Managing the abundance of bison in Yellowstone National Park, winter 2012

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EXECUTIVE SUMMARY

Background

Yellowstone National Park (YNP) developed a plan to manage the abundance of bison during the winter of 2012 using population data, modeled forecasts of movement, and a suite of wildlife management tools, consistent with the 2000 Interagency Bison Management Plan (IBMP) and subsequent adaptive management plans. Specifically, YNP is managing for an end-of-winter bison target of 3,000, while maintaining or progressing towards the following desired conditions:

- Bison abundance averages 3,000-3,500 per decade.
- Sex ratio of about 50% males and 50% females, and age structure of about 80% adults and 20% juveniles at the conclusion of winter in the central and northern breeding herds.
- Approximately equal abundance in the central and northern breeding herds.
- Maintain the processes of migration and dispersal.
- More than 50% decrease in brucellosis prevalence in bison.

In 2011, observers counted 3,720 bison in YNP, with 2,314 bison in the northern breeding herd and 1,406 in the central breeding herd. The sex ratio of bison observed in the central interior is skewed towards males. This is the largest number of bison ever observed in northern Yellowstone.

Population and movement models for bison were developed to explore strategies for reducing bison numbers towards an end-of-winter target of 3,000, while progressing towards equal abundance in each herd and sex ratios of 50% adult males and 50% adult females. Population and movement models, parameterized with environmental conditions, such as average snow pack and forage values, predicted with high certainty that more than 750 bison will migrate to the north boundary of YNP during the upcoming winter and more than 300 bison will migrate to the west boundary. Model-generated predictions of the number of bison surviving winter 2012 (November 2011-May 2012) without any hunting or management removals averaged 3,345 (95% confidence intervals = 2,800-3,969), including 2,141 (1,692-2,686) in the northern breeding herd and 1,205 (928-1,531) in the central herd. The certainty of total abundance being between 2,500 and 3,500 bison was 0.71, with an 88% chance of there being more than 3,000 bison.

Management Recommendations

Model results indicate that approximately 330 bison should be removed from the population during winter 2012. These efforts will increase the certainty of abundance being between 2,500 and 3,500 at the end of winter to more than 90%. Management removals of 30 adult male bison from the central herd bison and 300 bison (200 adult females, 50 yearlings, and 50 calves) from the northern herd should increase our certainty of progressing towards desired conditions in terms of age, herd, and sex structure. In the central herd, removal of 30 adult male bison could be accomplished through hunter harvest in Montana north of West Yellowstone. The 200 adult female bison from the northern herd could be removed through hunter harvest in Montana near Gardiner and the selective culling of bison likely to be infectious at boundary capture facilities. Fifty calf and 50 yearling bison from the northern herd could be removed through (1) hunter harvest, (2) shipment of seronegative bison to operational quarantine facilities on tribal or other lands, (3) shipment to research facilities, and (4) selective culling of seropositive individuals at boundary capture facilities. Additional bison (20-30) may be removed north of the park during a late-winter hunt that targets bulls resisting efforts to return them to the park.

Introduction

The conservation of Yellowstone bison from near extinction in the late 19th century to approximately 3,700 animals in summer 2011 has led to conflict regarding perceived overabundance, the potential for transmission of brucellosis from bison to cattle, and safety and property concerns when bison move into Montana. Prior to 1969, bison spent winter within Yellowstone National Park because decades of culling reduced numbers to less than 500 bison and there was a lack of tolerance for bison on winter ranges outside the park (Plumb et al. 2009). However, park managers ceased culling bison inside Yellowstone in 1969 and numbers increased to more than 2,200 by the mid-1980s. As numbers increased, seasonal migrations became the norm, with some bison moving from higher-elevation summer ranges to lower-elevations in and outside the park during winter (Bruggeman et al. 2009). The numbers of bison migrating increased with abundance, snow depth and hardness, and learning (Geremia et al. 2011).

The Yellowstone bison population is infected with brucellosis, which may induce abortions or the birth of non-viable calves and can be transmitted between bison and cattle (Rhyan et al. 2009). Thus, the federal government and the State of Montana agreed to a bison management plan in 2000 that established guidelines for cooperatively managing the risk of brucellosis transmission from bison to cattle. The plan emphasized conserving the bison population and allowing some bison to occupy winter ranges on public lands in Montana (U.S. Department of the Interior and U.S. Department of Agriculture 2000). Due to risk management and other concerns, more than 3,600 bison were removed from the population during 2001 to 2010, with more than 1,000 bison and 1,700 bison being removed from the population during winters 2006 and 2008, respectively. These culls unintentionally removed more calf and female bison from the central breeding herd which, if continued over time, could result in alterations of the sex and age structure of the population and consequent changes in demographic processes that could persist for decades (White et al. 2011). Also, productivity in the northern breeding herd increased, resulting in record abundance in 2011, with higher portions of females and calves in the herd.

There is a need to reduce large culls of bison and their potential long-term, unintended demographic and genetic effects by implementing smaller selective culls that dampen population growth (U.S. Department of the Interior et al. 2008). This plan provides a strategy for maintaining Yellowstone bison numbers near a target of 3,000, while maintaining or progressing towards the following desired conditions:
- Bison abundance averages 3,000-3,500 per decade (which should maintain 90-95% of existing genetic diversity over the next 200 years; Pérez-Figueroa et al. 2010).
- Sex ratio of about 50% males and 50% females, and age structure of about 80% adults and 20% juveniles at the conclusion of winter in the central and northern breeding herds.
- Approximately equal abundance in the central and northern breeding herds.
- Maintain the processes of migration and dispersal.
- More than 50% decrease in brucellosis prevalence in bison.

We developed a population model using data collected from Yellowstone bison during 1970-2011 and estimated the abundance, composition, and trends of each breeding herd to evaluate the relative impacts of harvests and other types of management removals. We integrated these estimates with a model of bison migration to predict the numbers of bison moving to the park boundary each winter. These tools combined long-term monitoring data with information gained from radio-collared bison to draw conclusions with articulated certainty about future conditions of Yellowstone bison.

We developed a decision-making process to advise the management of population abundance and trans-boundary movements of bison. During June and early July, we conducted population counts and age and gender classifications of each breeding herd. We then used long-term weather forecasts and the models described above to predict herd abundances and compositions at the end of the upcoming winter, and the

magnitude of numbers of bison migrating to park boundaries. We established annual removal objectives for bison based on abundance, disease, distribution, and demographic (age, herd, sex) goals. During autumn 2011, we will update the bison operations plan to incorporate our removal objectives and other possible management actions for the coming winter. As winter progresses, monthly aerial counts, snow model projections for the park, and revised long term weather forecasts will be used to refine our predictions of the timing and magnitude of trans-boundary movements to support decision-making during winter operations.

A variety of management tools will be used to reduce bison numbers as necessary, including (1) public and treaty harvests in Montana, (2) selective culling (shipment to slaughter) at boundary capture facilities to reduce the proportion of infectious bison, (3) selective culling (shooting, shipment to slaughter) in Montana to prevent brucellosis transmission to nearby livestock or due to human safety or property damage concerns, (4) transfer of bison to American Indian tribes or other organizations for quarantine and eventual release, and (5) transfer bison to research facilities. We attended a meeting in August, 2011 to discuss our removal objectives and harvests with Montana Fish, Wildlife, and Parks and American Indian tribes with recognized treaty rights for bison on unoccupied federal lands outside Yellowstone National Park in Montana. Pregnant bison will not be shipped to slaughter facilities during their third trimester (after March 1st). During winter 2012, we will monitor and document actual hunter harvest, winter-kill, predation off-take, and management culls.

Methods

We refer to bison that congregate during the breeding season in the Hayden valley as the central herd and those that gather in the Lamar valley and associated meadows as the northern herd (Figure 1). During winter, most central herd animals eventually move west from the Hayden and Pelican valleys into the Firehole River drainage, Madison River drainage, and/or Hebgen basin in Montana. Also, some central herd animals migrate to the northern portion of Yellowstone and interact with the northern herd during winter. While most central herd migrants return to the Hayden valley during the subsequent breeding season, some have dispersed into the northern herd in recent years (Geremia et al. 2011). Bison from the northern herd typically migrate west during winter towards lower-elevation areas near Mammoth, Wyoming and Gardiner, Montana. Dispersal from the northern herd to the central herd has been negligible.

We developed a population model that estimated the (1) annual size and composition of Yellowstone bison herds during 1970-2011, (2) numbers of culls and harvests from each herd, and (3) survival, fecundity, and fetal sex ratios. We combined estimates of herd abundance, composition, and survival with information on seasonal distributions to construct a movement model. We then combined the population and movement models to evaluate harvest strategies for the bison population during the upcoming winter. Specifically, we used the movement model to predict the magnitude of out-of-park movements by bison during a winter with below average, average, and extreme snow pack conditions. Next, we removed targeted numbers of bison from various demographic categories (age, sex) and herds, accounted for those removals in the population model, and predicted changes in herd sizes and compositions during the following summer. We also estimated the certainty with which the bison population was likely to be within desired conditions for abundance and herd and gender structure.

Population model.—We used a discrete-time, state-transition framework to construct the population model (Caswell 2001). Five stages were used to portray demography in the central and northern herds. The model updated on an annual time step that coincided with the onset of the breeding season during July. This time step was chosen because we could differentiate between herd membership based on spatial association during the breeding season. Bison reach reproductive maturity at 2 years of age and we identified sub-adult (1-2 years) and adult animals (greater than 2 years). We defined the stages S_1

through S_5 to represent central herd members, including S_1 as calves, S_2 as sub-adult females, S_3 as mature females, S_4 as sub-adult males, and S_5 as adult males. For northern herd members, we defined S_6 as calves, S_7 as sub-adult females, S_8 as mature females, S_9 as sub-adult males, and S_{10} as adult males. Transition probabilities were defined for fecundity (f), calf survival (s_j), adult survival (s_a), dispersal (i), and calf gender (g; Figures 2 and 3).

We assumed that sub-adults and adults had identical survival, but calves had lower probabilities (Meagher 1973). Empirical evidence suggests that the survival of adult female bison varies across time with changes in annual snow conditions (Fuller et al. 2007, Geremia et al. 2009). Thus, we represented adult survival as a function of accumulated snow water equivalents (SWE), which is the amount of water in a column of snow; Garrott et al. 2003). Modeled values of daily SWE in meters were generated across the bison range (Watson et al. 2006, Geremia et al. 2009) and summed during the snow-covered period (October-April) to provide single annual metrics of snow pack. Calf survival is undoubtedly affected by snow, but too few years of calf survival observations were available to model its influence. Therefore, we portrayed calf survival as constant.

