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Population Dynamics and Adaptive Management of Yellowstone Bison

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Executive Summary

During June and July 2015, up to 4,910 bison were counted in the Yellowstone population following calving, including approximately 3,600 bison in northern Yellowstone and 1,300 in central Yellowstone. Culls and harvests during winter 2015 (October 2014 - May 2015) totaled 737 bison, including 18 harvested from the western management area, 201 harvested from the northern management area, 507 consigned to meat processing facilities, 7 consigned to research facilities, and 4 that died within containment facilities. Removals included 276 males, 297 females, 161 calves, and 3 animals of unknown age and sex. The total sum of removals was below the recommended guideline of 800 to 900 animals – importantly, only 223 adult (at least two years old) females were removed, which was significantly below the recommended guideline of 410 adult females. The net result is a slightly larger bison population after calving.

We recommend removing 1,000 bison during the forthcoming winter, including 200 calves, 60 yearling females, 420 adult females, 40 yearling males, and 280 adult males. To reduce abundance and productivity, it is most important to meet the removal objectives for calves and females.

Predicted migrations suggest sufficient numbers of bison will move beyond park boundaries to facilitate the recommended removals. Hunter harvests can likely account for more than 300 of these removals with hunts occurring in both northern and western management areas. However, we recommend limiting harvest in the western management area to adult males because other central herd animals will likely be removed after migrating outside the northern park boundary. We also recommend the capture of bison in the northern management area and consignment to meat processing or research facilities. Removals through capture will likely need to be biased towards adult females, calves, and other juvenile animals to meet recommendations.

In 2008, IBMP managers decided to implement moderated culls in an attempt to avoid large annual fluctuations in the bison population, which occurred during the early IBMP period and could threaten long-term preservation of Yellowstone bison, cause societal conflict, and reduce hunting opportunities outside the park. The removal of 1,000 bison (as recommended above) next winter through hunting and culling should reduce abundance to approximately 3,800 before calving.

Need and Purpose

Yellowstone bison are managed under an Interagency Bison Management Plan (IBMP) that is primarily designed to reduce the risk of brucellosis transmission from bison to livestock. Pursuant to this plan, bison are supposed to be managed towards an end-of-the-winter guideline of 3,000 animals. Managers at Yellowstone National Park also want to maintain breeding herds of bison in the central and northern regions of the park, similar proportions of males to females, and an age structure of about 70% adults and 30% juveniles. Managers want to maintain the processes of migration and dispersal by bison, while avoiding annual reductions in bison numbers of more than 1,000 due to disease, property, and safety concerns near wintering areas in Montana. To meet these needs, the National Park Service developed a model capable of forecasting the future abundance and demographic conditions of the Yellowstone bison population.

General Population Modeling Approach

Adaptive management is a structured decision-making approach for improving resource management by systematic learning from management actions and outcomes. It involves the exploration of alternatives for meeting objectives; prediction of outcomes from alternatives using current understanding; implementation of at least one alternative; monitoring of outcomes; and using results to update knowledge and adjust actions. Adaptive management provides a framework for decision-making in the face of uncertainty and a formal process for reducing uncertainly to improve management and outcomes over time.

Model development is a component of the structured decision-making process that brings together data and uncertainty through testable hypotheses representing our understanding of the system and effects of management alternatives. Uncertainty arises from our lack of understanding of the ecological process, measurement error, environmental variability, and our lack of complete control over management actions.

The hierarchical Bayesian state-space modeling approach can be used to build complicated models that are suitable for incorporating these 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 revising 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.

Management Alternatives and Decision Criteria

After estimating the current conditions of the bison population, we forecast the numbers of bison in each age and sex class over the next year and determine the chances of meeting the following objectives under different management alternatives.

1. Meet an IBMP-mandated, end-of-winter, population target of 3,000 animals.

2. Maintain similar proportions of males and females (e.g. neither sex exceeds 60%).

3. Maintain an age structure of approximately 70% adults and 30% juveniles which resembles natural conditions (e.g., juvenile proportion from 22-34%).

