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Review

Management of Yellowstone bison and brucellosis transmission risk – Implications for conservation and restoration

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ABSTRACT

Yellowstone bison (*Bison bison bison*) are managed to reduce the risk of brucellosis (*Brucella abortus*) transmission to cattle while allowing some migration out of Yellowstone National Park to winter ranges in Montana. Intensive management near conservation area boundaries maintained separation between bison and cattle, with no transmission of brucellosis. However, brucellosis prevalence in the bison population was not reduced and the management plan underestimated bison abundance, distribution, and migration, which contributed to larger risk management culls (total >3000 bison) than anticipated. Culls differentially affected breeding herds and altered gender structure, created reduced female cohorts, and dampened productivity. The ecological future of plains bison could be significantly enhanced by resolving issues of disease and social tolerance for Yellowstone bison so that their unique wild state and adaptive capabilities can be used to synergize the restoration of the species. We recommend several adaptive management adjustments that could be implemented to enhance the conservation of plains bison and reduce brucellosis infection. These findings and recommendations are pertinent to wood bison (*Bison bison athabascae*), European bison (*Bison bonasus*), and other large ungulates worldwide that are managed using best practices within a risk framework.

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1. Introduction

Infectious diseases transmitted between wildlife and livestock are increasingly becoming one of the primary drivers threatening the long-term viability of wildlife populations through the isolation of protected areas (Newmark, 2008). The increase in human agricultural activities along the boundaries of wildlife reserves has augmented the sharing of diseases between wildlife, livestock, and humans. These multi-host situations, where the disease has been eradicated or is under control in domestic livestock, are exceptionally difficult to manage because a single transmission from wildlife to livestock can have severe consequences for public health, the region's economy, and wildlife conservation (Gortázar et al., 2007). As a result, wildlife hosts are often restricted to reserves which may not offer all the seasonal habitat requirements for survival and reproduction. This is the case for many migratory ungulates, where most protected areas do not include the entire migratory range and intact ungulate migrations have declined as these conservation areas have become increasingly insularized by human activities (Bolger et al., 2008). A consequence of restricting wildlife access outside reserves is the crowding of hosts within protected areas which can lead to an increase in disease transmission within the wildlife host populations (Lebarbenchon et al.,

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2007) and, ultimately, greater transmission risk to nearby livestock.

Decisions regarding management of wildlife diseases transmissible to humans and domestic livestock have complicated conservation of migratory ungulates worldwide. For example, bovine tuberculosis caused by *Mycobacterium bovis* infects wild ungulates and domestic livestock and is a major conservation problem in protected areas across the world. Wild ungulates infected with tuberculosis include buffalo (*Syncerus caffer*) in Kruger National Park (Cross et al., 2009) and Hluhluwe-Imfolozi Park (Jolles et al., 2005), South Africa; wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) in Doñana National Park, Spain (Gortázar et al., 2008); and elk (*C. elaphus*) in Riding Mountain National Park and wood bison (*Bison bison athabascae*) in Wood Buffalo National Park, Canada (Nishi et al., 2006). The wild state and genetic diversity of these ungulates could be used to synergize restoration efforts if issues of disease and social tolerance could be solved. Protected areas are needed as ecological baselines to discern natural change from those induced by human activities (Boyce, 1998; Sinclair et al., 2007), but the existence of wildlife disease reservoirs complicates wildlife management at conservation area boundaries.

The processes for long-term conservation of free-ranging ungulates operate on large landscapes over long periods of time, while the effectiveness of maintaining livestock health can be observed annually. Thus, management plans attempting to prevent disease transmission from infected wildlife to livestock, while conserving healthy wildlife populations, may have difficulties balancing both of these objectives. We used brucellosis management in Yellowstone bison (*B. b. bison*) as a case study to demonstrate the need for continually reviewing and integrating conservation practices into management policies to better protect migratory ungulates and facilitate the ecological role they play in the system. Though elk in the northern Yellowstone area are also chronically exposed to brucellosis (<5% seroprevalence; Barber-Meyer et al., 2007), we did not consider them in this assessment because transmission between bison and elk appears rare (Proffitt et al., 2010). Also, differences in behavior, distribution, infection rates, and tolerance for elk in Montana will likely lead to different strategies to mitigate brucellosis transmission risk from elk to cattle.

2. Brucellosis in Yellowstone bison

Yellowstone bison historically occupied approximately 20,000 km^2 in the headwaters of the Yellowstone and Madison rivers of the western United States (Schullery and Whittlesey, 2006). However, they were nearly extirpated in the early 20th century, with Yellowstone National Park providing sanctuary to the only relict, wild and free-ranging plains bison (Plumb and Sucec, 2006). The population was restored through husbandry, protection, and translocation (Meagher, 1973) and, today, more than 3000 bison in two breeding herds (central, northern) are an integral part of the northern portion of the greater Yellowstone ecosystem. These bison provide prey for predators and carrion for scavengers, contribute to the recycling of nutrients, and provide the visiting public with an opportunity to observe how this icon of the American frontier existed in the early settlement era (Freese et al., 2007; Sanderson et al., 2008).

The Yellowstone bison population has been infected with brucellosis since at least 1917 (Mohler, 1917), likely from cattle (Meagher and Meyer, 1994). Bovine brucellosis is a 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). When livestock are infected, economic loss from slaughtering infected cattle herds and imposed trade restrictions affect more than just the owner of the infected stock. The impacts are shared by others in the industry statewide. Brucellosis has been declared eradicated from cattle herds in the United States, but bison and elk persist as the last known reservoirs of infection in the greater Yellowstone area (Cheville et al., 1998). Approximately 40–60% of Yellowstone bison have been exposed to *B. abortus* and some of these animals migrate to winter ranges in Montana where there is a risk of brucellosis transmission to cattle that graze on public and private lands (Treanor et al., 2007; Plumb et al., 2009).

After intensively managing bison numbers for 60 years through husbandry and regular culling, Yellowstone National Park instituted a moratorium on culling ungulates within the park in 1969 and allowed numbers to fluctuate in response to weather, predators, and resource limitations (Cole, 1971). In response to livestock industry concerns over brucellosis, the National Park Service proposed a program to control bison at the boundary of the park and a series of four interim bison management plans through 1996 put specific boundaries and lethal control measures in place (United States Department of the Interior [USDI] and United States Department of Agriculture [USDA], 2000a). However, bison abundance increased rapidly under this management paradigm (Fig. 1) and migrations by hundreds of bison towards the park boundary during winter began during the 1980s when numbers exceeded 500–1000 bison on the northern and central ranges, respectively (Meagher, 1989a,b; Bruggeman et al., 2009). Attempts to deter these movements or bait animals back into the park failed (Meagher, 1989a,b) and deep snow and ice conditions in 1997 contributed to a large-scale migration of bison to the park boundary, seeking accessible forage at lower elevations. Implementation of the interim plan during this severe winter resulted in the removal of 1123 bison (1084 bison were shot or slaughtered and 39 were used for research purposes). Other bison died of starvation or other natural causes, decreasing population size from approximately 3500 bison in autumn 1996 to 2000 animals by spring 1997 (USDI and USDA, 2000a). In total, about 3100 bison were culled from the population during 1985–2000 for attempting to migrate outside the park.

These migrations and culls of Yellowstone bison led to a series of conflicts among various constituencies (environmentalists, stock growers) and management entities regarding issues of bison conservation and disease containment (Cheville et al., 1998). Since the management of bison outside the park in Montana is the prerogative of the state and the Gallatin National Forest on US Forest Service lands, the federal government and the state of Montana negotiated a court settlement in 2000 that established guidelines for cooperatively managing the risk of brucellosis transmission from bison to cattle. The so-called Interagency Bison Management Plan (IBMP) emphasized preserving the bison population as a natural component of the ecosystem and allowing some bison to occupy winter ranges on public lands in Montana (USDI and USDA, 2000a,b). The IBMP established a primary conservation area for bison that included all of Yellowstone National Park, two zones of intensive, adaptive management outside the north and west boundaries of the park where bison are allowed based on various contingencies, and three areas of the Gallatin National Forest where there are no significant wildlife–livestock conflicts and bison are allowed year-round (Fig. 2).

