Status Report on the Yellowstone Bison Population, October 2019

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Summary

- The maximum aerial count of bison during summer 2019 was 4,829, including 3,667 in northern Yellowstone (northern herd) and 1,162 in central Yellowstone (central herd).

- The removal of 600 to 900 bison this winter should decrease the number of bison to fewer than 4,100 by the end of winter.

- Removals should focus on the northern herd. We do not recommend harvesting or capturing bison west of the park (central herd).

- We recommend selectively removing 10 to 15% calves, 10 to 12% adolescents, 20 to 34% adult females, and 39 to 60% adult males.

- We recommend placing up to 120 juveniles and young adults into two to four new quarantine test groups at Stephens Creek and Corwin Springs this winter.

Contents

Population Size

Biologists completed two airplane surveys of the northern region (i.e., the northern herd) and central region (i.e., the central herd) of Yellowstone National Park and adjacent areas in the State of Montana. They counted 3,667 (June 12) and 3,540 (July 29) bison in the northern herd and 1,162 (June 13) and 1,124 (July 30) bison in the central herd. They photographed groups larger than 50 animals when feasible to improve counts.

We used an integrated population model to derive an estimate of 4,908 bison, within a 95% credible interval (i.e., range) of 4,588 to 5,256 bison (Figure 1). Our estimate indicated a 6% increase of about 300 animals since summer 2018 (4,613 bison). However, the population was stable, decreasing by 1% on average, over the past two years.

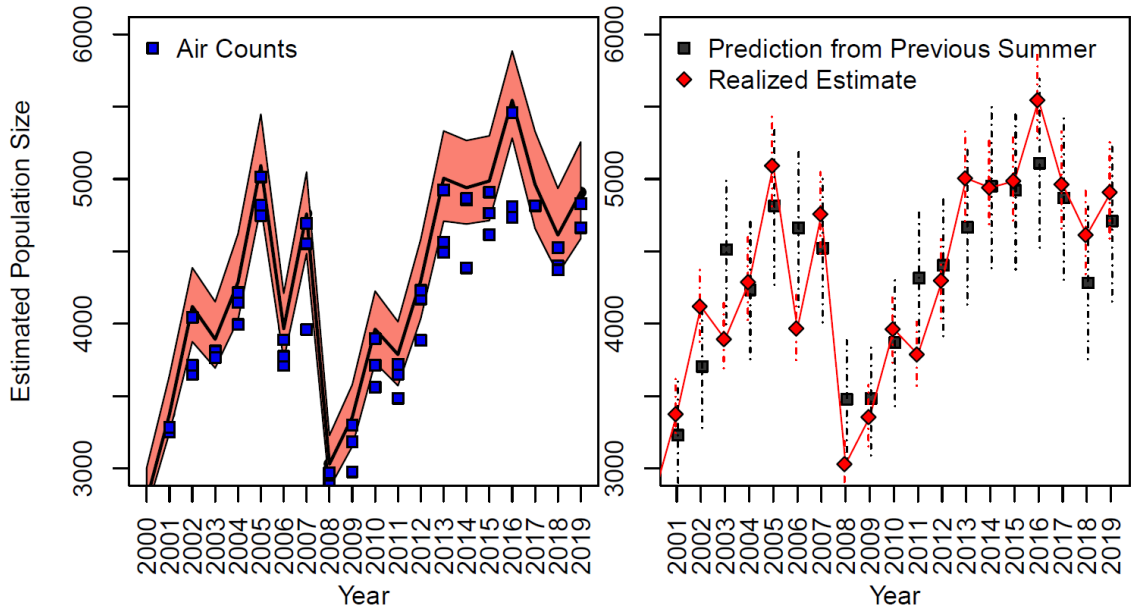

Figure 1.
(*Left)* Estimated size of the Yellowstone bison population based on an integrated population model (Appendix A). The black line connects averages during 2000-2019 while the red shaded area depicts the 95% credible interval (i.e., range) around population estimates. The blue boxes represent actual numbers of bison counted during aerial surveys. (*Right*) Predicted population abundance from the previous summer (black boxes) compared to estimates made once biologists collected data (red diamonds). Solid icons show averages and dotted lines depict ranges around estimates. Discrepancies between black and red icons suggest inaccurate counts.