We assume complete control over management interventions. We understand this is unrealistic because bison can only be removed after migrating to the park boundary during certain times of the year. However, we make this assumption to provide a reference point as to what level of removals would be necessary to reach our objectives. We compared three alternatives aimed to reduce the bison population by next summer, thus, alternatives were considered that exceeded the natural annual growth rate of the population of 15-17%. We compared management alternatives for removing 900 (18% of the current population size), 1,000 (20%), and 1,100 (22%) bison. Each alternative considered a removal of 70% adults, 10% yearlings, 20% calves, 60% females, and 40% males.

Results

The current bison population is estimated between 4,700 – 5,300 (95% credible interval) with a point estimate of 4,975 animals. In response to management, the bison population has been stable since summer 2013 with post-calving estimates varying among 4,900 and 5,000 animals each summer (Figure 1, Tables 1 & 3).

Removals from last winter included 737 bison, including 18 harvested from the western management area, 201 harvested from the northern management area, 507 consigned to meat processing facilities, 7 consigned to research facilities, and 4 that died within containment facilities (Tables 3 and 4). Removals included 276 males (all ages), 297 females (all ages), 161 calves (sex not determined), and 3 animals of unknown age and sex (Tables 3 and 4).

Removals were below the recommended guideline of 800-900 animals – importantly only 223 adult females (at least 2 years old) were removed, which was significantly below the recommended guideline of 410 adult females. Overall, harvests were heavily biased towards adult males (160 adult males, 35 adult females, 21 calves, and 3 unknowns) with more than 4 adults males harvested for each adult female. Capture and consignment of animals only occurred within the IBMP northern management area and was heavily biased towards calves and females. Consignments included 32 adult males and 194 adult females, 84 yearling males and 68 yearling females, and 140 calves. In line with recommendations and in an attempt to limit removals to the central herd, only 18 bison (12 male and 6 female) were removed from within the IBMP western management area.

The current bison population remains above the IBMP population size objective, but near the age and sex composition objectives of 70% adults and 30% juveniles, and neither sex exceeding 60% of the population (Figures 2 and 3). The most likely bison population composition is approximately 850 calves, 250 yearling females, 300 yearling males, 1,950 adult females, and

1,625 adult males (Table 2). Juveniles (calves and yearlings) make up 28% of the population (25 – 32 %, 95% credible interval). The sex ratio is 46% (41 – 51%, 95% credible interval) male and 54% (49 – 59%, 95% credible interval) female.

The northern herd increased from a high count of 3,519 to 3,627 individuals during 2014 – 2015 (Table 1). In turn, the central herd declined from 1,448 to 1,323 during 2014 – 2015 (Table 1). Removal recommendations for last winter were aimed to allow central herd growth and reduce the size of the northern herd. The lower central herd size is likely the result of net dispersal movements from the central to the northern herd, and some removal of central herd animals that migrated into the IBMP northern management area during winter (Tables 5 and 6). At least one radio-collared adult female from the central herd was removed through capture and consignment in the IBMP northern management area during winter 2014–15. Furthermore, two radio-collared adult females from the central herd that migrated to the northern range during winter did not return to the central area of Yellowstone. One radio-collared female dispersed from the northern to the central herd.

Predictions of Key Population Conditions May-July, 2016: We compared alternatives removing 900, 1,000, or 1,100 bison during winter 2015–16. Each alternative considered a removal of 70% adults, 10% yearlings, 20% calves, 60% females, and 40% males.

Remove:	900	1,000	1,100
End of winter 2015-16 size:	3,870 (2,950–5,020)	3,780 (2,880–4,920)	3,670 (2,800–4,750)
2016 calf crop	780 (480–1,200)	760 (465–1,180)	746 (450–1,150)
Post-calving size:	4,660 (3,650–5,900)	4,540 (3,570–5,750)	4,416 (3,470–5,590)
Post-removal			
Male to female ratio:	0.98 (0.55–1.62)	0.99 (0.55–1.67)	0.99 (0.55–1.69)
Juvenile proportion:	0.30 (0.22–0.40)	0.30 (0.22–0.40)	0.30 (0.22–0.40)

Management Recommendation

We recommend removing at least 1,000 bison during the forthcoming winter, including 200 calves, 60 yearling females, 420 adult females, 40 yearling males, and 280 adult males. To reduce abundance and productivity, it is most important to meet the removal objectives for females and calves. Removals could be implemented through public and treaty hunting in Montana and gather-and-consignment (shipment to meat processing or research facilities) at the northern boundary capture facility. We recommend that harvests be restricted to adult males in the western area.

