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Facing into the Blizzard: Resiliency and Mortality of Native and Domestic North American Ungulates to Extreme Weather Events

Jeff M. Martin [1,2,3]

[1] Center of Excellence for Bison Studies, South Dakota State University, Rapid City, SD 57703, USA; jeff.martin@sdstate.edu; Tel.: +1-605-394-2236
[2] Animal Science Department, South Dakota State University, Brookings, SD 57007, USA
[3] Natural Resource Management Department, South Dakota State University, Brookings, SD 57007, USA

Simple Summary: Unseasonably early blizzards in the northern Great Plains of the U.S. threaten large mammal populations unacclimated for winter conditions. This region averaged 22 blizzards per winter season during the 2010s and is anticipated to have 32 by the 2050s. Generally, expected weather-related deaths remain one of the highest non-predatory mortality causes for beef cattle and sheep at 16% for each species. But, for horses, expected weather-related deaths are correlated with colic, which represents 31% of equine mortality. For bison, expected weather-related deaths remain below 11%. However, in an early October 2013 blizzard that occurred across 16 counties of western South Dakota, the observed death loss of cattle was 223 times above expected background death loss, sheep were 63 times above expected, horses were 44 times above expected, and bison were 6.7 times above expected. Increased blizzard frequency in the future may threaten domestic ungulate populations in the northern Great Plains, but native ungulates may be well adapted to highly variable climates. For conservation and production systems, building adaptive capacity to support climate-resilient species will reduce losses economically and ecologically. Although similar mortality data for wildlife species other than bison are lacking, it seems plausible that other wildlife may share similar resilient traits to extreme weather events. Ranching bison may provide a ranch-scale alternative pathway for increasing red meat production resiliency in the face of climate change.

Abstract: Unseasonably early blizzards in the northern Great Plains threaten large mammal populations unacclimated for variable and extreme winter conditions. This region averaged 22 blizzards per winter season during the 2010s, up from 6 during the 1960s, and is anticipated to average 32 blizzards by the 2050s. In early October 2013, the fatal Atlas Blizzard affected four livestock and captive species in 16 counties of western South Dakota. Expected one-week total death losses for the study area were estimated from national average background mortality rates: 161 cattle, 102 sheep, 9 horses, and 6 bison. However, observed death loss varied significantly (McNemar's Test: $p < 0.001$) from the expected during the blizzard with: 35,682 cattle; 6428 sheep; 400 horses; and 40 bison. Observed proportional mortalities varied significantly from the expected proportional mortalities in cattle (83.9% vs. 58.0%); sheep (15.1% vs. 36.7%); horse (0.9% vs. 3.2%); and bison (0.1% vs. 2.1%; chi-squared goodness-of-fit: $\chi^2_3 = 16.85$, $p \leq 0.001$). Husbandry practices, animal behavior, and physiology may also explain some of the inequitable death losses for each species. Bison appear to be resilient to blizzards and blizzards are expected to increase due to climate change, therefore, bison may offer viability for ranchers in the face of blizzards and more variable weather.

Keywords: Atlas Blizzard; bison; cattle; death loss; horse; livestock; mortality; resiliency; sheep; wildlife

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1. Introduction

Death loss of animals during extreme weather events is an expected outcome for both wildlife conservation and livestock production systems—even in the fossil record, termed "catastrophic events" [1] and by the United State Department of Agriculture-Farm Service

Agency as "adverse weather events" [2,3]. However, the shared equity of death loss among species is often skewed beyond what is considered normal or expected. Sustainable conservation of wildlife and production of livestock ungulates on the northern Great Plains (NGP) of North America relies on taxa that are well-adapted to local weather and climatological trends, but weather trends are increasingly variable resulting in higher mortality rates [4–7]. In the NGP, the average growing season is less than 150 days and the average first frost occurs by mid-September, whereas the southern Great Plain's average growing season is often greater than 210 days and some places may not have frost every year [8]. Interannual precipitation variability in the NGP is projected to increase by 7.4% by the mid-21st century and 11.5% by the late 21st century and rising mean annual temperatures, and are projected to increase by an additional 3.0 °C and 5.3 °C over the same period [9], making the timing of seasonal transitions less predictable [10,11].

