# Status Report on the Yellowstone Bison Population, September 2018

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## Summary


- The aerial count of bison on August 4-5, 2018 was 4,527, including 3,337 in northern Yellowstone and 1,190 in central Yellowstone, which represents about a 6% decrease since summer 2017 and 17% decrease since summer 2016.

- A total of 1,171 bison were removed from the population during winter 2017-2018, including 375 harvests (including 6 dispatched [wounded] animals and 1 abandoned carcass), 694 animals sent to slaughter facilities, 3 animals that died in captivity, and 99 animals removed to a quarantine facility adjacent to the Stephens Creek capture facility.

- Management actions during winter 2017-2018 reduced the northern herd by 16% from a count of 3,969 in August 2017 to 3,337 in August 2018. This is the fewest number of animals counted in northern Yellowstone since 2012.

- A count of 1,190 bison in the central herd was near the average count of 1,338 since 2008. This count suggests the central herd was undercounted during August 2017.

- The removal of 600 to 900 animals during winter 2018-2019 will provide the highest chance the bison population is within a range of 4,200-4,500 animals after calving next summer.

- Bison should be removed selectively to retain the current age and sex structure: 90-140 calves, 60-90 adolescents (12-16 months), 200-300 adult females, and 250-370 adult males. Some captured bison may need to be held in the Stephens Creek facility through winter and released in spring to meet these removal composition objectives.

- Population management actions during winter 2018-2019 should focus on the northern herd. Bison migrating north of the park during winter are composed of animals from the northern and central breeding herds, while bison migrating west of the park are almost entirely from the central breeding herd. To focus on the northern herd, we recommend all state and tribal harvests and captures of bison occur in the northern management area.

- When the number of bison north of Mammoth Hot Springs exceeds 200, the National Park Service may initiate capture of bison at the Stephen's Creek facility. Some bison will be allowed to pass by the facility to provide treaty and state hunting opportunities.


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## Population Size

We completed three 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. We counted 3,641 (June 4), 3,337 (August 4), and 3,210 (September 3) bison in the northern herd and 758 (June 5), 1,190 (August 5), and 1,162 (September 2) bison in the central herd. Groups larger than 50 animals were photographed when feasible to improve counts. We used an integrated population model to derive an estimate of 4,585 bison, within a 95% credible interval (i.e., range) of 4,300-4,900 bison (Figure 1). Our estimate indicated a 7% decrease in abundance since summer 2017 (~ 4,930 bison), and a 17% decrease since 2016 (~5,500 bison). Counts during 2018 suggested the population was underestimated by up to 300 animals during summer 2017, primarily in the central herd.