We anticipate that hunts may remove more than 300 animals (Table 3). Additional bison will likely need to be removed through gather-and-consignment. We recommend that removals through gather-and-consignment are limited to the northern management area because central herd animals move to both the northern and western management areas and the central herd is estimated at approximately 1,300 animals (Table 1). To support hunting, gather-and-consignment could be implemented throughout the winter with relatively small numbers (e.g., 25-150) of animals removed weekly during January through March. This stepwise approach would limit animals held within capture facilities and minimize effects on hunting opportunities;

reduce logistical constraints of transporting large numbers of bison to meat processing facilities over brief periods; limit transporting females late in pregnancy to processing facilities (which could occur if gather-and-consignment occurred after the close of hunting seasons); and lower the chances of out-of-park abundance surpassing levels which exacerbates conflict. Under this approach, biologists could track the age and sex composition of harvests to appropriately adjust gather-and-consignment efforts as winter progresses.

We do not recommend the selective removal of bison based on their brucellosis exposure status. Removal of relatively small, entire groups of bison gathered through weekly efforts should mimic random culling, which is a preferable alternative for conservation. Management culling is the dominant source of mortality for Yellowstone bison. Random removal, in contrast to selective removal based on brucellosis exposure, avoids artificially allowing brucellosis to act as a key selective force on the bison population. We also recommend that vaccine-eligible individuals gathered in capture facilities are consigned during weekly efforts until removal guidelines are met.

If winter is severe, with hundreds of bison moving to the northern management by early winter, implementation of weekly gather-and-consignment of small, entire groups could begin in December. Using consistent, small consignments during early winter would reduce the chance of total harvests and consignments exceeding removal recommendations by late winter. At the close of hunting seasons, larger groups of bison could be gathered into the capture facility for holding and/or removal.

Space and time separation of bison and livestock has been effective at preventing the spillover of brucellosis from bison to cattle when the bison population has approximated 5,000 individuals. Furthermore, building evidence suggests that end of winter herd sizes of >2,500 northern and >1,500 central may be more appropriate for maintaining annual migrations where sufficient numbers of animals move beyond the northern park boundary to support state and tribal hunting outside of Yellowstone and removals that are large enough to offset growth. The IBMP partners agreed to implement moderated culls in an attempt to avoid large annual fluctuations in the bison population, which occurred during the early IBMP period and could threaten long-term preservation of Yellowstone bison. These fluctuations resulted from removals of more than 30% of the population in a given year, which then caused a much smaller population to increase rapidly because population sizes were insufficient to cause enough bison to leave the park.

Table 1. Aerial counts of the Yellowstone bison population completed during June-July, 2000-2015.

		Central Herd			Northern Herd		
		Total	Adults	Calves	Total	Adults	Calves
2000	June 4, 2000	2,060	1,734	326	553	460	93
	July 13, 2000	2,118			590		
	August 31, 2000	2,084			529		
2001	June 21, 2001	2,599	2,190	469	657	553	104
	July 25, 2001	2,564			719		
2002	June 25, 2002	3,100	2,560	540	548	477	71
	July 29, 2002	2,901			813		
	August 22, 2002	3,238			807		
2003	July 10, 2003	2,905	2,471	434	873	748	125
	August 8, 2003	2,923			888		
	August 28, 2003	2,772			994		
2004	July 21, 2004	2,811	2,310	501	1,337		
	July 28, 2004	3,027			968		
	August 4, 2004	3,339			876		
2005	July 19, 2005	3,553			1,266		
	July 26, 2005	3,394			1,353		
	August 1, 2005	3,531			1,484		
2006	July 19, 2006	2,430	2,146	284	1,283		
	July 26, 2006	2,512			1,377		
	August 2, 2006	2,496			1,279		
2007	June 14, 2007	2,734	2,385	349	1,820	1,499	321
	July 30, 2007	2,390			1,569		
	August 6, 2007	2,624			2,070		
2008	June 14, 2008	1,115	1,052	103	1,788	1,463	325
	July 8, 2008	1,540			1,341		
	July 15, 2008	1,469			1,500		
2009	June 12, 2009	1,462	1,293	169	1,839	1,520	319
	July 9, 2009	1,544			1,433		
	July 16, 2009	1,535			1,648		
2010	June 14, 2010	1,653	1,426	227	2,245	1,890	355
	July 8, 2010	1,735			1,980		
	July 22, 2010	1,713			1,850		
2011	June 21, 2011	976	880	96	2,675	2,188	487
	July 18, 2011	1,406			2,314		
	July 25, 2011	1,335			2,150		
2012	June 21, 2012	1,389	1,188	201	2,496	2,103	393
	July 8, 2012	1,640			2,531		
	July 22, 2012	1,561			2,669		
2013	June 6, 2013	1,338	1170	168	3,154	2,620	534
	July 15, 2013	1,504			3,420		
	July 22, 2013	1,337			3,228		
2014	June 20 ,2014	1,338	1,190	148	3,519	2,928	591
	July 18, 2014	1,448			2,938		
	July 25.2014	1,444			3,421		
2015	June 13-14, 2015	1,283	1,114	169	3,627	2,996	631
	July 12, 2015	1,291			3,325		
	July19-20, 2015	1,323			3,441		

