Status Report on the Yellowstone Bison Population, September 2017

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Summary

- The aerial count of bison on August 4-5, 2017 was 4,816, including 3,969 in northern Yellowstone and 847 in central Yellowstone, which represents about a 12% decrease in abundance since summer 2016.
- A total of 1,274 bison were removed from the population during winter 2016-2017, including 486 harvests (including 2 seized carcasses and 16 dispatched [wounded] animals), 748 animals sent to meat processing (slaughter) facilities, 2 animals that died in captivity, 3 animals shot after leaving the conservation area in Montana, and 35 animals held at the Stephens Creek capture facility in Yellowstone for possible quarantine.
- The count of 847 bison in central Yellowstone (i.e., the central herd) was a 42-48% decrease from summer 2016. This reduction was due to removals during winter 2016-2017 and the dispersal of bison from central to northern Yellowstone.
- Even though management actions during winter 2016-2017 focused on bison in northern Yellowstone, there were still nearly 4,000 bison counted in this region during summer 2017; likely due to the continued emigration of bison from central to northern Yellowstone. The precise causes of this emigration remain unknown.
- About 600 bison would need to be removed from the population during winter 2017-2018 to stabilize population growth. The removal of 1,000 bison (about 20% of the population) would likely decrease bison numbers to about 4,400 after calving next summer. We do not recommend removing more than 1,250 bison, which would be greater than 25% of the current population.
- When possible, bison should be removed in proportion to their occurrence in the population (73% adults, 12% yearlings, and 15% calves; 46% females and 56% males). Some captured bison may need to be held at the Stephens Creek facility through winter and released in spring to meet these removal composition objectives.
- Population management actions during winter 2017-2018 should focus on bison breeding in northern Yellowstone (i.e., the northern herd) by using telemetry data to inform the timing and magnitude of removals.
- We recommend using harvests in Montana and culling at Stephens Creek to meet population management objectives and reduce brucellosis transmission risk and other potential conflicts in local communities, while allowing hundreds of bison to migrate into, and disperse throughout, conservation areas in Montana.
- We do not recommend management removals or state and tribal harvests of bison in the western management area in Montana. Bison migrating west of the park during winter are almost entirely from the central breeding herd, which has decreased substantially in abundance during recent years.

Contents

Population Size

We completed two airplane surveys for bison in the northern region of Yellowstone National Park (i.e., the northern herd) and observed 3,619 bison on August 3 and 3,969 bison on August 5, 2017. We conducted 1 airplane survey for bison in the central region of the park (i.e., the central herd) on August 4 and observed 847 bison. Groups larger than 50 bison were photographed to enable more accurate counts after the flights, though this was not always possible due to movements of animals among groups, groups that were spread over large areas, and under/over exposure of photographs.

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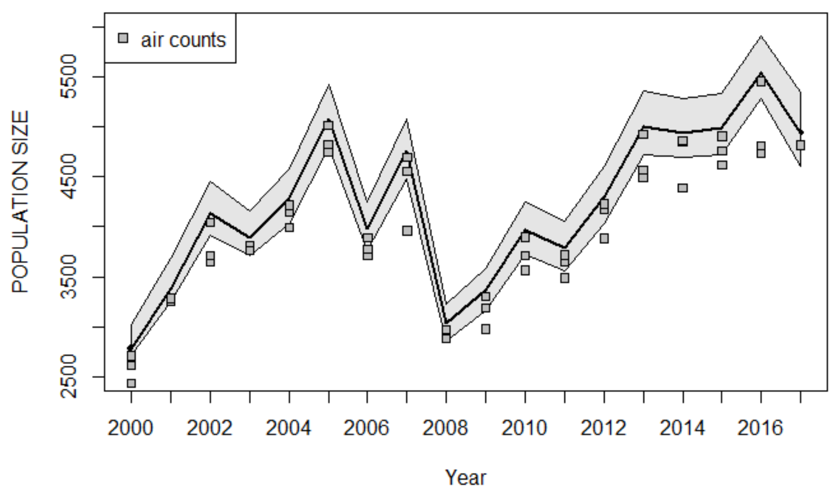
An integrated population model was used to derive an estimate of 4,930 bison in the Yellowstone population during summer 2017, within a 95% credible interval (i.e., range) of 4,578-5,342 bison (Figure 1). The population decreased by approximately 12% since summer 2016 when abundance was estimated near 5,540 animals. The decrease resulted from the removal of 1,274 animals during winter 2016-2017. We assessed differences between modeled outcomes that included the 2017 data and predictions that were made prior to collecting data in 2017 to determine whether the population changed as expected. Prior to collecting data, we estimated a 2017 bison population of about 4,840 animals, or 90 animals smaller than the estimate of 4,930 animals determined once all data was collected. We estimated similar sex ratios averaging 105 males per 100 females before data were collected compared to 107 males per 100 females after data were collected. We also estimated similar calf to adult female ratios (46:100 adult females before data collection; 43:100 adult females after) and juvenile proportions of the population (29% juveniles and 71% adults before; 27% juveniles and 73% adults after). The similarity of these measures suggests the 2016 and 2017 population estimates were precise estimates of actual conditions. The similarity also suggests bison abundance continued to increase according to average birth and survival rates, despite a relatively large population with more than 5,500 bison during summer 2016 and a winter with above-average snow conditions.

Figure 1. Estimated size of the Yellowstone bison population based on an integrated population model (Appendix A). The bold line connects annual estimates of abundance during 2000-2017, while the gray boxes represent actual numbers of bison observed during aerial counts and the gray shaded area depicts the 95% credible interval (i.e., range) around the population estimates.



