Influences of Precipitation on Bison Weights in the Northern Great Plains

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On the Ground

- We evaluated relationships between bison weights and prior precipitation during 1983 to 2015 for Wind Cave and 1998 to 2015 for Badlands National Parks.
- We generally found positive correlations between weights for most sex and age cohorts and precipitation during each of the preceding 7 years. The association was strongest for yearlings.
- We speculate that rainfall several years prior can improve forage, which affects the condition of cows, which affects neonatal weights and subsequent growth of young bison.
- Correlations were stronger for a moving average of previous precipitation, suggesting a cumulative effect.
- Our analysis demonstrates the importance of long-term monitoring for better understanding of grassland ecosystems.

Keywords: Badlands National Park, bison, *Bison bison*, precipitation, weight, Wind Cave National Park.

Rangelands 40(4):115–123
doi 10.1016/j.rala.2018.07.001

Weather and, more specifically, precipitation, is an ecological driver of Northern Great Plains grasslands. Precipitation influences plant composition and productivity, which in turn might affect the growth and mass of herbivores such as bison (*Bison bison*). However, confirming and understanding the relationship between precipitation and bison weights requires long-term datasets.

Wind Cave National Park, located in the Northern Great Plains, has played a critical role in bison conservation.[1] For almost a century the park has routinely rounded up and removed surplus animals for purposes of keeping the herd at desired abundance levels. Badlands National Park has managed bison similarly for nearly half a century. For the past several decades the parks have weighed the bison captured in the roundup operations.[2] The parks also collect weather data in collaboration with other agencies. We related these long-term datasets of bison weights to precipitation patterns to better understand the relationship and mechanisms between the two components of grassland ecosystems.

Study Areas

Wind Cave National Park lies about 6 km north of the town of Hot Springs, South Dakota, on the southern edge of the Black Hills. Fourteen bison were reintroduced to the site in 1913 and another six in 1916. The herd currently has access to about 11,330 ha within a woven-wire boundary fence. The park generally manages for a population of 350 to 500 bison. Park-reported estimates of the precull herd size from 1983 to 2015—derived primarily from periodic aerial counts, known cull sizes, and extrapolations using an estimated growth rate of 16%[3, 4]—averaged 445 bison (standard deviation [SD] = 47, n = 33). The herd has greater genetic diversity than most other bison herds[5] with no apparent inbreeding depression.[4] Although the herd appears healthy, the bison weigh less than bison at Badlands National Park in South Dakota and at Theodore Roosevelt National Park in North Dakota; the reasons for the disparity are not known.[2] Population estimates of other notable mammalian herbivores at the park from 1983 to 2015 include an average of 556 (SD = 64, n = 30) elk (*Cervus elaphus*), 67 (SD = 38, n = 22) pronghorn (*Antilocapra americana*), and 771 (SD =217, n = 15) ha of black-tailed prairie dogs (*Cynomys ludovicianus*), based on park internal reports. However, these reported population sizes are of questionable quality. For example, the park surveys only about half the prairie dog colonies in a year; to derive an annual park-wide estimate they carry over values of the unsurveyed colonies from prior years' surveys. Furthermore, routine monitoring of prairie dogs only began in the year 2000.

Vegetation within Wind Cave consists of a mosaic of mixed-grass prairie and ponderosa pine (*Pinus ponderosa*) forests. Dominant vegetation in the prairie includes blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyron smithii*), and little bluestem (*Schizachyrium scoparium*). The bison pasture produces about 24.5, 18.7, and 12.8 million kg of forage during favorable, normal, and unfavorable precipitation-years, respectively (values and terms from Natural Resources Conservation Service[6]). Assuming 450 bison, 550 elk, and 75 pronghorn; forage intake rates of 2.2%, 2.1%, and 2.1% of body mass; and average biomass per individual of 375, 250, and 35 kg; respectively, the herbivores would take about 9.9%, 12.9%, and 18.9% of the primary productivity in favorable, normal, and unfavorable precipitation-years.

Precipitation averaged 51.0 cm (SD = 11.4, n = 33) annually during 1983 to 2015 at a weather station located within the park.[7] Mean maximum July temperatures were 29.4°C in July and 3.9°C in January. An average of 306 ha was burned annually in the park during 1983 to 2015, although there was much variability among years (SD = 517, n = 30).