Table 2. Composition surveys of the Yellowstone bison population during June-July, 2003-2015.

		Survey 1							**Survey 2**						
Date		**Classified in Mixed Gender Groups**					**Air Count**		**Classified in Mixed Gender Groups**					**Air Count**	
		Male>1	Male1	Female>1	Female1	Calf	Bachelor	Mixed	Male>1	Male1	Female>1	Female1	Calf	Bachelor	Mixed
July 7-15, 2003	*central*	438	150	1,426	241	498	380	2,521							
	northern	159	23	176	12	46	77	795	133	11	227	15	110		
July 14-18, 2004	*central*	638	179	1,082	126	497	284	2,594	523	125	932	131	397		
	northern	247	35	331	33	164	125	1,145	232	26	458	49	145		
July 6-15, 2005	*central*	500	178	1,098	162	430			674	175	1,060	148	443		
	northern	276	63	441	51	153			205	49	324	37	97		
July 11-13, 2006	*central*	368	141	654	101	258	518	2,078	386	152	757	111	301		
	northern	102	27	202	40	103									
July 10-17, 2007	*central*	375	100	709	109	342			555	119	805	106	305		
	northern	300	139	637	101	339			173	28	366	28	169		
July 8-11, 2008	*central*	116	36	387	50	110	444	1,101							
	northern	198	87	433	61	232	178	1,158							
July 6-16, 2009	*central*	145	63	427	73	158	480	1,063	161	62	498	47	186		
	northern	244	84	414	53	237	191	1,239	224	83	391	53	179		
July 6-20, 2010	*central*	340	72	517	57	219	342	1,370	369	82	537	81	228		
	northern	228	126	934	140	391	20	1,755	298	150	679	121	344		
July 7-19, 2011	*central*	118	58	323	37	105	413	1,407	163	53	309	40	106		
	northern	303	131	915	99	361	185	2,103							
July 9-29, 2012	*central*	282	68	493	41	173	398	1,242	420	80	477	55	216	212	1,349
	northern	375	187	876	165	466	80	2,451	405	114	698	84	288	50	2,619
July 15-25, 2013	*central*	287	101	415	82	197	342	1,162	372	102	401	77	191	189	1,148
	northern	457	231	1,061	191	528	145	3,275	608	249	1,149	198	538	77	3,151
July 14-25, 2014	*central*	275	113	565	69	206	280	1,168	296	71	380	63	145	285	1,159
	northern	310	155	1,023	126	422	141	2,797	565	266	1,314	259	612	261	3,163
July 13-23, 2015	*central*	187	43	301	42	165	240	1,051	310	58	364	58	166	166	1,157
	northern	651	219	1,499	203	689	149	3,176	738	192	1,144	141	507	69	3,372

Table 3. Numbers of bison removed from Yellowstone National Park or nearby areas of Montana during winters from 1970-2014.