Population Composition (Age and Sex)

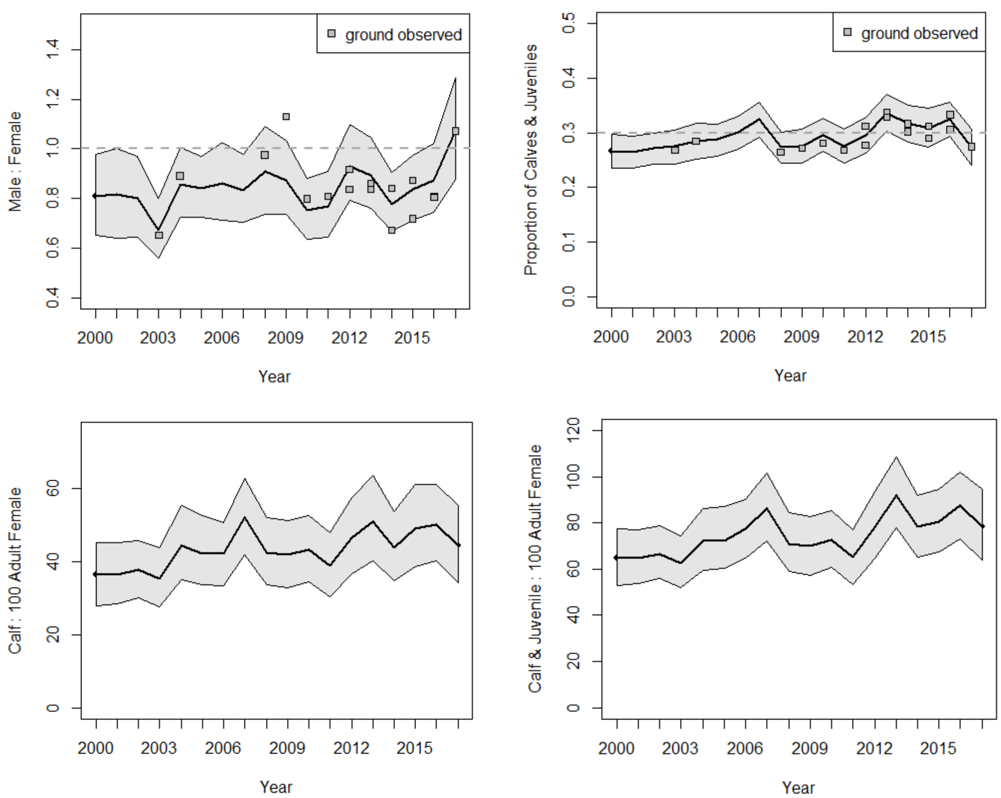
Park biologists conducted ground and aerial surveys during August to collect data on the age and sex composition of the bison population. Surveys occurred approximately two weeks later during 2017 compared to other years and were completed during the peak of the breeding period. We estimated a sex ratio of 107 males per 100 females (excluding calves), which equates to 52% males and 48% females. The sex ratio met our objective of maintaining a population with similar proportions of males and females (Figure 2) and has averaged 90 males per 100 females over the past five years. This was the first year it was more likely that males exceeded the number of females in the population since monitoring began in 2000. The proportional increase in males improves mate competition during the breeding season and dampens the growth rate of the population.

We estimated about 27% of the population was composed of pre-reproductive animals, which included calves and males and females between 12 and 16 months of age. Seventy-three percent of the population was composed of adults at least 2 years of age. Over the past five years, the age composition has averaged 31% juveniles and 69% adults, which met our objective of averaging 30% juveniles and 70% adults. It is likely the juvenile proportion of the population has been reduced below maximum values that approached 34% during 2013-2016. The current population consists of approximately 44 calves per 100 adult females, which is reduced from a high of 51 calves per 100 adult females measured during 2013 and 2016, but near the long-term average of 43 calves per 100 adult females. The ratio of pre-reproductive animals per 100 adult females was similarly reduced from a high of 92 in 2013 to 78 in 2017, which is near the long-term average of 75 per 100 adult females.

The removal of primarily adult females and juveniles during winter 2016-2017 aligned current conditions and 5-year averages of age and sex conditions with long-term objectives. We estimated about 750 calves survived through early August, which was about 25% lower than the 1,000 calves estimated to survive in 2016. We estimated about 600 juveniles (300 males and 300 females) in the population, which was about 20% lower than the 750 juveniles estimated in 2016. We estimated 1,700 adult females and 1,850 adult males were in the population, which was about 20% lower than the 2,100 females estimated in 2016, and about 13% higher than the 1,650 males estimated in 2016.

During 2000-2017, we estimated adult female annual survival at 0.94 (standard deviation [SD] = 0.01) and adult male survival at 0.94 (standard deviation [SD] = 0.03). In addition, we monitored 49 adult females using radio telemetry collars during June 1, 2016 through May 31, 2017 for survival and detected a single natural mortality of a 15 year-old in central Yellowstone that died during June 2016. Human harvest continued to be the overwhelming source of mortality, with 4 radio-collared bison (1 from central Yellowstone; 3 from northern Yellowstone) captured near the northern park boundary and sent to slaughter and 1 radio-collared bison from northern Yellowstone harvested by tribal hunters when it migrated beyond the northern park boundary. Calf survival, which excludes neonate mortality occurring between calving and surveys in early July, was estimated as 0.88 (SD = 0.05). Fertility, defined as the number of calves born per adult female that survive until age and sex counts in summer was 0.51 (SD = 0.03). The average population growth rate during 2000-2017 was 1.14, which indicates the bison population increased 14% per year, on average, in the absence of management removals.[2] After adjusting for removals, the natural growth rate of the population during 2016-2017 was 15%.

Figure 2. Estimated male to female ratio (*upper left)*, proportion of juveniles (*upper right*), calf to 100 adult female ratio (*lower left*), and juvenile to 100 female ratio (*lower right*) in the Yellowstone bison population. Bold lines connect average annual estimates, gray shaded areas show the 95% credible interval around the estimates, and gray boxes are observed ratios/proportions. The dotted lines indicate desired compositions (i.e., objectives).



[2] The population growth rate, λ, adjusted for removals was estimated as $N_{t+1} = \lambda\ (N_t - R_t)$, where N_t is the size of the population during the previous summer, N_{t+1} is the current population size, and R_t is the number of bison removed during the intervening winter.

Population Structure (Central and Northern Herds)

Historically, the Yellowstone bison population has been described by numbers of bison using and breeding in different geographic regions of the park, with the central herd spending summers in the Madison, Gibbon, Firehole, Hayden, and Pelican valleys, and the northern herd spending summers in Little America, the Lamar Valley, and adjacent higher-elevation areas (Figure 3). Movements of bison between these geographic regions of the park have increased during the implementation of the Interagency Bison Management Plan (2001-2017), but we continue to report counts of bison observed in these geographic areas each summer.