Prior to signing and implementing the IBMP, there was a concerted effort by federal and state agencies to predict the ecological impacts of various management actions on Yellowstone bison and the risk of brucellosis transmission to cattle. Since that time, the signatories have collected substantial information regarding bison, brucellosis, and the management of transmission risk. As biologists charged with implementing the IBMP for the National Park Service, we retrospectively evaluated if reality met expectations by comparing assumptions and predictions for the alternative selected

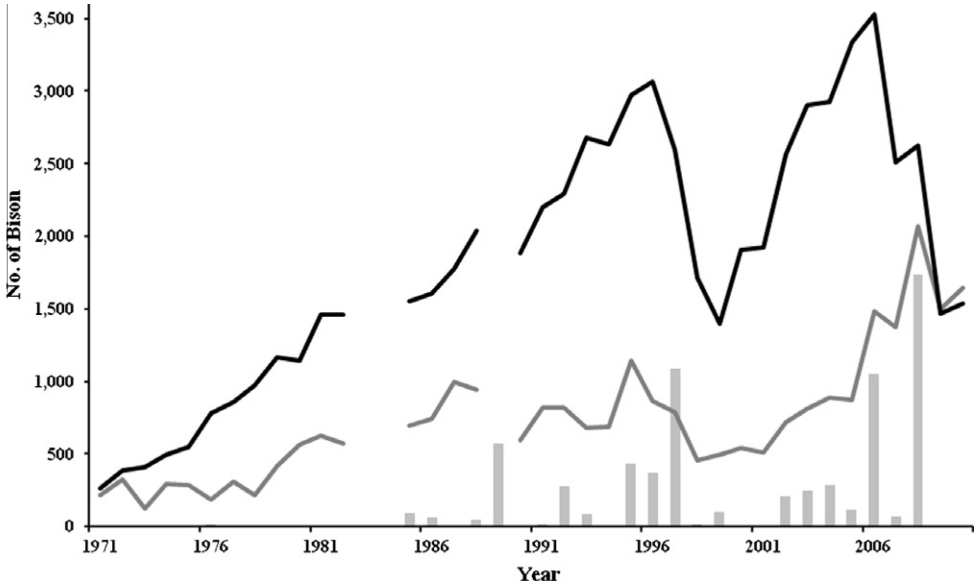

Fig. 1. Time series of central (black solid line) and northern (gray solid line) herd counts, and annual removals of bison in Yellowstone National Park during 1970–2010. Removals occurred during the 1-year period ending in the year indicated, while counts occurred during the previous summer.

from the Final Environmental Impact Statement and described in the Record of Decision for the IBMP (USDI and USDA, 2000a,b) with observed impacts and changes since implementation of the plan began in 2001. This assessment was used to develop adaptive management adjustments to the IBMP in 2008 and similar future assessments will be essential for effective management to conserve the largest free-ranging population of this iconic native species, while reducing brucellosis transmission risk to cattle.

3. Interagency bison management plan

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 (USDI and USDA, 2000b, pp. 11–13). During step 1, the agencies agreed to: (1) enforce spatial and temporal separation between bison and cattle; (2) use hazing by humans on horseback, all-terrain vehicles, or in helicopters to prevent bison egress from the park; (3) if hazing is unsuccessful, capture all bison attempting to leave the park and test them for brucellosis exposure; (4) send test-positive bison to slaughter; (5) vaccinate all test-negative bison except adult females during the third trimester of pregnancy (mid-January through May) when some research suggests vaccine-induced abortions could occur (Palmer et al., 1996); (6) temporarily hold all test-negative bison at the north boundary for release back into the park in spring; (7) release up to 100 test-negative bison at the west boundary and allow them to use habitat adjacent to the park until May 15; (8) conduct research on *Brucella* persistence in the environment to determine an adequate temporal separation period between bison and cattle; (9) conduct research on the safety and efficacy of strain RB51 vaccine; and (10) conduct research and development of a remote vaccine delivery system. The State of Montana also agreed to encourage voluntary vaccination of cattle that might graze on bison-occupied winter ranges outside the park. If 100% voluntary vaccination was not achieved in 1 year, the State of Montana agreed to make the vaccination of all female cattle greater than 4 months of age mandatory.

Step 2 was to begin when cattle no longer grazed during winter on the Royal Teton Ranch adjacent to the north boundary of the park, which was anticipated in winter 2003. Management actions initiated in step 1 were to be continued, except that: (1) up to 100 test-negative bison would be released at the north boundary and allowed to use habitat adjacent to the park until April 15 and (2) any calf and yearling bison that could not be captured at the west boundary would be vaccinated using a remote delivery system. Step 3 was expected to begin by winter 2006 once the agencies had determined an adequate temporal separation period between bison and cattle, gained experience in managing bison in allowable zones outside the park, and initiated a vaccination program for all calf, yearling, and adult female bison in the population, including remote delivery vaccination inside the park. The agencies would tolerate up to 100 untested bison to freely range in both the north and west boundary areas. The agencies would use capture facilities in these areas to maintain the population near 3000 bison, enforce tolerance levels (less than 100 bison), and ensure no bison were outside the park after the respective spring cut-off dates. The agencies could also pursue a quarantine facility to serve in better managing bison by developing a process to certify test-negative bison as brucellosis-free.

The IBMP was adjusted in 2005 to include bison hunting as a management action outside Yellowstone National Park (Montana Fish, Wildlife, and Parks and Department of Livestock, 2004). This adjustment authorized untested bison on winter ranges outside the park to provide for hunting opportunities by Montana-licensed hunters and American Indians with treaty rights. The IBMP was also adjusted in 2006 to: (1) define strategic hazing as a management tool to move bison outside the park to lower risk areas also outside the park; (2) describe increased tolerance for bull bison outside the park because there is virtually no risk of them transmitting brucellosis to cattle (Lyon et al., 1995); and (3) clarify that a population size of 3000 bison was an indicator to guide brucellosis risk management actions, not a target for deliberate population adjustment (USDI et al., 2006). In addition, adaptive management adjustments were approved in 2008 to further describe the circumstances for bison occupying habitats outside the park, to establish a precedent for minimizing consignment of bison to slaughter, to re-affirm the commitment to vaccinating bison, to develop a method for sharing decision documents with public constituencies,

