerning the park's forage base, bison movement ecology, retention of genetic diversity, brucellosis risk management, and prevailing social conditions.

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1. Introduction

Yellowstone National Park (YNP) of the western United States was created in 1872, and the successful conservation of bison (*Bison bison*) from a low of 23 animals in 1901 to a high near 5000 animals in 2005 has led to an enduring series of societal conflicts and disagreements among various publics and management entities regarding issues of perceived overabundance and the potential

transmission of the *Brucella abortus* pathogen to domestic livestock (Garrott et al., 1993; Cheville et al., 1998). Yellowstone bison historically occupied approximately 20,000 km² in the headwaters of the Yellowstone and Madison rivers in what is now referred to as the northern Greater Yellowstone Area (GYA; Fig. 1; Meagher, 1973; Schullery et al., 1998; Gates et al., 2005; Schullery and Whittlesey, 2006). However, by the early 20th century, YNP provided sanctuary to the only relict, wild and free-ranging bison remaining in the United States (Plumb and Sucec, 2006). Park ungulate management policies evolved in 1969 to preclude deliberate culling inside the park and allow ungulate abundance to fluctuate in

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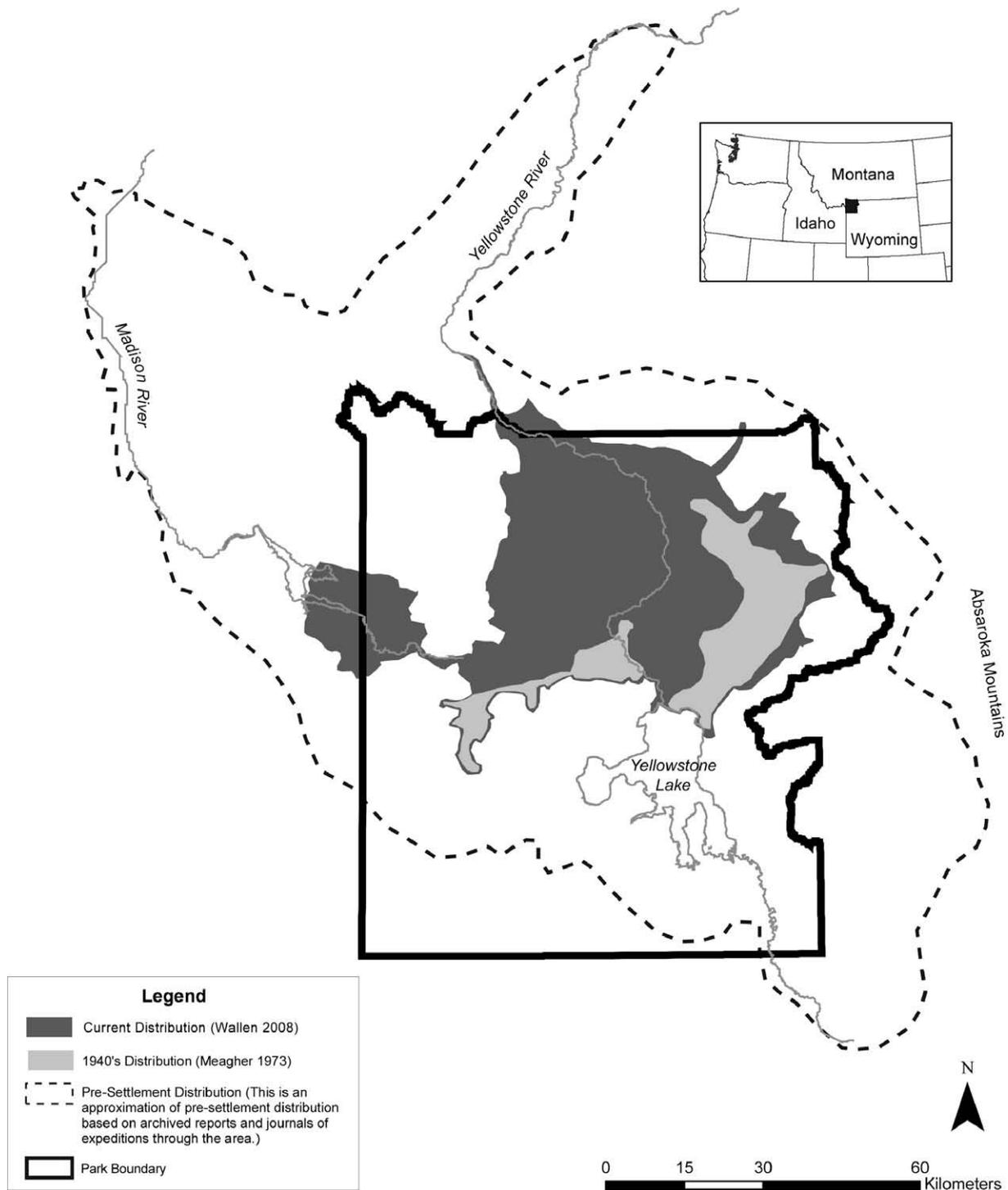


Fig. 1. Map depicting Yellowstone National Park and the pre-settlement, mid-20th century, and current distribution of Yellowstone bison.

response to weather, predators, resource limitations, and outside-the-park hunting and land uses (Cole, 1971). Bison numbers increased rapidly under this policy (Fig. 2) and, since the 1980s, increasing numbers have moved outside the park during winter where some have been culled or hunted by state, tribal, and federal agencies (Fuller et al., 2007a,b). The YNP policy of “natural regulation” (Cole, 1971) proved to be a highly contentious approach to wildlife management, with criticisms primarily focused on effects of perceived overabundance of wild ungulates on range health in the park (National Research Council, 2002). Bison movements

beyond the YNP boundary led to claims that bison were overabundant and had degraded the range health inside the park (Kay, 1998; Wagner, 2006). Such claims, in turn, have 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 (Hagenbarth, 2007; Kay, 2007; Schweitzer, 2007).