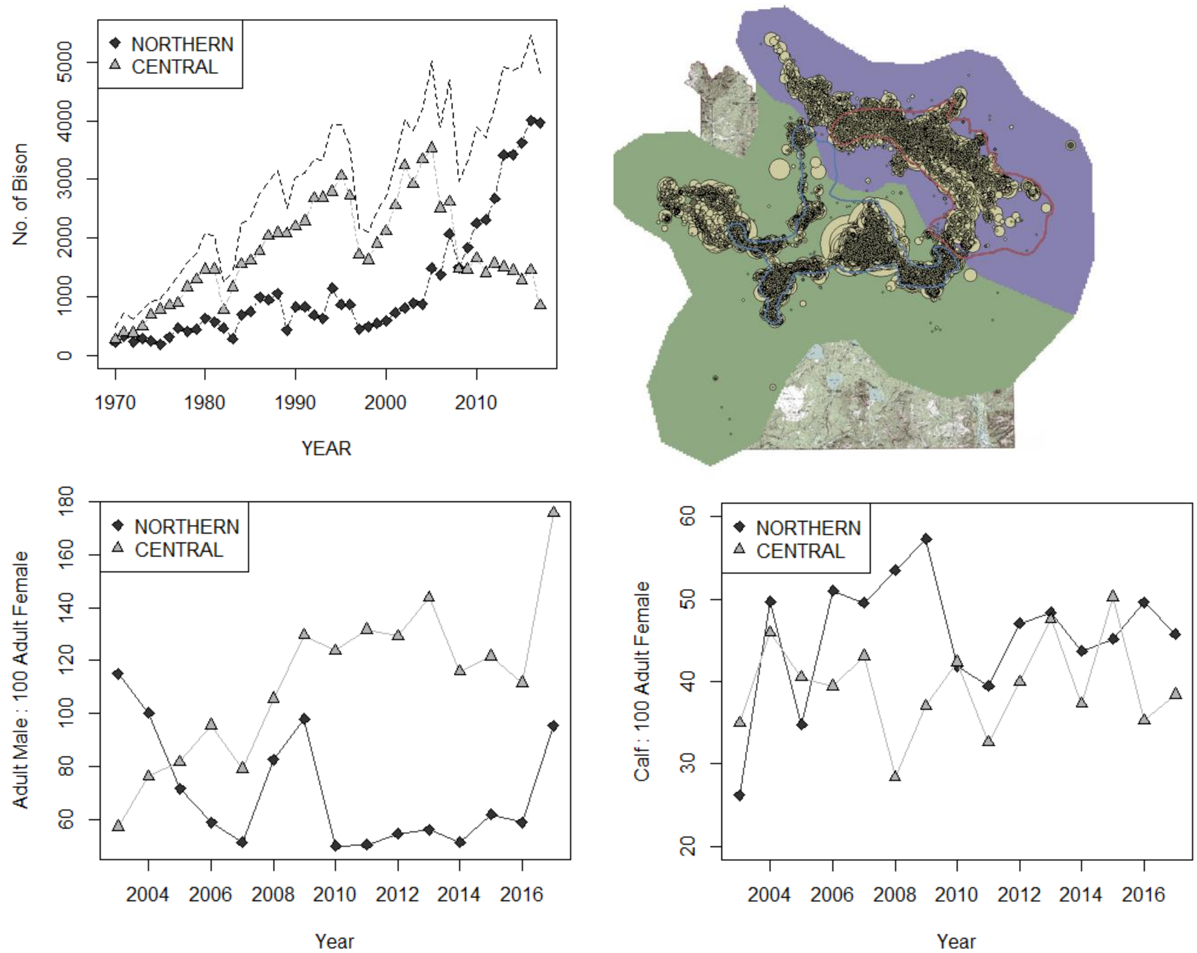
During August 2017, 847 bison were counted in central Yellowstone, which represented a decrease of 42-48% from counts of 1,451-1,638 animals during summer 2016. Prior to this decrease, summer counts of bison in central Yellowstone were similar during 2008-2016, averaging 1,470 animals. Counts of females in central Yellowstone decreased by 52% from 513 to 245 adults, whereas numbers of males decreased by 20% from counts of 572 to 431 adults. The decrease in adult females was probably not due to natural mortality because 11 of 12 radio-collared females in central Yellowstone did not die during winter 2016-2017 due to natural causes such as accidents, predation, or starvation. Rather, several hundred bison likely migrated from central to northern Yellowstone during winter in groups consisting of adult females and young animals. Many of these bison were likely removed (cull, harvest) near the northern park boundary or remained in northern Yellowstone during summer 2017. Six of the 11 radio-collared females that spent summer 2016 in the Hayden and Pelican valleys of central Yellowstone moved to winter ranges in the Firehole, Gibbon, and Madison valleys in west-central Yellowstone and nearby areas of Montana. However, the other 5 radio-collared females migrated to northern Yellowstone during winter, with 1 being captured near the northern park boundary and shipped to slaughter, 2 returning to the Hayden Valley by summer 2017, and 2 remaining in northern Yellowstone during summer 2017.

The central herd has exhibited lower potential for population growth since 2008. The juvenile proportion of bison counted in central Yellowstone averaged near 20% during 2008-2012 and 2017, which was substantially lower than the overall population objective of 30%. Also, the male to female ratio gradually increased over time, reaching a high of 62% males in 2017. In addition, biologists counted less than 300 adult female bison in the central herd during aerial surveys in summer 2017. As a result, additional migrations and dispersal of bison from central to northern Yellowstone, which likely increase during years with above-average snow conditions, could lead to future decreases in the number of bison living in central Yellowstone.

During the same time period, the number of bison counted in the northern Yellowstone increased by 275% from 1,500 bison in 2008 to 3,969 bison in 2017. Removals were aimed to reduce the northern herd beginning in 2012. We removed 3,148 bison near the northern park boundary compared to 289 bison near the western park boundary since 2012, yet growth was stabilized in the northern herd only during 2013-2014 and 2016-2017. Five of 6 radio-collared bison that began the winter in northern Yellowstone were captured near the northern park boundary (4) or harvested by hunters (1), suggesting that more than one-half of the 1,274 bison removed were from the northern herd. **C**ontinued emigration of bison from central to northern Yellowstone presents a persistent challenge to reducing the number of bison summering in northern Yellowstone and the precise causes of this emigration remain unknown. The sex ratio of bison counted in northern Yellowstone was 95 males per 100 females during 2017. The sex ratio had previously been biased towards females during 2010-2016 and averaged 63 males per 100 females (39% male, 61% female). The juvenile proportion of bison counted in northern Yellowstone was 29%.