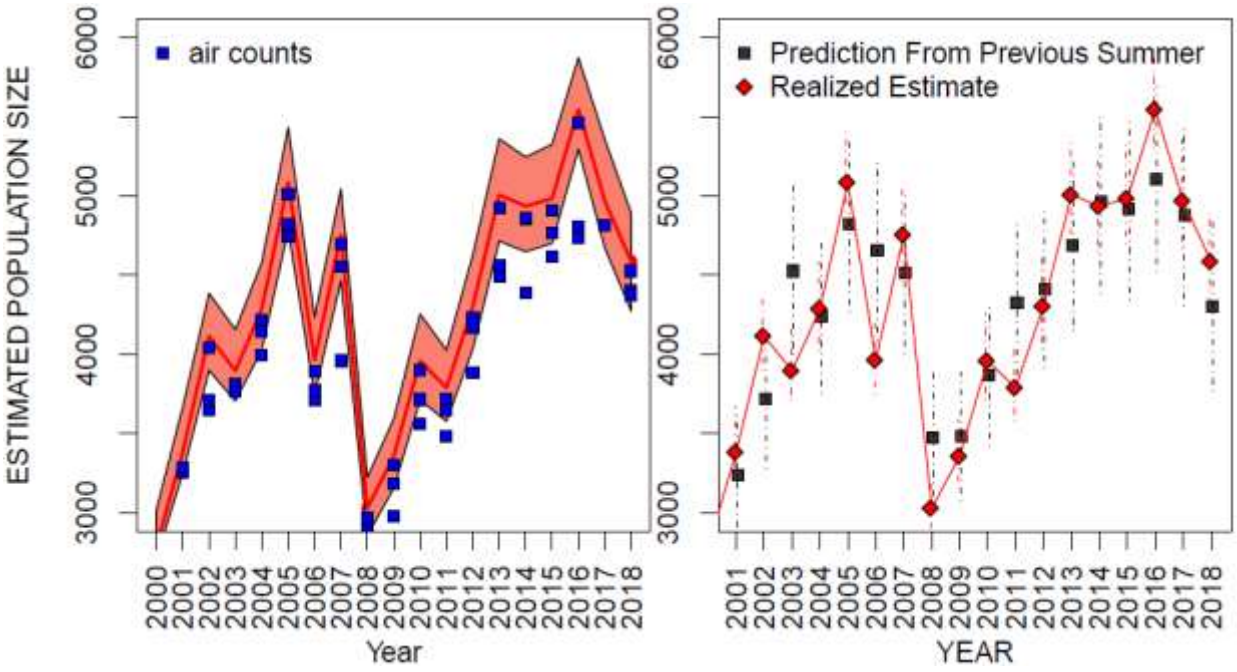


Figure 1. (*Left)* Estimated size of the Yellowstone bison population based on an integrated population model (Appendix A). The bold red line connects averages during 2000-2018 while the red shaded area depicts the 95% credible interval (i.e., range) around the population estimates. The blue boxes represent actual numbers of bison observed during aerial counts. (*Right*) Predicted population abundance made during the previous summer (black boxes) compared to estimates made once data were collected (red diamonds). Solid icons show averages and dotted lines depict ranges around estimates.

## Population Composition (Age and Sex)

Ground and aerial surveys were conducted during August 4 to August 10, 2018 to collect data on the age and sex composition of the bison population. Surveys were completed during the peak of the breeding period when males and females were concentrated in large groups. The current population is composed of approximately 730 calves (0-4 months), 180 female and 270 male adolescents (12-16 months), 1,605 adult females (≥2 years), and 1,800 adult males (≥2 years). Abundance decreased by approximately 300 animals since summer 2017, with most of this difference accounted for by a reduction of nearly 150 adolescents (1-2 years of age), 100 adult females, and 50 adult males.

We estimated a sex ratio of 117 males per 100 females (excluding calves), which equates to 54% males and 46% females. The sex ratio met our conservation objective of maintaining a population with similar proportions of males and females (Figure 2) and has averaged 95 males per 100 females over the past five years. We estimated 26% of the population was composed of juvenile animals, which included calves and adolescent males and females (12-16 months of age). Of the juvenile component, we estimated 45 calves per 100 adult females and 73 juveniles per 100 adult females. Over the past five years, the age composition has averaged 31% juveniles and 69% adults. Current conditions met our conservation objective of maintaining a population composed of nearly 30% juveniles and 70% adults.

During 2000-2018, we estimated adult female annual survival 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 29 (23 northern herd, 6 central herd) adult females that were initially fit with radio telemetry collars prior to June 1, 2016. Eighteen additional adult female bison were captured and fit with radio collars during autumn 2018. Eighty-nine percent (42 of 47) of radio-collared bison survived through August 1, 2018, with 3 bison harvested by hunters and 2 bison captured and sent to slaughter. No bison died of natural causes during winter 2018.

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 4-5, 2018 detected 728 calves. Ground counts during August, while not a complete census, detected 512 calves in the northern herd and 126 calves in the central herd.

The average population growth rate during 2000-2018 was 1.14, which indicates the bison population increased 14% per year after adjusting for management removals.[2] The natural growth rate of the population during 2017-2018 was -7% when removals were included, but increased to 18% after adjusting for removals, suggesting the population would have continued to increase exponentially if management removals were not used to control abundance.

[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.