Population Composition (Age and Sex)

Biologists conducted ground and aerial surveys during July 30 to August 6, 2019, to estimate the age and sex composition of the bison population. They completed surveys during the peak of the breeding period when males and females concentrate in large groups. The current population is composed of approximately 735 calves (0 to 4 months), 288 female and 292 male adolescents (12 to 16 months), 1,667 adult females (≥2 years), and 1,925 adult males (≥2 years).

We estimated a sex ratio of 114 males per 100 females (excluding calves), which equates to 53% males and 47% females. The sex ratio met our conservation objective of maintaining a population with similar proportions of males and females (Figure 2) and has averaged 102 males

per 100 females over the past five years. We estimated 27% of the population was composed of juvenile animals (0 to 16 months of age). Of the juvenile component, we estimated 44 calves per 100 adult females and 79 juveniles (i.e., calves, yearling females, and yearling males) per 100 adult females. Over the past five years, the age composition has averaged 29% juveniles and 71% adults. Current conditions met our conservation objective of maintaining a population composed of nearly 30% juveniles and 70% adults.

We estimated annual adult female survival during 2000 to 2019 at 0.95 (standard deviation [SD] = 0.01), adult male annual survival at 0.95 (standard deviation [SD] = 0.03), and calf annual survival, which excludes neonate mortality occurring between calving and surveys in July, as 0.90 (SD = 0.04). These estimates do not include mortality resulting from capture and slaughter or hunter harvest. We monitored 46 (36 northern herd, 10 central herd) adult females that were initially fit with radio telemetry collars prior to June 1, 2018. Eighty percent (37 of 46) of radio-collared bison survived through August 1, 2019. Of these radio-collared animals, hunters harvested two bison, management operations captured three bison and sent them to slaughter, and four bison died of natural causes.

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). Aerial counting on June 12-13, 2019, detected 821 calves (672 northern, 149 central), which was higher than our final projection of about 735 calves, which incorporated ground counts in August.

Birth and survival rates during 2000 to 2019 suggested the population has the potential to increase annually by 11% ($\lambda = 1.11$) in the absence of management removals. Observed growth rates when adjusting for management removals[1] averaged 14.5% per year (range: -8% to 27%) and were higher than the population potential due to skewed sex and age proportions and counting inaccuracies. The population increased by 6.4% during 2018-2019. The population would have increased by 13% to about 5,220 animals during summer 2019 if managers did not remove 460 bison last winter.

[1] 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.