A central question in this debate is whether bison move outside the park because their abundance has surpassed levels that can be supported by the forage base in the park, considering year-to-year

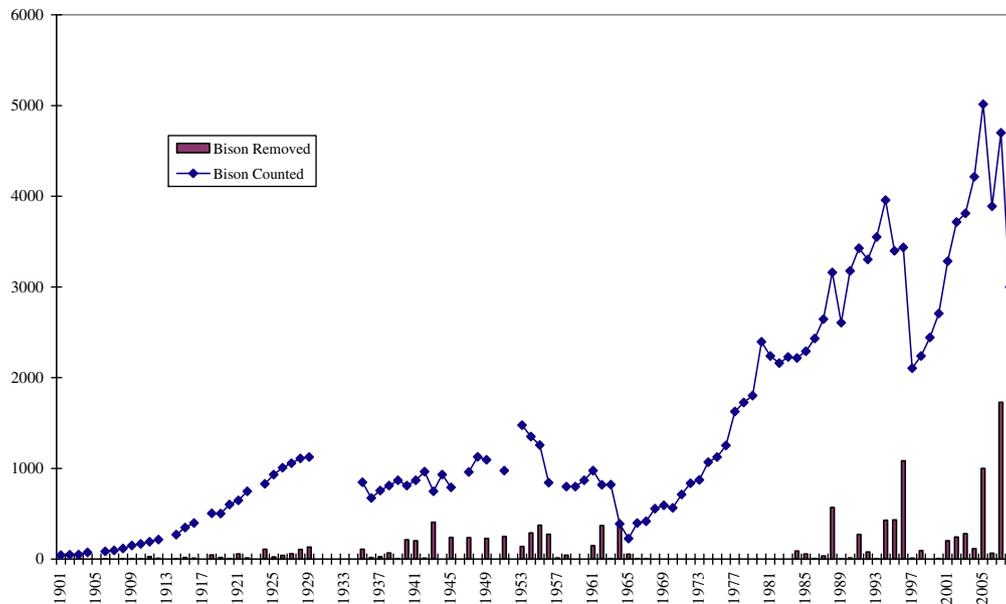


Fig. 2. Time series of counts and removals for bison in Yellowstone National Park during 1901–2008. Counts occurred in the summer of the year indicated, while removals occurred during the following winter and spring.

variations in food production, habitat use, diet selection, and energy balance. This review contributes new insights into the debate over Yellowstone bison conservation and management by synthesizing information from recent analytical efforts to: (1) evaluate whether bison numbers have exceeded their theoretical food-limited carrying capacity in the park; (2) examine potential explanations for bison movements outside the park during winter and spring; (3) assess the role of interspecific competition and recreation during winter on bison carrying capacity and movements; and (4) appraise the implications of perceived overabundance and zoonotic disease for long-term bison conservation.

2. Study system

The park encompasses 9018 km² in the western United States, including portions of Idaho, Montana, and Wyoming. Approximately 3175 km² of this area currently serves as principal bison habitat (Fig. 1). The bison population consists of central and northern herds that occupy ranges comparable in size (Hess, 2002), but with different plant communities, precipitation patterns, and densities of elk (*Cervus elaphus*). A comprehensive aerial survey during fall 2008 documented a total population of 3000 bison (Wallen, 2008). The range of the northern herd encompasses a decreasing elevation gradient (2200–1600 m) extending approximately 90 km between Cooke City and Gardiner, Montana (Fig. 3). The northern range is drier and warmer than the rest of the park, with mean snow–water equivalents decreasing from 30 to 2 cm along the east–west elevation gradient. Bison predominantly feed on graminoids, sedges (*Carex* spp.), and rushes (*Juncus* spp.) on the extensive grasslands of the northern range (Meagher, 1973). Bison share this range with a large elk herd, which increased from approximately 3200 to >19,000 counted elk during 1968–1994 and then decreased to <7000 by 2006 (White et al., 2007).

The range of the central herd extends from the Hayden and Pelican valleys in the east (2400 m) to the lower-elevation, Madison headwaters in the west (2070 m) (Fig. 3). Winter conditions are severe with snow–water equivalents averaging 35 cm and temperatures reaching -42°C , though windswept areas in the upper portions of the Hayden Valley and patchily distributed geothermal

areas reduce snow cover and costs for accessing food, traveling, and thermoregulation. The central range includes a higher proportion of mesic meadows than the northern range and dominant forages include grasses and sedges. The central bison herd coexists with 100–600 elk during winter (Garrott et al., 2005).

All elk and bison populations in the GYA are variably and chronically exposed and infected with *B. abortus*. Northern GYA elk exhibit relatively low seroprevalence levels (1–5%), whereas southern GYA elk associated with feed grounds can exhibit much higher seroprevalence levels (15–35%; US Animal Health Association, 2006). Since the initial detection of this non-native pathogen in Yellowstone bison in 1917, with transmission presumably from infected livestock, up to 60% of this population has tested positive for antibodies indicating exposure to the brucellosis pathogen (Cheville et al., 1998). Many livestock producers and animal health interests contend that any risk of “spillback” brucellosis transmission from Yellowstone bison to livestock is unacceptable (Cheville et al., 1998). Thus, they advocate taking all necessary steps to eliminate brucellosis from bison and elk in the GYA (US Animal Health Association, 2008).

To manage the risk of brucellosis transmission from Yellowstone bison to livestock, the federal government and State of Montana agreed to the Interagency Bison Management Plan (IBMP) in 2000. This plan established guidelines for implementing hazing, test-and-slaughter, hunting, and other actions affecting bison abundance and distribution near the park boundary (US Department of Interior, 2000a,b). The IBMP established a primary conservation area of approximately 9050 km² for the bison population that includes all of YNP, two zones of intensive, adaptive, risk management outside the northern and western boundaries of the park where limited numbers of bison are allowed under various contingencies, and three areas of the Gallatin National Forest adjacent to YNP where there are no significant wildlife–livestock conflicts and bison are allowed year-round (Fig. 1).