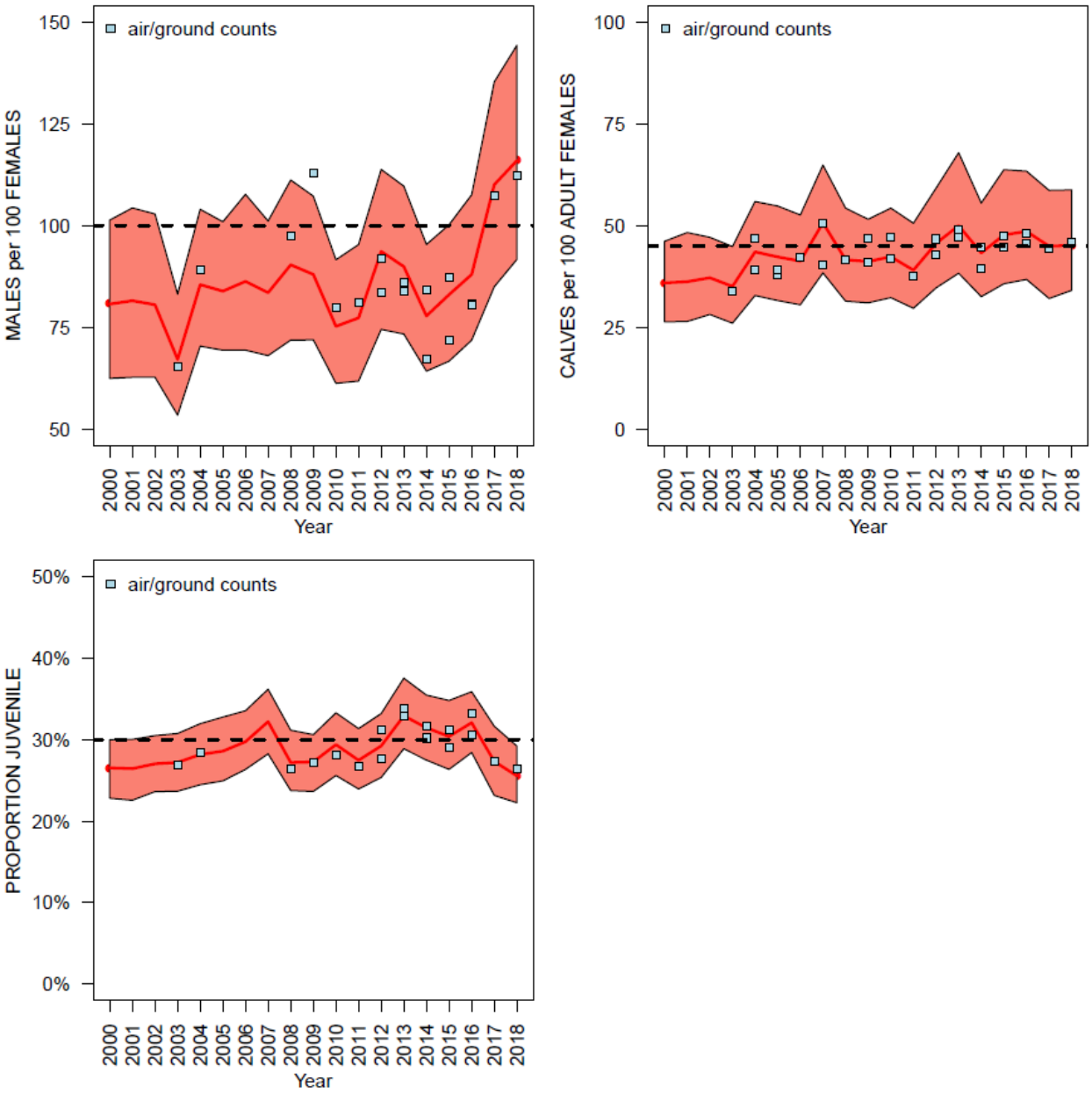


Figure 2. (*Top left)* Estimated male to female ratio, (*right*) calf to adult female ratio, and (*lower left*) and proportion of calf and adolescent bison in the population. The bold red line connects annual mean estimates during 2000-2018, while the red shaded area depicts the 95% credible interval (i.e., range). The blue boxes represent actual numbers of bison observed during aerial and ground composition counts, while black dotted lines show conservation objectives.

## Population Structure (Central and Northern Herds)

Since the 1980s, the Yellowstone bison population has been described by numbers of bison using and breeding in the central and northern 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. Movements of bison between these geographic regions of the park have

increased during the implementation of the Interagency Bison Management Plan (Figure 3), but we continue to report counts of bison observed in these geographic areas each summer.