Vital rates, demographic composition, movements, and genetic structure are important aspects of the bison population that require continued monitoring to ensure undesired impacts are not occurring. We intend to increase the number of radio-collared females in central Yellowstone prior to winter 2017-2018 to help track movements of central herd bison into northern areas of the park as winter progresses. Additionally, we intend to continue collaborative genetic studies with Texas A&M University to further evaluate distributions of the endemic and introduced lineages of Yellowstone bison.

Figure 3. *Top left*: Annual maximum counts of bison observed in the central and northern regions of Yellowstone National Park during June 1-August 31 from 1970-2017. *Top right*: Geographic regions used to delineate the northern herd (purple) and the central herd (green). Red and blue lines represent previously used boundaries for these herds, while yellow graduated circles show bison locations recorded during aerial counts from 1970-2017. *Bottom*: Numbers of bison in age and sex categories determined from summer aerial and ground surveys.



Removals during Winter 2016-2017

A total of 1,274 bison were culled or harvested during winter 2016-2017, which was within the recommended range of removing at least 900 but fewer than 1,400 bison (Table 1). Culled bison totaled 753 animals, including 748 animals consigned to meat processing facilities, 2 animals that died during processing, and 3 animals that were shot when moving beyond the boundary of the conservation area in Montana. Harvests, seized carcasses, and dispatched wounded animals totaled 389 bison in the northern management area and 97 bison in the western management area. Thirty-five male bison were held in an isolation pen at the Stephens Creek facility near the northern park boundary to evaluate quarantine procedures.

The age and sex composition of removals included 492 adult females, 209 adult males, 342 calves, and 195 juveniles (1 year of age). Classification of 44 animals was not determined. The age composition of bison removed was 28% calves, 15 % juveniles, and 57% adults compared to recommendations for 20% calves, 10% juveniles, and 70% adults. The sex ratio of adult bison removed was 30% males and 70% females, which was skewed from the recommendation of 40% males and 60% females. About 342 of the 1,000 calves (34%) estimated to be in the population during summer 2016 were removed during winter operations. Removals also were biased towards females and young animals when more than 1,000 animals were removed during the winters of 2005-2006 and

2007-2008. Groups consisting of pregnant females and young animals appear to disproportionately migrate outside the park during years with severe winter conditions.

Table 1. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 2008-2017. See the Appendix B for data from all winters since 1970.

	Maximum No. Bison Counted Previous June-August			Sent to Slaughter/ Management Culls		Hunter Harvest		Sent to Quarantine Research		Total	Age and Gender Composition of Culls/Harvests			
Winter	North	Central	Total	N	W	N	W	N	W		M	F	C	Unk
2007-08	2,070	2,624	4,694	1,288	160	59	107	112	0	1,726	516	632	332	246
2008-09	1,500	1,469	2,969	0	4	1	0	0	0	5	5	0	0	0
2009-10	1,837	1,464	3,301	3	0	4	0	0	0	7	7	0	0	0
2010-11	2,246	1,652	3,898	6	0	Unk	Unk	53	0	260	106	102	52	0
2011-12	2,314	1,406	3,720	0	0	15	13	0	0	28	14	12	2	0
2012-13	2,669	1,561	4,230	0	0	148	81	0	0	250	116	85	28	0
2013-14	3,420	1,504	4,924	258	0	258	69	60	0	645	202	287	152	4
2014-15	3,424	1441	4,865	511	0	201	18	7	0	737	276	297	161	3
2015-16	3,627	1,282	4,910	101	0	378	24	49	0	552	175	227	146	4
2016-17	4,008	1,451	5,459	753	0	389	97	35	0	1,274	311	585	342	36

Predicting Population Growth under Different Management Scenarios

We predicted bison abundance and composition during July 2018 after simulating the removals of up to 1,500 bison of various age and sex compositions during winter 2017-2018. We report the findings for two key removal strategies, which we refer to as the "nonselective" and "proportional" strategies. The nonselective strategy was based on the observed composition of removals when large numbers of bison were removed during the winters of 2005-2006, 2007-2008, and 2016-2017. Primarily pregnant females and young bison migrated outside the park during these relatively severe winters and the composition of removals, averaged among years, was 60% adults, 14% yearlings, and 26% calves (62% females and 38% males). Thus, the composition of the nonselective strategy represents what likely would be removed if nearly all migrants were culled or harvested during a large migration. In the proportional strategy, we considered removing bison proportional to their occurrence in the population and according to a composition of 73% adults, 12% yearlings, and 15% calves (46% females and 56% males). Thus, the proportional strategy provides a reference for selective removals that maintains the population near desired conditions for age and sex composition.

The removal of no bison during winter 2017-2018 would likely result in a population size of about 5,550 bison the following summer after calving (Figure 4, Table 2). The removal of approximately 600 bison would be needed to stabilize population growth, and the removal of 1,000 animals would likely result in a population size near 4,400 bison, which would be about 10% smaller than the current population. The removal of 600 bison would include about 90 calves under the proportional strategy or 156 calves under the nonselective strategy; 36 yearling females under either strategy; 36 (proportional) or 48 (nonselective) yearling males; 198 (proportional) or 240 (nonselective) adult females; and 240 (proportional) or 120 (nonselective) adult males. If 1,000 bison were removed, totals for each age and sex composition under each strategy would include 150 (proportional) or 260 (nonselective) calves; 60 yearling females under either strategy; 60 (proportional) or 80 (nonselective) yearling males; 330 (proportional) or 400 (nonselective) adult females, and 400 (proportional) or 200 (nonselective) adult males.