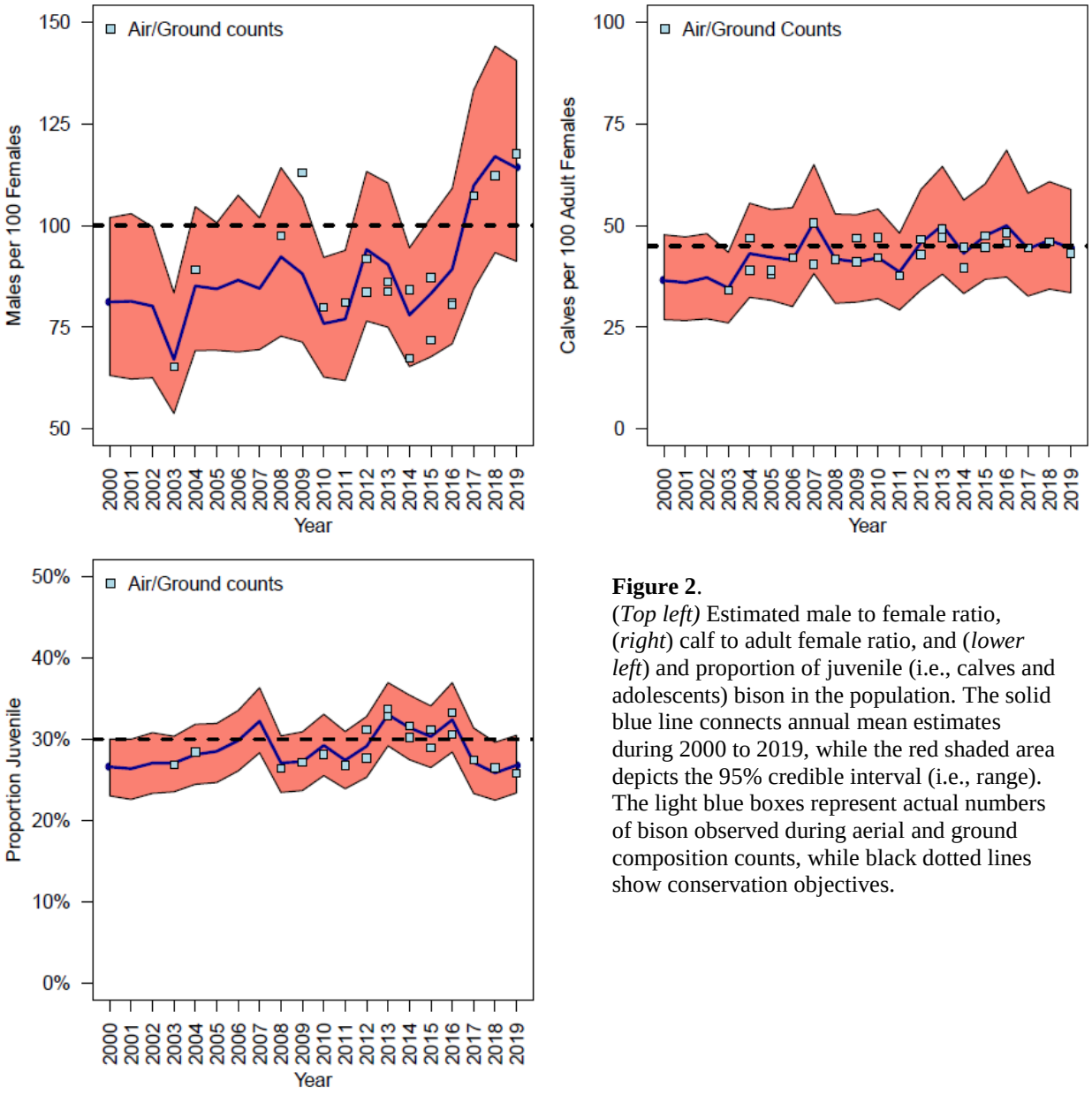

Figure 2.
(*Top left)* Estimated male to female ratio, (*right*) calf to adult female ratio, and (*lower left*) and proportion of juvenile (i.e., calves and adolescents) bison in the population. The solid blue line connects annual mean estimates during 2000 to 2019, while the red shaded area depicts the 95% credible interval (i.e., range). The light blue boxes represent actual numbers of bison observed during aerial and ground composition counts, while black dotted lines show conservation objectives.

Population Structure (Northern and Central Herds)

Since the 1980s, the Yellowstone bison population has been described by numbers of bison using and breeding in the northern and central geographic regions of the park, with the northern herd spending summers in Little America, Lamar Valley, and adjacent higher-elevation areas, and the central herd spending summers in the Madison, Gibbon, Firehole, Hayden, and Pelican valleys. While movements of bison between these geographic regions of the park increased during the implementation of the Interagency Bison Management Plan (2001 to 2019), we continue to report counts of bison observed in these geographic areas each summer.

Bison abundance in the northern herd increased 10% from a count of 3,337 in August 2018 to 3,667 in July 2019. Counts of the northern herd averaged 3,722 over the last five years and were

relatively stable (range: 3,337 to 4,008). The calf to cow ratio was 0.44 (5-year average = 0.47), the juvenile proportion was 27% (5-year average = 30%), and the male to female ratio was 1.06 (5 year average = 0.88). The age and sex structure of the northern herd meets the composition objectives of a juvenile proportion of 30% and near equal sex ratio.

Bison abundance in the central herd remained stable from a count of 1,190 during August 2018 to a count of 1,162 during July 2019. Counts of the central herd over the last five years were similar and averaged 1,186. The central herd continues to exhibit a lower potential for population growth compared to the northern herd. During August 2019, there were approximately 330 adult female bison in the central herd, the calf to cow ratio was 0.39 (5-year average = 0.40), the juvenile proportion of the herd was 20% (5-year average = 23%), and the male to female ratio was 1.77 (64% male; 5-year average = 60%; Figure 3). The age and sex structure of the central herd does not meet composition objectives, specifically the low juvenile proportion and high male to female ratio.