Previous findings indicate that brucellosis infection decreases fecundity, but it is otherwise relatively constant between years (Fuller et al. 2007, Geremia et al. 2009). We used a single parameter (f) to estimate the probability of birth and neonate survival. We did not differentiate mortality occurring immediately after birth since annual calf counts occurred during June, which is after peak-calving (Jones et al. 2010). Dispersal of Yellowstone bison is largely unidirectional with individuals moving from the central herd to the northern herd between breeding seasons (White et al. 2011). Thus, we portrayed dispersal as constant across time.

Our analytical approach was to obtain posterior distributions of model parameters and numbers of bison in demographic stages across time. We created a hierarchy in our model structure by differentiating between true and observed numbers of bison in each demographic stage. True numbers of bison were conditional on our model parameters (Figures 2 and 3) and process error (Clark 2007). Our observations were conditional on true states and measurement error (Clark 2007). We incorporated the results of detailed studies on Yellowstone bison as informative prior distributions for model parameters. We also incorporated long-term population counts and classification data as likelihoods of true states conditional on parameters, and observations conditional on true states (Appendix I).

Initial numbers of bison in each demographic stage were estimated. The bison population experienced a prolonged period of selective culling within the park to reduce brucellosis prevalence during 1950-1966. Females were preferentially removed, which created a population biased towards males (Meagher 1973). We used compositions of harvests recorded during 1964-1966 (Meagher 1973) and aerial counts during 1970 (Taper et al. 2000) to estimate the initial number of animals in each age and gender class.

Bison exiting park boundaries were historically shot by agency personnel since animals were not allowed outside of Yellowstone National Park due to threats of brucellosis transmission to livestock (Cheville et al. 1998). Fewer than 10 bison were culled during any winter until 1984-1985 when 88 animals were removed outside the northern park boundary. Thereafter, episodic removals of more than 500 migrating bison occurred during some winters as animals were either shot by state hunters or agency personnel, or gathered and shipped to domestic slaughter facilities by federal and state personnel (White et al. 2011). We needed to attribute removals occurring to each herd to model the bison population. Central herd bison exclusively exited the western park boundary, while both central and northern herd bison exited the northern park boundary. Also, while total numbers of removals were known, only partial information was available on composition and herd membership. The annual composition of bison removed near the western boundary of the park was estimated from the subset of observed age and gender composition. Similarly, all north boundary removals during 1970-1993 were attributed to the northern herd.

Thereafter, north boundary removals were composed of members of each herd, with central herd size influencing the number of central herd animals removed (Geremia et al. 2011).

Removals were subtracted from model estimates of the true numbers of bison prior to updating. The number of bison in each demographic stage was treated as a lognormal random variable, which is an appropriate error distribution for a multiplicative process such as population growth. Process model predictions were based on (1) a transition matrix of survival, birth, and dispersal, (2) the log of the number of bison in demographic stages adjusted by removals, and (3) process model variance on the log scale.

We created several data models to relate the likelihood of the initial conditions (e.g., starting numbers of bison in each demographic stage during 1970) and process model predictions (e.g., unobserved number of bison in each demographic stage during 1971-2010) to our observations during long-term monitoring efforts. Aerial breeding season counts of Yellowstone bison herds were completed during June-August from 1970-2010 with between one and three annual surveys. Bison are highly visible during the breeding season as animals congregate in large groups in open areas for the rut (Hess 2002). However, some unknown component of the population was missed by aerial observers and we accounted for this uncertainty by explicitly modeling observation error using replicated counts.

In addition, a single aerial count was completed during most years at the conclusion of the birthing period, which generally occurred in the beginning of June. Neonate calves were differentiated from other bison during counting. We also completed annual composition counts of the bison population during July 2002-2010. Efforts began with a comprehensive aerial survey where numbers of bison in mixed gender and bachelor groups were counted. The presence of calves that are bright orange in color simplified identification of mixed gender groups. Ground observers subsequently surveyed areas occupied by mixed gender groups encountering more than 80% of herd members during single-day efforts. Numbers of calves, male and female sub-adults, and male and female adults located in mixed gender groups were recorded.

Removal scenarios.—We identified several desired conditions supportive of long-term conservation and preservation goals (White et al. 2011), and assessed the certainty of the Yellowstone bison population existing within these quantifiable ranges under alternate removal scenarios. Desired conditions included (1) a population between 2,500 and 3,500 individuals, (2) 1,250-1,750 individuals in each herd, (3) a ratio of males to females in each herd between 0.90-1.10, and (4) a ratio of juveniles to adults in each herd between 0.15-0.25. These criteria were assessed at the conclusion of the projected 2012 winter and were adjusted by proposed removals for that year. Model forecasts were made assuming average snow and forage conditions since current long-term forecasts predict near normal precipitation and temperature during August 2011 through May 2012.

Movement model.—Success in implementing the proposed removals will be influenced by the numbers and timing of bison movements to boundary areas of Yellowstone National Park during winter. Thus, we developed mechanistic, nonlinear models to predict bison migration to the park boundary and evaluate the likelihood of being able to meet the removal objectives (Appendix II; Geremia et al. 2011).

We considered 142 aerial counts of bison completed near the northern and western boundaries of Yellowstone during October-May, 1990-2009. We counted all bison that were outside the park boundary or within a 5-km buffer inside the park boundary to account for animals that had left the park, were poised to leave the park, or had possibly been hazed back inside the park prior to counting. We summed these counts with the total number of bison that had migrated beyond the park boundary and were culled prior to counting to improve our measure of migration. Culls included bison that were harvested by hunters, shot by agency personnel, moved to out-of-park research or quarantine facilities, sent to slaughter, or held

in fenced paddocks until release during spring. Culls were known for each year and aerial surveys provided accurate estimates of numbers because bison are highly visible and often congregate in large groups in open areas (Hess 2002). We defined two responses measuring migration since herds differentially move towards each park boundary and are exposed to different climate conditions. $Y_{N,t}$ where $t \in [1990, 2009]$ was our observation of migration beyond the northern boundary and was represented as the annual maxima of counts of bison near the northern boundary and culls occurring prior to counting. $Y_{W,t}$ was our observation of migration beyond the western boundary and defined as the annual maxima of counts of bison near the western boundary and culls occurring prior to counting.

Covariates were defined for density, snow pack severity, and above-ground dried biomass. We completed annual breeding season counts of the northern and central herds during July-August, 1990-2009 as a surrogate for density. Bison located in the Madison, Firehole, Hayden, and Pelican valleys were considered part of the central herd, while bison on the Mirror Plateau and in the upper Lamar River valley were included in the northern herd. We defined $x_{central,t}$ as the annual count of central herd animals and $x_{north,t}$ as the annual count of the northern herd. We used a validated snow pack simulation model (Watson et al. 2006, 2009) to estimate daily SWE by averaging values across all 28.5 x 28.5-meter pixels within a 99% kernel of bison use. We summed daily model-generated averages during October 1st through April 31st, and created single accumulated annual values for the northern range ($x_{snowN,t}$), central interior ($x_{snowC,t}$), and entire park ($x_{snow,t}$).

We generated above-ground, dried, biomass (grams per square meter) estimates using modeled monthly net primary productivity from NASA's Carnegie-Stanford-Ames-Approach (CASA; Potter et al. 1993, 2007). CASA, a biophysical ecosystem model, incorporates temperature, precipitation, solar radiation, vegetation cover, and the normalized differential vegetation index (NDVI) from Landsat satellite data as inputs during the April to October growing season (Crabtree et al. 2009, Huang et al. 2010).   We considered all pixels within the 99% kernel of bison use, except for forested areas that were clipped from analysis because bison are predominantly grazers. The resulting analysis area consisted of approximately 33 meadows greater than 1 square kilometer in size and distributed across the elevation gradient of the northern and central ranges. We censored areas affected by cloud cover within years, resulting in marginal differences in the size of the analysis area between years. Due to this difference, we summed values across available pixels for each year and divided by the number of pixels. We defined $x_{forageN,t}$ for the northern range, $x_{forageC,t}$ for the central interior, and $x_{forage,t}$ for the entire park. The covariate does not exactly reflect annual plant biomass production over the growing season or standing biomass available for bison during winter due to herbivore off take during April through October. However, our measurement provides an excellent assessment of the quality of the growing season. Further, all covariates were standardized to indicate the percentage by which each was above or below 20-year averages. This facilitated model convergence and allowed us to compare the relative importance of each control on numbers of migrants.

Results

Population model.—The model-generated average abundance of the Yellowstone bison population during July 2011 was 3,654 (95% credible interval = 3,444-3,866; Figure 4). There were an estimated 2,321 (2,158-2,482) bison in the northern herd and 1,333 (1,199-1,468) bison in the central herd (Figure 5). Male to female ratios were 0.75 (0.62-0.95) in the northern herd and 1.00 (0.81-1.20) in the central herd (Figure 6). The annual median of the probability of bison being in bachelor groups ranged from 0.06-0.29, and the 2011 probability was estimated at 0.16 (0.11-0.23). However, more animals than anticipated (0.34) were observed in bachelor groups during the classification of the central herd in summer 2011, and the true male to female ratio was likely near the upper end of the credible interval. The proportions of bison in each age class were 0.76 (0.65-0.80) adults, 0.12 (0.10-0.14) juveniles, and

0.12 (0.11-0.13) calves in the central herd, and 0.72 (0.70-0.74) adults, 0.11 (0.09-0.12) juveniles, and 0.17 (0.16-0.19) calves in the northern herd. We generated productivity estimates as the ratio of juvenile (calf and yearling bison) to adult animals (male and female; Skalski et al. 2005). Northern herd productivity (0.40; 0.35-0.43) was greater than central herd productivity (0.32; 0.28-0.36), indicating the increased capacity for future growth.

We detected differential survival between adults and calves, with lower adult survival during years characterized by increased snow pack establishment (Table 1). For example, adult survival was 0.92 (0.90-0.95) when snow pack establishment was near the 42-year average, 0.87 (0.79-0.93) when 50% above average, and 0.80 (0.62-0.92) when 100% above average. Females produced 0.57 (0.53-0.61) calves each year after reaching maturity at 3 years of age (Table 1), with a slightly higher probability of male calves (0.53, 0.51-0.56).