The nonselective removal of less than 500 animals would likely have limited effects on the average sex ratio and age structure. The nonselective removal of up to 1,250 animals likely would skew the average sex ratio to 57% males and 43% females, and the age structure to 24% juveniles and 76% adults. To lessen the potential consequences of nonselective removals, we recommend bison be removed in proportion to their occurrence in the population; especially as the total number of removals exceeds 500 bison. We do not recommend removing more than 1,250 bison, which would be greater than 25% of the current population. These recommendations should maintain population conditions near composition objectives and lessen the need for widely disproportionate removals in subsequent years that would likely be difficult to implement.

Figure 4. Predicted size of the bison population during July 2018 considering management removals of up to 1,500 animals. Predictions were made assuming a removal composition near current conditions.

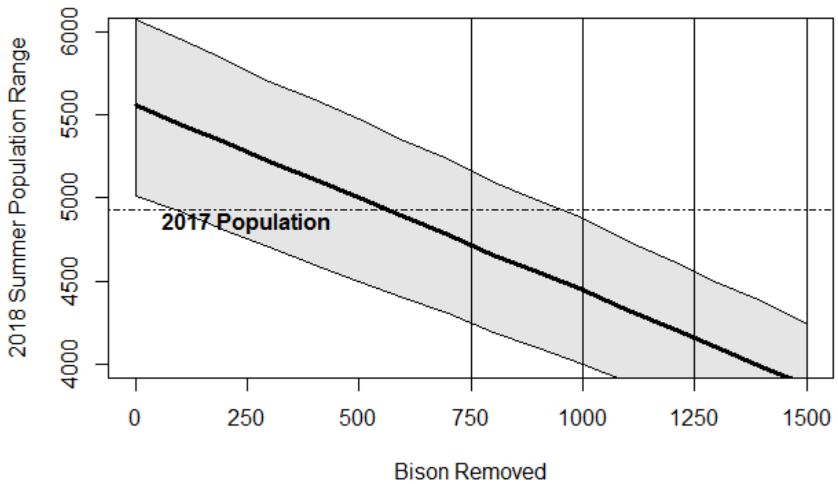


Table 2. Predicted population sizes, male to female ratios, and juvenile to adult ratios of the Yellowstone bison population during July 2018 with standard deviations in parentheses. The proportional strategy columns show predictions based on a removal composition of 73% adults, 12% yearlings, and 15% calves (46% females and 56% males), while the nonselective strategy columns show predictions based on a removal composition of 60% adults, 14% yearlings, and 26% calves (62% females and 38% males).

Bison	PROPORTIONAL STRATEGY			NONSELECTIVE STRATEGY		
Removed	**Abundance**	**M:F Ratio**	**% Juvenile**	**Abundance**	**M:F Ratio**	**% Juvenile**
0	5,545 (649)	1.12 (0.30)	0.28 (0.04)	5,545 (649)	1.12 (0.30)	0.28 (0.04)
100	5,443 (646)	1.12 (0.30)	0.28 (0.04)	5,443 (637)	1.13 (0.30)	0.27 (0.04)
200	5,326 (628)	1.12 (0.30)	0.28 (0.04)	5,327 (627)	1.14 (0.31)	0.27 (0.04)
300	5,223 (615)	1.12 (0.30)	0.28 (0.04)	5,205 (612)	1.15 (0.31)	0.27 (0.04)
400	5,107 (604)	1.11 (0.30)	0.28 (0.04)	5,101 (605)	1.16 (0.32)	0.27 (0.04)
500	4,989 (589)	1.11 (0.30)	0.28 (0.04)	4,976 (588)	1.18 (0.32)	0.26 (0.04)
600	4,896 (588)	1.11 (0.30)	0.28 (0.04)	4,873 (586)	1.19 (0.32)	0.26 (0.04)
700	4,785 (575)	1.11 (0.30)	0.28 (0.04)	4,760 (573)	1.21 (0.34)	0.26 (0.04)
800	4,662 (550)	1.11 (0.30)	0.28 (0.04)	4,632 (556)	1.22 (0.34)	0.26 (0.04)
900	4,551 (543)	1.10 (0.30)	0.28 (0.04)	4,521 (554)	1.23 (0.35)	0.25 (0.04)
1,000	4,438 (529)	1.10 (0.31)	0.28 (0.04)	4,403 (544)	1.24 (0.36)	0.25 (0.04)
1,100	4,315 (522)	1.10 (0.31)	0.28 (0.04)	4,292 (529)	1.27 (0.36)	0.25 (0.04)
1,200	4,212 (514)	1.10 (0.31)	0.28 (0.04)	4,179 (530)	1.29 (0.37)	0.24 (0.04)
1,300	4,100 (503)	1.09 (0.31)	0.28 (0.04)	4,073 (512)	1.31 (0.38)	0.24 (0.04)
1,400	3,996 (496)	1.09 (0.31)	0.28 (0.04)	3,947 (501)	1.33 (0.38)	0.23 (0.04)
1,500	3,879 (481)	1.09 (0.31)	0.28 (0.04)	3,848 (501)	1.35 (0.40)	0.23 (0.04)

Management Recommendations for Winter 2017-2018

We recommend implementing the following guidelines that balance conservation objectives and conflict resolution constraints for managing bison that migrate to the park boundary and into Montana:

1. Focus population management reductions on the northern herd by using location information from radio-collared bison to inform the timing and magnitude of bison captures near the northern park boundary such that captures primarily remove bison that lived and bred in northern Yellowstone during summer 2017.

2. Maintain approximately 200-450 animals north of Mammoth Hot Springs and within the existing conservation area to Yankee Jim Canyon to support state and tribal harvests, while reducing potential conflicts (e.g., human safety, property damage) in the local community.

3. Capture bison at the Stephen's Creek facility throughout the winter, including during state and tribal hunts, to maintain the number of bison north of Mammoth Hot Springs within the range of 200-450 animals. Up to 150-200 bison may be removed weekly during January through March.

4. Remove more bison if winter is severe and large numbers migrate into the Gardiner basin, but restrict removals to less than 25% (1,250 bison) of the preceding summer population. If there is a mass migration of bison into the basin, some bison may need to be held in pastures at the Stephens Creek facility and released during spring.

5. Track the age and sex composition of removals throughout the winter to approximate removing bison in proportion to their occurrence in the population; especially as the total number of removals exceeds 500 bison. If adult females and young bison are disproportionately captured, which is typical during severe winters, some of these animals may need to be held in the Stephens Creek facility for release during spring.