Badlands National Park is located about 11 km south of Wall, South Dakota. In 1963 to 1964, 53 bison were reintroduced to the site.[4] Another 20 bison were added in 1984.[8] The herd currently has access to about 19,500 ha, composing about half of the park's North Unit. The park manages for a postcull population of about 700 animals, a target that is considered conservative.[1] Park-reported precull population estimates from 1998 to 2015—derived from ground counts, known cull sizes, and extrapolations using estimated growth rates—averaged 1,001 animals (SD = 405, n = 18). Other large grazers in the park include pronghorn and bighorn sheep (*Ovis canadensis*); their abundance within the bison pasture is not known, but is assumed to be small and their plant utilization negligible. Within the bison pasture are about 1,400 ha of black-tailed prairie dogs. As was done at Wind Cave, the park attempts to survey all the colonies over 2-year periods (although that was not always done) and started the monitoring program in the year 2000.

About a third of the area within the bison pasture is composed of sparsely vegetated badlands topography. In the prairie areas the dominant vegetation includes western wheatgrass, green needlegrass (*Nassella viridula*), and little bluestem. The bison pasture produces about 33.3, 26.2, and 14.9 million kg of forage during favorable, normal, and unfavorable precipitation-years, respectively.[6] Assuming a herd of 1,000 bison, an intake rate of 2.2%, and an average biomass of 450 kg per bison, the herd would take about 10.8%, 13.8%, and 24.1% of the primary productivity in favorable, normal, and unfavorable precipitation years.

Precipitation averaged 48.2 cm (SD = 12.7, n = 18) annually from 1998 to 2015 at a weather station located at Interior, South Dakota.[7] The station is about 35 km from the center of the

Table 1. Number of bison weighed at Wind Cave and Badlands National Parks

	Wind Cave NP (1983-2015)		Badlands NP (1998-2015)	
	Years with weight data	Average number per year with data	Years with weight data	Average number per year with data
Female				
Calves	10	31.7	10	84.6
Yearlings	25	35.1	11	76.9
2.5 year olds	25	14.1	11	40.8
3.5 year olds	23	11.2	11	26.3
4.5 year olds	24	8.5	11	20.9
5.5 year olds	24	56.1	11	137.8
Male				
Calves	10	30.8	10	83.2
Yearlings	25	37.1	11	75.7
2.5 year olds	24	13.8	11	37.5
3.5 year olds	24	5.8	11	17.9
4.5 year olds	18	2.6	11	11.2
10.5 year olds	14	5.2	11	10.7

NP indicates National Park.

Badlands bison pasture. Mean maximum temperatures were 31.5° C in July and 2.2° C in January. Burns were infrequent.

Methods

Between September and October of most years both parks round up bison primarily to remove surplus animals.[2] At Wind Cave helicopters typically have been used since the 1960s to drive bison into holding corrals. The roundups capture most if not all of the cow–calf herds; however, mature bulls are normally ignored because they are difficult and dangerous to handle and less desired by recipients of the park's surplus bison. An aerial census of uncaptured bison is routinely conducted during the roundup. At Badlands the bison are typically pushed into the corrals by vehicles and people on horseback. Population estimates are typically conducted by observers on horseback.

At both parks captured animals are individually pushed into a restraining chute where they are weighed. Unmarked animals are marked with a uniquely numbered passive microchip injected subcutaneously behind the right ear. The almost yearly frequency of the roundups means that most of the captured animals without marks were calves or yearlings; cohorts that can generally be correctly aged based on tooth eruption, pelage color, and other characteristics. Surplus animals are transferred to other entities; the remaining captured animals are released back into the park.

We used Wind Cave bison capture records from 1983 to 2015. Although records with weight information were available from 1966 to 1968, we did not use those because of concerns about methods used at the time and accuracy of the scale. Weight information was not collected in the intervening years because there was no functioning scale. We used Badlands data from 1998 to 2015. Although weights were also occasionally recorded earlier at that park,[8] sample sizes were small and the data did not appear to be systematically collected; therefore, we excluded the prior years. Because of the longer time series of data for Wind Cave we relied on that dataset for most of our inferences. We used the Badlands data to corroborate the Wind Cave findings as appropriate.