The IBMP allows for the removal of bison in park boundary areas, where they are likely to move beyond the primary conservation area and co-mingle with livestock. The Final Environmental Impact Statement for the IBMP anticipated a total average brucellosis risk management removal of 159–246 bison per year, with larger removals occurring during years with severe winter condi-

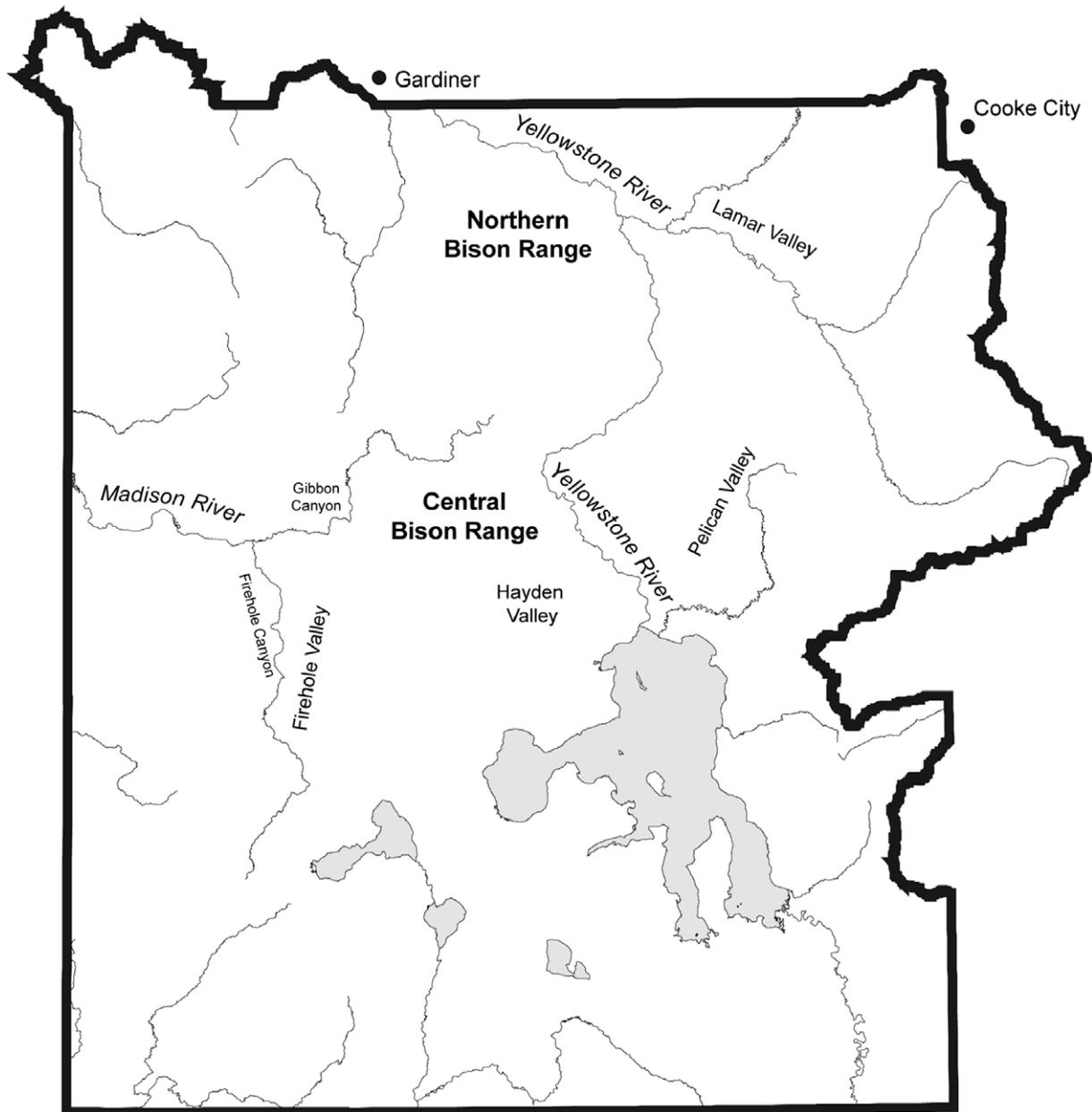


Fig. 3. Map depicting place names of current distribution of Yellowstone bison.

tions (US Department of Interior, 2000a,b). However, the IBMP also provides for non-lethal options, including vaccinating and holding seronegative bison in capture pens until they can be released back into the park during spring (US Department of Interior, 2000a,b) or a quarantine protocol to provide live, disease-free bison for tribal governments and requesting organizations (Montana Fish, Wildlife, and Parks and the United States Department of Agriculture, 2006).

3. Food-limited carrying capacity

The term *carrying capacity* is one of the most common and confusing terms used in wildlife management because it denotes a variety of meanings (McCullough, 1992; Wagner et al., 1995). 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 (represented by K of the logistic equation) that populations tend towards via

density-dependent effects from lack of food, space, cover, or other resources. Environmental variations produce random fluctuations around this equilibrium, with the variability determined by the strength of density dependence. The definition of ecological carrying capacity is often simplified to the number of herbivores in dynamic equilibrium with the forage base (i.e., food-limited carrying capacity; Caughley, 1976, 1979).