6. We do not recommend management removals or state and tribal harvests of bison in the western management area in Montana. Bison migrating west of the park during winter are almost entirely from the central breeding herd, which has decreased substantially in abundance during recent years.

Appendix A: Population Modeling Methods

The hierarchical Bayesian state-space modeling approach can be used to build complicated models that are suitable for incorporating multiple sources of uncertainty and comparing forecasted outcomes of a system under management. These approaches support adaptive management by incorporating new data as it becomes available and revises future predictions as outcomes of management are monitored. In the state-space approach, we begin by estimating the initial conditions of the bison population. This includes the number of bison in age and sex stages which can be summed to identify total herd and population sizes. Next, we predict the bison population during the next year based on survival, birth, and winter removals. These quantities, which are referred to as states are assumed to be unobserved, meaning we never know their exact value. As the year passes, we collect data on the bison population through aerial counting, completing age and sex composition surveys, and monitoring collared animals. These data are compared to model predictions made before the data were collected to refine estimation. These data are imperfect because we cannot count or track every single individual. Therefore, even after data are collected, we still do not know the exact values of the states of interest. We repeat this process of forecasting the state of the bison population during the next year and collecting data to check and improve our predictions. Over time, predictions improve because repeating these comparisons each year improves our understanding of the system.

The Yellowstone bison population contains 2-3 genetic lineages deriving from about 23 indigenous bison remaining in the central region (Pelican Valley) of the Yellowstone National Park during 1901 and 18 pregnant female bison from northwestern Montana introduced with 3 male bison from Texas to the northern portion of the park (Lamar Valley) in the early 1900s. The indigenous (central) and introduced (northern) herds began mixing and interbreeding to some extent after several decades, but were still were believed to be distinct breeding subpopulations when the Interagency Bison Management Plan began being implemented during the early 2000s. However, larger herd sizes during recent decades have resulted in increased mixing of bison from these herds/regions, suggesting this substructure may no longer be intact or sustained over time. Therefore, we assumed a single, intermixing population. We created five life-cycle stages for bison. We estimated the number of bison in these stages during June each year since the inception of the Interagency Bison Management Plan in 2000. Life cycle stages were newborn calves, pre-reproductive (one-year-old) female or male bison, and reproductive ($\geq$2-year-old) female or male bison. We assumed there were three different survival rates. Calf survival was the rate for the first year, from June until the next June, and excluded mortality occurring immediately after birth. Pre-reproductive and reproductive-aged animals were given the same survival rate. However, male survival was assumed to vary from female survival. We assumed all reproductive-aged females exhibited similar birth rates. Birth rate included offsets due to neonate morality occurring between birth and June 1. Bison could produce up to one calf each year. We assumed birth rates were unaffected by population size; thus, our model was an exponential growth model. That is, the rate of population growth could not decrease as the bison population increased in size.

A Bayesian matrix model was used to estimate the bison population. We began by estimating the numbers of bison in each life-cycle stage during June 2000. Each ensuing year, we estimated the number of bison based on survival, reproduction, and winter removals. Statistically, we represented the bison population as $\mathbf{Z}_t = \mathbf{A}(\mathbf{Z}_{t-1}-\mathbf{H}_t)+\varepsilon_1$ using a lognormal model. In this equation, $\mathbf{Z}_t$ is the number of bison in each life-cycle stage during the current year, $\mathbf{Z}_{t-1}$ is the number of bison in each life-cycle stage during the previous year, $\mathbf{A}$ is a matrix of survival and reproduction rates, and $\mathbf{H}_t$ is the number of bison removed during winter harvests and culls. The term ε_1 accounts for types of uncertainty about the natural processes of population growth and brucellosis transmission that we overlooked, such as different survival rates among bison in northern and central Yellowstone and age-effects on reproduction. The matrix $\mathbf{A}$ included survival and reproduction rates. We estimated survival rates using the logistic model where $s = \mathit{invlogit}(s_0 + s_1 + s_2 + \varepsilon_2)$. The elements of $\mathbf{s}$ were survival coefficients for age and sex classes and the term ε_2 accounted for other sources of uncertainty (e.g., weather effects) in annual survival that we overlooked. Similarly, we used a logistic model to estimate reproduction rate.

We collected data on the bison population through aerial counting, completing age and sex composition surveys, monitoring collared animals, and testing for previous brucellosis exposure of bison at capture facilities. These data were used to refine estimation of survival and birth rates, and numbers of bison in each life-cycle stage over time. Fifty-six aerial surveys were completed during June through August, 2000-2017 to count bison in the population. We assumed the bison population did not change during the summer count interval, meaning bison were not born and did not die among counts. We assumed aerial counts were nearly a census where every single individual was counted. Bison are highly visible during the summer and congregate in large groups in open areas. However, we expected some differences among counts and actual abundance due to observer error, such as missing groups that moved out of survey units or into timbered areas. As a result, observers could under-count the bison population, but could not over-count the bison population. We related counts to the model predicted population size using a beta-binomial model $Y1_t = p\mathbf{Z}_t + \sigma_1$ where $Y1_t$ was a population count, $\mathbf{Z}_t$ was the number of bison in each age and sex class, p was a sighting parameter, and σ_1 was error. We assumed the sighting parameter p was not a single value (e.g., 0.97). Instead, p represented a range of values described by a mean and standard deviation (e.g., 0.97, 0.92 – 0.99).

Aerial and ground composition surveys were completed during July. Bison segregate into mixed age and gender and adult male only (e.g., bachelor) groups during summer. Aerial counts determined the number of bison found in mixed gender and bachelor groups. We used a beta-binomial model to estimate the annual proportion of bison found within bachelor groups *m*, $Y2_t = mN2_t + \sigma_2$ where $Y2_t$ was the number of animals found in mixed groups and $N2_t$ was the total aerial count. Ground counts determined the number of calves, juvenile males and females, and adult males and females found within mixed groups. The proportion of bison found in mixed gender groups was used to correct ground count observations for bulls that were missed because ground counts were restricted to mixed gender groups. We used the beta-binomial model to relate our ground counts to model predicted numbers of bison in each age and sex class. For female and young, $Y3_{t,i} = c_i N3_t / m + \sigma_3$ where c_i was the model predicted proportion of bison in the i^{th} age and sex class, $Y3_{t,i}$ was the number of bison in the given age and sex class counted in mixed groups, and $N3_t$ was the total number of bison counted in mixed groups. For adult males, $Y3_{t,i} = mc_i / (1 - mc_i) N3_t + \sigma_3$.