Table 2. Pearson correlation coefficients, along with *P* values and sample sizes, of Wind Cave bison weights between sex and age cohorts 1983-2015

	M Calf	F 1.5	M 1.5	F 2.5	M 2.5	F Adult	M Adult
F Calf	**0.732**	0.330	0.024	0.208	0.001	0.216	0.154
	$P = 0.016$	$P = 0.321$	$P = 0.945$	$P = 0.564$	$P = 0.998$	$P = 0.550$	$P = 0.672$
	n = 9	n = 10	n = 10	n = 9	n = 9	n = 9	n = 9
M Calf		0.032	0.079	0.051	0.125	0.136	0.135
		$P = 0.931$	$P = 0.829$	$P = 0.897$	$P = 0.749$	$P = 0.728$	$P = 0.728$
		n =10	n = 10	n = 9	n = 9	n = 9	n = 9
F 1.5			**0.890**	**0.634**	**0.730**	**0.579**	0.101
			$P = 0.001$	$P = 0.001$	$P = 0.001$	$P = 0.003$	$P = 0.673$
			n = 25	n = 24	n = 23	n = 24	n = 20
M 1.5				**0.713**	**0.812**	**0.626**	0.241
				$P = 0.001$	$P = 0.001$	$P = 0.001$	$P = 0.306$
				n = 24	n = 23	n = 24	n = 20
F 2.5					**0.800**	**0.583**	0.001
					$P = 0.001$	$P = 0.003$	$P = 0.996$
					n = 23	n = 24	n = 20
M 2.5						**0.691**	0.193
						$P = 0.001$	$P = 0.428$
						n = 23	n = 19
F Adult							0.016
							$P = 0.946$
							n = 20

Note: Significant correlations ($P < 0.05$) are in bold.
F indicates female; M, male.

Table 3. Correlations, along with *P* values and sample sizes, between Wind Cave bison weights and precipitation in current (lag0; 0-11 months prior) and previous years (lag1-9)

Females	1.5 yrs	2.5 yrs	3.5 yrs	4.5 yrs	5.5+ yrs	Males	1.5 yrs	2.5 yrs	3.5 yrs	4.5 yrs	10.5+ yrs	Mean
lag0	0.386	0.172	0.132	0.072	0.036		**0.436**	0.162	0.072	0.273	0.278	0.146
	P = 0.056	*P* = 0.412	*P* = 0.548	*P* = 0.738	*P* = 0.867		*P* = 0.029	*P* = 0.449	*P* = 0.739	*P* = 0.273	*P* = 0.337	
	25	25	23	24	24		25	24	24	18	14	
lag1	0.144	0.127	0.314	0.095	0.050		0.183	0.002	0.256	0.315	0.041	0.123
	P = 0.492	*P* = 0.544	*P* = 0.144	*P* = 0.659	*P* = 0.816		*P* = 0.381	*P* = 0.993	*P* = 0.228	*P* = 0.203	*P* = 0.889	
	25	25	23	24	24		25	24	24	18	14	
lag2	0.392	0.357	0.377	**0.515**	**0.509**		**0.599**	**0.539**	0.338	0.439	**0.794**	0.486
	P = 0.053	*P* = 0.080	*P* = 0.077	*P* = 0.010	*P* = 0.011		*P* = 0.002	*P* = 0.007	*P* = 0.106	*P* = 0.068	*P* = 0.001	
	25	25	23	24	24		25	24	24	18	14	
lag3	**0.460**	**0.473**	0.355	0.156	0.275		**0.431**	**0.412**	0.099	0.135	0.322	0.312
	P = 0.021	*P* = 0.017	*P* = 0.097	*P* = 0.467	*P* = 0.193		*P* = 0.032	*P* = 0.046	*P* = 0.647	*P* = 0.593	*P* = 0.262	
	25	25	23	24	24		25	24	24	18	14	
lag4	**0.609**	0.222	0.244	0.231	0.054		**0.549**	0.237	0.101	0.041	0.041	0.225
	P = 0.001	*P* = 0.286	*P* = 0.262	*P* = 0.277	*P* = 0.803		*P* = 0.005	*P* = 0.266	*P* = 0.637	*P* = 0.870	*P* = 0.889	
	25	25	23	24	24		25	24	24	18	14	
lag5	0.303	0.052	0.046	0.099	0.206		0.208	0.156	0.242	0.228	0.066	0.121
	P = 0.141	*P* = 0.804	*P* = 0.836	*P* = 0.645	*P* = 0.333		*P* = 0.319	*P* = 0.467	*P* = 0.255	*P* = 0.363	*P* = 0.822	
	25	25	23	24	24		25	24	24	18	14	
lag6	**0.429**	0.379	0.340	0.360	0.366		**0.404**	**0.488**	0.129	0.014	0.470	0.335
	P = 0.032	*P* = 0.062	*P* = 0.113	*P* = 0.084	*P* = 0.079		*P* = 0.045	*P* = 0.016	*P* = 0.548	*P* = 0.955	*P* = 0.090	
	25	25	23	24	24		25	24	24	18	14	
lag7	0.032	0.170	0.037	0.219	0.061		0.049	0.220	0.131	0.058	0.166	0.049
	P = 0.880	*P* = 0.416	*P* = 0.869	*P* = 0.304	*P* = 0.777		*P* = 0.817	*P* = 0.302	*P* = 0.542	*P* = 0.820	*P* = 0.569	
	25	25	23	24	24		25	24	24	18	14	
lag8	0.028	0.047	0.080	0.252	0.024		0.185	0.016	0.186	0.175	**0.577**	0.021
	P = 0.896	*P* = 0.823	*P* = 0.717	*P* = 0.234	*P* = 0.913		*P* = 0.377	*P* = 0.942	*P* = 0.384	*P* = 0.488	*P* = 0.031	
	25	25	23	24	24		25	24	24	18	14	
lag9	0.219	0.091	0.224	0.122	0.287		0.303	0.115	0.025	0.374	0.357	0.132
	P = 0.293	*P* = 0.667	*P* = 0.305	*P* = 0.571	*P* = 0.174		*P* = 0.140	*P* = 0.594	*P* = 0.909	*P* = 0.127	*P* = 0.211	
	25	25	23	24	24		25	24	24	18	14	