While total numbers of annual removals from the population were known (White et al. 2011), seasonal mixing and interchange of bison between herds complicated a simple analysis of attributing removals occurring at the northern park boundary to the northern herd and attributing removals occurring at the western park boundary to the central herd. Thus, our modeling approach simultaneously estimated within-year interchange, dispersal, and herd-specific removals. Winter migration of central herd bison to the northern park boundary began during the mid-1990s and increased with bison abundance in the central herd (p_0 = -1.78, -2.70 - -0.87; p_1 = 4.80, 2.98-6.69). Dispersal of central herd bison to the northern breeding herd was 0.02 (0.01-0.03). Prior to implementation of the Interagency Bison Management Plan (1971-1999), removals of bison from the central herd near the western park boundary consisted of 548 (428-721) males, 426 (321-601) females, and 108 (57-197) calves (Figure 7). Removals near the northern boundary of the park included 653 (531-801) males, 490 (388-625) females, and 142 (94-210) calves from the northern herd, and 336 (261-434) males, 249 (192-330) females, and 138 (101-186) calves from the central herd (Figure 8). During implementation of the Interagency Bison Management Plan (2000-2011), removals of bison near the northern boundary of the park were skewed towards females and calves from the central herd. These removals included 314 (219-435) males, 428 (298-600) females, and 173 (115-256) calves from the northern herd, and 595 (460-759) males, 1,075 (890-1,280) females, and 542 (453-637) calves from the central herd (Figure 8).

Movement model.—Migration beyond the northern park boundary was affected by herd size, accumulated SWE, and above-ground dried biomass. There was greater than a 95% probability that increases in central and northern herd sizes, and accumulated SWE, increased numbers of bison migrating beyond the northern park boundary. There was also greater than a 95% probability that fewer bison migrated with increases in above-ground dried biomass.

We found a greater than 95% probability of more bison moving beyond the western boundary with increases in central herd size, increases in accumulated SWE, and decreases in above-ground dried biomass. We plotted process predictions of the modified logistic model compared to observed counts and predicted true states, and model performance decreased beginning around 2001. This finding suggests an important control on recent migrations (e.g., learning) was not included in the model. Modeling of future migrations indicated that large and episodic migrations of bison beyond the northern and western boundaries of Yellowstone would occur during the next decade.

The National Oceanic and Atmospheric Administration (NOAA) temperature and precipitation forecasting models predict average temperatures and precipitation during August 2011 through May 2012 (Table 2). Also, field assessments indicate there has been average to above-average forage production during summer 2012. Thus, the forecast for winter 2012 is average snow and forage conditions (100%) for more than 2,000 bison in the northern herd and less than 1,500 bison in the central herd. Given this

forecast, we predict more than 750 bison will migrate to the northern boundary of Yellowstone National Park and more than 300 bison will migrate to the western boundary during winter 2012 (Table 3).

Management Implications

Average productivity (ratio of juvenile to adult bison) in the central herd was high during 2002-2005 (2002: 0.42 ± 0.02 SD; 2003: 0.37 ± 0.02; 2004: 0.41 ± 0.02; 2005: 0.42 ± 0.02). Females out-numbered males (Figure 6) and several winters of below-average snow conditions resulted in high survival which facilitated growth. The central herd rapidly increased and reached record levels of abundance in 2005 (Figure 5), after which repeated, large removals at the northern and western park boundaries decreased the herd by more than 65%, altered the gender ratio, and diminished productivity to the lowest estimated value (0.24 ± 0.01) in the entire 42-year time series. Concurrently, northern herd productivity consistently increased from 0.27 ± 0.01 in 2002 to 0.40 ± 0.01 in 2011 as the herd substantially increased to record abundance in 2011 and shifted towards a greater proportion of females.

We developed removals strategies for the Yellowstone bison population to meet desired conditions for conservation, while moderating large-scale alterations to either breeding herd. Model-generated predictions of the average number of bison surviving the 2012 winter without any hunting or management removals were 3,345 (2,800-3,969), including 2,141 (1,692-2,686) bison in the northern herd and 1,205 (928-1,531) in the central herd. The certainty of total abundance being between 2,500 and 3,500 bison was 0.71, with an 88% chance of there being more than 3,000 bison. Hunting or management removals of approximately 330 bison during winter 2012 would increase the certainty of abundance being between 2,500 and 3,500 at the end of winter to more than 90%, while providing equal certainty (0.5) of there being more or less than 3,000 bison.

Disparate trends in productivity and gender ratios between the central and northern herds indicate that removals should be targeted towards juvenile and adult female members of the northern herd. Removals of 30 adult male bison from the central herd bison and 300 bison (200 adult females, 50 yearlings, and 50 calves) from the northern herd would increase our certainty of progressing towards desired conditions in terms of age, herd, and sex structure (Figure 9). Thirty adult male bison from the central herd could be removed though hunter harvest in Montana north of West Yellowstone. The 200 adult female bison from the northern herd could be removed through hunter harvest in Montana near Gardiner, and the selective culling of bison likely to be infectious at boundary capture facilities. Fifty calf and 50 yearling bison from the northern herd could be removed through (1) hunter harvest, (2) shipment of seronegative bison to operational quarantine facilities on tribal or other lands, (3) shipment to research facilities, and (4) selective culling of seropositive individuals at boundary capture facilities.

Success in implementing the proposed removals will be influenced by numbers of animals moving to boundary areas. The models predicting bison migration to the boundaries of Yellowstone National Park suggest that migration should be sufficient to meet the removal objectives during winter 2012. Model forecasts indicate these removals would provide for 0.97 certainty of fewer than 1,500 surviving central herd bison, with an equal certainty of a male to female ratio above or below 1.0 and a juvenile to adult ratio of 0.14 (Table 4). We do not recommend removal of any juvenile or adult female members from the central herd since such management would decrease the certainty of meeting desired demographic conditions. The proposed removals from the northern herd would increase the certainty of meeting desired conditions (Table 4). However, current abundance and age and gender structure will require removals of northern herd animals for several years to attain desired conditions.

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Table 1. Posterior distributions of parameters of a population model of Yellowstone bison herd during 1970-2011. Abbreviations are standard deviation (SD), credible interval (CI), logit transformation of adult female survival ($s_{a,1}$), logit transformation of the effect of snow on adult female survival ($s_{a,2}$), calf survival (s_j), fecundity (f), fetal gender (g), dispersal (i), process variance (σ), logit transformation of the proportion of central herd animals included in north boundary removals (p_0), logit transformation of the effect of central herd size on the proportion of central herd animals included in north boundary removals (p_1), observation error of replicated aerial counts of bison (σ_{obs}), and model deviance (deviance).

Parameter	Mean	SD	2.5% CI	50.0% CI	96.5% CI
$s_{a,1}$	2.48	0.19	2.15	2.46	2.87
$s_{a,2}$	-1.09	0.31	-1.66	-1.10	-0.43
s_j	0.78	0.03	0.73	0.78	0.84
f	0.57	0.02	0.53	0.57	0.61
g	0.53	0.01	0.51	0.53	0.56
i	0.02	0.004	0.01	0.02	0.03
σ	0.03	0.02	0.02	0.03	0.04
p_0	-1.78	0.47	-2.70	-1.78	-0.87
p_1	4.80	0.95	2.98	4.79	6.69
σ_{obs}	144.01	10.83	124.45	143.58	166.97
deviance	3084	25.20	3037	3084	3136

Table 2. Predictions of the National Oceanic and Atmospheric Administration (NOAA) temperature and precipitation forecasting models at <http://www.longrangeweather.com/Long-Range-Monthly-Weather-Forecasts.htm>.

	Temperature reported as departure from average	Precipitation reported as departure from average
August 2011	- 1 to 2 Degrees	+ 10 %
Sept 2011	Normal to - 1	+ or – 10 %
Oct 2011	Normal to - 1	Normal to minus 10 %
Nov 2011	- 1 Degrees	Normal to + 10 %
Dec 2011	- 1 to 2 Degrees	+ or – 10 %
Jan 2012	- 4 to 5 Degrees	+ 10 %
Feb 2012	- 2 to 4 Degrees	+ 20 %
Mar 2012	- 1 to 3 Degrees	+ 10 %
Apr 2012	+ 1 to – 2 Degrees	Normal to + 10 %
May 2012	Normal to + 1	+ 10 %

Table 3. Predicted annual maxima of bison migrating beyond the northern and western boundaries of Yellowstone National Park generated using a modified logistic process equation that incorporates the effects of central herd and northern herd size, accumulated SWE, aboveground dried biomass, and an interaction between herd size and accumulated SWE. Table values indicate approximate maxima abundances with 95% probability, e.g. the probability that there will be no more than the listed number of bison outside of the park is 0.95 given central and northern herd sizes, and accumulated SWE (snow) and aboveground dry biomass (forage) as percentages of 20-year averages.

Central	Northern		NORTH	BOUNDARY						
		Snow	60%	60%	100%	100%	100%	130%	130%	130%
		Forage	100%	60%	130%	100%	60%	130%	100%	60%
1,000	1,000	--	135	185	210	275	360	390	500	635
1,500	1,000	--	175	240	250	335	440	460	580	740
2,000	1,000	--	215	285	305	400	525	550	700	890
1,000	1,500	--	255	340	320	415	535	510	630	785
1,500	1,500	--	330	445	410	520	675	605	765	960
2,000	1,500	--	400	530	485	625	810	725	915	1,150
1,000	2,000	--	470	600	510	645	810	690	860	1,040
1,500	2,000	--	620	790	650	830	1,040	870	1,070	1,300
2,000	2,000	--	740	950	785	1,000	1,250	1,040	1,290	1,560
Central	Northern		WEST	BOUNDARY						
		Snow	60%	60%	100%	100%	100%	130%	130%	130%
		Forage	100%	60%	130%	100%	60%	130%	100%	60%
1,000	--	--	150	170	140	160	185	155	180	205
1,500	--	--	235	270	255	295	335	315	360	415
2,000	--	--	260	300	260	300	345	295	340	390

Table 4. Model-generated certainties of meeting desired conditions of age, gender, and herd structure of Yellowstone bison at the conclusion of the 2011-2012 winter comparing no removals and our recommended removal (i.e., culls and harvests) of 330 bison. Desired conditions measured at the end of winter include maintaining or progressing towards (1) a population between 2,500 and 3,500 individuals, (2) 1,250-1,750 individuals in each herd, (3) a ratio of males to females in each herd between 0.90-1.10, and (4) a ratio of juveniles to adults in each herd between 0.15-0.25.