Bison were removed through state and tribal harvests, or capture and consignment to meat processing or research facilities. Total removals were treated as known for each winter. However, the age and sex class of some removals were unknown during some years. We estimated these unknown removals as the product of total removals for each year and the age and sex proportions identified from the subset of known removals.

Model parameters and latent quantities were estimated using Markov chain Monte Carlo techniques. All analyses were completed using program R. We assessed the ability of our model to make predictions using posterior predictive checking and out of sample prediction. Posterior predictive checks evaluate the ability of the model to simulate data that resembles the data that were actually collected. Out of sample prediction compares data that were not used in fitting the model to new data sources that were collected. We found using these techniques that annual aerial calf counts of the population systematically undercounted the likely number of calves in the population. Also, we monitored whether adult females fit with collars produced calves each year and determined that the calf to female ratio from these data was much higher than population averages estimated in June. Therefore, these data sources have no longer been used in model fitting.

Appendix B: Summaries of Counts, Classifications, and Removals during 2000-2017

Table B1. Aerial counts of the Yellowstone bison population completed during June-July, 2000-2017[a].

		Park Total	Central Herd			Northern Herd		
			Total	Adults	Calves	Total	Adults	Calves
2000	June 4, 2000	2,613	2,060	1,734	326	553	460	93
	July 13, 2000	2,432	1,924			508		
	August 31, 2000	2,708	2,118			590		
2001	June 21, 2001	3,256	2,595	2,126	469	661	557	104
	July 24-25, 2001	2,859	2,564			719		
2002	June 25, 2002	3,648	3,100	2,560	540	548	477	71
	July 29, 2002	3,715	2,902			812		
	August 22, 2002	4,045	3,240			805		
2003	July 10, 2003	3,778	2,900	2,466	434	878	753	125
	August 8, 2003	3,811	2,923			888		
	August 28, 2003	3,766	2,770			996		
2004	July 21, 2004	4,148	2,811	2,310	501	1,337		
	July 28, 2004	3,995	3,027			968		
	August 4, 2004	4,215	3,339			876		
2005	July 19, 2005	4,819	3,553			1,266		
	July 26, 2005	4,747	3,394			1,353		
	August 1, 2005	5,015	3,531			1,484		
2006	July 19, 2006	3,713	2,430	2,146	284	1,283		
	July 26, 2006	3,889	2,512			1,377		
	August 2, 2006	3,775	2,496			1,279		
2007	June 14, 2007	4,554	2,734	2,385	349	1,820	1,499	321
	July 30, 2007	3,959	2,390			1,569		
	August 6, 2007	4,694	2,624			2,070		
2008	June 14, 2008	2,943	1,150	1,047	103	1,793	1,468	325
	July 8, 2008	2,881	1,540			1,341		
	July 15, 2008	2,969	1,469			1,500		
2009	June 12, 2009	3,301	1,464	1,295	169	1,837	1,518	319
	July 9, 2009	2,977	1,544			1,433		
	July 16, 2009	3,183	1,535			1,648		
2010	June 14, 2010	3,898	1,652	1,425	227	2,246	1,891	355
	July 8, 2010	3,715	1,730			1,985		
	July 22, 2010	3,563	1,708			1,855		
2011	June 21, 2011	3,651	976	880	96	2,675	2,188	487
	July 12, 2011		NA			2,288		
	July 18, 2011	3,720	1,406			2,314		
	July 25, 2011	3,485	1,330			2,155		
2012	June 21, 2012	3,885	1,395	1,194	201	2,490	2,097	393

	July 8, 2012	4,171	1,640			2,531		
	July 22, 2012	4,230	1,561			2,669		
2013	June 6, 2013	4,492	1,327	1,159	168	3,165	2,631	534
	July 15, 2013	4,924	1,504			3,420		
	July 22, 2013	4,565	1,334			3,231		
2014	June 20 ,2014	4,857	1,340	1,192	148	3,517	2,926	591
	July 18, 2014	4,386	1,444			2,942		
	July 25.2014	4,865	1,441			3,424		
2015	June 13-14, 2015	4,910	1,282	1,113	169	3,628	2,997	631
	July 12, 2015	4,616	1,291			3,325		
	July19-20, 2015	4,764	1,323			3,441		
2016	June 18 & 28, 2016	5,459	1,451	1,280	171	4,008	3,312	696
	July 18, 2015	4,736	1,584			3,152		
	July 25, 2016	4,809	1,638			3,171		
	August 8, 2016		NA			4,042		
2017	August 03, 2017		NA			3,619		
	August 4-5, 2017	4,816	847			3,969		

[a] Flight totals were reevaluated during summer 2017 using updated count areas for each herd based on an improved understanding of bison movements.

Table B2. Composition surveys of the Yellowstone bison population during June-August, 2003-2017.

		Classified in Mixed Gender Groups					Air Count	
Year	Herd	Male>1	Male1	Female>1	Female1	Calf	Bachelor	Mixed
2003	C	438	150	1,426	241	498	379	2,521
	N	159 (133)	23 (11)	176 (227)	12 (15)	46 (110)	83	795
2004	C	638 (523)	179 (125)	1,082 (932)	126 (131)	497 (397)	217	2,594
	N	247 (232)	35 (26)	331 (458)	33 (49)	164 (145)	127	1,210
2005	C	500 (674)	178 (175)	1,098 (1,060)	162 (148)	430 (443)		
	N	276 (205)	63 (49)	441 (324)	51 (37)	153 (97)		
2006	C	368 (386)	141 (152)	654 (757)	101 (111)	258 (301)	352	2,078
	N	102	27	202	40	103		
2007	C	375 (555)	100 (119)	709 (805)	109 (106)	342 (305)		
	N	300 (173)	139 (28)	637 (366)	101 (28)	339 (169)		
2008	C	116	36	387	50	110	439	1,101
	N	198	87	433	61	232	183	1,158
2009	C	145 (161)	63 (62)	427 (498)	73 (47)	158 (186)	481	1,063
	N	244 (224)	84 (83)	414 (391)	53 (53)	237 (179)	194	1,239
2010	C	340 (369)	72 (82)	517 (537)	57 (81)	219 (228)	338	1,370
	N	228 (298)	126 (150)	934 (679)	140 (121)	391 (344)	230	1,755
2011	C	118 (163)	58 (53)	323 (309)	37 (40)	105 (106)	444	962
	N	303	131	915	99	361	185	2,103
2012	C	282 (420)	68 (80)	493 (477)	41 (55)	173 (216)	398 (212)	1,242 (1,349)
	N	375 (405)	187 (114)	876 (698)	165 (84)	466 (288)	80 (50)	2,451 (2,619)