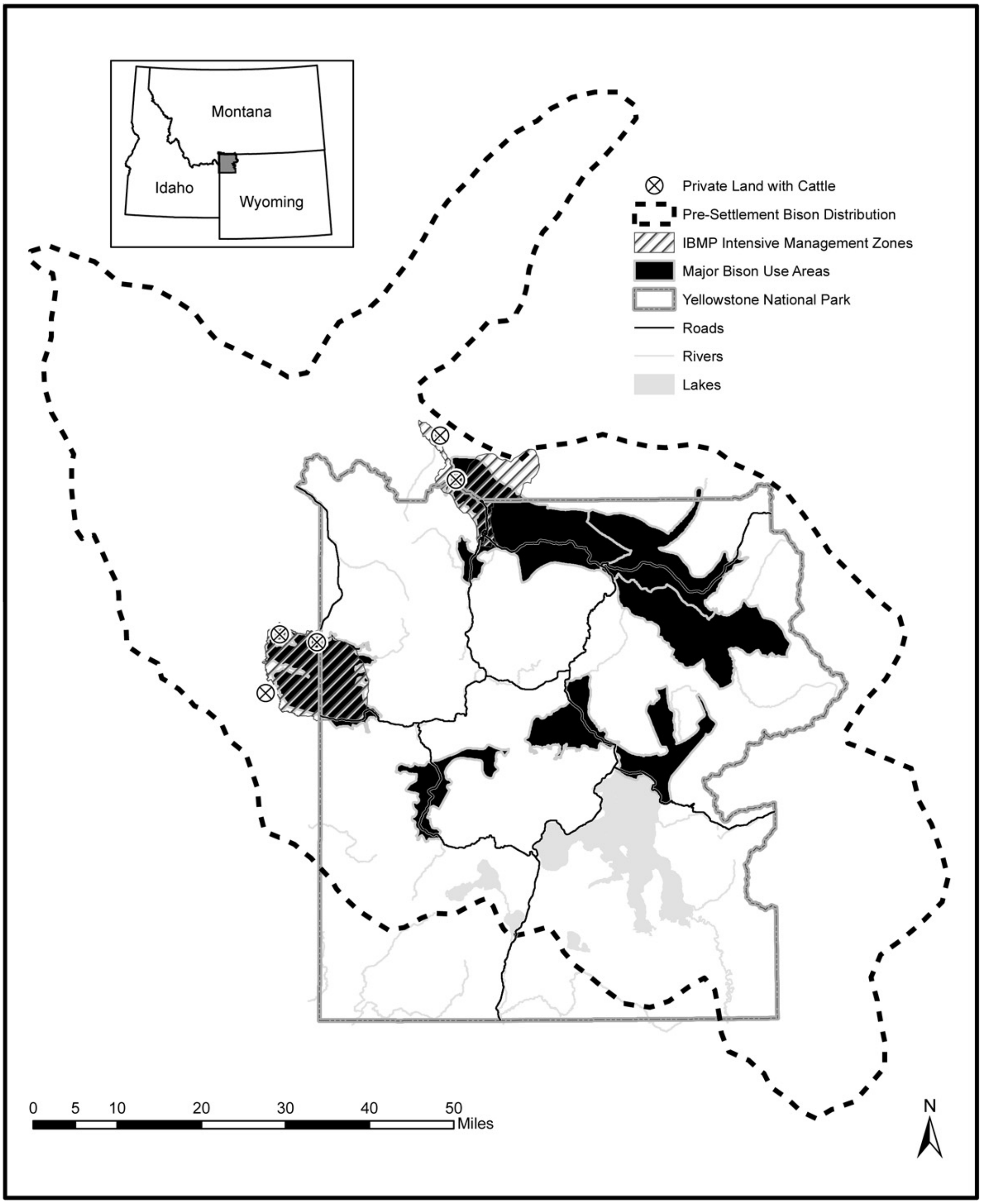

Fig. 2. Map depicting bison management zones and major use areas in and near Yellowstone National Park.

and to develop a metric for annual monitoring of and reporting on IBMP actions (USDI et al., 2008).

4. Risk of brucellosis transmission

Wildlife management practices to prevent or control the spread of infectious diseases have been limited and focused primarily on economically important zoonotic diseases (Wobeser, 2002). Host populations are generally managed by immunization, altering the distribution or density of the population, or extirpation (Choquette et al., 1972; Pech and Hone, 1988; Murray et al., 1996; Henderson et al., 1999; Steelman et al., 2000). The IBMP uses risk management procedures to maintain spatial and temporal separation between bison and cattle around Yellowstone National Park. For bison to transmit brucellosis directly to cattle, infected bison must leave Yellowstone National Park where there are no cattle, enter areas where cattle graze, shed infectious birth tissues via abortions or live births, and have cattle contact infected tissues before they are removed from the environment or the *Brucella* bacteria die. Under prevailing conditions, the risk of brucellosis transmission from bison to cattle is low during winter and spring, with no cattle in the management zone west of the park and less than 50 cattle in the north management zone (Kilpatrick et al., 2009). With the exception of a few male bison that provide no significant risk of

Table 1
Management expectations regarding the prevention of brucellosis transmission from bison to cattle in the Final Environmental Impact Statement for the Interagency Bison Management Plan (IBMP; USDI and USDA, 2000a) and the state of progress or changed circumstances by 2010.

Factors	Assumptions in 2000	New knowledge by 2010
Separation of bison and cattle	Bison will not be allowed to intermingle with cattle (p. 177). Hazing will be used to prevent bison movements outside of identified conservation areas (pp. 180, 184)	The IBMP agencies have successfully maintained spatial and temporal separation between bison and cattle. Every recent brucellosis transmission to cattle has been attributed to elk (Galey et al., 2005; Beja-Pereira et al., 2009)
Brucellosis seroprevalence	The population seroprevalence rate would decrease from about 50% to 33% in 10 years (p. 433)	The proportion of adult females in the population that are test-positive has increased or remained constant at about 60% (Hobbs et al., 2009; Kilpatrick et al., 2009)
Brucellosis viability in the environment	The separation of bison and cattle on public grazing allotments by 45 days will be adequate to eliminate the risk of cattle being exposed to viable *Brucella* bacteria—as few as 5 days in mid-June could be sufficient (pp. 189, 291)	The birth synchrony and cleaning behavior of bison, along with scavenging of birth tissues and bacterial degradation, quickly remove infected tissue from the environment and kill *Brucella*. Transmission risk to cattle is very low by June 1 and essentially non-existent by June 15 (Aune et al., 2007; Jones et al., 2010)
Cattle near bison winter range in Montana (outside the park)	There are about 300 cattle outside the north boundary and 397 cattle outside the west boundary of the park where bison could range if allowed (pp. 305–308)	During winter, there are no cattle outside the west boundary and less than 50 cattle outside the north boundary with the potential to overlap with bison on the winter range. During summer, when bison are in the park, about 220 cattle occupy bison winter range outside the park (White et al., 2009)
Tolerance limits for bison in Montana (outside the park)	Never more than 100 bison (initially seronegative; later untested) in particular areas outside the park's north and west boundaries (pp. 432–433)	More than 400 bison were in the west management area during spring 2009 and 2010. A 30-year livestock grazing restriction and bison access agreement to remove livestock from the Royal Teton Ranch, north of the park's boundary, will allow 25–100 bison to use habitats along the Yellowstone River up to 10 miles away from the park boundary, beginning in 2009
Bison culls	A total average brucellosis risk management cull of 159–246 bison per year (8% of population), with larger culls occurring during years with severe winter conditions that increase migration to park boundary areas (pp. 430–431). Over 18 years, about 1382 bison would be sent to slaughter, while another 3792 would be shipped to quarantine (pp. 434–435). Sixty-five percent of the total bison culled will be from the north boundary and 35% will be from the west boundary (p. 380)	An average of 369 bison (range = 5–1726) were culled each year. In 10 years (2001–2010), 3207 bison were sent to slaughter or shot during management operations, 216 were sent to quarantine, and 270 were harvested by hunters. About 80% of the bison were culled near the north boundary and 20% were culled near the west boundary
Capture and testing for brucellosis risk management	If hazing becomes infeasible, bison will be captured, tested, and animals testing seropositive for brucellosis will be slaughtered at both the north and west boundaries of the park (pp. 180, 184)	During 2001, 2004, and 2005, captured bison were tested for brucellosis and only exposed animals were sent to slaughter. Thus, few test-positive calves were culled. Conversely, bison were not tested before being sent to slaughter during 2003, 2006, and 2008. Thus, an unknown number of test-negative bison and more than 30% of calves were culled from the population during winters 2006 and 2008. Untested and brucellosis-exposed females approaching parturition were held for release during 2006
Quarantine facility	A quarantine facility will be designed and used to hold seronegative bison captured when the tolerance level of the boundary area is reached, the late winter bison population is >3000, or when hazing bison back into the park becomes ineffective (pp. 178–179, 194)	A 5-year research program was initiated in 2005 to determine the latent expression of brucellosis and test the sensitivity of quarantine procedures for detecting the bacteria in multiple generations. This study demonstrated it is possible to certify bison as free from brucellosis (Montana Fish, Wildlife, and Parks, 2009)
Hunting	Hunting inside Yellowstone National Park is not authorized by Congress and longstanding policy prohibits hunting in National Park units unless specifically authorized by Congress (16 USC I, V § 26). However, recreational hunting could limit bison abundance and distribution in Montana, with shipment to slaughter or quarantine used as back-up measures (pp. 401–405)	The IBMP was adjusted in 2005 to include hunting as an action authorized outside Yellowstone National Park (Montana Fish, Wildlife, and Parks and Department of Livestock, 2004). This adjustment authorized untested bison on winter ranges outside the park during November 15 to February 15 to provide opportunities for Montana-licensed hunters and American Indian treaty hunters
Hazing to prevent bison dispersal	Bison will be hazed back into the park at or near the time when bison historically can return based on snow and weather conditions (pp. 180, 184)	The hazing of bison back into the park typically occurs before the "natural" migration in June. During late April and May, there is new growth of grasses in low-elevation meadows, but snow generally still covers higher-elevation summer ranges in the park
Release of untested bison outside the park	Up to 100 untested bison will be allowed in Montana outside both the north and west boundaries of the park after the agencies have collected adequate data and experience in managing bison in each area for a minimum of 2 years (pp. 179–180, 429–430)	Hundreds of untested bison have been tolerated in the Horse Butte area outside the west park boundary for several winters due to the lack of cattle. Cattle were also removed from ranch land adjacent to north boundary of the park in 2008. A limited number of test-negative bison will now be allowed to occupy portions of these lands so managers can gain experience for the eventual release of untested bison (USDI et al., 2008)
Vaccination of bison at capture facilities near the park boundary	The agencies will use vaccination of bison and cattle to reduce transmission risk (p. 177). Seronegative calves and yearlings that are captured would be vaccinated with a safe vaccine (pp. 179, 184)	Yellowstone National Park initiated a vaccination program in 2004 by vaccinating 112 yearling and calf bison. In 2005, nine yearling bison were vaccinated at the Duck Creek capture facility. In 2008, 24 yearling and calf females were vaccinated
Vaccination of bison inside the park	A remote calfhood vaccination program that protects about 53% of calves would eventually reduce the seroprevalence of the bison population to about 11% (p. 437)	The National Park Service has prepared a draft environmental impact statement to decide whether to proceed with implementation of remote delivery vaccination of bison in the park (USDI, 2010). A decision is expected by winter 2012