Desired Condition	Distribution	No Removals	Remove 300 Bison
2,500-3,500 bison	park-wide	0.71	0.91
1,250-1,750	central	0.32	0.27
	northern	<0.01	0.07
0.90-1.10	central	0.32	0.31
male:female	northern	0.23	0.29
0.15-0.25	central	0.02	0.14
juvenile:adult	northern	<0.01	0.69

Figure 1. Major use areas of bison in Yellowstone National Park including bison management zones identified in the Interagency Bison Management Plan beyond which bison were rarely observed during 1990-2009.
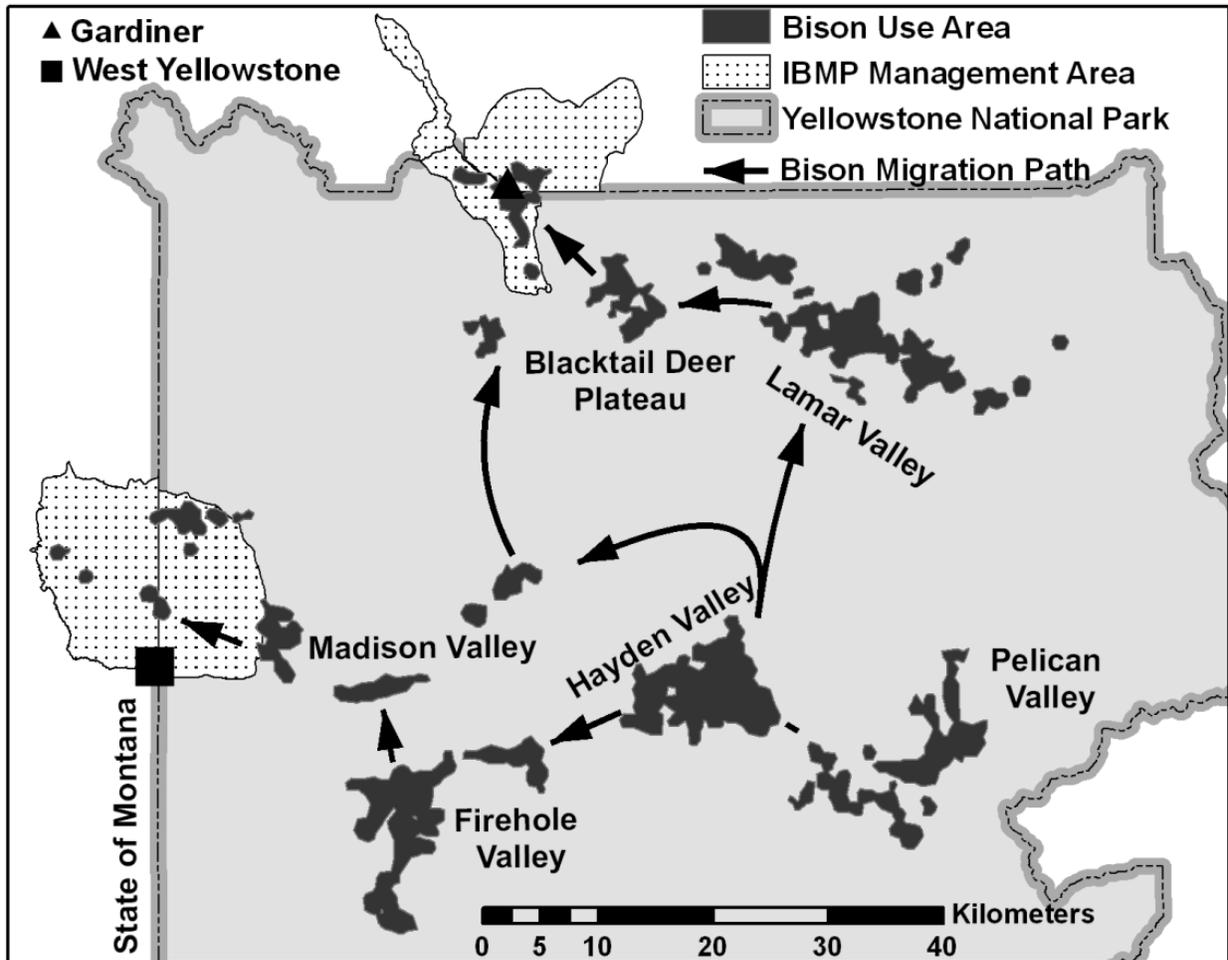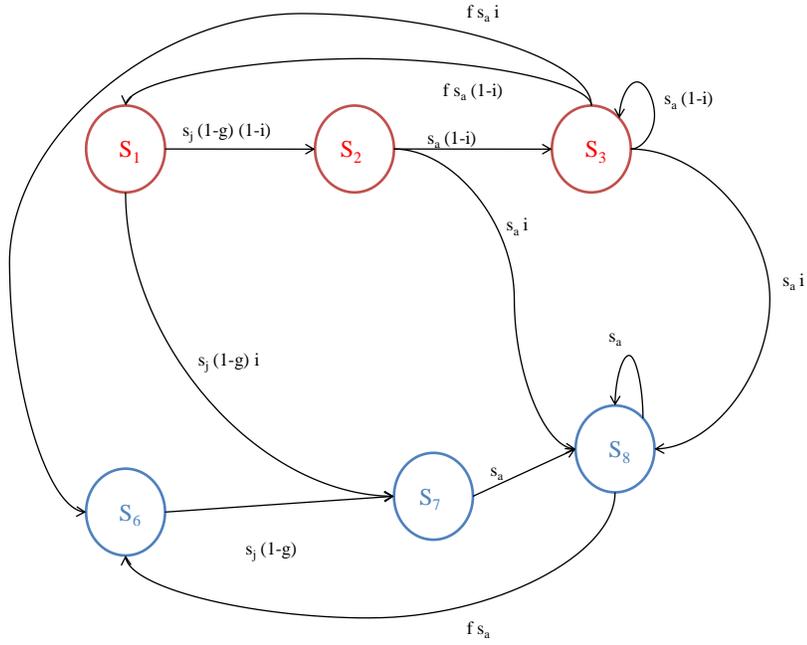
Figure 2. A conceptual model of the life cycle of calf and female Yellowstone bison. Stages S_1 through S_3 represent central herd bison, while stages S_6 through S_8 represent northern herd bison. Stages S_1 and S_6 represent calves, stages S_2 and S_7 represent sub-adult females, and stages S_3 and S_8 represent adult females. Parameters for transition probabilities were fecundity (f), calf survival (s_j), adult survival (s_a), calf gender ratio (g), and dispersal to the northern herd (i).

Figure 3. A conceptual model of the life cycle of calf and male Yellowstone bison. Stages S_1, S_4, and S_5 represent central herd bison, while stages S_6, S_9, and S_{10} represent northern herd bison. Stages S_1 and S_6 represent calves, stages S_4 and S_9 represent sub-adult males, and stages S_6 and S_{10} represent adult males. Parameters for transition probabilities were calf survival (s_j), adult survival (s_a), calf gender ratio (g), and dispersal to the northern herd (i).
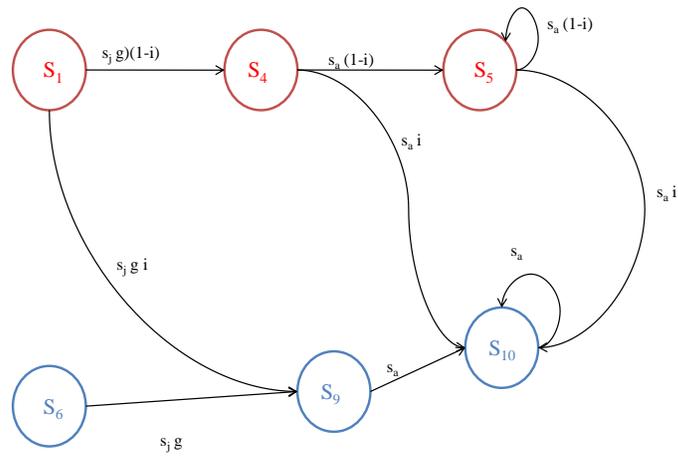
Figure 4. Model generated predictions of the abundance of bison (excluding new-born calves) in July during 1970-2014. The solid line depicts the predicted average population size, while the dotted lines depict the interval of 95% credibility. Open circles indicate the highest annual aerial counts completed each year.
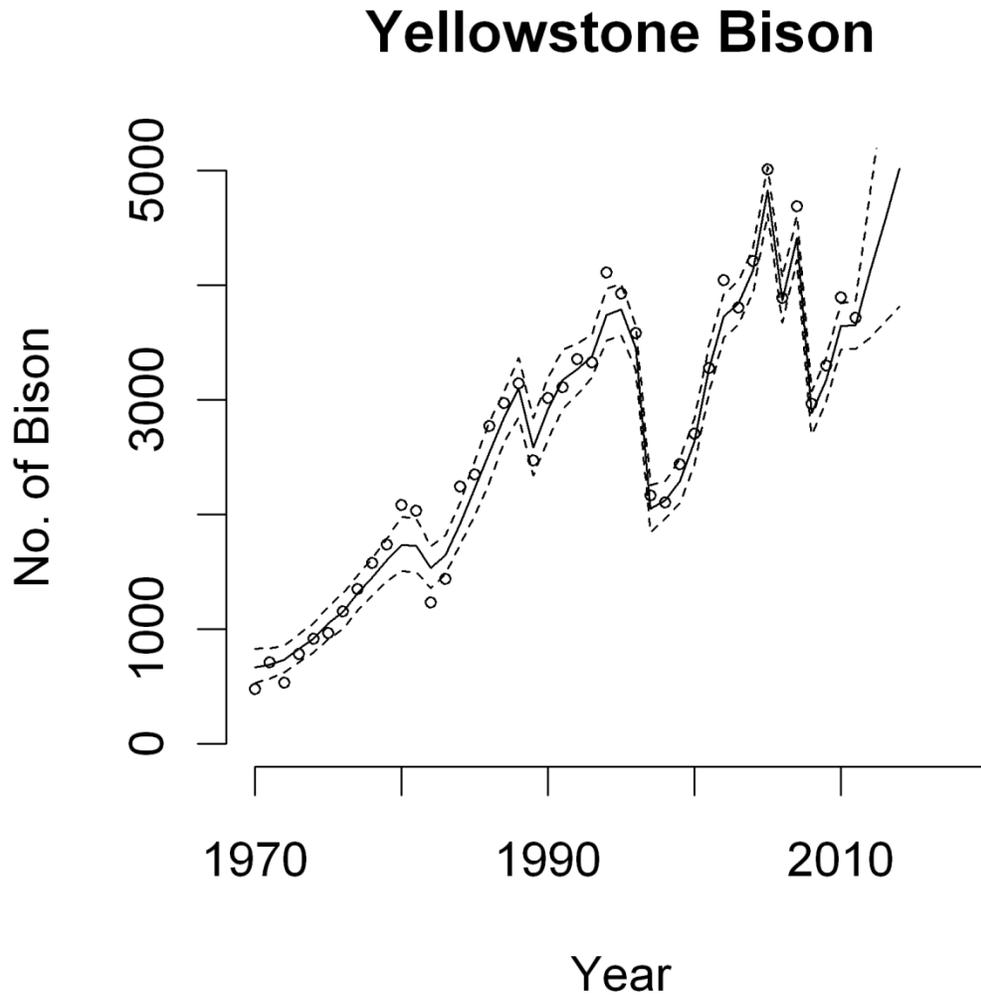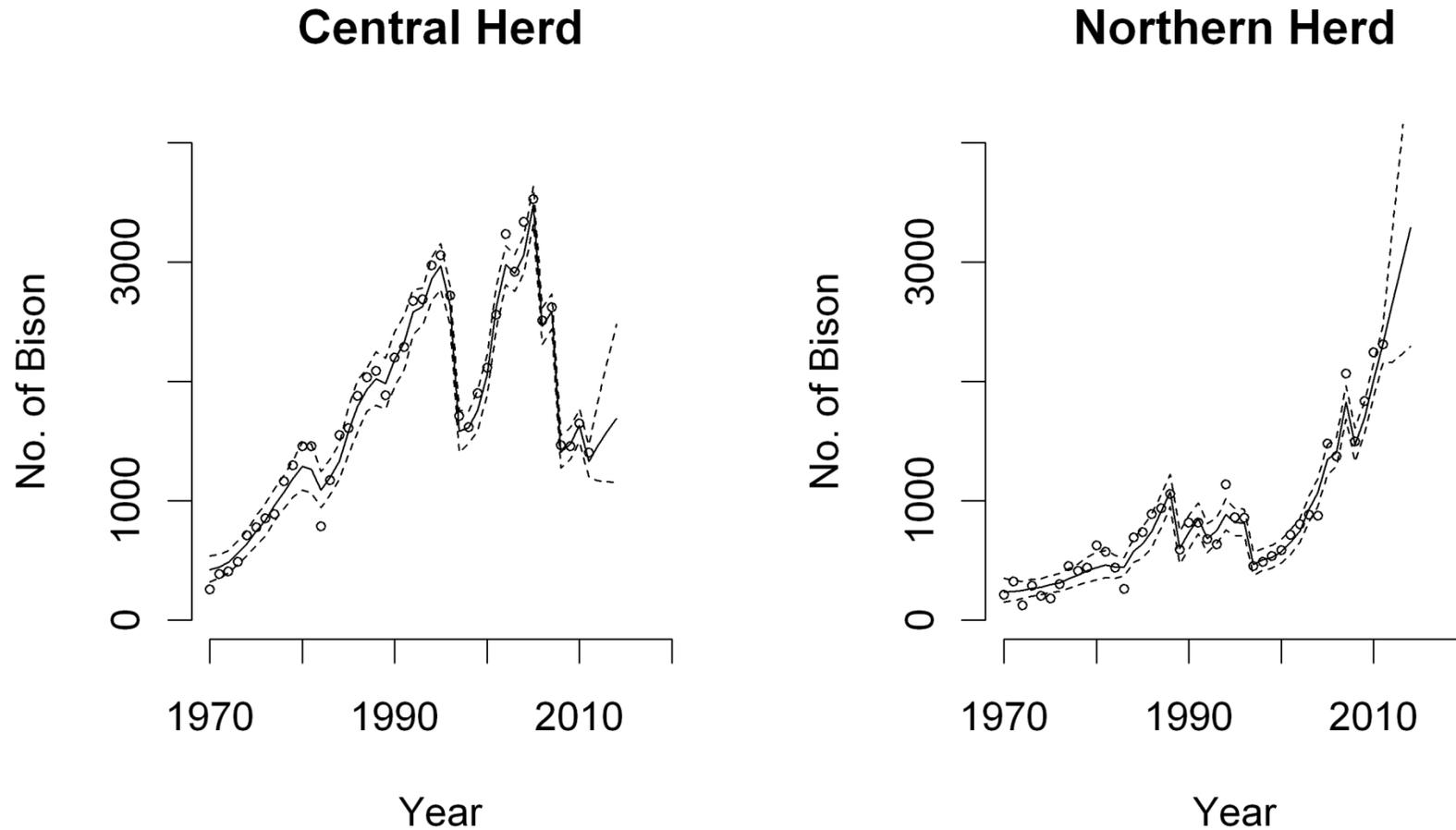
Figure 5. Model generated predictions of bison abundance (excluding new-born calves) in the central and northern breeding herds in July during 1970-2014. Solid lines depict the predicted average herd sizes, while dotted lines depict the intervals of 95% credibility. Open circles indicate the highest annual aerial counts completed each year.