	Maximum No. Bison Counted Previous July-August			Sent to Slaughter/ Management Culls		Hunter Harvest[a]		Sent to Quarantine		Total	Age and Gender Composition of Culls/Harvests			
Winter	**North**	**Central**	**Total**	**North**	**West**	**North**	**West**	**North**	**West**		**Male**	**Female**	**Calf**	**Unknown**
1970-84				0	0	13	0	0	0	13	4	7	0	2
1985	695	1,552	2,247	0	0	88	0	0	0	88	42	37	8	1
1986	742	1,609	2,351	0	0	41	16	0	0	57	42	15	0	0
1987	998	1,778	2,776	0	0	0	7	0	0	7	5	2	0	0
1988	940	2,036	2,976	0	0	2	37	0	0	39	27	7	0	5
1989	NA[b]	NA[b]	NA[b]	0	0	567	2	0	0	569	295	221	53	0
1990	592	1,885	2,477	0	0	1	3	0	0	4				4
1991	818	2,203	3,021	0	0	0	14	0	0	14				14
1992	822	2,290	3,112	249	22	0	0	0	0	271	113	95	41	22
1993	681	2,676	3,357	0	79	0	0	0	0	79	9	8	9	53
1994	686	2,635	3,321	0	5	0	0	0	0	5				5
1995	1,140	2,974	4,114	307	119	0	0	0	0	426	77	66	31	252
1996	866	3,062	3,928	26	344	0	0	0	0	370[c]	100	71	10	189
1997	785	2,593	3,378	725	358	0	0	0	0	1,083[d]	329	330	144	280
1998	455	1,715	2,170	0	11	0	0	0	0	11				11
1999	493	1,399	1,892	0	94	0	0	0	0	94	44	49	1	0
2000	540	1,904	2,444	0	0	0	0	0	0	0				
2001	508	1,924	2,432	0	6	0	0	0	0	6	6	0	0	0
2002	719	2,564	3,283	0	202	0	0	0	0	202	60	42	16	84
2003	813	2,902	3,715	231	13	0	0	0	0	244	75	98	43	28
2004	888	2,923	3,811	267	15	0	0	0	0	282	58	179	23	22
2005	876	3,339	4,215	1	96	0	0	0	17	114	23	54	20	17
2006	1,484	3,531	5,015	861	56	32	8	87	0	1,044	205	513	245	81
2007	1,377	2,512	3,889	0	4	47	12	0	0	63	53	6	0	4
2008	2,070	2,624	4,694	1,288	160	59	107	112	0	1,726	516	632	332	246
2009	1,500	1,469	2,969	0	4	1	0	0	0	5	5	0	0	0

2010	1,839	1,462	3,301	3	0	4	0	0	0	7	7	0	0	0
2011	2,245	1,653	3,898	6	0	Unk	Unk	53	0	260	106	102	52	0
2012	2,314	1,406	3,720	0	0	15	13	0	0	28	14	12	2	0
2013	2,669	1,561	4,230	0	0	148	81	0	0	229	116	85	28	0
2014	3,420	1,504	4,924	258	0	258	64	60	0	640	200	284	152	4
2015	3,421	1,444	4,865	511	0	201	18	7	0	737	276	297	161	3

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

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

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

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

Table 4. Brucellosis exposure status and disposition of bison tested at boundary management facilities in and near Yellowstone National Park.

	No. captured[a]		**Tested[b]**		**Positives slaughtered[c]**		**Negatives slaughtered[c]**		**Untested slaughtered**		**Consigned to quarantine**		**Negatives**		**Positives released**		**Untested**		**Capture pen mortalities**		**Management shootings**	
Winter	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**	**W**	**N**
2001	14[d]	0	14[d]	0	5	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	1	0
2002	251[d]	0	118[d]	0	113	0	41	0	45	0	0	0	52	0	0	0	0	0	0	0	3	0
2003	20[d]	231	16[d]	0	8	105	4	104	0	22	0	0	8	0	0	0	0	0	0	0	1	0
2004	21	463	18	407	10	227	0	31	3	6	0	0	8	198[e]	0	0	0	0	0	1	2	2
2005	186[d]	0	168[d]	0	79	0	0	0	17	0	17	0	73	0	0	0	0	0	0	0	0	1
2006	59	1,253	0	98	0	384	0	451	50	14	0	87	0	0	0	0	9	308[f]	0	9[g]	6	3
2007	56	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	52[h]	0	0	0	0
2008	158	1,647	0	539	0	711	0	560	158	5	0	112	0	191	0	18[i]	0	44[j]	0	6[g]	2	6
2009	3	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3