Table 2

Numbers of Yellowstone bison that were captured, tested, and culled or released near the northern and western boundaries of Yellowstone National Park during the implementation of the Interagency Bison Management Plan. Data from west-side operations were obtained from reports by the Montana Department of Livestock, while data from north-side operations were obtained from reports by the National Park Service, Yellowstone National Park.

Winter	No. captured[a]		Tested[b]		Positives slaughtered[c]		Negatives slaughtered[c]		Untested slaughtered		Consigned to quarantine		Negatives released		Positives released		Untested released		Capture pen mortalities		Management shootings	
	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N
2001	14[d]	0	14[d]	0	5	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	1	0
2002	251[d]	0	118[d]	0	113	0	41	0	45	0	0	0	52	0	0	0	0	0	0	0	3	0
2003	20[d]	231	16[d]	0	8	105	4	104	0	22	0	0	8	0	0	0	0	0	0	0	1	0
2004	21	463	18	407	10	227	0	31	3	6	0	0	8	198[e]	0	0	0	0	0	1	2	2
2005	186[d]	0	168[d]	0	79	0	0	0	17	0	17	0	73	0	0	0	0	0	0	0	0	1
2006	59	1253	0	98	0	384	0	451	50	14	0	87	0	0	0	0	9	308[f]	0	9[g]	6	3
2007	56	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	52[h]	0	0	0	0
2008	158	1647	0	539	0	711	0	560	158	5	0	112	0	191	0	18[i]	0	44[j]	0	6[g]	2	6
2009	3	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3

[a] Captures include bison gathered into capture facilities, but exclude management shootings.
[b] Field testing occurred during handling at capture facilities.
[c] Disease exposure status determined during handling at capture or processing at slaughter facilities.
[d] Totals may be incorrect due to inconsistencies in agency reports concerning individual animals captured and tested multiple times.
[e] Twenty-eight animals retested at the Montana Department of Livestock diagnostic laboratory tested positive for disease exposure status.
[f] Total excludes two untested newborn calves born within containment facilities during holding.
[g] Total excludes four failed births that occurred within containment facilities during holding.
[h] Fifty-two mixed age and gender bison were captured nearby the western park boundary during June and released at the Stephen's Creek Facility.
[i] These seropositive bison were released back into the park because managers did not want to send females late in the third trimester of pregnancy to slaughter.
[j] Total excludes 80 untested newborn calves born within containment facilities during holding.

brucellosis transmission (Lyon et al., 1995), the agencies have successfully maintained spatial and temporal separation between bison and cattle on these ranches. During mid-June and July, about 1800 cattle are released onto public and private lands north and west of the park (White et al., 2009). By this time, however, Yellowstone bison are following the progressive green-up of grasses back into the park interior as snow melts at higher elevations (Gates et al., 2005), and any bison that remain on boundary ranges outside the park are hazed back into the park or lethally removed (USDI et al., 2008). To date, no documented transmission of brucellosis from Yellowstone bison to cattle has occurred due to the cumulative effects of management to maintain separation between cattle and bison, synchrony of bison parturition events (i.e., parturition concentrated in a short period, with abortion cycle earlier than the live birth cycle), bison parturition locations (i.e., spatial separation from cattle summer ranges), bison behavior (i.e., thorough cleaning of birth sites), environmental degradation of *Brucella* (i.e., short persistence period in late spring weather conditions), and scavenger removal of potentially infectious birth tissues that makes it unlikely that substantial quantities of viable *B. abortus* would remain for cattle to encounter (Jones et al., 2010). Thus, transmission risk to cattle is low by June 1 and extremely low by June 15 (Aune et al., 2007; Jones et al., 2010).

Though implementation of the IBMP has nearly eliminated the risk of brucellosis transmission from bison to cattle (Kilpatrick et al., 2009), there is no evidence that it has contributed to a reduction in brucellosis exposure or infection within the bison population (Table 1). The proportion of adult females in the population that are seropositive for brucellosis exposure has increased or remained constant at about 60% (Hobbs et al., 2009). Some aspects of the IBMP were never completely or consistently implemented and, as a result, progress was slow at completing the plan's successive adaptive management steps designed to increase tolerance for bison outside the park and decrease brucellosis seroprevalence (United States Government Accountability Office, 2008). For example, with the exception of 2001, 2004, and 2005, bison migrating outside the park were not consistently captured and tested for brucellosis, with test-positive bison sent to slaughter and test-negative bison vaccinated (Table 2). Instead, bison near the north boundary, where they were not tolerated outside the park during step 1 of the IBMP, were often captured once hazing was no longer effective at keeping them in the park and, without testing, either sent to slaughter or held without vaccination for release back into the park during spring. Also, 216 test-negative calves were sent to a quarantine facility to develop a process to certify test-negative bison as brucellosis-free rather than being vaccinated and released back into the park. Furthermore, remote delivery vaccination of bison was not implemented outside the west boundary of the park, and all cattle near the bison conservation area were not vaccinated (Diemer et al., 2008). Thus, little progress was made on the vaccination efforts envisioned in the IBMP. However, managers committed to increased vaccination in the 2008 adaptive management plan for the IBMP and the National Park Service has initiated environmental review and compliance to decide whether to implement remote delivery vaccination of bison inside the park (USDI et al., 2008; USDI, 2010).