Note: Significant correlations ($P < 0.05$) are in bold.

Female bison at Wind Cave increase in weight annually until 5.5 years of age, when weights level off with no statistically significant differences among the older age classes.[2] Males appear to increase in weight until about 10.5 years of age.[2] Therefore, we analyzed weights by age up to 4.5 years for females and grouped all older females into an "adult" class (although females can breed at younger ages). For males, we analyzed weights by age up to 4.5 years of age and then grouped all males ≥ 10.5 years into an "adult" class (although they too can breed at younger ages). The sample size of male cohorts aged 5.5 to 9.5 was insufficient for our analyses.

We retrieved weather data from a National Oceanic and Atmospheric Administration website[7] for the time period corresponding to the respective bison datasets and preceding years. Badlands weather came from a station near the town of Interior (USC00394184), located about 35 km from the center of the bison pasture. Although there was a weather station closer to the bison, it did not consistently report precipitation data for the time period of interest. Wind Cave weather data came from a station (USC00399347) within the bison pasture. Because roundups were typically conducted in late September or early October, we summed up precipitation from the prior 12 months (i.e., October of the preceding year to September of the roundup year) and refer to that as "growth year" precipitation.

We calculated Pearson correlation coefficients to evaluate linear relationships between bison weights, the response variable, and precipitation and other potential influential variables. Precipitation explanatory variables included values for the current growth year (lag0) and for growth years as far back as 10 years (lag1, …, lag9). We also considered moving averages including growth years up to 6 years earlier, such as ma2 = (lag0 + lag1)/2, ma3 = (lag0 + lag1 + lag2)/3, etc. Multiple linear regression was conducted to evaluate the joint effects of more than one explanatory variable. The other variables included the reported size of the bison, elk, and pronghorn populations; area occupied by prairie dogs; area burned in a year and average area burned over the prior 3 years; and the dates of the roundups. Data was nonexistent or inadequate for other potential explanatory variables including reproductive status of individual animals, soil moisture, snow cover, and various measures of vegetation. For both the correlation and multiple regression analyses, observations (e.g., mean weight of an age-sex cohort in a particular year) were weighted by sample sizes. We claimed a relationship as statistically significant if $P < 0.05$. We used Excel and SAS Version 10 for analyses.

Findings

Bison roundups were conducted at Wind Cave in 25 of 33 years during 1983 to 2015. Of the 5,179 capture records with weight data, 1,805 were of yearlings for an average of 72.2 yearlings per roundup, split almost evenly between the sexes (Table 1). An average of 56.1 females ≥ 5.5 years of age were weighed per roundup (excludes 1983 which did not include any adult female records with weight data, for unknown reasons). Bison roundups were conducted at Badlands in 11 of 18 years during 1998 to 2015, and 6,896 records had weight information. At Badlands an average of 152.6 yearlings and 137.8 females ≥ 5.5 years of age were weighed per roundup (Table 1).