2011	0	797	0	694	0	0	0	0	0	0	0	53	0	392	0	249	0	100[k]	0	3	0	3
2012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2014	0	353	0	353	0	145	0	113	0	0	0	60	0	21	0	14	0	0	0	0	0	0
2015	0	519	0	481	0	181	0	293	0	33	0	7	0	0	0	0	0	1	0	4	0	0

a - Captures include bison gathered into capture facilities, but exclude management shootings.

b - Field testing occurred during handling at capture facilities.

c - Disease exposure status determined during handling at capture or meat processing facilities.

d -Totals may be incorrect due to inconsistencies in agency reports concerning individual animals captured and tested multiple times.

e - Twenty-eight animals retested at the Montana Department of Livestock diagnostic laboratory tested positive for disease exposure status.

f - Total excludes two untested newborn calves born within containment facilities during holding.

g - Total excludes four failed births that occurred within containment facilities during holding.

h - Fifty-two mixed age and gender bison were captured nearby the western park boundary during June and released at the Stephen's Creek Facility.

i – These seropositive bison were released back into the park because managers did not want to send females late in the third trimester of pregnancy to meat processing facilities.

j - Total excludes 80 untested newborn calves born within containment facilities during holding.

k - Total excludes 169 untested newborn calves born within containment facilities during holding.

Table 5. Survival and reproduction of radio-collared, adult, female bison in and near Yellowstone National Park.

Survival					**Birth**				
	Central		**Northern**			**Central**		**Northern**	
year	lived	total	lived	total	year	birthed	total	birthed	total
1996	0	0	10	10	1996	0	0	3	3
1997	0	0	19	20	1997	2	2	6	8
1998	16	16	21	22	1998	3	7	9	14
1999	11	13	17	20	1999	9	15	10	14
2000	14	14	17	19	2000	7	10	8	13
2001	9	9	14	15	2001	5	8	9	13
2002	2	2	1	2	2002	0	0	0	0
2003	6	6	1	1	2003	3	4	0	0
2004	6	6	1	1	2004	14	17	0	0
2005	21	21	1	1	2005	15	25	0	0
2006	33	36	1	1	2006	11	19	0	0
2007	36	39	1	1	2007	19	29	8	10
2008	31	33	11	11	2008	14	23	18	27
2009	22	28	43	44	2009	8	14	14	19
2010	19	20	43	45	2010	11	13	15	18
2011	15	19	33	34	2011	7	10	17	19
2012	15	15	31	31	2012	9	14	15	17
2013	16	17	27	28	2013	10	14	11	16
2014	14	14	27	29	2014	8	12	9	14

Table 6. Vital rates of the Yellowstone bison population estimated from radio-collared bison and air and ground counts.

Rate	Mean	SD
Adult female survival	0.94	0.01
Neonate survival (May 1 – 31)	0.75	0.06
Calf survival (remainder of 1st year)	0.88	0.05
Male survival	0.94	0.03
Probability of a newborn calf being female	0.47	0.02
Birth rate	0.69	0.02

Figure 1. Estimated Yellowstone bison abundance from aerial counts conducted during the Interagency Bison Management Plan. Bold lines indicate mean abundance and thin lines show 95% credible intervals.