In summary, the IBMP was not completely or consistently implemented as planned, which underscores the difficulties of implementing multi-agency plans and collaboratively attempting to measure progress towards objectives such as reducing brucellosis infection in bison. It is also difficult and, at times, ineffective to consistently apply plans derived from our limited understanding of the processes of wildlife ecology and disease transmission and infection. Given that agencies have spent more than $2 million annually to implement the IBMP since 2002, and another nearly $15 million to purchase land, a conservation easement, and grazing rights north of the park (United States Government Accountability Office, 2008), it is imperative to have rigorous research and surveillance to attain necessary information, measure progress towards objectives, and periodically assess the effects and effectiveness of management actions in light of new information and changed circumstances.

5. Bison conservation

The movement patterns of bison are substantially different than envisioned in the IBMP, with larger numbers moving to the

Table 3
Comparisons of expectations and reality regarding the conservation of the Yellowstone bison population since the implementation of the Interagency Bison Management Plan (IBMP). Page numbers in the Final Environmental Impact Statement (USDI and USDA, 2000a) are provided for each assumption.

Factors	Assumptions and predictions in 2000	New knowledge by 2010
Bison abundance	The population would be managed to a limit of 3000 bison (pp. 193, 429). Abundance would increase from about 2100–3700 bison in 8–9 years (average increase of 4.6% per year), where it would remain over the life of the plan (pp. 433–434)	Abundance has approached 5000 bison under favorable conditions, but fluctuated erratically between 2400 and 5000 due to sporadic, large-scale culls and intervening exponential population growth (Fuller et al., 2009)
Population structure	Sex ratios of about 50% males and 50% females (p. 280). Age structure of about 73% adults, 11% yearlings, and 16% calves (pp. 280–281). Management actions (e.g., culls) will not measurably affect the age/sex distribution of the population (p. 431)	Overall, the population sex ratio increased from 0.5 to 1 male per female during 2003–2009, but there were fewer males in the northern herd and more males in the central herd. Age structure is about 70% adults, 12% yearlings, and 18% calves. More than 30% of calves were culled from the population during winters 2006 and 2008, creating reduced cohorts (Geremia et al., 2011)
Vital rates	Pregnancy: 50%; Birthing: 50%; Survival: unknown (pp. 280–282, 378, 382). Management actions will not affect the reproductive rates of the population (p. 431)	Pregnancy: 60–90%; Birthing: 60–90%; Survival (adult females): 91% with culls censored; 83% with culls treated as deaths (Geremia et al., 2009). Large-scale culls of females apparently reduced the productivity and actual growth rate of the central herd
Bison distribution	There are two distinct winter herds with 30% of the bison in the northern herd and 70% in the central herd (pp. 381–382)	Numbers of bison were about equal (1500) between herds due to higher culling of the central herd and emigration from the central herd to the northern herd (Geremia et al., 2011)
Migratory movements	The northern breeding herd migrates northwest along the Yellowstone River towards the northern boundary of the park during winter, while the central breeding herd primarily migrates west along the Madison River towards the west boundary of the park (p. 31)	Bison from the northern herd move to the north boundary of the park during severe winters. About 50% of bison in the central herd have migrated to the west boundary in some winters, while 30% have migrated to the north boundary in some winters (Clark et al., 2005; National Park Service, unpublished data)
Percent bison migrating to the park boundary	On average, 5% of the population will leave the park, with 65% crossing the north boundary and 35% crossing the west boundary (p. 380). Percentages range from 0% to 10% of the central herd to almost 100% of the northern herd during severe snow pack winters (pp. 381–382, 388)	Zero to 60% of northern herd migrates to the north boundary area during winter, while 50–90% of central herd migrates to the north and west boundaries during winter (National Park Service, unpublished data)
Genetics	Management prescriptions that result in non-random, selective culling of bison can negatively influence the genetic integrity and viability of a population (p. 288)	More than 1000 bison were culled from the population during winters of 2006 and 2008. A disproportionate level of calf–mother pairs were likely culled (Halbert, 2003; Geremia et al., 2011). However, there is no evidence that culling to date has threatened the long-term genetic viability or persistence of the population (USFWS, 2007; Pérez-Figueroa et al., 2010)

boundary and significant movements from the park interior (central herd) to both the north and west boundaries (Table 3). The central and northern bison herds have not reached a theoretical food-limited carrying capacity of approximately 5500–7500 bison inside Yellowstone National Park (Coughenour, 2005; Plumb et al., 2009). However, bison began to migrate to lower-elevation ranges in and outside the park as numbers increased and climatic factors (i.e., snow, drought) interacted with bison density to limit food availability (Gates et al., 2005; Geremia et al., 2011). Also, bison from the central herd began immigrating into the northern herd beginning in the 1980s, and this dispersal increased substantially from 1996 to present (Taper et al., 2000; Coughenour, 2005; Fuller et al., 2009; Bruggeman et al., 2009).

Large annual migrations of bison to low-elevation winter ranges north and west of the park boundary highlight the importance of these areas as winter habitat for bison (Bruggeman et al., 2009; Plumb et al., 2009). Migration during winter allows bison to access food resources that are more readily available in lower snow depth areas of their range, and serves to release portions of the bison range in the park from intensive use for a portion of the year (Bjornlie and Garrott, 2001; Gates et al., 2005). Most bison migration into Montana occurs during mid- to late winter, with peak numbers moving to the north boundary in late February and March and to the west boundary in April and May as vegetation begins to green-up on low-elevation ranges (Ferrari and Garrott, 2002; Clark et al., 2005; Thein et al., 2009). Migration back to interior park ranges typically occurs during May through June, following the wave of growing vegetation from lower to higher elevations, similar to other ungulates in this system (Frank and McNaughton, 1993; White et al., 2007, 2010). Thus, hazing operations to move all bison back into the park during mid-May often occur at a time when bison are undernourished at the end of winter, have vulnerable newborn calves, and may want to remain on low-elevation ranges with new grasses because there is typically still substantial snow on their higher-elevation summer ranges (Gates et al., 2005; Kilpatrick et al., 2009; Newman and Watson, 2009; Watson et al., 2009; Jones et al., 2010). The reluctance of bison to be returned to the park before sufficient vegetation green-up at higher elevations is evidenced by the repeated attempts of hazed bison to return to lower-elevation ranges with new grasses in Montana during May and early June (White et al., 2009).

If migration by bison into Montana is restricted (such as bison being forced to remain within the park by humans) or shortened (such as bison being hazed back into the park by humans before spring forage conditions are suitable), then bison numbers would ultimately be regulated by food availability in the park, with bison reaching high densities (Coughenour, 2008) before substantial winterkill (starvation) occurs. These high densities could cause significant deterioration to other park resources such as vegetation, soils, other ungulates, and processes as the bison population approaches or overshoots their food capacity in the park. Alternatively, managers could limit bison abundance at low numbers (less than 500 per breeding herd) to reduce the likelihood of large migrations to the park boundary (Geremia et al., 2011). Until the late 1970s, bison persisted at relatively low numbers (less than 1500 total) and generally remained isolated in interior park valleys by deep snows (Meagher, 1998). However, recent demographic and genetic analyses suggest that an average of more than 3000 bison total on a decadal scale is likely needed to maintain a demographically robust and resilient population that retains its adaptive capabilities with relatively high genetic diversity (Gross et al., 2006; Freese et al., 2007; Plumb et al., 2009; Pérez-Figueroa et al., 2010).

Table 4

Actual and predicted number of bison culled from the population near the north and west boundaries of Yellowstone National Park during 1974–2010. Predicted values were taken from Table 51 (p. 431) of the Final Environmental Impact Statement for the Interagency Bison Management Plan (USDI and USDA 2000a) which, in turn, was based on projections in Angliss (2003).