Weights of Wind Cave bison were generally strongly correlated across age and sex classes with the exception of calves and fully grown males (≥ 10.5 years of age; Table 2), suggesting that most of the herd was responding synchronously to external factors influencing weights. The mean weight and standard deviation (SD) across years from 1983 to 2015 (unweighted by annual sample size) of the female and male yearlings was 268.7 kg ± 25.4 SD and 287.8 kg ± 27.7 SD, whereas for females ≥ 5.5 years of age it was 429.6 kg ± 9.9 SD, indicating that the external factors influencing weights were acting most strongly on the younger animals, excluding calves. Female and male calf weights were correlated across years, but were not significantly correlated to other age classes or precipitation patterns, even when we included time of roundup as an explanatory variable in a multiple regression analysis to account for that potentially confounding variable.

We related the weights of female and male yearlings at Wind Cave to the current growth year's precipitation (i.e., preceding 12 months, lag0); temperature; bison, elk, and pronghorn herd sizes; prairie dog acres; acres burned; time of roundup; and year. All explanatory variables were insignificant ($P > 0.05$) except for precipitation and pronghorn herd size. Male yearling weights were significantly correlated with current year's precipitation ($P = 0.029$, $r = 0.436$); female yearling weights were also strongly correlated, but not significantly so ($P = 0.056$, $r = 0.386$). The correlation between yearling female and male bison weights and the size of pronghorn herd was negative and significant (respectively, $P = 0.011$, $r = -0.617$; $P = 0.012$, $r = -0.611$). We doubt this correlation was causative, but rather both variables were responding to the same external factor (precipitation) in opposite ways. We also correlated female and male yearling weights to 3-year moving averages of the variables listed previously and found no significant correlations ($P < 0.05$) except for precipitation (respectively, $P = 0.010$, $r = 0.506$; $P < 0.001$, $r = 0.638$).

Weights of Wind Cave bison were often strongly correlated to rainfall in each prior growth year going back as far as 7 years (Table 3). Yearlings generally responded more strongly to previous rainfall amounts than did other age classes, especially rainfall in lag years four to six. Across most sex-age classes correlations between bison weights and previous growth years, rainfall was strongest for lag2 (i.e., 24-35 months prior; mean $r = 0.486$ unweighted by sample size). Weights of bison from Badlands tended to follow a similar pattern despite a shorter time series, with the correlations between yearlings and prior rainfall becoming negligible around at lag7 (Fig. 1).

Bison weights were more strongly correlated to moving averages of several prior years' rainfall than to rainfall in any single year, suggesting a cumulative relationship (Table 4).

Table 4. Correlation between Wind Cave bison weights and a moving average of prior years' precipitation (ma2 is average of current year and previous year, ma3 is average of current year and previous 2 years, etc.)

Females	1.5 yrs	2.5 yrs	3.5 yrs	4.5 yrs	5.5+ yrs	Males	1.5 yrs	2.5 yrs	3.5 yrs	4.5 yrs	10.5+ yrs	Mean
ma2	0.377	0.199	0.309	0.023	0.011		**0.429**	0.117	0.222	**0.491**	0.193	0.192
	P = 0.063	*P* = 0.341	*P* = 0.152	*P* = 0.917	*P* = 0.961		*P* = 0.032	*P* = 0.587	*P* = 0.297	*P* = 0.039	*P* = 0.509	
	25	25	23	24	24		25	24	24	18	14	
ma3	**0.506**	0.336	**0.461**	0.250	0.264		**0.638**	0.349	0.335	**0.557**	0.231	0.393
	P = 0.010	*P* = 0.101	*P* = 0.027	*P* = 0.239	*P* = 0.213		*P* = 0.000	*P* = 0.095	*P* = 0.109	*P* = 0.016	*P* = 0.427	
	25	25	23	24	24		25	24	24	18	14	
ma4	**0.606**	**0.481**	**0.559**	0.300	0.336		**0.712**	**0.483**	0.330	**0.573**	0.305	0.469
	P = 0.001	*P* = 0.015	*P* = 0.006	*P* = 0.155	*P* = 0.108		*P* = 0.000	*P* = 0.017	*P* = 0.115	*P* = 0.013	*P* = 0.289	
	25	25	23	24	24		25	24	24	18	14	
ma5	**0.735**	**0.449**	**0.545**	0.344	0.291		**0.777**	**0.468**	0.304	0.446	0.238	0.460
	P = 0.000	*P* = 0.024	*P* = 0.007	*P* = 0.100	*P* = 0.168		*P* = 0.000	*P* = 0.021	*P* = 0.149	*P* = 0.064	*P* = 0.413	
	25	25	23	24	24		25	24	24	18	14	
ma6	**0.766**	**0.438**	**0.490**	0.261	0.331		**0.778**	**0.505**	0.369	**0.475**	0.246	0.466
	P = 0.000	*P* = 0.029	*P* = 0.018	*P* = 0.217	*P* = 0.114		*P* = 0.000	*P* = 0.012	*P* = 0.076	*P* = 0.046	*P* = 0.397	
	25	25	23	24	24		25	24	24	18	14	
ma7	**0.843**	**0.502**	**0.543**	0.342	**0.412**		**0.829**	**0.600**	0.370	0.432	0.344	0.532
	P = 0.000	*P* = 0.011	*P* = 0.007	*P* = 0.102	*P* = 0.045		*P* = 0.000	*P* = 0.002	*P* = 0.075	*P* = 0.073	*P* = 0.229	
	25	25	23	24	24		25	24	24	18	14	