A rudimentary estimate of bison density and abundance in YNP can be obtained using an allometric relationship between population densities and body masses of herbivorous mammals (Peters and Raelson, 1984; Nudds, 1993). A conservative estimate of mean body mass for a Yellowstone bison population of variable age and sex is three-fourths of the mean adult female body mass (450 kg), or 338 kg (Meagher, 1973) which, in turn, generates an allometric density of 0.405 Yellowstone bison per km². Accordingly, if we assume that bison populations behave similar to other mammalian herbivores, and there is no *a priori* reason to assume otherwise (Nudds, 1993), an allometric density of 0.405 bison per km²

applied to YNP yields an expected population of 3652 bison. Such predictions must be considered within the context of wide confidence intervals common at the extremes of allometric relationships (95% CI = $0 \leq 0.405 < 1700$ bison per km², Nudds, 1993).

More-complex estimates of food-limited carrying capacity for large herbivores require information on fundamental processes involved in linkages between forage production and use, habitat qualities and nutrition, and nutritional status and demographic responses of populations. The feedback of herbivory onto forage

growth rate is central to interactive plant-herbivore models in which forage intake is a function of forage abundance, and forage abundance is determined by the net outcome of forage production, forage availability, and forage use (Caughley and Lawton, 1975; Noy-Meir, 1975; Caughley, 1979). Plant-herbivore models can be analytically or numerically solved for the population density at which there is equilibrium between the rate of forage production and the rate of forage use. Weather-induced fluctuations in forage production, availability, or mortality produce dynamic equilibria

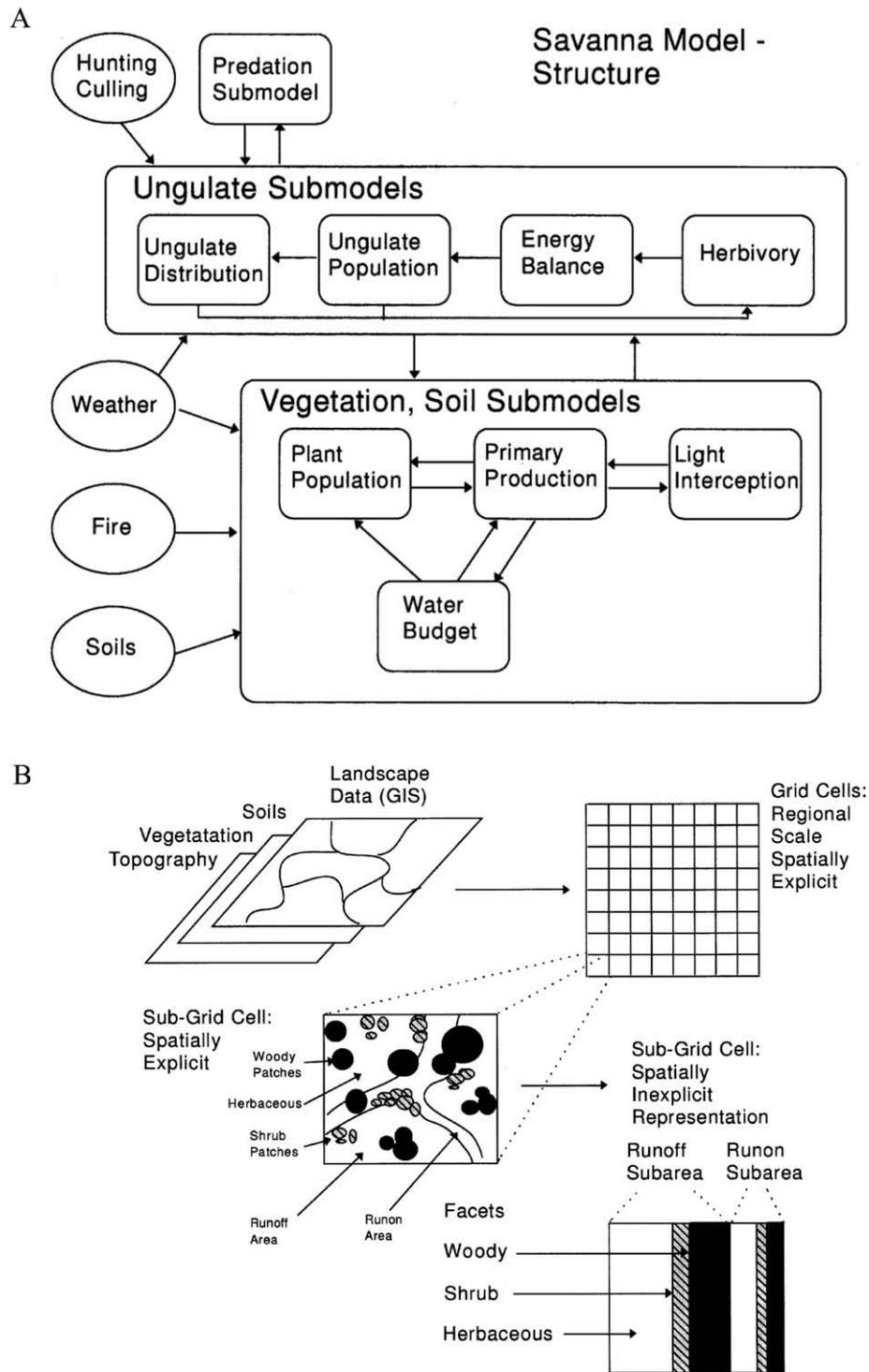


Fig. 4. (A) Primary components of the SAVANNA model and (B) spatial structure of the model.

and, if weather fluctuations are sufficiently unpredictable, the plant-herbivore system may be disequilibriumal (Coughley, 1987; Ellis and Swift, 1988).

Another key component of an explanatory approach must be a dynamic model of animal energy balance, where energy balance is modeled as the net outcome of energy intake through foraging, and expenditures resulting from metabolism and activity. Such energy and nitrogen balance models have been constructed for many years (Moen, 1973; Swift, 1983; Hudson and White, 1985; Coppock and Detling, 1986; Hobbs, 1989; Ilius and Gordon, 1992). The third key component is the explicit linkage between nutrition and population processes (Getz and Owen-Smith, 1999; Ilius and O'Connor, 2000; Owen-Smith, 2002a,b), which can be incorporated by making animal birth and death rates functions of their condition indices (Coughenour, 1993; Coughenour and Singer, 1996a).