Central Herd

Northern Herd

Figure 6. Model generated predictions of the ratios of males to females in the central and northern breeding herds during July from 2000-2011. Solid lines depict the predicted average ratios, while dotted lines represent the intervals of 95% credibility.
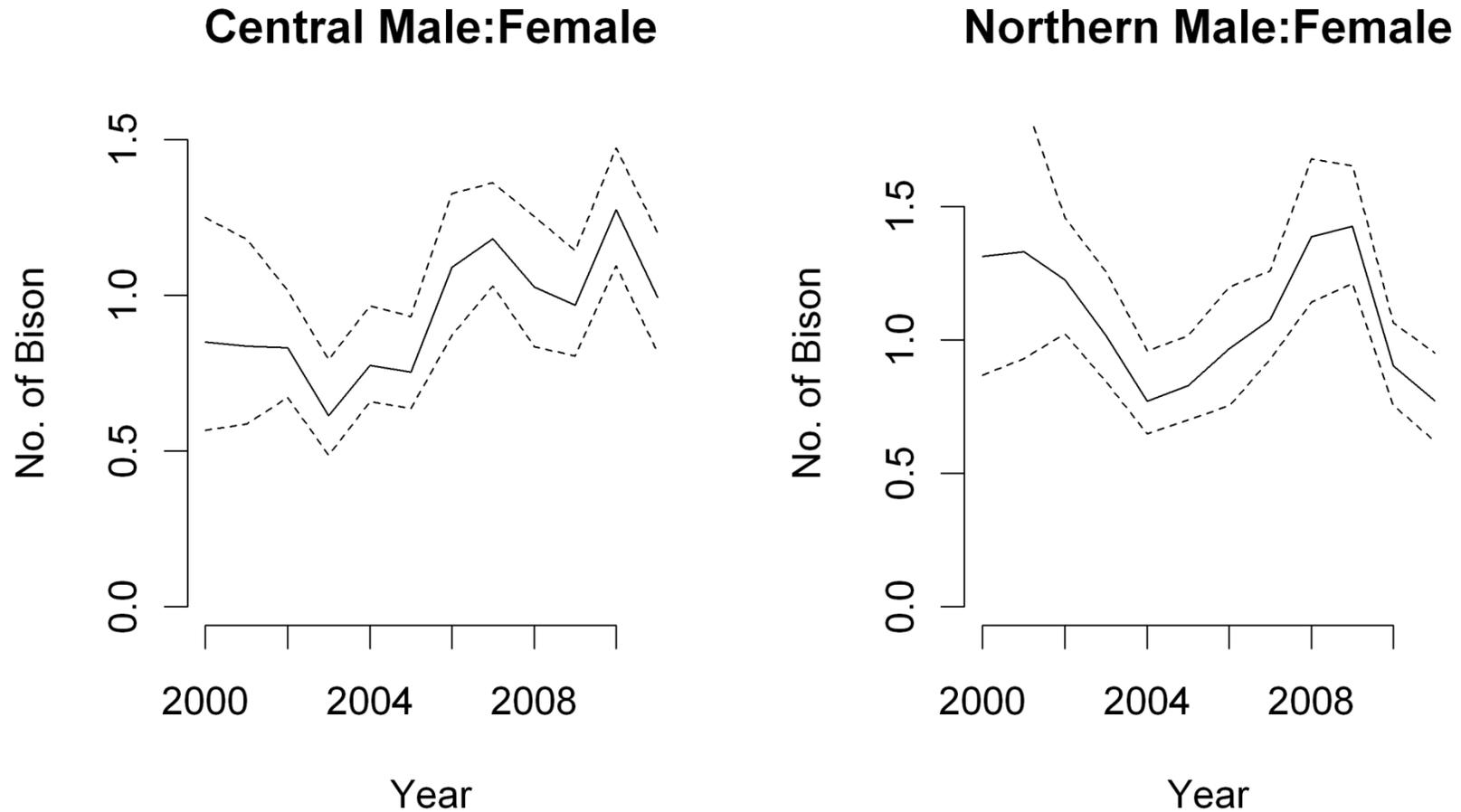
Figure 7. Model generated predictions of bison removals (harvests, management culls) from the central herd near the western boundary of Yellowstone National Park before (1971-1999) and after (2000-2011) implementation of the Interagency Bison Management Plan. Circles depict the predicted averages, while lines represent the intervals of 95% credibility.
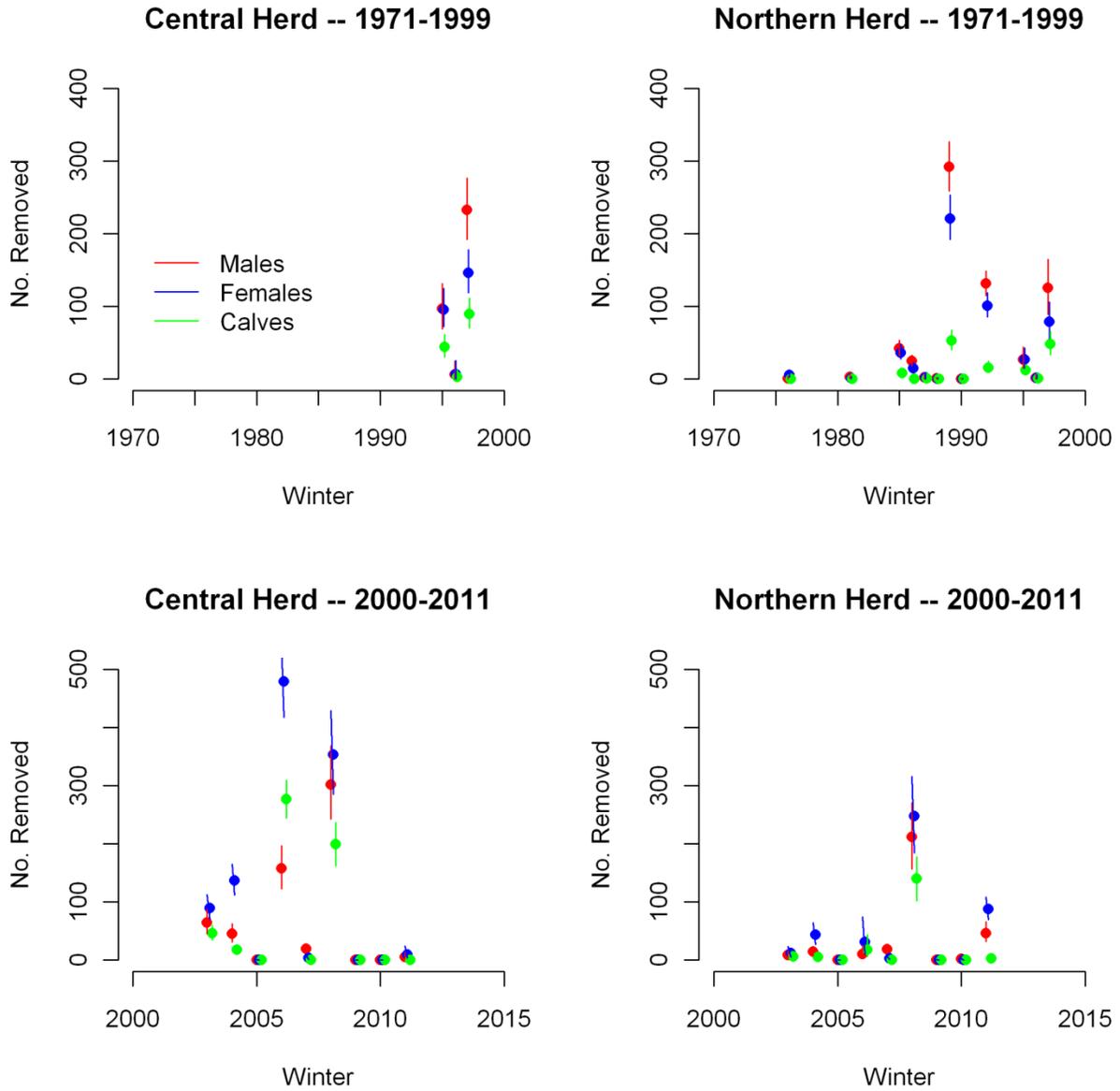