During August 2018, 1,190 bison were counted in the central herd, which represented an increase of 41% from a count of 847 animals during summer 2017. This difference suggests we likely undercounted the park-wide bison population by approximately 300 animals during summer 2017. Over the past three years, central herd counts fluctuated between 1,451 (2016), 847 (2017), and 1,190 (2018), suggesting we likely missed groups of animals in central herd count areas during August 2017. We attributed management removals to the lower count for the central herd during 2016-2017,[3] though now it appears inaccurate counting also contributed. After counting 847 bison during August 2017, we counted 1,398 bison during December 2017, 749 during March 2018, 758 during June 2018, and 1,190 during August 2018. This pattern of counts suggests large movements of bison between northern and central herd count units occurred throughout the year.

Bison abundance in the northern herd decreased 16% from a count of 3,969 in August 2017 to 3,337 in August 2018. This is the fewest number of bison counted in northern Yellowstone since 2012, when 2,669 were observed.

The central herd continues to exhibit lower potential for population growth compared to the northern herd. During August 2018, there were about 400 adult female bison in the central herd, the number of calves per adult female was 0.39 (5-year average = 0.40), the juvenile proportion of bison was 21% (5-year average = 24%), and the male to female ratio was 1.53 males per female (61% male; 5-year average = 57%; Figure 4). 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. The age and sex structure of the northern herd meets composition objectives, with a juvenile proportion of 28% (5-year average = 33%) and a male proportion of 50% (5-year average = 41%; Figure 4).

[3] Geremia, C. R. Wallen, and P.J. White. Status report of the Yellowstone bison population, September 2017. Available at http://ibmp.info/Library/OpsPlans/2017_StatusYellowstoneBisonPopulation_Sep2017_Final.pdf.