Winter	Maximum no. bison counted previous July–August			Sent to slaughter/management culls		Hunter harvest[a]		Sent to quarantine			Age and gender composition of culls/harvests				Deterministic model predictions of culls		
	North	Central	Total	North	West	North	West	North	West	Total	Male	Female	Calf	Unknown	North	West	Total
1970–1984				0	0	13	0	0	0	13	4	7	0	2			
1985	695	1552	2247	0	0	88	0	0	0	88	42	37	8	1			
1986	742	1609	2351	0	0	41	16	0	0	57	42	15	0	0			
1987	998	1778	2776	0	0	0	7	0	0	7	5	2	0	0			
1988	940	2036	2976	0	0	2	37	0	0	39	27	7	0	5			
1989	NA[b]	NA[b]	NA[b]	0	0	567	2	0	0	569	295	221	53	0			
1990	592	1885	2477	0	0	1	3	0	0	4				4			
1991	818	2203	3021	0	0	0	14	0	0	14				14			
1992	822	2290	3112	249	22	0	0	0	0	271	113	95	41	22			
1993	681	2676	3357	0	79	0	0	0	0	79	9	8	9	53			
1994	686	2635	3321	0	5	0	0	0	0	5				5			
1995	1140	2974	4114	307	119	0	0	0	0	426	77	66	31	252			
1996	866	3062	3928	26	344	0	0	0	0	370[c]	100	71	10	189			
1997	785	2593	3378	725	358	0	0	0	0	1083[d]	329	330	144	280	0	55	55
1998	455	1715	2170	0	11	0	0	0	0	11				11	0	56	56
1999	493	1399	1892	0	94	0	0	0	0	94	44	49	1	0	38	20	58
2000	540	1904	2444	0	0	0	0	0	0	0					39	0	39
2001	508	1924	2432	0	6	0	0	0	0	6	6	0	0	0	0	0	0
2002	719	2564	3283	0	202	0	0	0	0	202	60	42	16	84	0	0	0
2003	813	2902	3715	231	13	0	0	0	0	244	75	98	43	28	106	53	159
2004	888	2923	3811	267	15	0	0	0	0	282	58	179	23	22	109	56	244[e]
2005	876	3339	4215	1	96	0	0	0	17	114	23	54	20	17	109	56	246[e]
2006	1484	3531	5015	861	56	32	8	87	0	1044	205	513	245	81	109	56	245[e]
2007	1377	2512	3889	0	4	47	12	0	0	63	53	6	0	4	109	56	245[e]
2008	2070	2624	4694	1288	160	59	107	112	0	1726	516	632	332	246	109	56	245[e]
2009	1500	1469	2969	0	4	1	0	0	0	5	5	0	0	0	109	56	245[e]
2010	1644	1539	3183	3	0	4	0	0	0	7	7	0	0	0	109	56	245[e]
IBMP total				2651	556	143	127	199	17	3693					869	445	1874[f]

[a] Total includes bison harvested by game wardens and State of Montana hunters during 1973 through 1991, and state and tribal hunters after 2000.

[b] Aerial survey data not available during summer survey period (July–August).

[c] The Final Environmental Impact Statement reported 433 bison, but records maintained by Yellowstone National Park only indicate 370 bison.

[d] Total does not include an unknown number of bison (less than 100) captured at the north boundary and consigned to a research facility at Texas A&M University.

[e] Total includes additional culls of 79–81 bison at either boundary to reduce the population to 3000 animals.

[f] Based on summing mean culls across an 18-year span of model projections (1997–2011), a stochastic model by G. Sargeant, US Geological Survey, Northern Prairie Wildlife Research Center, predicted a total of 1382 bison would be sent to slaughter and another 3792 bison would be sent to quarantine (US Department of the Interior and US Department of Agriculture, 2000a, p. 435).

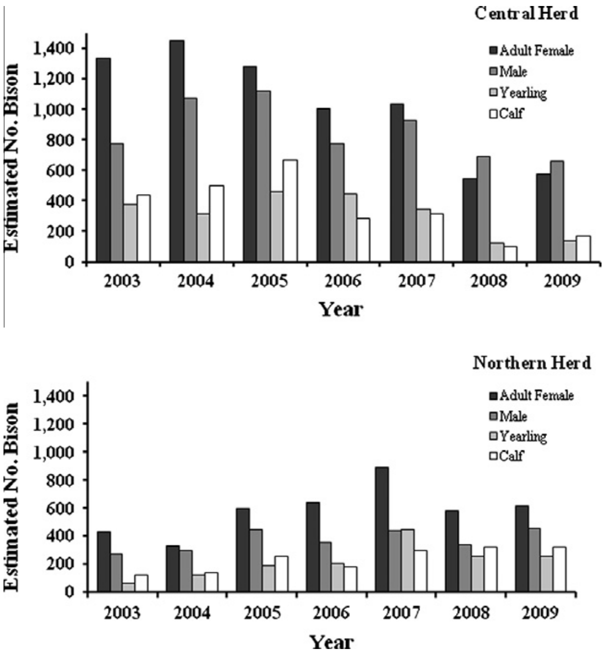

Fig. 3. Abundance of adult (greater than 1 year-old), yearling, and calf bison in the central and northern herds based on ground and air composition surveys in Yellowstone National Park during July 2003–2010. Estimates were derived using cluster sampling methods (Steinhorst and Samuel, 1989; Samuel et al., 1992).

Brucellosis risk management actions have been periodically implemented under the IBMP to reduce the numbers of bison attempting to move outside the park. However, more than 1000 bison (21%) were culled from the population during winter 2006 and 1700 bison (37%) were culled during winter 2008 because hazing was no longer effective at keeping them in the park or adjacent conservation areas, as required during step 1 of the IBMP (Fig. 1; Table 4). Frequent large-scale, non-random culls could have unintended effects on the long-term conservation of bison, similar to demographic side effects detected in other ungulate populations around the world (Ginsberg and Milner-Gulland, 1994; Schaefer et al., 2001; Coulson et al., 2001; Raedeke et al., 2002; Nussey et al., 2006). For example, bison sent to slaughter from the west ($n = 556$) and north ($n = 2650$) boundaries during 2003–2008 were female-biased (1.8 females per male in 2003, 3.0 in 2004, 2.3 in 2005, 5.3 in 2006, and 1.2 in 2008) and likely contributed to changes in the gender ratio of bison greater than 1 year-old in the central herd from 1.7 ± 0.2 (standard deviation) females per male in 2003 to 0.9 ± 0.2 female per male in 2009 (Fig. 3). In contrast, the sex ratio of the northern herd remained nearly constant from 1.6 ± 3.0 females per male in 2003 to 1.4 ± 1.2 females per male in 2009 owing to fewer culls of females from this herd and dispersal of female and juvenile groups into the northern herd from the central herd.

Skewing bison sex ratios in favor of males could increase mate competition among males and result in higher levels of aggression and mortality during the breeding season. Also, over-winter survival is usually lower in males than females in large sexually dimorphic species such as bison due to the expenditure of resources during the rut (Clutton-Brock et al., 1982). For male Yellowstone bison, internal resources depleted during the autumn rut cannot be replenished until new forage is produced in the spring. Thus, management actions that skew the sex ratio in favor of males may further reduce male over-winter survival by increasing the intensity of competitive interactions during the breeding season.