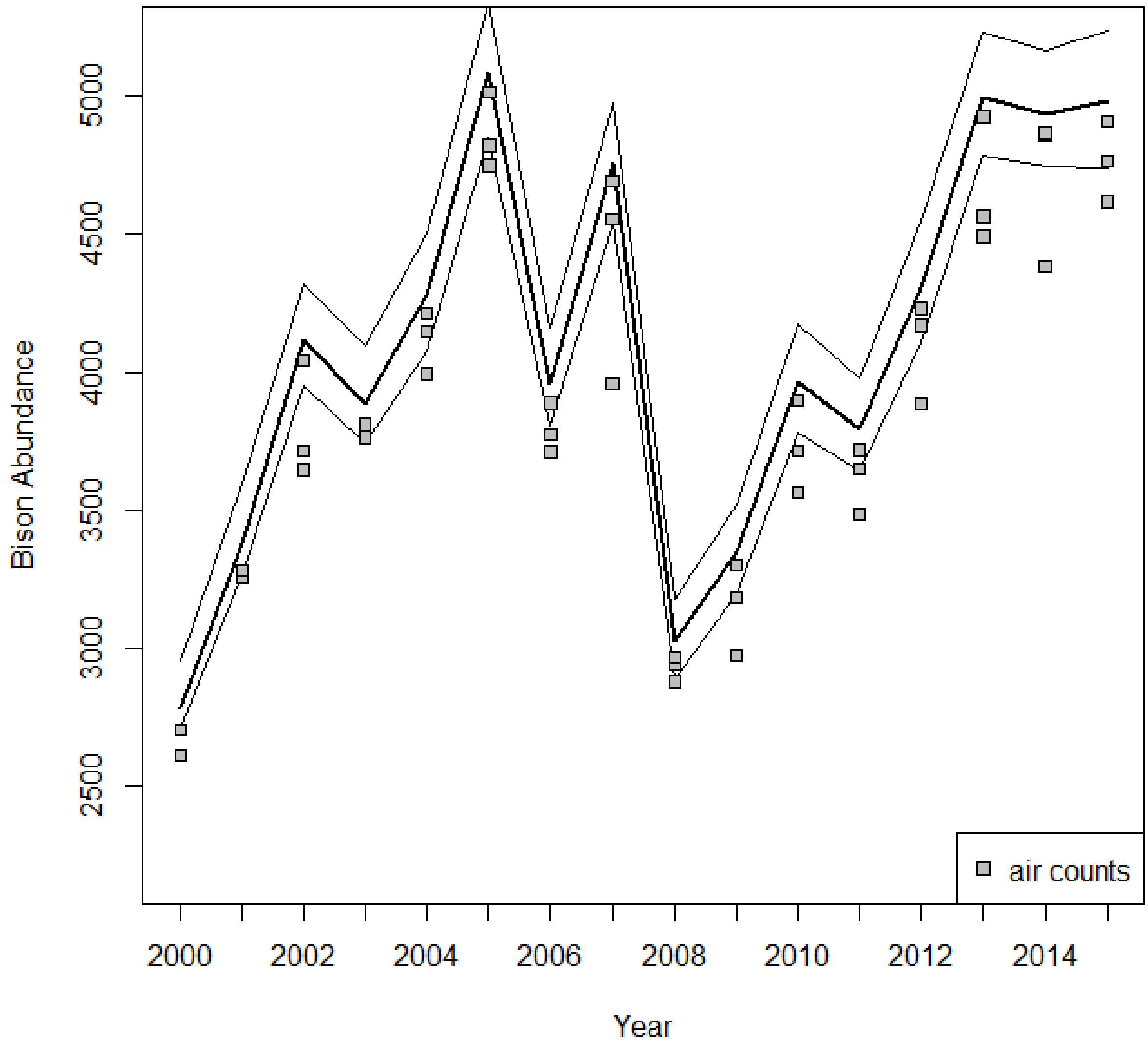
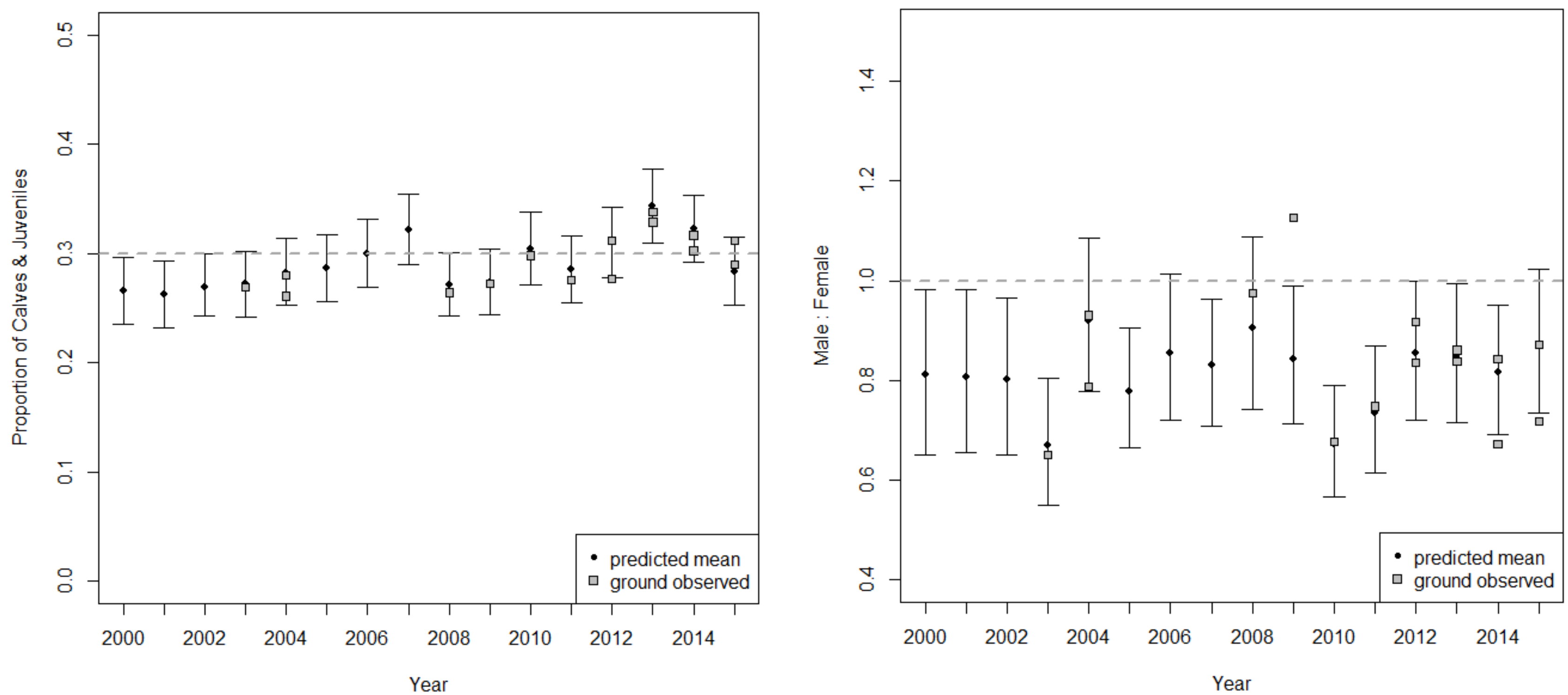