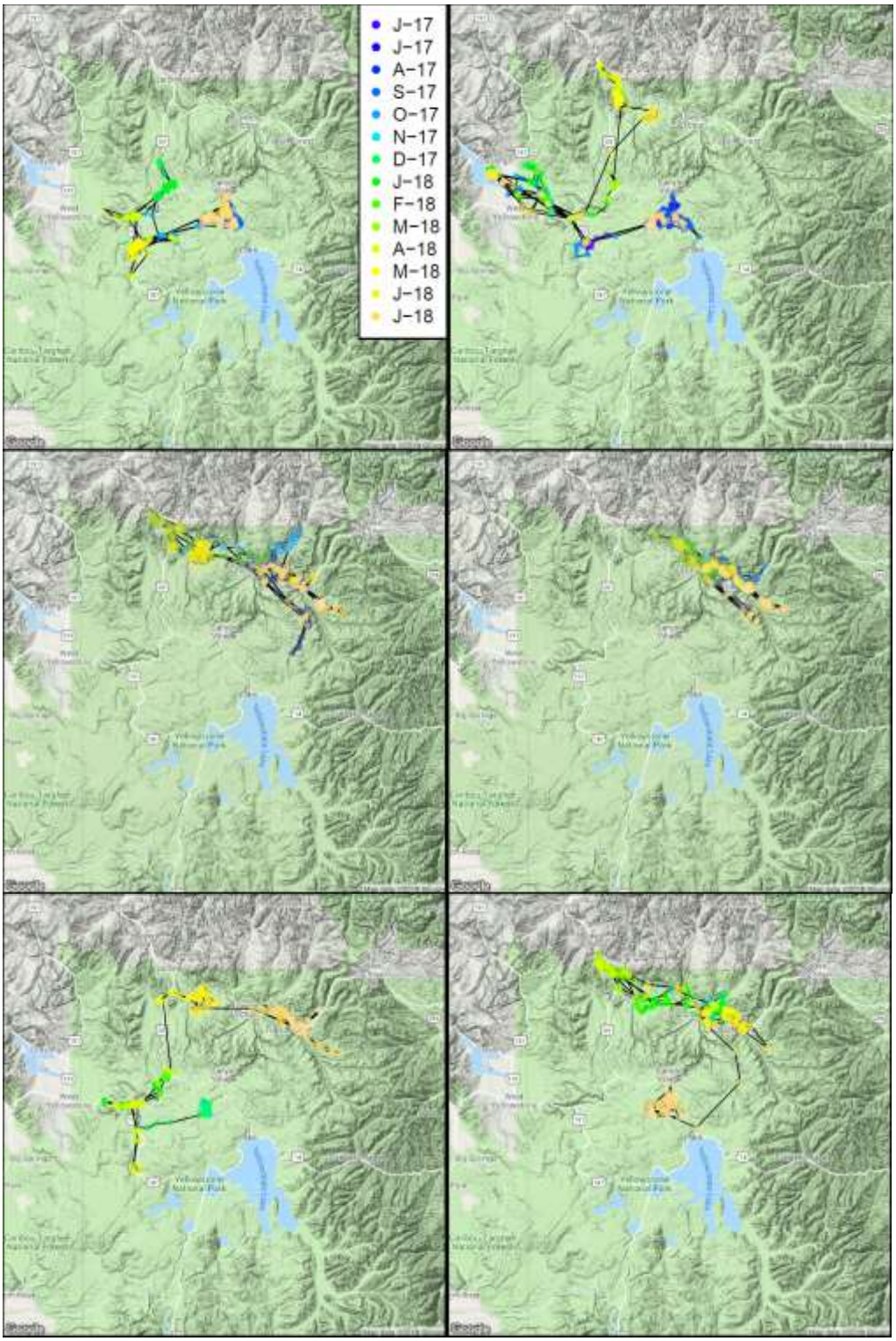

Figure 3. Movement summaries of GPS collared bison during summer 2017 to summer 2018, including (*top row*) central herd animals that remained in central areas (3 of 5, including 1 harvested West Yellowstone) or moved to the northern range during winter (2 of 5, including 1 culled Gardiner); (*middle row*) northern herd animals that exited the park (8 of 10, including 1 culled Gardiner) or remained in the interior northern range (2 of 10); and animals originally collared during fall 2017 that remained in northern areas (9 of 13), remained in central areas (1 of 13), (*bottom row*) moved from north to central areas (1 of 13), or moved from central to northern areas (2 of 13).