Large-scale culls also contributed to a substantial reduction in juvenile cohorts when captured bison were not tested for brucellosis exposure before being removed from the population. Bison captured during winter 2004 were tested for brucellosis and only test-positive animals were culled from the population. Since relatively few calves show positive responses on serological tests (Treanor et al., 2007), few calves were culled during this winter. During winters 2006 and 2008, however, the majority of captured bison were not tested for brucellosis because managers did not want to fill capture facilities with test-negative bison in early winter and hold them for several months until spring. Thus, many seronegative

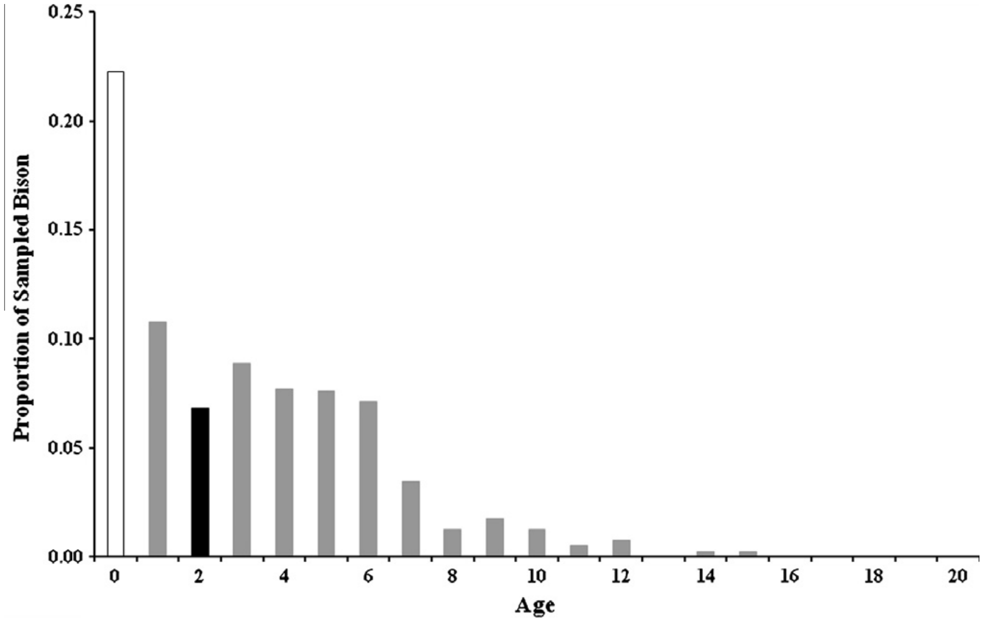

Fig. 4. Relative age-specific proportions of 488 female bison processed at the Stephen's Creek capture facility near the northern boundary of Yellowstone National Park during winter 2008–2009. Ages were determined using incisor eruption patterns and cementum annuli analysis. The darkened column corresponds to the reduced cohort resulting from culling nearly one-third of surviving calves during winter 2005–2006, and white column illustrates that more than one-half of the 2008–2009 calf crop was culled. Age could not be determined on some (0.19) bison >=5 years of age and, as a result, figure proportions do not sum to one.

bison were culled rather than being held and released back into the park, including 245 and 332 calves in winters 2006 and 2008, respectively, which equates to between one-third and one-half of the calves from the population. These culls created reduced cohorts (Fig. 4), similar to predicted gaps in population age structure of bison in Wind Cave National Park, South Dakota when large numbers of calf and yearling bison were culled every 2–3 years (Millspaugh et al., 2008).

In addition, large-scale culls of females apparently reduced the productivity of the central herd, which decreased from between 0.71 and 0.75 ± 0.01 juvenile (calves and yearlings) per female greater than 2 years-old during 2004–2007 to 0.49 ± 0.10 in 2008 and 0.63 ± 0.01 in 2009. Conversely, there is some indication that the productivity of the northern herd has increased (i.e., 0.59 ± 0.01 in 2005, 0.74 ± 0.01 in 2006, 0.79 ± 0.01 in 2007, 0.88 ± 0.11 in 2008, and 0.86 ± 0.01 in 2009). The highest reproductive value for Yellowstone bison is for animals between 3 and 6 years of age (Fuller et al., 2007), and reduced calf cohorts from 2006 and 2008 owing to large, non-random culls are entering these age classes, which may be contributing to the diminished productivity detected in the central herd.

Overall, differential culling of bison from the central herd lowered the actual (including culls) growth rate of the herd ($\lambda = 0.94$), while the actual growth rate of the northern herd was relatively high ($\lambda = 1.11$) during the IBMP era (Table 3). The central herd has the potential to rebound if management culls become fewer and less frequent because its maximum potential growth rate was moderate ($\lambda = 1.07–1.08$) entering the IBMP era (Fuller et al., 2007). However, the actual growth rate of the central herd during years 2007 and 2009 when culls were minimal was only $\lambda = 1.04$ (Geremia et al., 2009; unpublished data).

The expected long-term effect of continued, sporadic, large-scale culls is a slower-growing bison population with large fluctuations in abundance. Removing juvenile cohorts creates gaps in the population age structure, while removing young adult females that contribute the most to population productivity could reduce the resiliency of Yellowstone bison to quickly recover from reductions. Also, the large-scale culling of Yellowstone bison could have consequences that persist for multiple generations after culling has ceased. In long-lived, age-structured populations such as bison, a rapid increase in population density after release from culling can lead to a sequence of changes in age-specific fecundity and survival that affect fluctuations in population size for many years (Eberhardt, 2002). For example, different vital rates responded to increased density at different rates in red deer, causing long-term changes to the demographic structure of the population that persisted for decades (Coulson et al., 2004). Thus, sporadic, non-random, large-scale culls of bison have the potential to maintain population instability (i.e., large fluctuations) by altering age structure and increasing the variability of associated vital rates. Long-term bison conservation would likely benefit from management practices that maintain more population stability and productivity.

To date, the bison population has shown remarkable resiliency to recover from large-scale culling for population and brucellosis control (United States Fish and Wildlife Service [USFWS], 2007). The overall abundance of Yellowstone bison during the IBMP period (2001–2010), based on counts during July–August, was between 2432 and 5015, with a count of 3900 bison in 2010 despite culls of more than 1000 bison in 2006 and 2008 (White et al., 2009, unpublished data). Culling has not substantially altered the migratory behavior of bison which continue to move out of Yellowstone National Park during winter in search of food (Plumb et al., 2009). Also, there is no evidence that culling has significantly altered the genetic structure or diversity in the Yellowstone bison population. However, our analyses suggest the continuation of erratic, large-scale culls over the coming decades could have unintended consequences on the demography of Yellowstone bison. We certainly have not established a causal link between culls and possible demographic effects, and acknowledge that other reasonable hypotheses exist. However, given the potential effects identified herein, we recommend that best management practices for preventing disease transmission should be conservative to avoid undermining long-term conservation efforts where impacts are more subtle and occur over a longer time period. While managers can annually monitor and react to prevent disease transmission from wildlife to livestock, some of the effects to wildlife associated with these actions may not be detectable for decades (e.g., genetic diversity) and, as a result, unintended consequences may occur. Thus, it is difficult to balance competing objectives to prevent disease transmission from infected wildlife to livestock, while conserving healthy wildlife populations.

6. Implications

Today, there are more than 500,000 plains bison in North America and the species is no longer susceptible to demographic extinction (Boyd, 2003). However, less than 4% (20,000) of these bison are in herds managed primarily for conservation and less than 1.5% (7500) can be classified as having no evidence of genes from inter-breeding with cattle (Halbert and Derr, 2007; Hedrick, 2009). Instead, most bison are selectively bred and fed for meat production, mixed with cattle genes, protected from natural predators, and managed in fenced pastures (Sanderson et al., 2008). Thus, the majority of bison no longer have the significant influence they once did on grasslands and other ecosystems, including shaping the landscape by creating a mosaic of grazing intensities, providing a key link in nutrient cycling, competing with other ungulates, making wallows and small wetlands, and serving as a major converter of grass to animal biomass that provided food for American Indians, European settlement, predators, scavengers, and decomposers (Knapp et al., 1999; Truett et al., 2001; Freese et al., 2007; Sanderson et al., 2008). As a result, Freese et al. (2007) concluded that plains bison were ecologically extinct across the Great Plains and other grassland regions of North America.