Figure 2. Estimated proportion of juveniles (*left*) and male to female ratio (*right*) of the Yellowstone bison population during the Interagency Bison Management Plan. Solid lines indicate 95% credible intervals and square boxes show observed values among replicate composition surveys. The dotted lines show objective compositions.



Methods

The bison population has been sub-structured into at least two breeding herd units over much of the past century. However, larger herd sizes during recent years have resulted in increased mixing of these units suggesting this substructure may no longer be 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. Survival: We assumed that there were four different survival rates. Neonate survival was the rate for May, the first month of life, when calves are more susceptible to dying. Calf survival was the rate for the remainder of the first year, from June until the next June. Pre-reproductive and reproductive-aged animals were given the same survival rate. However, male survival was assumed to be slightly lower than female survival. Reproduction: We assumed that all reproductive-aged females exhibited similar birth rates. Bison could produce up to one calf each year. We assumed that birth rates were unaffected by population size. Our model was an exponential growth model. That is, the rate of population growth could not decrease as the bison population increased in size.

Predicting the Bison Population 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 **A** included survival and reproduction rates. We estimated survival rates using the logistic model where $s=invlogit(s_0 + s_1 + s_2 + s_3 + \varepsilon_2)$. The elements of **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.

Data Collection and Incorporation in the Model: 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.

Forty-seven aerial surveys were completed during June through August, 2000 – 2014 to count bison in the population (Table 1). We assumed that the bison population did not change during the summer count interval, meaning bison were not born and did not die among counts. We assumed that 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 difference 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. 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 that 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 (Table 2). 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 (Tables 3 and 4). 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.

Data on adult female survival and calving were recorded by tracking radio-collared bison since 1995 (Table 5). These data were related to model predictions of survival and birth rates using a binomial model.

Model Implementation: Model parameters and latent quantities were estimated using Markov chain Monte Carlo techniques. All analyses were completed using program R.