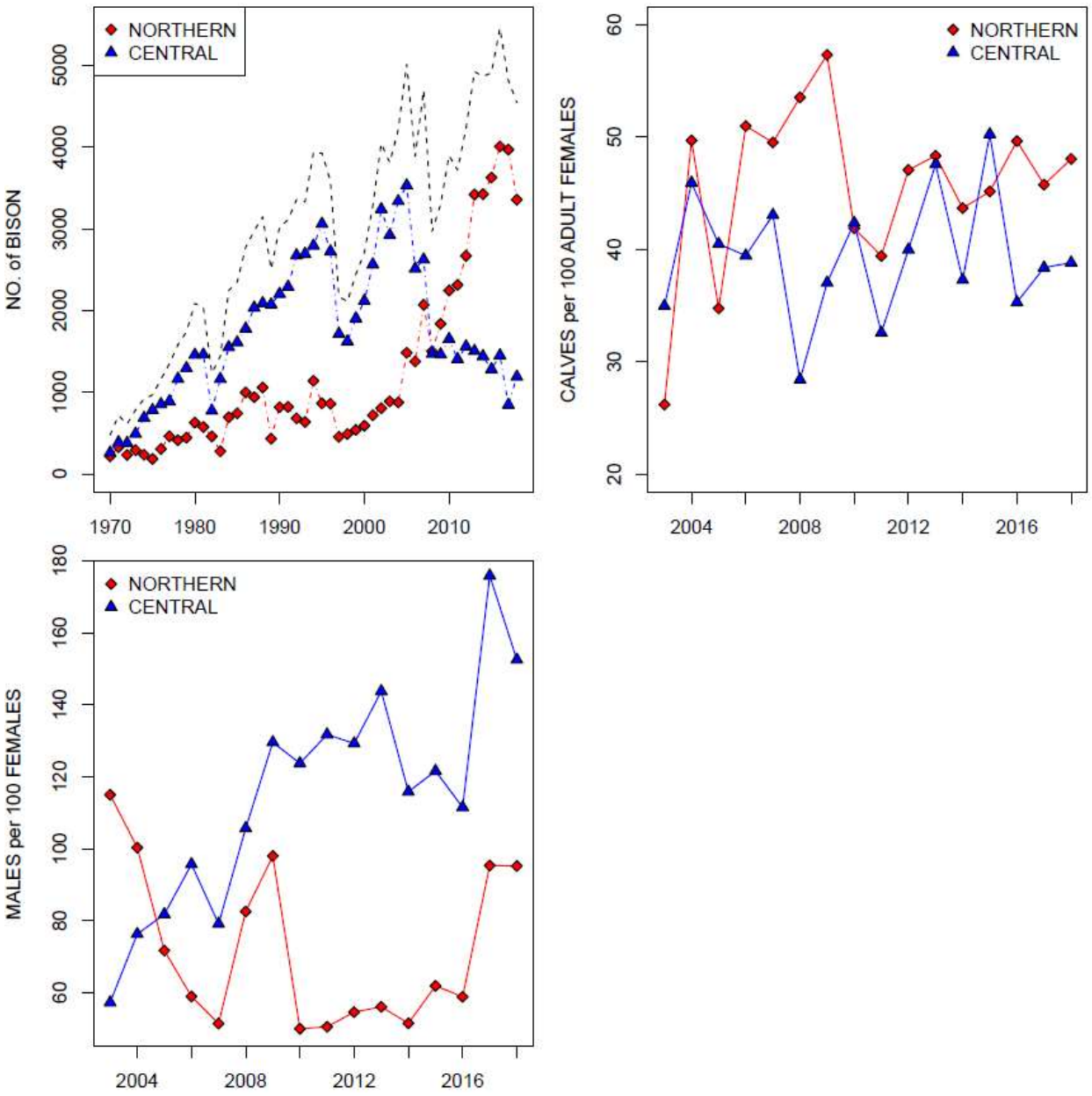


Figure 4. (*Top left*) Annual maximum counts of bison observed in central and northern herd count units during June 1-August 31 from 1970-2018. (*Top right, bottom left*) Numbers of bison in age and sex categories counted during summer aerial and ground surveys.

## Removals during Winter 2018-2019

A total of 1,171 bison were culled or harvested during winter 2017-2018 (Table 1). This total was within the range (at least 600, but fewer than 1,250) recommended by the National Park Service.[4] Eight hundred and ninety eight bison were captured at the Stephens Creek capture

[4] Geremia, C. R. Wallen, and P.J. White. Status report of the Yellowstone bison population, September 2017. Available at http://ibmp.info/Library/OpsPlans/2017_StatusYellowstoneBisonPopulation_Sep2017_Final.pdf.

facility, of which, 694 were transported to slaughter facilities, 99 were removed into nearby quarantine pastures, 3 died during holding, 26 were released back into the park, and 76 escaped the facility after fences were illegally vandalized. Harvests, seized carcasses, and dispatched wounded animals totaled 285 bison in the northern management area and 90 bison in the western management area.

Recommendations during the winter of 2017-2018 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. The actual age and sex composition of removals included 387 adult females, 185 adult males, 288 calves, and 219 adolescents (12-16 months). The age and sex classification of 92 bison was not recorded. The age composition of removed bison was 27% calves, 20% adolescents, and 53% adults. The sex ratio of adult bison removed was 68% adult females and 32% adult males. As a result, the 2018 population continued to move away from objectives for sex ratio and juvenile proportion.

Since winter 2013-2014, more than 1,100 calves and nearly 700 adolescents (12-16 months) have been removed from the bison population. Removing large numbers of calves and adolescents disproportionately reduces the number of animals reaching reproductive maturity. About 342 of the 1,000 calves estimated to be in the population during summer 2016 were removed during winter 2016-2017, with about 219 additional animals removed as juveniles during winter 2017-2018. Thus, 561 (56%) of the 2016 calf cohort was removed prior to reaching adulthood. Also, more than 1,500 adult females were removed since winter 2013-2014 compared to about 900 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.

Table 1. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 2009-2018. 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 |

## Predicting Population Growth under Different Management Scenarios

We predicted bison abundance and composition during July 2019 after simulating the removals of up to 1,500 bison of various age and sex compositions during winter 2017-2018 (Figure 5, Table 2). 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 more than 1,000 bison (primarily pregnant females and young) were removed during relatively severe winters. The composition of these 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 selectively to maintain current age and sex compositions of about 74% adults, 10% yearlings, and 16% calves (46% females and 54% males).