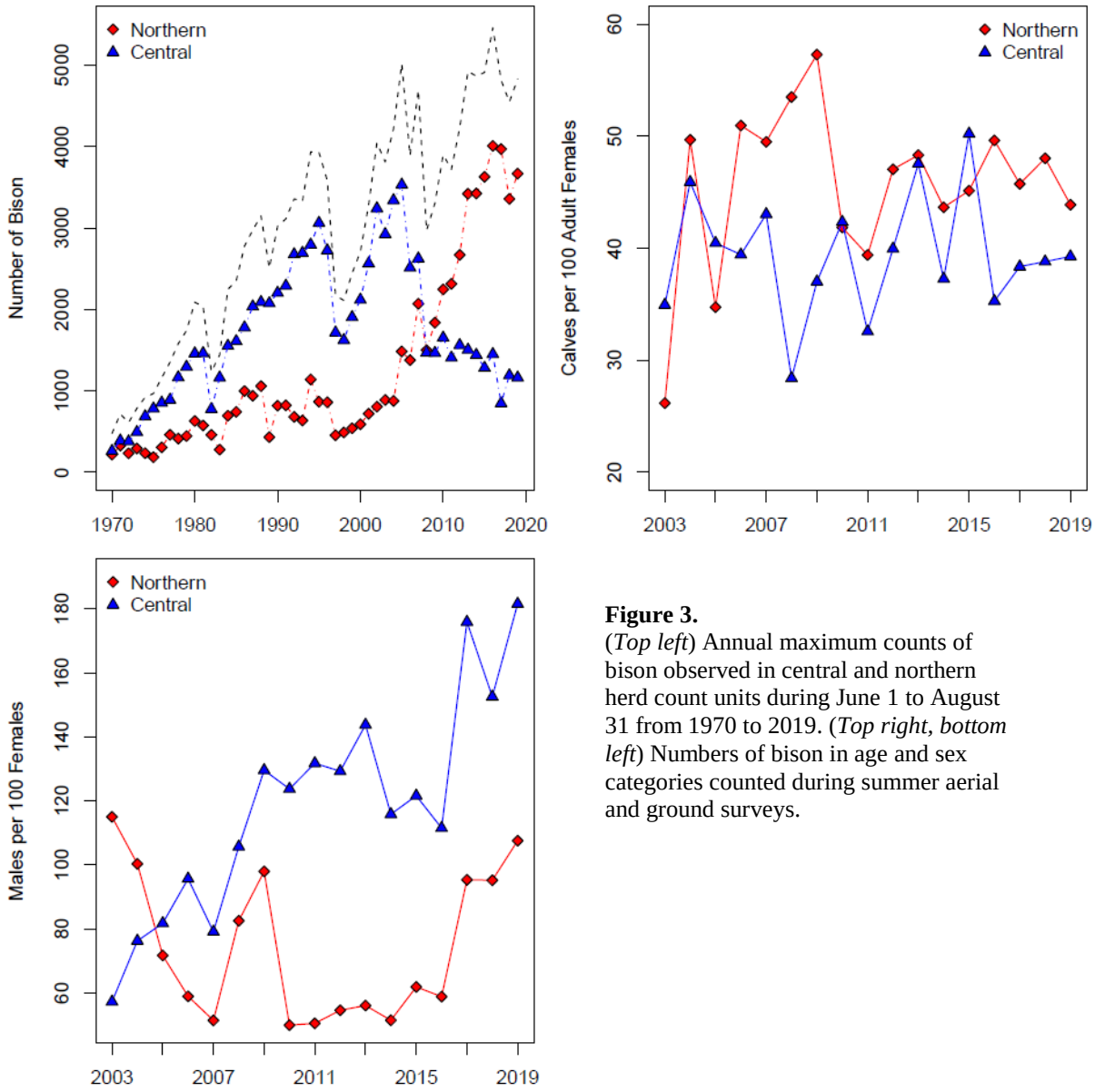

Figure 3.
(*Top left*) Annual maximum counts of bison observed in central and northern herd count units during June 1 to August 31 from 1970 to 2019. (*Top right*, *bottom left*) Numbers of bison in age and sex categories counted during summer aerial and ground surveys.