19
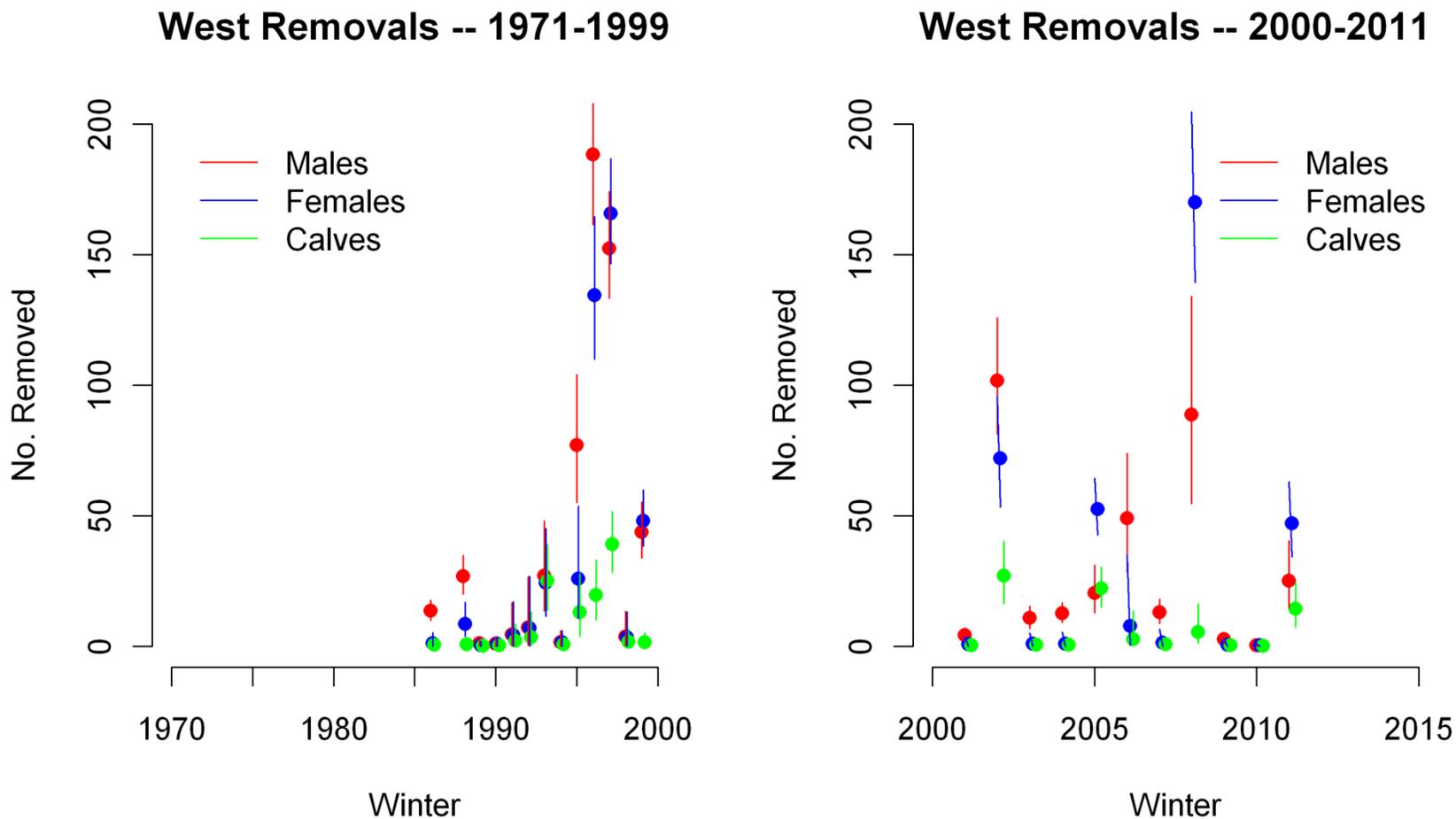
Figure 8. Model generated predictions of bison removals (harvests, management culls) near the northern boundary of Yellowstone National Park before (1971-1999) and after (2000-2011) implementation of the Interagency Bison Management Plan. Circles depict the predicted averages, while lines represent the intervals of 95% credibility.

Figure 9. Model generated predictions of abundance for the central and northern breeding herds in Yellowstone National Park during July from 2000-2012. Solid lines depict the predicted average herd sizes, while dotted lines depict the intervals of 95% credibility. Red solid and dotted lines represent predicted herd sizes (including new-born calves), provided the recommended removals of 330 bison are implemented during winter 2011-12. The recommended removals are 30 adult males from the central herd, and 200 adult females, 25 juvenile females, 25 juvenile males, and 50 calves from the northern herd.
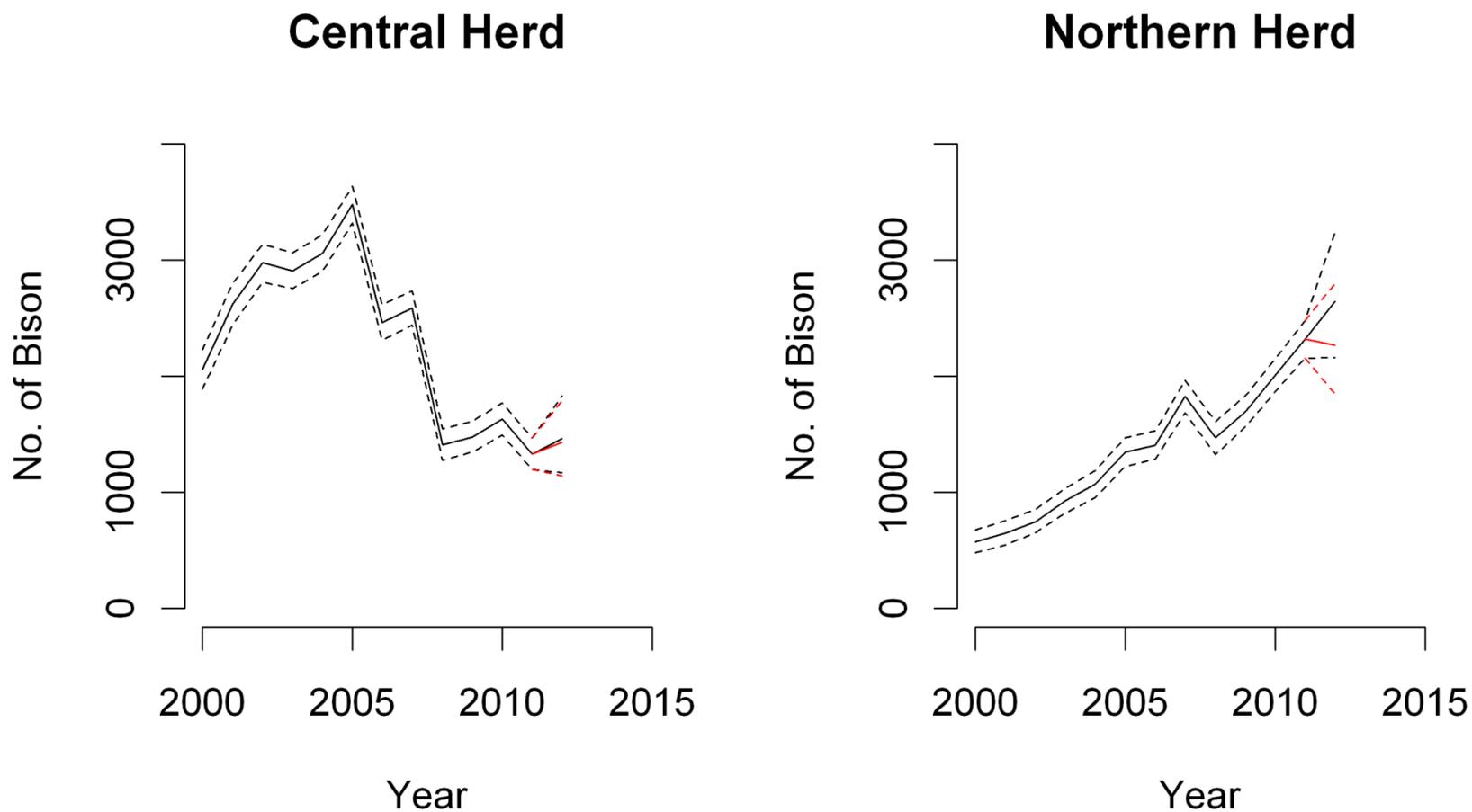
Appendix I: Development of a Stage-Structured Model of the Yellowstone Bison Population

Population model parameters and prior information.—Prior distributions of adult survival, fecundity, and herd interchange were estimated from mark-recapture data collected during 1995-2011. We defined fecundity (*f*) as the probability of observing a calf in close proximity to a dam during the parturition period. Data were aggregated with existing information on Yellowstone bison (Fuller et al. 2007, Geremia et al. 2009) and included 266 observations of 132 female bison at least 2 years of age. We treated the number of observations of dams with calves (*y*) as a binomial distributed random variable such that

$$P(f|y,n) \propto binomial(y|f,n) \times uniform(f|0,1)$$

We assumed that increasing snow pack diminished survival and coalesced recent data with existing information (Fuller et al. 2007, Geremia et al. 2009) to consider 377 observations from 96 female bison at least 1 year of age. We accumulated snow pack metrics (Garrott et al. 2003) across each winter as our measure of snow pack establishment (Watson et al. 2006). Bison that were culled or harvested were not considered during the year of removal. Abbreviations were x_s as the vector of standardized snow pack metrics, $s_{a,0}$ as the probability of survival, $s_{a,1}$ as the contribution of snow pack establishment, t_i as the subset of years that each animal remained in the study, and Y as the matrix of observations of survival status. Each individual observation was treated as a random Bernoulli variable such that

$$P(s_{A,0}, s_{A,1}|Y, x_S)$$

$$\propto \prod_{i=1}^{96} \prod_{t \in t_i} Bernoulli\ (y_{i,t}|invlogit(s_{A,0} + s_{A,1}x_s)) \times normal(s_{A,0}|0,1000)$$
$$\times normal(s_{A,1}|0,1000)$$