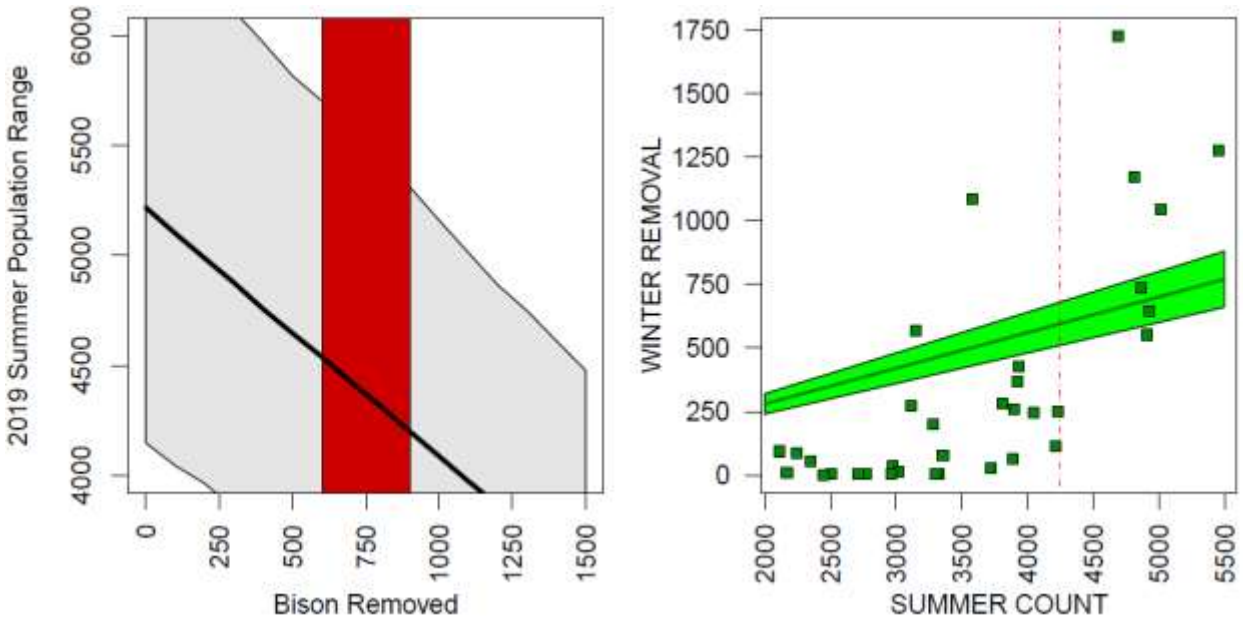


Figure 5. (*Left*) Predicted size of the bison population during July 2019 considering management removals of up to 1,500 animals. Predictions were made assuming a removal composition near current age and sex structure. The red shaded area shows the recommended removal of 600-900 animals which provides the highest chance of a 2019 population between 4,200-4,500 animals. (*Right*) Numbers of bison removed during winter (1984-2018) and corresponding population sizes during the summer. The green shaded area shows the number of bison within a range that must be removed to offset growth and lead to a population that is no larger during the subsequent summer.

The removal of 600 to 900 animals will provide the highest chance the bison population is within the range of 4,200-4,500 animals after calving the following summer. By selectively removing animals to retain the current age and sex structure, a removal of 600-900 bison would include about 90-140 calves, 60-90 adolescents (12-16 months), 200-300 adult females, and 250-370 adult males. Removing 600-900 bison without regard to age and sex composition would continue to skew the population toward males, resulting in a sex ratio of 1.28-1.34 adult males per adult female.