Note: Significant correlations ($P < 0.05$) are in bold.

Yearlings again showed the strongest correlations, with an average correlation coefficient across seven moving averages of 0.766 for females and 0.778 for males for Wind Cave bison. Fully grown females and males tended to show the weakest correlations to moving averages of prior years' rainfall. Across all sex-age cohorts the 2-year moving average of rainfall correlation to bison weights was 0.192 (unweighted by sample size), but for longer moving averages the mean correlation was 0.400.

The temporal pattern of yearling bison weights at Wind Cave during 1983 to 2015 visually synchronizes with the 7-year moving average of prior rainfall (Fig. 2). Conversely, annual precipitation exhibited great among-year variability and did not show an obvious relationship with yearling bison weights.

Discussion

That bison weights can correlate to precipitation is of little surprise, although we were somewhat surprised to find the correlations were substantial and statistically significant at the two parks as the stocking rates are very low.[1] An even greater surprise was the long-term nature of the relationship. Yearling bison were markedly affected by precipitation in the growth year immediately preceding measurement and up to 7 years prior. Weights of bison in other age classes were only modestly affected by precipitation in the immediate growth year but were also often strongly related to precipitation several years earlier. The strongest correlations were between weights of Wind Cave bison and moving averages of precipitation extending back 7 years. The Badlands dataset spanned only 18 years and weight records were collected in only 11 of those years, nevertheless, that dataset generally corroborated the Wind Cave results.

The primary proximal cause of changes in bison weights over time was likely changes in the plant community over time. However, comprehensively evaluating temporal changes in the plant community and correlating those changes to changes in bison weights at the parks was not possible in our study because of the lack of suitable vegetation data. We explored the use of remote imagery to assess vegetation conditions but could not find high-quality data that covered our period of interest (i.e., starting in the late 1970s). Furthermore, remote imagery has limited value for assessing potentially relevant plant community characteristics such as species composition. The parks have recently initiated comprehensive long-term plant community monitoring that records data on composition, structure, ground cover, and other vegetation characteristics; however, that effort only began in the year 2011. Information from that study in combination with known information on nutritional characteristics of rangeland plants and remote sensing information that can capture characteristics such as plant phenology, can shed more light on proximal causes; however, we believe data covering at least one wet-dry cycle is needed before such analysis would be appropriate.

Nevertheless, it seems reasonable to speculate that changes to the plant community were the primary proximal cause to changes in bison weights. In the grassland region of the United States aboveground net primary productivity is strongly associated with precipitation.[9] The amount of change in plant productivity and composition can be amplified by sequences of wet or dry years.[10] Our strongest correlations