Counts in the central herd fluctuate seasonally due to movements of bison between central and northern areas of the park[2,3]. However, central herd counts during winter 2018-2019 were stable, suggesting relatively few central herd animals moved to northern Yellowstone during the period management removals occurred. For example, we counted 1,139 (bison) during September 2018, 1,024 during December 2018, and 1,104 during March 2019. Moreover, management operations and hunting removed five radio-collared adult female bison near the northern park boundary and all of these animals migrated from northern areas of the park. We did detect two radio-collared adult females summering in northern Yellowstone during 2019 that previously summered in central Yellowstone during 2018. Dispersal of adult females from central to northern areas of the park, compounded by the age and sex structure of the central herd, continues to stabilize population growth of this herd unit in the absence of management removals.

Removals during Winter 2018-2019

Managers culled or harvested 460 bison during winter 2018-2019 (Table 1). This total was below the range of 600 to 900 recommended by biologists from Yellowstone National Park[3]. Bison migrations occurred during an abbreviated period from March 7 to April 7, 2019, during which more than 200 bison were regularly near the northern park boundary. Managers captured 348 bison at the Stephens Creek facility while hunters harvested 109 animals outside the park in Montana. Managers transported all captured bison to slaughter facilities except for one that died during holding. Managers did not place any animals into quarantine.

Recommendations during winter 2018-2019 were to remove bison in proportion to their occurrence in the population (73% adults [46% females and 54% males], 12% adolescents, and 15% calves), particularly if the total cull exceeded 500 animals[3]. The actual age and sex composition of removed bison was 56% adults (63% females and 37% males), 19% adolescents, and 25% calves. As a result, the 2019 population continued to move away from objectives for juvenile proportion and sex ratio – although 5-year averages remained within desired ranges.

Since winter 2013-2014, managers have removed more than 1,233 calves and nearly 800 adolescents (12 to 16 months) from the bison population. Removing large numbers of calves and adolescents disproportionately reduces the number of animals reaching reproductive maturity. Managers removed about 33% of the 2016-calf cohort, 74% of the 2017-calf cohort, and 51% of the 2018-calf cohort. In addition, managers removed more than 1,733 adult females since winter 2013-2014 compared to about 1,005 adult males. Continued removal of pre-reproductive and adult female bison has the potential to create a skewed population structure overrepresented by males and older females. Continued biased removal of juvenile and adult female bison holds high potential to shift the bison population out of desired ranges.

[2] Geremia, C. R. Wallen, and P. J. White. Status report of the Yellowstone bison population, September 2018. Available at http://ibmp.info/Library/OpsPlans/2018_StatusYellowstoneBisonPopulation_Sep2018_Final.pdf.
[3] Geremia, C., P. J. White, J. A. Hoeting, R. L.Wallen, F. G. R. Watson, D. Blanton, and N. T. Hobbs. 2014. Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecological Applications*, *24*(2), 346-362.

Table 1. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 2009 to 2019. See 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
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
2017-18	3,969	847	4,816	697	0	285	90	99	0	1,171	300	491	288	92
2018-19	3,337	1,190	4,527	348	0	109	3	0	0	460	144	200	116	0

Predicting Population Growth under Different Management Scenario

We predicted bison abundance and composition during July 2020 after simulating removals of up to 1,100 bison of various age and sex compositions during winter 2019-2020 (Figure 4, Table 2). We report the findings for three key removal strategies, referred to as "proportional," "conservation," and "non-selective" strategies. The proportional strategy maintains existing demographic conditions by removing bison according to the existing population structure of 73% adults (46% females and 54% males), 15% calves, and 12% adolescents. The conservation strategy aims to align demographic conditions with conservation goals by selectively removing male and adult bison according to 80% adults (25% females and 75% males), 10% calves, and 10% adolescents. The nonselective strategy removes bison according to observed demographic proportions (primarily pregnant females and young) when large culls occur (e.g., more than 1,000) of 60% adults (62% females and 38% males), 14% adolescents, and 26% calves. The composition of the nonselective strategy represents what managers likely would remove if they culled or harvested nearly all migrants during a large migration.

The removal of 500 to 700 animals provides the highest chance of stabilizing the population near 4,000 animals at the end-of-winter and 4,900 bison after calving (Figure 4). The proportional strategy would remove 75 to 105 calves, 60 to 84 adolescents (12 to 16 months old), 170 to 238 adult females, and 195 to 273 adult males (Table 2). The conservation strategy would remove 50 to 70 calves, 40 to 70 adolescents, 100 to 140 adult females, and 300 to 420 adult males.