Spatially-explicit, ecosystem models incorporating these linkages have been used to estimate food-limited carrying capacity and ungulate population dynamics in a wide range of environments (Coughenour, 1999, 2002; Coughenour and Singer, 1996b; Boone et al., 2002; Weisberg et al., 2002). Ecological carrying capacity can be determined by running the model until it reaches a dynamic equilibrium with no management removals. The carrying capacity is estimated by the mean number of animals in long-term dynamic equilibrium with other components of the ecosystem, particularly plants and soils. Spatial heterogeneity plays a critical role in most grazing ecosystems and “key resources” (Ilius and O'Connor, 2000) or temporally variable distributions of weather, soils, vegetation, plant growth, and herbivores can be readily represented on actual landscapes using geographic information systems (GIS) data (Coughenour, 1999, 2002). The ecosystem modeling approach links plant growth, nutrient cycling, and soil water budgets using process-based realism, thereby permitting explanatory assessments of the effects of spatially heterogeneous grazing intensities on plants and soils across the landscape.

Boyce (1998) argued that establishing quantitative and measurable standards of ecosystem processes is likely beyond the ability of managers for any park system because the wide-ranging dynamics of interacting abiotic variables and biotic processes obstruct attempts to characterize the precise structure and function of ecosystems and predict the effects of manipulations. While heeding this warning, it became necessary for the various reasons outlined above to rigorously estimate a benchmark of food-limited carrying capacity for bison in YNP. Thus, Coughenour (2005) evaluated whether or not Yellowstone bison had reached a food-limited carrying capacity by parameterizing and testing a spatially-explicit ecosystem model (SAVANNA, version 5a; Coughenour, 2002) for the YNP ecosystem that integrated data from 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 submodels (Fig. 4, also see Coughenour, 2005 at <http://www.greateryellowstonescience.org/topics/biological/mammals/bison/projects/coughenour> for full disclosure of source data, parameterization, and time series analyses). The model simulated the central and northern bison herds, as well as the two resident wintering elk herds (northern, 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 was sensitive to spatial position and used GIS data for soils, vegetation, topography, and other variables, and was driven by weather data from 29 different climate and snow telemetry sites located in and near the park. Precipitation and temperature maps were generated using elevation-corrected spatial interpolation, and a validated snow model simulated the accumulation and melting of

snow, thereby generating maps of snow depth and water content. Simulated bison population dynamics agreed well with observed data.

When the model was run for eight simulations for the northern and central herds simultaneously over 50 years as a closed population (no dispersal) with stochastic weather, the northern herd increased to a mean of 2417 bison (range = 1820–3530, median = 2670, skewness = -0.59, kurtosis = 0.122, probability not normal <0.001, Chi square, Kolmogorov–Smirnov) and the central herd increased to a mean of 3776 bison (range = 2430–5630, median 4030, skewness = 0.41, kurtosis = 0.19, probability not normal <0.001, Chi square, Kolmogorov–Smirnov). The actual maximum total count of Yellowstone bison within a year was 3531 bison in the central herd and 1484 bison in the northern herd during summer 2005, with an estimated sightability of 0.97 (Wallen, 2008). Thus, neither the central nor the northern bison herds have exceeded the estimated mean food-limited carrying capacities in the park, though simulations suggest there should be extensive inter-annual variations in estimated carrying capacity due to variations in weather, forage availability, competition, and other factors (Coughenour, 2005). Most of the simulated inter-annual variations in abundance were underpinned by fluctuations in recruitment rates, wherein simulated calf:cow ratios declined during severe winters with increased nutritional stress in gestating females and were variable between herds due to variations in winter weather regimes (Coughenour, 2005). During severe winters, the energy balance model predicted that the populations would be under nutritional stress well below food-limited carrying capacity and, as a result, the population model predicted considerable calf mortality and small increases in adult mortality due to starvation (Coughenour, 2005).

4. Migration

Migration is defined as movement from one spatial unit to another, with a return component (Baker, 1978; Stenseth and Lidicker, 1992). After near extirpation in the early 20th century, bison in the Lamar and Pelican valleys of YNP were subject to intense animal husbandry during 1902–1938 and reintroduced into the Hayden and Firehole valleys of YNP in 1936 (Meagher, 1973). As numbers increased, seasonal migrations along altitudinal gradients within YNP became the norm, with some bison in both the central and northern herds moving from higher-elevation summer ranges to lower-elevations during autumn through winter, until bison returned to the summer ranges in June (Meagher, 1989b; Bjornlie and Garrott, 2001; Bruggeman et al., 2009c). Seasonal movements of the central herd from the higher-elevation Hayden Valley to the lower-elevation Madison headwaters that also contains geothermal habitat were initially detected inside YNP by the 1970s, when bison abundance was low (<500 bison) and the summer range should have provided ample resources for bison year-round (Meagher, 1993, 1998; Bruggeman, 2006). Thus, Yellowstone bison were partially migratory several decades before their abundance began to approach the estimated food-limited carrying capacity of their range inside YNP (Bruggeman et al., 2009c). However, more bison began migrating earlier to lower-elevation winter ranges as density increased, suggesting migration served to increase per capita access to food resources (Meagher, 1998; Bruggeman et al., 2009c).