Yellowstone bison comprise the largest (2400–5000) conservation population of plains bison, and are unique in that they have existed in a wild state since prehistoric times (Gates et al., 2005). Yellowstone bison are managed as wildlife in multiple, large herds that migrate and disperse across an extensive landscape (>90,000 ha) they share with a full suite of native ungulates and predators, and are subject to natural selection factors such as competition for food and mates, predation and survival under substantial environmental variability (Becker et al., 2009; Plumb et al., 2009). Thus, they have retained the adaptive capabilities of plains bison, which is an essential quality for restoring other wild populations, and contribute significant and unique genetic diversity to plains bison (Halbert, 2003; USFWS, 2007). The ecological future of plains bison could be significantly enhanced by resolving issues of disease and social tolerance for Yellowstone bison so that their wild state and genetic diversity are retained and can be used to synergize the recovery of the species and the restoration of grassland biodiversity across central and western North America (Freese et al., 2007; Sanderson et al., 2008; USDI, 2008; Gates et al., 2010). Thus, in the remainder of this section we recommend several adaptive management adjustments to the IBMP that can be grouped into three strategic categories: (1) managing brucellosis transmission risk; (2) conserving a viable population of wild bison; and (3) reducing the prevalence and transmission of brucellosis.

Yellowstone bison will continue to migrate into Montana during winter, with higher numbers migrating as bison abundance and winter severity increase (Geremia et al., 2011). Without human intervention, some bison will not migrate back into Yellowstone National Park during spring, but will attempt to expand their range into suitable habitat areas in Montana (Plumb et al., 2009). Thus, a deliberate risk management strategy such as the IBMP is necessary to maintain separation between bison and cattle and prevent the tangible risk of brucellosis transmission between these species (Flagg, 1983; Davis et al., 1990; Cheville et al., 1998). However, migrations by hundreds of bison into Montana have resulted in large culls when attempts to deter these movements failed (Plumb et al., 2009). Also, there are political and social concerns about allowing these massive wild animals in Montana, including human safety and property damage, conflicts with private landowners, depredation of agricultural crops, competition with livestock grazing, lack of local public support, and lack of funds for state management (Boyd, 2003). Thus, there is a desire by managers of the IBMP to limit bison abundance below the estimated food-limited carrying capacity (5500–7500) of the park (Coughenour, 2005) to reduce the frequency of large migrations by bison into Montana, and the use of large shipments of bison to domestic slaughter facilities to limit their abundance and distribution (White et al., 2009). Developing and implementing a plan to regulate the bison population between approximately 2500–4500 animals should satisfy collective interests concerning the park's forage base, bison movement ecology, brucellosis risk management, and prevailing social conditions (Plumb et al., 2009). Also, recent genetic analyses and computer simulations indicate that 95% of existing allelic diversity should be maintained for more than 100 years with a fluctuating population size that increases to more than 3500 bison and averages approximately 3000 bison, regardless of the culling strategy (Pérez-Figueroa et al., 2010).

Hunting in Montana by state and treaty hunters could play a more significant role in limiting bison numbers and distribution outside the park to reduce brucellosis transmission risk and the frequency of large shipments of bison to domestic slaughter facilities (USDI et al., 2008). However, a successful hunting paradigm would necessitate increased tolerance for bison in Montana, better access for hunters, and creative harvest strategies with non-traditional seasons in late winter and spring. Increased tolerance for wild bison in areas of Montana adjacent to Yellowstone National Park should be attainable without increasing the risk of brucellosis transmission, given the removal of cattle from most of these areas and spring turn-on dates used by cattle operators in close proximity occur in mid- to late June, at which time the risk of brucellosis transmission is about zero (Aune et al., 2007; Jones et al., 2010). Kilpatrick et al. (2009) showed that areas of transmission risk from bison to cattle are localized in time and space, which offers great potential for management actions such as vaccination of bison and cattle, fencing, hazing, delaying cattle turn-on dates, and private land conservation incentives to provide greater tolerance for bison on low-elevation winter ranges in Montana while maintaining spatial and temporal separation between bison and cattle (USDI et al., 2008). Thus, IBMP managers should work with public agencies and willing landowners to identify areas of habitat for bison without cattle and adjust zone boundaries in the plan to reflect this increased tolerance.

In addition, the ecological and genetic value of Yellowstone bison to facilitate the conservation of plains bison warrants efforts to relocate some disease-free Yellowstone bison to suitable quarantine and restoration sites (Freese et al., 2007; Sanderson et al., 2008; Gates et al., 2010). Diverse constituencies that cross many social and economic layers of society support the re-location of surplus Yellowstone bison to suitable restoration areas in North America. For example, managers at Yellowstone National Park consult with 26 associated American Indian tribes and 83 other tribes that consider bison culturally significant to their heritage. Thus, managers of Yellowstone bison should engage with stakeholders to develop feasible options for sending "surplus," brucellosis test-negative, bison to suitable quarantine facilities operated and funded by tribal governments and other organizations for further surveillance and eventual release for conservation purposes.

Bison management and vaccination conducted only at boundary capture facilities is unlikely to yield significant long-term reductions in brucellosis infection (Treanor et al., 2007). Thus, efforts to reduce the prevalence of brucellosis in bison through vaccination or a combination of methods would be most effective through a sustained, park-wide effort that can consistently and reliably deliver vaccine to a large portion of eligible bison each year over decades. Such a program will be controversial, logistically challenging, expensive, and intrusive, with no guarantee of successfully reducing brucellosis prevalence to near zero. The primary reasons for implementing actions to suppress brucellosis would be to reduce transmission of the disease among bison and possibly to cattle, and increase tolerance for bison on essential winter ranges in Montana. However, there is no guarantee of a substantial increase in tolerance due to non-disease political and social concerns (USDI, 2010). Chronic brucellosis infection does not adversely affect the long-term viability of Yellowstone bison (Fuller et al., 2007; Geremia et al., 2009), though it has prevented the use of their unique wild state and adaptive capabilities to synergize the restoration of the species in the greater Yellowstone area and elsewhere (Freese et al., 2007; Sanderson et al., 2008; Gates et al., 2010). Thus, an essential step for the National Park Service is to complete environmental analyses and decide if a comprehensive vaccination effort for Yellowstone bison is desirable, feasible, and sustainable.

Nishi (2010) explored current management issues for plains and wood bison infected with transmissible livestock diseases and recommended the application of best management practices within an adaptive management process to reduce transmission risk, increase social tolerance, and facilitate the restoration of bison. The IBMP managers attempted to implement similar practices within a risk framework and adaptive process and, as a result, the findings and implications in this article are pertinent to the management of wood bison, European bison or wisent (*Bison bonasus*), and other large ungulates worldwide that are intensively managed within conservation boundaries due to transmissible livestock diseases or social intolerance. For example, free-ranging wisent in the Białowieża Primeval Forest (1500 km^2) that straddles the Polish-Belarussian border are occasionally culled to stabilize population size, which could unintentionally reduce the already low genetic variability of the population (Pucek, 2004; Mysterud et al., 2007). Thus, management adjustments and increased tolerance are needed to allow natural selection to operate more freely on this population and facilitate reintroductions to establish bison metapopulations (Olech and Perzanowski, 2002; Perzanowski et al., 2004; Perzanowski and Olech, 2007). African buffalo testing positive for bovine tuberculosis are being culled in Hluhluwe-Imfolozi Park (Jolles et al., 2005), South Africa, while vaccination of buffalo is being considered as a means of controlling the disease in Kruger National Park, South Africa (Cross and Getz, 2006). Alternatively, movement restrictions for cattle and culling of wild boar and red deer have been proposed to control bovine tuberculosis in Doñana Biosphere Reserve (Gortázar et al., 2008). Similar to the situation in the greater Yellowstone ecosystem with bison and elk, alternate wildlife species that can serve as spill-over hosts or maintain disease infection independently complicate disease management.

In summary, the risk of disease transmission from migratory ungulates to livestock near reserve boundaries often restricts ungulates to areas that do not contain all the seasonal habitats necessary for their survival. Even relatively large reserves such as Yellowstone National Park generally contain only a subcomponent of the habitat needed by migratory ungulates. Long-term conservation of plains bison requires restoring populations to other locations. Yellowstone bison provide the wild state and adaptive capabilities needed for restoration but, to date, the brucellosis issue has prevented their use in restoration efforts. Thus, management plans should incorporate a conservation component that does not limit wildlife to isolated reserves, but facilitates responsible restoration efforts for long-term conservation.

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