We do not recommend the strategy of non-selectively removing all migrants during a large migration because it will further shift the population away from conservation objectives – increasing the population to 56% male and 44% female, and 25% juvenile and 75% adult.

Skewing the population towards adult males holds potential to alter movement patterns, reduce the proportion of animals that migrate out of the park (Figure 4), increase the bison population size, and create larger episodic, weather-driven, out-of-park migrations. Skewing the population towards adult males also reduces mate competition, requiring a larger population size to preserve population genetics.

Regardless of winter severity, enough bison migrate outside the park for managers to remove and stabilize the population when there are between 4,250 and 5,000 bison during summer (Figure 4). We expect migrations during winter 2019-2020 to support the removal of at least 500 to 700 animals. If winter is severe, more bison may be available for removal to reduce the population below 4,900 animals after calving in summer 2020.

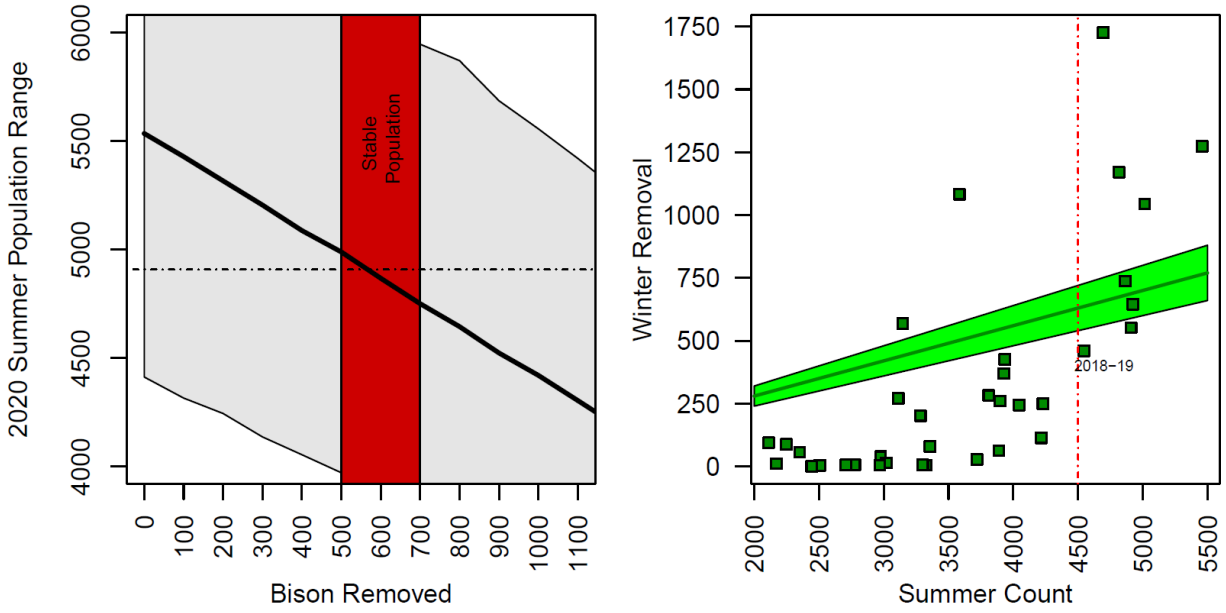

Figure 4.
(*Left*) Predicted size of the bison population during July 2020 considering management removals of up to 1,100 animals. We made predictions assuming a removal composition near current age and sex structure. The solid black line represents the estimated summer population size according to varying management removals, and the gray polygon represents the 95% credible interval. The dashed black line represents the current population size of approximately 4,900 animals. The red shaded area shows the removal of 500 to 700 animals to offset growth. (*Right*) Numbers of bison removed during winters from 1984 to 2019 and corresponding population sizes during the summer. The green shaded area represents the number of bison within a range that managers must remove to offset growth and lead to a population that is no larger during the subsequent summer.

Table 2. Predicted population sizes, male to female ratios, and juvenile to adult ratios of the Yellowstone bison population for July 2020 with standard deviations in parentheses. The proportional strategy (gray) shows predictions based on a removal composition using the current age and sex structure of 73% adults (46% females and 54% males), 15% calves, and 12% adolescents. The conservation (white) strategy shows predictions based on a removal composition of 80% adults (25% females and 75% males), 10% calves, and 10% adolescents and aims to realign demographic conditions with conservation objectives. The nonselective strategy (blue) shows predictions based on a removal composition of 60% adults (62% females and 38% males, 14% adolescents, and 26% calves and represents the likely composition if nearly all migrants were removed during winter.