Some of the annual variability in the proportion of bison migrating each winter is explained by density-independent climate covariates that limit their access to food. 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., 2009c). Thus, snow is the primary factor that reduces foraging efficiency and bi-

son prefer patches with minimal snow pack 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, even though many geothermal areas contain low biomass and/or relatively poor quality forage (Meagher, 1989a,b; Bruggeman, 2006; Bruggeman et al., 2009c). Also, snow melts earlier at lower elevations and, as a result, there is earlier green-up and energy-efficient foraging opportunities while upper-elevation portions of the winter range are still covered with snow (Bjornlie and Garrott, 2001; Bruggeman et al., 2006). Thus, the numbers and timing of bison migrating from the summer range to the winter range is positively related to snow build-up on the summer range, while return migration from lower elevation winter ranges aligns with temporal and spatial patterns of onset phenology (Thein et al., 2009). Upon initiation, onset phenology occurs progressively at the rate of approximately 10 days for every 300 m of elevation gained (Despain, 1986), suggesting Yellowstone bison may employ a conditional migration strategy based on climate variability (Bjornlie and Garrott, 2001; Bruggeman, 2006; Bruggeman et al., 2006).

5. Dispersal

Dispersal is defined as movement from one spatial unit to another, without return (at least in the short term; Stenseth and Lidicker, 1992), while range expansion is the outward dispersal of animals beyond the limits of the traditional distribution for a population (Gates et al., 2005). Increases in the winter range areas used by migratory bison in the central and northern herds of YNP were detected in the 1980s and continued as bison numbers increased, eventually including movements to winter range areas outside the park (Taper et al., 2000; Gates et al., 2005). There were also pulses of emigration from the central herd to the northern range during this time period (Coughenour, 2005; Fuller et al., 2007a; Bruggeman et al., 2009c). Wood bison (*Bison bison athabascæ*) exhibit density-driven (resource limitation) range expansion and random (nomadic) movements (Gates and Larter, 1990; Larter and Gates, 1990; Larter et al., 2000). Adult male and female wood bison display differential spatial behaviors, with single and small groups of adult males having life history flexibility to explore new habitat patches, yet return to core breeding areas where the female herds are located (Komers et al., 1992, 1993). Several authors suggested that range expansion and emigration among Yellowstone bison enabled relatively stable instantaneous densities (i.e., density equalization) during winter as population size increased (Taper et al., 2000; Coughenour, 2005; Gates et al., 2005). Range expansion may delay responses to food limitations since new ranges provide additional forage and limitations will become apparent primarily when new ranges can no longer be colonized (Messier et al., 1988). 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; creating a positive feedback cycle (Coughenour, 2005).

Increasing density regulates ungulate populations by decreasing per capita resources and, in turn, negatively influencing nutrition, body condition, reproduction, and survival (Sinclair, 1975; Caughley, 1976). Movements to lower-elevation winter ranges along the boundary of YNP began when population size increased above 1500 bison for the central herd and 550 for the northern herd (Gates et al., 2005). These thresholds are well below mean estimates of food-limited carrying capacity (e.g. ~2400 northern herd; ~3800 central herd; Coughenour, 2005), but above an allometric-based estimate of dispersal-threshold density (0.41 bison/

km²) and abundance (1285) derived by applying this density to an estimate of current bison distribution (Fig. 1; 3175 km²) in YNP. Similar dispersal-threshold densities have been reported for bison in Wood Buffalo National Park (>0.4 bison/km²; Nudds, 1993) and Mackenzie Bison Sanctuary (0.5–0.8 bison/km²; Gates and Larter, 1990). There were indications of nutritional stress via decreasing minimum body condition and calf:cow ratios in simulations of Yellowstone bison dynamics during 1969 through the mid-1990s as bison and elk numbers increased (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). Residence times in winter foraging areas were negatively correlated with bison numbers, suggesting that competition increased in high-quality foraging areas as more bison moved onto the winter range and bison travel and redistribution increased (Bruggeman, 2006). Cheville et al. (1998) suggested an increasing probability of larger bison movement beyond the park boundary when their abundance exceeded 3000. More-recent analyses of data collected during 1970–2008 suggest that limiting the population to <3500 bison in the central herd and <1200 bison in the northern herd could abate most large-scale movements outside the park during near-average winter conditions (Jeremia et al., 2009).

The stochastic effects of climate can exacerbate density-related effects on ungulates by further decreasing the availability of forage and/or increasing energetic costs (Sæther, 1997; Gaillard et al., 2000). Gates et al. (2005) concluded that bison move beyond park boundaries in winter in response to forage limitation caused by interactions between population density, variable forage production driven by growing season precipitation, snow conditions, and competition between bison and elk. Simulated numbers of bison outside the western boundary during 1980–1997 were significantly but variably affected by snow, little affected by population size, and strongly affected by an interaction between snow and population size (Coughenour, 2005). Conversely, the number of animals expected outside the northern boundary was highly related to snow depth, but not related to the size of the northern herd (Coughenour, 2005). Severe winter snow conditions have prompted large movements of bison to low-elevation meadows beyond their historic winter range and outside YNP that offer lesser snow pack and more energy efficient foraging (Meagher, 1989a,b; Cheville et al., 1998; Gates et al., 2005). Also, pulses of emigration from the central herd to the northern range were generated by an interaction between density and severe snow pack (Fuller et al., 2007a; Bruggeman et al., 2009c). Since the mid-20th century, and more recently under the IBMP, range expansion beyond park boundaries was precluded by culling and hazing bison back into the park during winter and spring to reduce the risk of brucellosis transmission to livestock.

In simulations that represented a brucellosis risk management-induced off-take of 45% of bison leaving the park, the northern herd fluctuated between 200 and 400 animals and the central herd fluctuated between 1700 and 2500 animals (Coughenour, 2005). This simulation can be thought of as representing a dispersal sink, wherein some bison would normally leave the higher, elevation park landscape and not return. Dispersal movements and sinks are common in wildlife populations (Owen-Smith, 1983) and should be expected in nomadic, wide-ranging species such as bison. Intermittent brucellosis risk-management removals at the park boundary, combined with over-winter natural mortality, of >1000 bison in 1997, 2006, and 2008 temporarily reduced the density of bison and likely diminished the magnitude of density dependent effects on demography and movements. Conversely, in the absence of hunting or brucellosis risk management remo-

vals, hazing bison back into the park likely maintained the density-dependent effects of exploitative competition (Gates et al., 2005), and increased retention of learned movement behaviors that otherwise would be lost in a management-induced “dispersal sink.” Without this intensive management intervention, there is little doubt that bison would have continued to expand their winter range and dispersed to suitable habitat areas outside the northern and western boundaries of the park.