Pulses of immigration from the central herd to the northern herd have occurred since the early 1980s (Fuller et al. 2007) and we assumed that interchange was unidirectional. We treated annual numbers of dispersing central herd bison as random binomial variables. Dispersal was indicated by a central herd animal that was located on the northern breeding range during the subsequent summer. We defined *Y* as the vector of observations and *n* as the vector of numbers of central herd study animals, where

$$P(i|Y,n) \propto \prod_{i=1}^{16} binomial(y_i|i, n_i \times uniform(i|0,1)$$

Fetal gender ratios were estimated from several individual studies of Yellowstone bison that identified the sex of fetuses associated with dams that were harvested during boundary reductions. Studies occurred during 1931-1932 (*n* = 208), 1940-1941 (*n* = 263), 1945-1946 (*n* = 212), 1949-1950 (*n* = 238), and 1988-1989 (*n* = 82; Meagher 1973, Pac and Frey 1990). We defined *g* as the probability that a fetus was male, *n* as the vector of numbers of fetuses examined during each study, and *y* as the vector of observed male fetuses per study, where

$$P(g|\boldsymbol{y}, \boldsymbol{n}) \propto \prod_{i=1}^{5} binomial(y_i|g, n_i) \times Uniform(g|0,1)$$

These analyses provided prior distributions for parameters used in the population model:

Parameter	Mean	SD	Prior distribution
f	0.66	0.03	Beta (f_0 | 164, 84)

$s_{A,0}$	2.40	0.19	Normal ($s_{A,0}$ | 2.40, 0.19)
$s_{A,1}$	-0.44	0.45	Normal ($s_{A,1}$ | -0.44, 0.45)
i	0.05	0.01	Betal(i | 10.69, 216.83)
g	0.55	0.02	Beta(j | 340,278)

<u>Estimating harvest composition.</u>—Bison were removed near the northern or western park boundary after exiting the park during 1984-2011. Numbers of annual removals were known, but records were incomplete for age and gender classification (White et al. 2011). We assumed that *H* was a matrix of random variables where $H = H_W + H_N$ with H_W representing western and H_N as northern removals. We needed to differentiate removals occurring at different boundaries because bison from both herds exited the northern boundary after approximately 1992 while only animals from the central herd exited the western boundary. Intuitively, our approach estimated the number of animals removed from each demographic stage as the product of known composition of western removals and the total removed from the western boundary, and the product of known composition of northern removals, the total removed from the northern boundary, and probability that a removal was a member of the central herd.

Proportions of animals removed from each demographic stage were considered to be Dirichlet random variables. We defined the matrix r_W as the true composition of west boundary removals. Components of r_W for northern herd bison were set to zero to attribute all western removals as occurring to central herd members. We defined y_W as our observed annual totals of west boundary removals from each demographic stage and evaluated

$$P(r_W|y_W) \propto \prod_{t=1}^{41} Dirichlet(r_{W,t}|y_{W,t} + 1)$$

We defined R_W as the vector of total annual western removals and estimated western removal composition as $H_W = R_W r_W$. A similar approach was used for estimating north boundary removals during 1970-1992 when only northern herd animals were speculated to exit the northern boundary. We defined y_N as observed annual totals of north boundary removals. Components of r_N for central herd bison were set to zero. We considered R_N as the vector of total annual northern removals and estimated north boundary removal composition as $H_N = R_N r_N$ such that

$$P(r_N|y_N) \propto \prod_{t=1}^{23} Dirichlet(r_{N,t}|y_{N,t} + 1)$$

After 1993 we needed to account for some unknown component of northern removals as occurring to central herd members. We defined the matrix *c* as the proportion of animals removed at the northern boundary from calf, sub-adult female, adult female, sub-adult male, and male demographic stages. We evaluated $r_N = cp$ for components of r_N describing central herd demographic stages and $r_N = c(1-p)$ for components of r_N describing northern herd demographic stages. We also defined y_N as observed annual totals of north boundary removals and incorporated an informative prior distribution for p (the probability that a removal was a member of the central herd) such that

$$P(c,p|y_W) \propto \prod_{t=1}^{41} Dirichlet(c_t|y_{W,t} + 1) \times normal(p_0| - 2.31, 0.63) \times normal(p_1|5.24, 1.27)$$

R_N represented the vector of total annual northern removals and we estimated northern removal composition as $H_N = R_N r_N$. The informative prior distribution for p was evaluated from mark-recapture observations of central and northern herd collared bison during 1995-2011. Herd size affected the number of central herd members migrating to the northern boundary (Geremia et al. 2011) and we evaluated $p = invlogit (p_0 + p_1 x_C)$ where x_C were annual counts of central herd animals. Study animals were observed at the northern park boundary during six winters. We treated y as a vector of random

binomial variables indicating the number of central herd study animals captured at the north boundary processing facility and n as the vector of all captured study animals, where

$$P(p_0, p_1 | \boldsymbol{y}, \boldsymbol{n}, x_c) \propto \prod_{i=1}^{6} binomial(y_i | invlogit(p_0 + p_1 x_c), n_i) \times Uniform(p|0,1)$$

Note: next year we will attempt to update this to a multinomial to decrease uncertainty around the composition estimates.

Estimating numbers of bison in various demographic stages during 1970-2011.—Within park gather-and-removal operations were completed during 1964-1966 to reduce brucellosis prevalence which we used to estimate the starting composition of the population during 1970. We defined $z_{0,i}$ as uniform random variables representing initial numbers of animals in each herd and demographic stage. Within park reductions during 1964-1966 provided observations of the composition of each herd at model initiation. We defined the matrix $\boldsymbol{y_0}$ as random multinomial variables of the observed number of bison in each demographic stage where the vector n_0 was the total number of observations of central and northern herd members. Vectors of multinomial probabilities (p_0) were defined by $\frac{z_{0,i}}{\sum z_0}$ $i \in 1:5$ for central herd stages and $\frac{z_{0,i}}{\sum z_0}$ $i \in 6:10$ for northern herd stages. We specified the initial conditions component of the posterior distribution as

$$P(\boldsymbol{y_0}, p_0 \sigma_0 | z_0, n_0) \propto \prod_{i=1}^{10} uniform(z_{0,i} | 0,200) \times multinomial(y_0 | p_0, n_0)$$

Process model.—We defined $\boldsymbol{Z}$ as a 10 by 42 matrix of lognormal distributed random variables representing true numbers of bison in each demographic stage during 1971-2010. Rows of the matrix $\boldsymbol{Z}$ corresponded to demographic stages, with row 1 portraying central herd calves (2 months of age), row 2 portraying central herd juvenile females (14 months of age), row 3 portraying central herd adult females (more than 26 months of age), row 4 portraying central herd juvenile males (14 months of age), row 5 portraying central herd adult males (more than 26 months of age), row 6 portraying northern herd calves, row 7 portraying northern herd juvenile females, row 8 portraying northern herd adult females, row 9 portraying northern herd juvenile males, and row 10 portraying northern herd adult males.

We defined the vector $\dot{z}_t$ as the log of the median of A $(\boldsymbol{Z_t} - \boldsymbol{H_t})$ where $\boldsymbol{Z_t}$ was the tth column of $\boldsymbol{Z}$, and $\boldsymbol{H_t}$ as the tth column of $\boldsymbol{H}$. $\boldsymbol{H}$ represented the matrix of removals to each demographic stage per year. A was defined as the transition matrix of survival, fecundity, and dispersal probabilities between demographic stages where

$$A = \begin{bmatrix} 0 & 0 & s_a f(1-i) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ (1-g)s_j(1-i) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_a(1-i) & s_a(1-i) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ gs_j(1-i) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_a(1-i) & s_a(1-i) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_a f i & 0 & 0 & 0 & 0 & s_a f & 0 & 0 \\ (1-g)s_j I & 0 & 0 & 0 & 0 & (1-g)s_j & 0 & 0 & 0 & 0 \\ 0 & s_a I & s_a i & 0 & 0 & 0 & s_a & s_a & 0 & 0 \\ gs_j I & 0 & 0 & 0 & 0 & gs & 0 & 0 & 0 & 0 \\ 0 & s_a I & s_a I & 0 & 0 & 0 & s_a & s_a & 0 & 0 \end{bmatrix}$$

We defined σ as model process variance on the log scale and used an uninformative prior distribution. We also used an uninformative prior distribution for our calf survival parameter. Otherwise, informative prior distributions were used for model parameters determined from observations of collared animals (described above). We specified the process model component of the posterior distribution as,

$$P(A, Z_{t-1}, \sigma | Z_t, x_c, x_s, H)$$
$$\propto \prod_{t=2}^{42} \prod_{i=1}^{10} lognormal(Z_{t,i} | AZ_{t-1},\sigma) \times normal(s_{A,0} | 2.40, 0.19) \times normal(s_{A,1} |$$
$$- 0.44, 0.45) \times uniform(s_J | 0,1) \times beta(f | 164, 84) \times beta(g | 340, 278) \times normal(i |$$
$$- 2.98, 0.37) \times normal(i_1 | - 1.61, 1.07) \times gamma(\sigma | 0.001, 0.001)$$

<u>Data models</u>.—Between one and three aerial counts of the northern and central herds were completed during June-August, 1970-2011. While bison are highly visible during the rut when they are congregated in large groups, counts were imperfect and we used a gamma-Poisson mixture model to explicitly model observation error (σ_{obs}). We treated each count as a Poisson random variable. Y_N and Y_C were matrices of counts for the northern and central herds and we defined t_i as the number of counts occurring during each year, and

$$P(Z, \sigma_{obs} | Y_N, Y_C)$$
$$\propto \prod_{t=1}^{42} \prod_{i \in t_i} gamma\left(\lambda_{c,t,i} \Big| \frac{\sum_{j=1}^{5} Z_{j,t}}{\sigma_{obs}^2}, \sum_{j=1}^{5} Z_{j,t}\right) \times gamma\left(\lambda_{n,t,i} \Big| \frac{\sum_{j=6}^{10} Z_{j,t}}{\sigma_{obs}^2}, \sum_{j=6}^{10} Z_{j,t}\right)$$
$$\times \prod_{t=1}^{42} \prod_{i \in t_i} Poisson(Y_{c,t,i} | \lambda_{c,t,i}) \times Poisson(Y_{n,t,i} | \lambda_{n,t,i}) \times uniform(\sigma_{obs} | 1,500)$$