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 74% adults, 10% yearlings, and 16% 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 | SELECTIVE STRATEGY | | | NONSELECTIVE STRATEGY | | |
|---|---|---|---|---|---|---|
| Removed | Abundance | M:F Ratio | % Juvenile | Abundance | M:F Ratio | % Juvenile |
| 0 | 5,200 (601) | 1.19 (0.33) | 0.28 (0.04) | 5,205 (595) | 1.19 (0.32) | 0.28 (0.04) |
| 100 | 5,094 (592) | 1.19 (0.33) | 0.28 (0.04) | 5,091 (594) | 1.20 (0.33) | 0.28 (0.04) |
| 200 | 4,985 (582) | 1.19 (0.33) | 0.28 (0.04) | 4,980 (585) | 1.22 (0.33) | 0.28 (0.04) |
| 300 | 4,861 (568) | 1.19 (0.33) | 0.28 (0.04) | 4,862 (577) | 1.23 (0.33) | 0.27 (0.04) |
| 400 | 4,752 (555) | 1.19 (0.33) | 0.28 (0.04) | 4,743 (564) | 1.24 (0.34) | 0.27 (0.04) |
| 500 | 4,641 (549) | 1.19 (0.33) | 0.28 (0.04) | 4,638 (554) | 1.27 (0.35) | 0.27 (0.04) |
| 600 | 4,521 (526) | 1.19 (0.33) | 0.28 (0.04) | 4,512 (543) | 1.28 (0.36) | 0.27 (0.04) |
| 700 | 4,409 (518) | 1.19 (0.33) | 0.28 (0.04) | 4,393 (532) | 1.30 (0.36) | 0.27 (0.04) |
| 800 | 4,301 (502) | 1.19 (0.33) | 0.28 (0.04) | 4,281 (513) | 1.29 (0.34) | 0.26 (0.04) |
| 900 | 4,188 (492) | 1.19 (0.33) | 0.28 (0.04) | 4,173 (506) | 1.34 (0.38) | 0.26 (0.04) |
| 1,000 | 4,076 (488) | 1.18 (0.34) | 0.28 (0.04) | 4,054 (488) | 1.37 (0.40) | 0.26 (0.04) |
| 1,100 | 3,952 (481) | 1.18 (0.34) | 0.28 (0.04) | 3,936 (486) | 1.40 (0.41) | 0.25 (0.04) |
| 1,200 | 3,849 (455) | 1.18 (0.34) | 0.28 (0.04) | 3,822 (478) | 1.42 (0.41) | 0.25 (0.04) |
| 1,300 | 3,736 (450) | 1.18 (0.34) | 0.28 (0.04) | 3,700 (461) | 1.45 (0.43) | 0.24 (0.04) |
| 1,400 | 3,620 (432) | 1.18 (0.34) | 0.28 (0.04) | 3,587 (458) | 1.48 (0.44) | 0.24 (0.04) |
| 1,500 | 3,513 (428) | 1.18 (0.34) | 0.28 (0.04) | 3,475 (451) | 1.51 (0.46) | 0.23 (0.04) |

## Management Recommendations for Winter 2018-2019

- Use harvests and captures to remove 600 to 900 bison, which should result in an end-of-winter population of 3,500-3,800 bison and a post-calving population of 4,200-4,500 bison.
  - The National Park Service may initiate capture operations at Stephens Creek when more than 200 bison are observed north of Mammoth Hot Springs. Some bison will be allowed to pass by the facility to provide treaty and state hunting opportunities.
- Focus removals on the northern herd to decrease numbers below 3,000 bison (3,337 bison counted during summer 2018).
  - The National Park Service intends to target northern herd animals by monitoring the movements of radio-collared bison and during aerial counts in December to February.
  - The State of Montana should consider using temporary capture facilities in the northern management area near Yankee Jim Canyon to allow hunters increased access to bison before capture, provided hunters allow some bison to disperse north of the park.
- Limit removals from the central herd (1,337 bison counted during summer 2018).
  - Some bison from the central herd will migrate to the northern boundary of Yellowstone National Park and be inadvertently captured and removed. However, the National Park Service does not recommend the harvest or capture of any bison west of the park.
- Do not remove more than 900 bison, even if winter is severe and large numbers of bison migrate into the Gardiner basin.
  - Some bison may need to be held at Stephens Creek and released during spring if there is a mass migration of bison. If adult females and young bison are disproportionately captured, adolescent females may be held for release during spring.
- Capture 25-50 juvenile male bison at Stephens Creek for quarantine, provided there is space in the quarantine pastures at Stephens Creek or Corwin Springs, Montana.

## 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, **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 $\varepsilon_1$ 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 **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 **s** were survival coefficients for age and sex classes and the term $\varepsilon_2$ 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 $\sigma_1$ 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 2000-2018

Table B1. Aerial counts of the Yellowstone bison population completed during June-July, 2000-2018[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 | | |

[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, 2003-2018. 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 |

Table B3. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 1970-2018.

| | 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 |

[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.