6. Other factors influencing migration and dispersal

There are certainly other factors that influence bison carrying capacity and movements because some animals exhibit long-distance movements at lower densities or before significant snow build-up on their summer range (Bruggeman, 2006). Bison movements are undoubtedly influenced by learned behaviors (Gates et al., 2005). Also, interactions between bison and elk are significant for predicting the food-limited carrying capacity of bison because their diets overlap considerably, particularly with fine-leaved, upland grasses (Singer and Norland, 1994; Coughenour, 2005). Counts of northern Yellowstone elk decreased from 13,400 to <7000 since 2001, which is likely to indirectly increase bison population growth rates and their ecological carrying capacity (White and Garrott, 2005). The effect of competition between bison and elk on bison food-limited carrying capacity was assessed by Coughenour (2005), where simulated elk numbers were held at 5000 and bison were allowed to reach their food-limited carrying capacity. With elk held to 5000, in years 28–50 of 50 year simulations, the northern herd reached a mean of 3219 (sd = 490) bison, as compared to 2611 (sd = 335) bison without elk limitations. The central herd reached 5129 (sd = 841) bison, compared to 3217 (sd = 604) bison without elk limitation (paired *t*-tests comparing means were significant at $P < 0.001$). Thus, under these simulations, elk abundance affected the ecological carrying capacity for bison, with increased bison movements outside the park boundary with increased elk numbers (Coughenour, 2005).

Meagher (1993) suggested that road grooming or mechanical snow packing used for oversnow vehicles, increased survival rates and facilitated movements of bison to park boundaries. Several independent analyses concluded road grooming did not change the population growth rates of bison relative to what may have been realized in the absence of road grooming (Gates et al., 2005; Fuller et al., 2007a; Wagner, 2006; Bruggeman et al., 2007). Rather, these authors concluded the observed increase in winter range used by bison was likely a natural response to increasing population density (Bjornlie and Garrott, 2001; Gates et al., 2005; Bruggeman et al., 2009a,b). The rapid increase in bison numbers during 1969–1995 followed a fundamental shift in the management of bison, whereby the park switched from husbandry and culling of bison to achieve target densities (1934–1968) to a regime of ecological management under which the bison population in the park was allowed to fluctuate with minimal human manipulation (Cole, 1971). Bison apparently reached levels of decreased foraging efficiency when they were limited to their historical Hayden and Pelican Valley winter ranges deep within the interior of the park. This decreased nutritional intake, combined with their nomadic nature and ability to travel through deep snow, made it likely that migration to the Madison headwaters and range expansion beyond was an inevitable outcome (Coughenour, 2005).

Winter travel by bison was negatively correlated with road grooming and there was no evidence that bison preferentially used groomed roads in central YNP during winter (Bjornlie and Garrott, 2001; Bruggeman et al., 2006, 2009a). In fact, the amount of bison travel, both on and off roads, was reduced during winter because bison decreased movements as snow pack accumulated to con-

serve energy (Bruggeman et al., 2006). Rather, the probability of bison movements and the spatial distribution of travel corridors were affected by topographic and habitat attributes including slope, landscape roughness, habitat, and distances to streams, foraging areas, and forested habitats (Bruggeman et al., 2007). Streams are the most influential landscape feature affecting the bison winter travel network (Bruggeman et al., 2009b). Simulations by Gates et al. (2005) indicated that inter-range movements of bison in the park interior were generally not constrained by winter snow pack in non-road grooming scenarios during most winters.

It is impossible to determine through retrospective analyses if groomed roads facilitated redistribution and the extension of winter ranges by bison because no detailed data on bison travel patterns existed prior to road grooming and bison are now familiar with destination ranges at lower elevations (Bruggeman et al., 2007, 2009b). Anecdotal information suggests that bison can break trail for considerable distances through deep snow (>1 m; Gates et al., 2005) and repeated use of trails by bison traveling in single file lines maintain them in a “self-groomed” state, an adaptation for saving energy while traveling in snow (Telfer and Kelsall, 1984; Bjornlie and Garrott, 2001; Bruggeman et al., 2007, 2009b). As noted above, bison largely follow travel corridors that align with stream courses, but also use road corridors that may enable efficient movement through landscape bottlenecks, including the Fire-hole and Gibbon canyons (Gates et al., 2005; Bruggeman et al., 2007, 2009b). Coughenour (2005) asserted an increased proportion of travel on packed snow could provide minor energetic savings which, without brucellosis risk management removals of bison, could compound over the course of many winters to affect population growth. In addition, there could be an effect on instantaneous decision-making by bison because individual animals decide to travel or not based upon the immediate energetic costs imposed by snow conditions (Coughenour, 2005).

7. Implications for bison conservation

Yellowstone bison have not exceeded estimates of their theoretical food-limited carrying capacity in YNP of approximately 2400 in the northern herd and 3800 in the central herd. However, bison began to expand their winter range to lower elevations in and outside the park as numbers increased and climatic factors (i.e., snow, drought) interacted with density to limit nutritional intake and foraging efficiency. This behavioral response enabled bison to maintain relatively stable population growth and increase their food-limited carrying capacity as numbers increased. These findings suggest the concept of food-limited carrying capacity is somewhat different for Yellowstone bison than the classic Caughley (1976) model because decreased foraging efficiency or intake induces dispersal movements well below ecological carrying capacity and large-scale starvation of animals.