A single aerial count of the northern and central herds at the conclusion of the calving season was completed during 1970-2011. We defined Y_N and Y_C as the total count of calves, and N_N and N_C as the total count of all bison in each herd, and

$$P(Z | Y_N, Y_C, N_N, N_C) \propto \prod_{t=1}^{42} binomial\left(Y_{c,t} \Big| \frac{Z_{1,t}}{\sum_{j=1}^{5} Z_{j,t}}, N_{c,t}\right) \times \prod_{t=1}^{42} binomial\left(Y_{n,t} \Big| \frac{Z_{6,t}}{\sum_{j=6}^{10} Z_{j,t}}, N_{n,t}\right)$$

We began comprehensive composition counts of park herds during July 2002. At least one aerial survey was completed to identify locations and numbers of bison congregating in mixed gender and bachelor groups. We defined m as the probability of a bison being in a mixed gender group. We assumed that between-year variations in m resulted from delays in the onset of the breeding season which influenced the probability of being in a mixed gender group. We defined Y as vector of number of bison counted in mixed groups during each survey; N as the vector of total number of bison counted during each survey; s_1 and s_2 as shape parameters of a beta random variable (m); and specified a random effect to model such that

$$P(m, s_1, s_2 | Y, N)$$
$$\propto \prod_{i=1}^{16} binomial(Y_i | m, N_i) \times beta(m | s_1, s_2) \times gamma(s_1 | 0.001, 0.001)$$
$$\times gamma(s_2 | 0.001, 0.001)$$

Ground observers then encountered >80% of bison identified in mixed gender groups and counted numbers of calf, male and female sub-adults, and male and female adults. We had to account for male bison that were not classified because of residing in bachelor groups. We began by treating matrices (Y) of observed bison from each demographic stage as random binomial variables. It followed that the probability p_i of observing an individual in the ith demographic stage was $\frac{z_i}{m \sum z_i}$ for calf, male and female sub-adults, and adult female bison. However, the probability p_i for adult male bison was $\frac{z_i - \sum z_i (1-m)}{m \sum z_i}$ such that

$$P(\mathbf{Z}, s_1, s_2 | \mathbf{Y}) \propto \prod_{t=32}^{42} \prod_{i=1}^{10} binomial\left(y_{t,i} \middle| p_i, \sum y_t\right) \times gamma(s_1 | 13.58, 1.17)$$
$$\times\ gamma(s_2 | 18.77, 13.7)$$

Note: next year we will consider one sightability parameter for males in each herd.

Appendix II: Development of a Model of Seasonal Bison Distributions

Model development and evaluation.—We obtained posterior distributions for model parameters using Monte Carlo Markov chain methods in a hierarchal Bayesian framework. Our observed responses ($Y_{N,t}$, $Y_{W,t}$) were counts which were measured imperfectly, and the hierarchal framework allowed us to estimate posterior distributions of the unobserved, but true numbers of bison beyond park boundaries. We defined true annual maxima of bison beyond the northern park boundary as $Z_{N,t}$ and western boundary as $Z_{W,t}$.

Process model.—We anticipated that increasing bison population size and accumulated SWE would increase numbers migrating, and population size would interact with accumulated SWE such that larger incremental increases would occur with higher population size and snow measures. We hypothesized that increases in above-ground dried biomass may moderate the impetus for bison to move. Thus, our process equations included terms for population size, accumulated SWE, average above-ground dried biomass, and an interaction between population size and accumulated SWE.

We proposed alternate forms of process equations representing competing hypotheses of migration. A linear relationship was deemed infeasible because numbers migrating cannot exceed population size and numbers of bison exiting park boundaries far exceeded linear model predictions during 2000-2009. Only bison from the central herd have migrated outside the western park boundary, while bison from both the central and northern herds have migrated beyond the northern boundary. We began by using a logistic deterministic process equation portraying the probability that bison exit the north boundary

$$p_{N,t} = \frac{1}{1+e^{-(\beta_0+\beta_1 x_{north,t}+\beta_2 x_{central,t}+\beta_3 x_{snow,t}+\beta_4 x_{forage,t}+\beta_5 (x_{north,t}+x_{central,t})x_{snow,t})}}$$

and west boundary

$$p_{W,t} = \frac{1}{1+e^{-(\beta_0+\beta_1 x_{central,t}+\beta_2 x_{snowC,t}+\beta_3 x_{forageC,t}+\beta_4 x_{central,t}x_{snow,t})}}$$

Bruggeman et al. (2009) suggested that Yellowstone bison were partially migratory, with both migratory and resident components. We proposed the modified logistic process equation where a is a saturation parameter to represent this non-migrant component

$$p_{N,t} = \frac{a}{1+e^{-(\beta_0+\beta_1 x_{north,t}+\beta_2 x_{central,t}+\beta_3 x_{snow,t}+\beta_4 x_{forage,t}+\beta_5 (x_{north,t}+x_{central,t})x_{snow,t})}}$$

and

$$p_{W,t} = \frac{a}{1+e^{-(\beta_0+\beta_1 x_{central,t}+\beta_2 x_{snowC,t}+\beta_3 x_{forageC,t}+\beta_4 x_{central,t}x_{snow,t})}}$$

Bison may maintain a relatively stable winter density and higher numbers may move beyond park boundaries under moderate covariate levels. Variations of the negative exponential functional form are often used in ecology to represent responses that initially increase and reach a plateau. We considered the negative exponential form portraying saturation as occurring at the population size

$$p_{N,t} = (1-e^{-(\beta_0+\beta_1 x_{north,t}+\beta_2 x_{central,t}+\beta_3 x_{snow,t}+\beta_4 x_{forage,t}+\beta_5 (x_{north,t}+x_{central,t})x_{snow,t})})$$

and

$$p_{W,t} = (1-e^{-(\beta_0+\beta_1 x_{central,t}+\beta_2 x_{snowC,t}+\beta_3 x_{forageC,t}+\beta_4 x_{central,t}x_{snow,t})})$$

We also considered the modified negative exponential indicating saturation occurring at lower levels

$$p_{N,t} = a(1-e^{-(\beta_0+\beta_1 x_{north,t}+\beta_2 x_{central,t}+\beta_3 x_{snow,t}+\beta_4 x_{forage,t}+\beta_5 (x_{north,t}+x_{central,t})x_{snow,t})})$$

and

$$p_{W,t} = a(1 - e^{-(\beta_0 + \beta_1 x_{central,t} + \beta_2 x_{snowC,t} + \beta_3 x_{forageC,t} + \beta_4 x_{central,t} x_{snow,t})})$$

Process and observation model stochasticity.—Uncertainty in each process equation was included by treating $Z_{N,t}$ and $Z_{W,t}$ as binomial distributed random variables where

$$Z_{N,t} \sim Binomial(p_{N,t}, x_{central,t} + x_{north,t})$$
$$Z_{W,t} \sim Binomial(p_{W,t}, x_{central,t})$$

The binomial distribution is discrete and often used to model the number of successes in a sample of known size. Individual successes are not treated as independent, and we considered success as representing a bison that exited the park and failure as a bison that remained in the park. We took the sample size of bison that may exit the north boundary as the sum of preceding summer counts of each herd ($x_{central,t}$, $x_{north,t}$) and west boundary as the preceding summer count of the central herd ($x_{central,t}$). Uncertainty in observations was included by assuming observed responses ($Y_{N,t}$, $Y_{W,t}$) were also binomial distributed random variables such that

$$Y_{N,t} \sim Binomial(d, Z_{N,t})$$
$$Y_{W,t} \sim Binomial(d, Z_{W,t})$$

where d is a detection parameter. Here, we treated a success as an observation of bison exiting the park.

Model specification.—We denoted $\mathbf{Y_N}$ and $\mathbf{Y_W}$ as vectors consisting of all annual observations, and $\mathbf{Z_N}$ and $\mathbf{Z_W}$ as vectors of process model predictions for all years. We also denoted $\mathbf{x_{central}}$, $\mathbf{x_{north}}$, $\mathbf{x_{snow}}$, $\mathbf{x_{snowC}}$, $\mathbf{x_{forage}}$, and $\mathbf{x_{forageC}}$ as vectors of covariates. The prior distribution of d was provided by Hess (2002) and we used uninformative prior distributions for other parameters. Likelihoods in the following model specification are easily identified as statements of states and observations conditional on parameters and covariates, and priors are statements of parameters conditional on distribution shape parameters. For convenience, we included the saturation parameter a in the following model specification, but this parameter was only present in the modified functional forms. The posterior distribution of migration beyond the northern boundary was specified as

$$P(\mathbf{Z_N}, a, \beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, d \mid \mathbf{Y_N}, \mathbf{x_{central}}, \mathbf{x_{north}}, \mathbf{x_{snow}}, \mathbf{x_{forage}})$$

$$\propto \prod_{t=1}^{19} Binomial(Z_{N,t} \mid p_{N,t}, x_{central,t}, x_{north,t}, x_{snow,t}, x_{forage,t})$$

$$\times \prod_{t=1}^{19} Binomial(Y_{N,t} \mid d, Z_{N,t}) \times Normal(\beta_0 \mid 0, 0.001) \times Normal(\beta_1 \mid 0, 0.001) \times Normal(\beta_2 \mid 0, 0.001)$$

$$\times Normal(\beta_3 \mid 0, 0.001) \times Normal(\beta_4 \mid 0, 0.001) \times Normal(\beta_5 \mid 0, 0.001) \times Beta(d \mid 2866, 250)$$

$$\times Uniform(a \mid 0,1)$$

and beyond the western boundary as

$$P(\mathbf{Z_W}, a, \beta_0, \beta_1, \beta_2, \beta_3, \beta_4, d \mid \mathbf{Y_w}, \mathbf{x_{central}}, \mathbf{x_{snowC}}, \mathbf{x_{forageC}})$$

$$\propto \prod_{t=1}^{19} Binomial\,(Z_{W,t} \mid p_{W,t}, x_{central,t}, x_{snowC,t}, x_{forageC,t})$$

$$\times \prod_{t=1}^{19} Binomial\,(Y_{W,t} \mid d, Z_{W,t}) \times Normal(\beta_0 \mid 0, 0.001) \times Normal(\beta_1 \mid 0, 0.001) \times Normal(\beta_2 \mid 0, 0.001)$$

$$\times Normal(\beta_3 \mid 0, 0.001) \times Normal(\beta_4 \mid 0, 0.001) \times Beta\,(d \mid 2866, 250) \times Uniform(a \mid 0, 1)$$