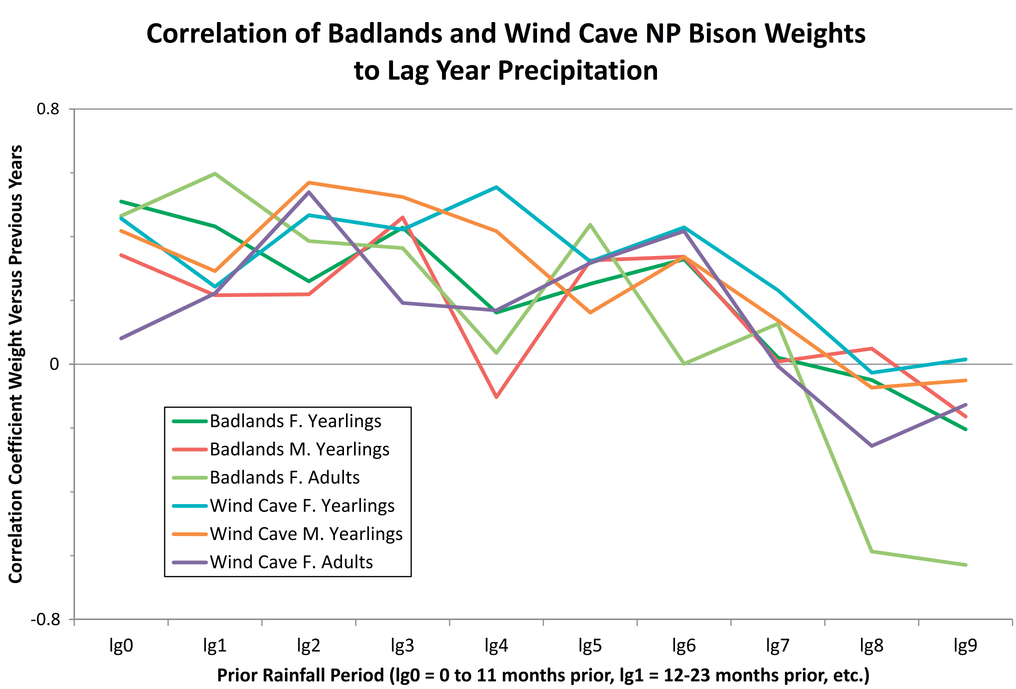

Figure 1. Correlations between bison weights and prior years precipitation for bison from Wind Cave and Badlands National Parks (NP).

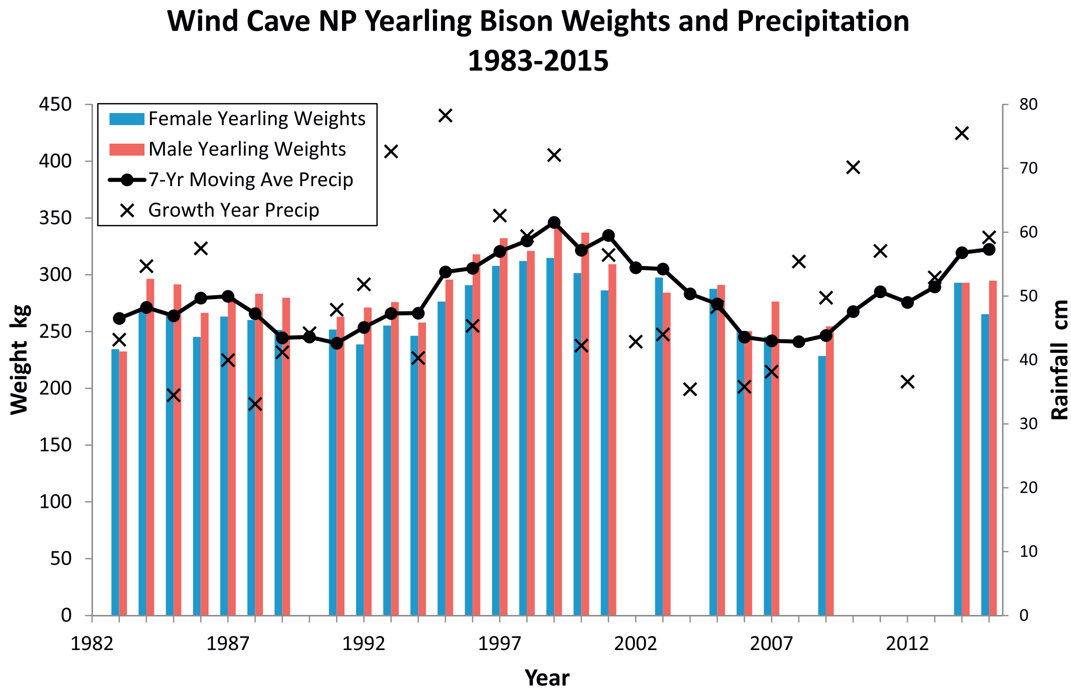

Figure 2. Yearling bison weights and a 7-year moving average of precipitation at Wind Cave National Park (NP) 1983-2015.