Applying ecological understanding to complex management problems requires developing an understanding of properties and processes and assembling that understanding reliably across space and time (Hobbs, 2003). One of the defining characteristics of ungulates is their mobility. They can traverse large areas of space in relatively brief intervals of time and, consequently, respond to landscape heterogeneity expressed across a broad range of scales (Hobbs, 2003). Perhaps the most well-known example is the wildebeest (*Connochaetes taurinus*) migration on the Serengeti of East Africa in response to seasonal rainfall patterns (Maddock, 1979). Similarly, plains bison evolved in the spatially and temporally variable climatic environments in the North American central grasslands (McHugh, 1972), and they adapted to this variability through large-scale movements (Moodie and Ray, 1976; Hanson, 1984). Bison occupying the Yellowstone and Madison River water-

sheds historically operated at a scale larger than YNP (Gates et al., 2005) and recent density-related dispersal movements by Yellowstone bison represent an attempt to operate at this larger scale. In natural populations, animals often disperse to marginal habitats in response to food competition and nutritional stress in core, high quality habitats. Thus, the dispersal area acts as a population sink (Owen-Smith, 1983; Coughenour, 2008). In a situation like YNP, these movements are a natural process resulting from successful conservation and population increases inside the park. Though potential bison habitats adjacent to YNP should not be considered marginal, lethal brucellosis risk management in these areas can serve as a surrogate for the dispersal sink that would otherwise be an expected part of natural ecosystem processes. Thus, the role of winter range expansion at densities below estimated food-limited carrying capacity, and the resulting lower numbers of bison in the park due to this dispersal sink (Coughenour, 2005), should be acknowledged when considering the optimal abundance, carrying capacity, and distribution of Yellowstone bison.

For much of the past 100 years, as Yellowstone bison recovered from near extirpation, they were constrained to 2–3 relatively independent breeding groups that migrated into three discrete wintering areas, but did not regularly and extensively venture outside the park. This has led to the popular belief that Yellowstone bison should always remain in YNP, and is reflected in the status and authority for management afforded to bison adjacent to the park in the GYA states. The Comprehensive Wildlife Conservation Strategy for Idaho mentions bison as species of concern that is critically imperiled, but the state agricultural regulations do not recognize wild bison and consider them livestock (<http://www.wildlifeactionplans.org/idaho.html>). Wyoming has designated specific areas adjacent to Grand Teton National Park and YNP where bison are considered wildlife—elsewhere they are considered livestock (<http://www.gf.state.wy.us/wildlife/CompConvStrategy/index.asp>). Montana considers the Yellowstone bison population to be wildlife, with disease control management under the lead authority of the Montana Department of Livestock and hunting on lands adjacent to the park managed by the Montana Department of Fish, Wildlife and Parks (<http://www.fwp.mt.gov/specieshabitat/strategy/fullplan.html>). In addition, for the purposes of brucellosis management, the United States Department of Agriculture, through the auspices of the Animal and Plant Health Inspection Service, considers all bison removed from YNP, for purposes other than consignment directly to slaughter, as alternate livestock (9 United States Code of Federal Regulations 78). Thus, even if the risk of brucellosis transmission could be eliminated from bison, it is unlikely these massive wild animals would be tolerated in most areas outside YNP due to social and political barriers such 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 GYA states, the prevailing social carrying capacity of Yellowstone bison is perhaps most limiting.

Freese et al. (2007) documented that the North American bison is ecologically extinct across its former range and, along with Sanderson et al. (2008), called for urgent measures to conserve the remaining wild and free-ranging bison, and restore the species as wildlife in focal areas across its historic range. Conservation of the migratory and nomadic tendencies of bison, as well as their genetic integrity and ecological role, is paramount for the perpetuation of the species. Yellowstone bison can be characterized as a single population with two genetically distinguishable breeding groups or subpopulations (Halbert, 2003; Gardipee, 2007). Analyses estimate that 1000–2000 bison likely are needed in each of

the central and northern breeding herds to retain enough genetic diversity to enable bison to adapt to a changing environment through natural selection, drift, and mutation (Gross and Wang, 2005; 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). Thus, while the IBMP initially indicated that 2100 bison would satisfy conservation values (US Department of Interior, 2000a,b), strong scientific and management support has developed for managing the Yellowstone population above a minimum conservation target of 2500 bison. Given the spatial and temporal scales aligned with this primary conservation area, this objective should be possible, with appropriate levels of management-induced dispersal sink conditions (e.g., hunting and brucellosis risk management) (Millspaugh et al., 2008). Indeed, the recent development of hunting of Yellowstone bison in Wyoming and Montana, outside of YNP, enhances their stature as wildlife, and is consistent with management of other wild ungulates that seasonally occupy the park, yet move outside the park within their annual home ranges.

While evidence indicates the Yellowstone bison population has not exceeded the park's food-limited carrying capacity of approximately 6200, it also appears that the interactive effects of severe winters with population levels greater than 4700 bison could induce large-scale movements of bison to lower-elevation winter range outside YNP (Geremia et al., 2009). Such large movements jeopardize brucellosis risk management objectives by overwhelming manager's abilities to maintain separation between bison and livestock. Thus, we propose that a Yellowstone bison population that varies on a decadal scale between 2500 and 4500 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. Within this range of abundance, management agencies should continue to prioritize conservation of bison migration to essential winter range areas within and adjacent to the park, while also actively preventing dispersal and range expansion via hunting, outside YNP, and periodic brucellosis risk-management (i.e., dispersal sink).

Acknowledgments

We thank Wayne Brewster for asking tough questions. S. Lewis, T. Olliff, T. Reid, J.F. Wilmshurst, and four anonymous reviewers provided helpful comments on earlier versions of this manuscript. The views and opinions in this article are those of the authors and should not be construed to represent any views, determinations, or policies of the National Park Service. The parameterization and testing of 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. The funders had no role in model design or testing, decision to publish, or preparation of the manuscript. The authors have declared that no competing interests exist.

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