2013	C	287 (372)	101 (102)	415 (401)	82 (77)	197 (191)	342 (186)	1,162 (1,148)
	N	457 (608)	231 (249)	1,061 (1,149)	191 (198)	528 (538)	145 (80)	3,275 (3,151)
2014	C	275 (296)	113 (71)	565 (380)	69 (63)	206 (145)	276 (282)	1,168 (1,159)
	N	310 (565)	155 (266)	1,023 (1,314)	126 (259)	422 (612)	145 (261)	2,797 (3,163)
2015	C	187 (310)	43 (58)	301 (364)	42 (58)	165 (166)	240 (166)	1,051 (1,157)
	N	651 (738)	219 (192)	1,499 (1,144)	203 (141)	689 (507)	149 (69)	3,176 (3,372)
2016	C	350 (327)	106 (37)	457 (316)	79 (25)	185 (95)	169 (142)	1,415 (1,496)
	N	770 (839)	316 (304)	1,510 (1,570)	248 (200)	763 (766)	123 (56)	3,029 (3,115)
2017	C	388	44	275	39	106	88	759
	N	1,167	221	1,279	231	585	59	3,910

Table B3. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 1970-2017.

	Maximum No. Bison Counted Previous June-August[h]			Sent to Slaughter/ Management Culls		Hunter Harvest[a]		Sent to Quarantine Research		Total	Age and Gender Composition of Culls/Harvests			
Winter	North	Central	Total	N	W	N	W	N	W		M	F	C	Unk
1970-84				0	0	13	0	0	0	13	4	7	0	2
1984-85	695	1,552	2,247	0	0	88	0	0	0	88	42	37	8	1
1985-86	742	1,609	2,351	0	0	41	16	0	0	57	42	15	0	0
1986-87	998	1,778	2,776	0	0	0	7	0	0	7	5	2	0	0
1987-88	940	2,036	2,976	0	0	2	37	0	0	39	27	7	0	5
1988-89	1,058[h]	2,089[h]	3,147[h]	0	0	567	2	0	0	569	295	221	53	0
1989-90	432[h]	2,075[h]	2,507[h]	0	0	1	3	0	0	4	0	0	0	4
1990-91	818	2,203	3,021	0	0	0	14	0	0	14	0	0	0	14
1991-92	822	2,290	3,112	249	22	0	0	0	0	271	113	95	41	22
1992-93	681	2,676	3,357	0	79	0	0	0	0	79	9	8	9	53
1993-94	636[h]	2693[h]	3329[h]	0	5	0	0	0	0	5	0	0	0	5
1994-95	1,140	2,974	4,114	307	119	0	0	0	0	426	77	66	31	252
1995-96	866	3,062	3,928	26	344	0	0	0	0	370[c]	100	71	10	189
1996-97	860[h]	2,724[h]	3,584[h]	725	358	0	0	0	0	1,083[d]	329	330	144	280
1997-98	455	1,715	2,170	0	11	0	0	0	0	11	0	0	0	11
1998-99	489[h]	1,622[h]	2,111[h]	0	94	0	0	0	0	94	44	49	1	0
1999-00	540	1,904	2,444	0	0	0	0	0	0	0	0	0	0	0
2000-01	590[h]	2,118[h]	2,708[h]	0	6	0	0	0	0	6	6	0	0	0
2001-02	719	2,564	3,283	0	202	0	0	0	0	202	60	42	16	84
2002-03	805[h]	3,240[h]	4,045	231	13	0	0	0	0	244	75	98	43	28
2003-04	888	2,923	3,811	267	15	0	0	0	0	282	58	179	23	22
2004-05	876	3,339	4,215	1	96	0	0	0	17	114	23	54	20	17
2005-06	1,484	3,531	5,015	861	56	32	8	87	0	1,044	205	513	245	81
2006-07	1,377	2,512	3,889	0	4	47	12	0	0	63	53	6	0	4

2007-08	2,070	2,624	4,694	1,288	160	59	107	112	0	1,726	516	632	332	246
2008-09	1,500	1,469	2,969	0	4	1	0	0	0	5	5	0	0	0
2009-10	1,837[h]	1,464[h]	3,301[h]	3	0	4	0	0	0	7	7	0	0	0
2010-11	2,246[h]	1,652[h]	3,898[h]	6	0	Unk	Unk	53	0	260	106	102	52	0
2011-12	2,314	1,406	3,720	0	0	15	13	0	0	28[e]	14	12	2	0
2012-13	2,669	1,561	4,230	0	0	148	81	0	0	250[f]	116	85	28	0
2013-14	3,420	1,504	4,924	258	0	258	69	60	0	645[g]	202	287	152	4
2014-15	3,424[h]	1441[h]	4,865	511	0	201	18	7	0	737	276	297	161	3
2015-16	3,627[h]	1,282[h]	4,910[h]	101	0	378	24	49	0	552	175	227	146	4
2016-17	4,008	1,451	5,459	753	0	389	97	35	0	1,274	311	585	342	36

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

[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 captured at the north boundary and consigned to a research facility at Texas A&M University (about 100 bison).

[e] There is a report of 29 removals with differences owing to reported harvests.

[f] There is a report of 260 removals with differences owing to reported harvests.

[g] There is a report of 650 removals with differences owing to reported harvests.

[h] Flight totals were reevaluated during summer 2017 using updated count areas for each herd and including flights occurring June 1-August 31.