Bison	Proportional to Current Conditions			Move towards Conservation Objectives			Non-selective Removal		
Removed	Abundance	M:F Ratio	% Juvenile	Abundance	M:F Ratio	% Juvenile	Abundance	M:F Ratio	% Juvenile
0	5,549 (639)	1.18 (0.32)	0.27 (0.04)	5551 (645)	1.18 (0.32)	0.27 (0.04)	5,550 (625)	1.18 (0.32)	0.27 (0.04)
100	5,428 (626)	1.18 (032)	0.27 (0.04)	5431 (635)	1.16 (0.31)	0.28 (0.04)	5,429 (624)	1.19 (0.32)	0.27 (0.04)
200	5,316 (606)	1.18 (0.32)	0.27 (0.04)	5323 (615)	1.15 (0.31)	0.28 (0.04)	5,315 (614)	1.21 (0.32)	0.27 (0.04)
300	5,198 (600)	1.18 (0.32)	0.27 (0.04)	5227 (604)	1.13 (0.3)	0.28 (0.04)	5,198 (614)	1.22 (0.33)	0.27 (0.04)
400	5,093 (597)	1.18 (0.32)	0.27 (0.04)	5119 (585)	1.11 (0.3)	0.28 (0.04)	5,075 (599)	1.23 (0.34)	0.26 (0.04)
500	4,990 (589)	1.19 (0.33)	0.27 (0.04)	5009 (583)	1.09 (0.3)	0.28 (0.04)	4,968 (593)	1.25 (0.34)	0.26 (0.04)
600	4,876 (571)	1.18 (0.32)	0.27 (0.04)	4900 (573)	1.08 (0.29)	0.29 (0.04)	4,854 (576)	1.26 (0.35)	0.26 (0.04)
700	4,755 (555)	1.18 (0.33)	0.27 (0.04)	4802 (559)	1.06 (0.29)	0.29 (0.04)	4,748 (566)	1.28 (0.36)	0.25 (0.04)
800	4,642 (549)	1.18 (0.33)	0.27 (0.04)	4690 (540)	1.03 (0.28)	0.29 (0.04)	4,617 (553)	1.30 (0.37)	0.25 (0.04)
900	4,525 (536)	1.18 (0.33)	0.27 (0.04)	4587 (538)	1.01 (0.27)	0.29 (0.04)	4,506 (550)	1.31 (0.37)	0.25 (0.04)
1,000	4,418 (524)	1.18 (0.33)	0.27 (0.04)	4485 (527)	0.99 (0.27)	0.29 (0.04)	4,392 (533)	1.33 (0.38)	0.25 (0.04)
1,100	4,299 (504)	1.18 (0.33)	0.27 (0.04)	4376 (501)	0.97 (0.27)	0.30 (0.04)	4,277 (522)	1.36 (0.39)	0.24 (0.04)

Operational Quarantine

The National Park Service, APHIS, State of Montana, and Fort Peck tribes continued quarantine of male and female individual test groups within Yellowstone National Park. Fifty-eight of 73 juvenile male bison placed into quarantine during February-March 2018 remained brucellosis-free during August 2019. The National Park Service transferred 55 of these males to the Fort Peck tribes to undergo one additional year of assurance testing before final release from the quarantine program. Managers placed three of the brucellosis-free males with 21 female bison, also removed into quarantine during February-March 2018, for breeding. In addition, APHIS transferred five adult males to the Fort Peck tribes during winter 2018-2019 after these animals completed research studies and subsequent quarantine at facilities in Corwin Springs, Montana. APHIS is continuing quarantine testing of additional animals.

Quarantine provides an alternative to slaughter when managers capture bison during winter operations. Bison must test brucellosis negative to qualify for the program. Based on brucellosis prevalence and capturing 300 to 500 animals during winter 2019-2020, we expect the following animals could qualify for the program: 40 to 65 male calves, 30 to 60 female calves, 30 to 50 young males, 20 to 40 juvenile females, and 40 to 70 adult females. We can accept new animals into the program by selecting individual test groups of bison of the same age and sex. Based on completion dates of existing test groups undergoing quarantine in pastures at Stephens Creek and Corwin Springs, we may be able to accept one to five new test groups of 20 to 40 animals each this winter, which could include up to 120 bison. To maximize the number of animals moving into and completing quarantine, we recommend capturing test groups of juvenile females and young males.