were with the yearling class and when we averaged precipitation over 7 years prior to the weighing. Increased rainfall over a several-year period would likely improve range conditions. That change could increase the preparturition condition and weight of cows. That in turn could affect the birth weight of bison calves, as is the case with cattle (*Bos taurus*) where the birth weight of calves averages approximately 7% of the weight of the dam.[11] Similarly, heavier bison mothers appear to produce heavier calves.[12] These heavier calves appear to continue their size advantage to the yearling age.[2]

Although we detected significant correlations between precipitation and bison age classes ≥ 1.5 years of age, we failed to detect a correlation between calf weights and any precipitation patterns, even after we accounted for the dates of the roundup. The lack of apparent correlations could have been due to the small sample size of that age class (only 10 years of data at Wind Cave). It also could have been due to among-year differences in parturition dates, as that would influence the age of the calves (in days) at the time of the roundup. Peak parturition dates are known to vary at Wind Cave by perhaps a couple of weeks.[13] The actual dates and reasons for the variation in peak parturition dates are unknown, and therefore we could not account for changes in parturition dates into our model.

In cattle the correlation between precipitation and weights are known to be especially strong under heavy stocking.[14] However, the parks in this study are stocked well below ecological carrying capacity, with bison consuming only about 19% to 24% of the aboveground net primary productivity in dry years at Wind Cave and Badlands, respectively, and only 10% to 11% in wet years. Therefore, it appears that the mediating factor at the parks is forage quality more than quantity. Precipitation is known to change the ratio of C_3 to C_4 grasses in grassland ecosystems.[15] Wet winters and springs, a pattern that would increase C_3 grasses, increased postgrazing-season weights of Hereford cattle in a northern mixed-grass prairie.[16] Research in the tallgrass region correlated increased weight gain of adult and young bison to changes in vegetation quality, not quantity.[17]

We found that multiyear wet periods are associated with heavier bison. What this means under climate change is uncertain. Although there could be an increase in annual precipitation amounts in the Northern Great Plains, that increase could come in the winter in the form of intense short-term events.[18] The potential increase could also be offset by higher temperature and therefore lower soil moisture, which would likely degrade bison forage. Throughout the North American bison range, warmer areas were associated with smaller bison.[19] Conversely, future Northern Great Plains growing seasons could be longer, which could result in an increase in net primary production in the region that in turn would result in an increase in cattle and bison production.[20]

Ecological studies are often limited by short time spans. Our results show some potential pitfalls of such studies. For example, in our study yearling bison weights at Wind Cave ranged from an average of 228.5 in the lightest year to 314.8 kg in the heaviest year for females and 232.5 to 342.6 kg for males. The only apparent explanation is changes in prior rainfall patterns. Using weight information derived from a single year for planning or other purposes could result in inaccuracies and miscalculations.

The Wind Cave bison roundup dataset, and to a lesser extent the Badlands dataset, are unique and extremely valuable in part because of their longevity. The parks should continue to systematically record bison weights as part of roundup operations. Ideally, we would like to see four to five wet-dry cycles covered by the datasets, meaning that another two to three decades of bison and precipitation data are needed to increase confidence in our results and perhaps better explain the mechanisms involved. Yet after just a couple of wet-dry cycles, we found a strong correlation between bison weights and long-term precipitation patterns, even on lightly stocked sites.

This study necessarily is observational in nature because direct experimentation of ecosystems by manipulating precipitation is not feasible. Nonetheless, these results have two important implications. First, although components of prairie ecosystems can respond immediately to drivers such as weather, they also exhibit cumulative longer-term responses and mechanisms. Second, the discovery and understanding of such long-term relationships requires consistent monitoring and study for extended periods of time.

Management Implications

Our findings demonstrate that changes in annual precipitation can influence bison weights as long as 7 years later. Therefore, managers need to take a long-term perspective in assessing range and the condition of large herbivores. Weight gains from increased precipitation can be realized even on lightly grazed sites in the Northern Great Plains. Researchers need to take a long-term perspective when assessing, studying, and reporting on grassland ecosystems.

Acknowledgments

We thank the park staff who collected bison weight data. A special thank you to Barb Muenchau and Eddie Childers who oversaw and maintained the parks' bison roundup databases. We thank Justin Reeves for helping us interpret the preliminary results. We thank two anonymous reviewers.

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This research did not receive a specific grant from funding agencies in the public, commercial, or not-for-profit sectors.