Management Recommendations for Winter 2019-2020

- The maximum aerial count of bison during summer 2019 was 4,829, including 3,667 in northern Yellowstone (northern herd) and 1,162 in central Yellowstone (central herd).
- The removal of 600 to 900 bison this winter should decrease the number of bison to fewer than 4,100 by the end of winter.
- Removals should focus on the northern herd. We do not recommend harvesting or capturing bison west of the park (central herd).
- We recommend selectively removing 10 to 15% calves, 10 to 12% adolescents, 20 to 34% adult females, and 39 to 60% adult males.
- We recommend placing up to 120 juveniles and young adults into two to four new quarantine test groups at Stephens Creek and Corwin Springs this winter.

Appendix A: Population Modeling Methods

We use the hierarchical Bayesian state-space modeling approach to build models suitable for incorporating multiple sources of uncertainty and comparing forecasted outcomes of a system under management. This approach supports adaptive management by incorporating new data as it becomes available and revising future predictions based on outcomes of management. We begin by estimating the initial conditions of the bison population, including the number of bison in age and sex stages, which we sum 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, called states, are 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 radio-collared animals. We compare these data to model predictions made before collecting the data 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 two or three genetic lineages derived from about 23 indigenous bison remaining in the central region (Pelican Valley) of Yellowstone National Park during 1901 and 18 pregnant female bison from northwestern Montana introduced with three 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 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. We assigned the same survival rate to pre-reproductive and reproductive-aged animals. However, male survival varied from female survival. We assumed all reproductive-aged females exhibited similar birth rates. Birth rate included offsets due to neonate mortality 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, we used an exponential growth model. That is, the rate of population growth could not decrease as the bison population increased in size.

We used a Bayesian matrix model to estimate bison population growth. 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 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 $s=invlogit(s_0 + s_1 + s_2 + \varepsilon_2)$. 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 radio-collared animals, and testing for previous brucellosis exposure of bison at capture facilities. We used these data to refine estimation of survival and

birth rates, and numbers of bison in each life-cycle stage over time. Biologists completed 56 aerial surveys during June through August from 2000 to 2019 to count bison in the population. We assumed the bison population did not change during the summer count interval. In other words, we assumed no bison were born or died between counts. We assumed aerial counts were nearly a census with every single individual 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).

We completed aerial and ground composition surveys 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. We used the proportion of bison found in mixed gender groups to correct ground count observations for bulls 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, $Y3_{t,i} = mc_i / (1 - mc_i) N3_t + \sigma_3$.

Managers removed bison through state and tribal harvests, or capture and consignment to meat processing or research facilities. We treated total removals as known quantities 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 not used to fit the model to new data collected during monitoring. We found that annual aerial calf counts of the population systematically undercounted the likely number of calves in the population. In addition, we monitored whether adult females fit with radio-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, we did not use these data sources in model fitting.

Appendix B: Summaries of Counts, Classifications, and Removals during 2000-2019

Table B1. Aerial counts of the Yellowstone bison population completed during June-July, 2000 to 2019[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					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					3,619		
	August 4-5, 2017	4,816	847			3,969		
2018	June 4-5, 2018	4,401	758	679	79	3,643	2,994	649
	August 4-5, 2018	4,527	1,190			3,337		
	September 2-3, 2018	4,372	1,162			3,210		
2019	June 12-13, 2019	4829	1,162	1013	149	3,667	2995	672
	July 29-30, 2019	4664	1,124			3,540		

[a] We reevaluated flight totals 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 to 2019. Numbers in parentheses show results from repeated counts.

		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
2018	C	405	59	324	34	126	105	1,085
	N	983	179	1,065	134	512	35	3,302
2019	C	317	37	213	27	84	106	1,018
	N	1,065	192	1,140	195	500	175	3,365

Table B3. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 1970 to 2019.

	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
2017-18	3,969	847	4,816	697	0	285	90	99	0	1,171	300	491	288	92
2018-19	3,337	1,190	4,527	348	0	109	3	0	0	460	97	159	204	0

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