Mis-matched seasonal autumnal phenology may affect how well large mammals prepare for winter seasons, such as attempting to obtain adequate adipose tissue with meager available forage due to drought [12], growing a winter haircoat [13], and ensuring all body maintenance has been recovered prior to winter (i.e., sufficient backgrounding and conditioning) [14]. Autumnal forage senescence closely tracks photoperiod, drought conditions, and the timing of precipitation [15]. Late growing season forage quality and availability determine animal conditioning, reproductive status, and survival success [12,16]—the timing of winter haircoat growth and molt may also be linked with the interaction of photoperiod and forage nutrient availability [14]. Untimely blizzard storms early in the autumn season may disproportionally affect ungulates unprepared for the coming winter season. In this same region, several common species of large-bodied ungulates are predominantly used for conserving wildlife species and producing livestock for agricultural commodities. While North American plains bison (*Bison bison*; hereafter referred to as bison) exist in both domains, the livestock-only species include beef cattle (*Bos taurus*), sheep (*Ovis aries*), and horses (*Equus caballus*).

Large biota, inclusive of large herbivores, are disproportionately influential on ecosystem form and functioning [17]. Bison are keystone species that engineer the landscape geomorphology [18,19], plant and arthropod biodiversity [20,21], and nutrient cycles [22,23] because of their behavioral actions. Two behaviors of bison, creating and maintaining wallows, and site selection and duration of grazing, outweigh other behavioral actions because of their broad biological interactions. Bison wallows, shallow excavated soil depressions, have multiple roles: (1) exposing the seed bank in the soil for germination of forbs that create plant biodiversity hotspots [20,24,25], (2) serving as ephemeral vernal catchments for anuran breeding [26], and (3) increasing landscape mosaic of bare soil and vegetation that increases solitary native pollinating arthropod biodiversity [27–29]. Over multiple decades, these attributes of bison behaviors eventually compound and accrue into increasing plant biodiversity [20]. Loss of bison on the landscape, therefore, eventually loses ecological resiliency for ecosystem function [20,23]. Loss of bison today, as opposed to the infamous late 18th-century population bottleneck [30], is driven by management choices and extreme adverse weather [31]. Management-wise, bison are a unique species that co-occur in both conservation and production systems, termed the "Bison Management System" (BMS) by Martin et al. [32].

In the 1960s the Great Plains from southern Alberta to northern Texas averaged 5.9 blizzards per winter season, predominately occurring in Minnesota, North Dakota, and South Dakota [33]. The 2010s averaged 21.6 blizzards per winter season, and by the 2050s, the frequency of blizzards is predicted to increase to 32 $\pm$ 5.3 per season [33]. Although average blizzard size has decreased by half, the frequencies have increased, the geographic distribution has increased, and the disaster declarations—agricultural and urban inclusive—have increased totaling more than $8.6 billion in losses over the past four decades and will likely increase with additional blizzard occurrences [33].

Atlas Blizzard occurred on 3–5 October 2013, observations recorded from the National Weather Service office in Rapid City, showed record-setting snowfall (0.3–0.6 m in the plains and 0.9–1.5 m in the higher elevations of the Black Hills), plunging temperatures (preceding 7-day daily maximum temperature averaged 18 °C and during the Atlas Blizzard daily maximum temperature averaged −1 °C), freezing rain, strong winds (110 km/h: 30.5 m/s), and blowing/drifting snow. The estimated wind chill of ambient dry bulb temperature and wind speed was −12.5 °C.

Across the United States, average annual expected background mortality rates have been 1.5% for cattle, 4.4% for sheep, 1.4% for horses, and 2.3% for bison [31,34–36]. Of those mortality rates, weather-related death loss is a top-three contributor in cattle, a top-two contributor in sheep, an indirect top-three contributor in horses, and a top-four in bison. Explaining average annual total death losses for each species; weather-related deaths account for approximately 16% for both cattle [34] and sheep [35]. For horses, weather-related deaths remained unreported in the USDA report [36]—colic, however, represented 31% of horse death loss between the ages of 1–20 y and colic-related deaths represented 13% of horses >20 y and colic has been correlated with highly variable weather conditions [37–39]. Whereas, for bison weather-related death losses remain below 11% of all death losses [31]. It is interesting to note that parturition-related deaths are unreported in both horses and bison mortality reports—unlike in the cattle industry, calving is unassisted in the bison industry.

Discrepancies between each species' long-term weather-related death losses may offer insight into how each taxon might respond to short-term extreme weather events, such as blizzards. Disparities in weather-related death loss, mortality rates, and proportional mortality (see Box 1) across these species may be related to physiological and husbandry differences. Here, this paper evaluates observed death loss, mortality rates, and proportional mortality during the Atlas winter storm blizzard (hereafter, "Atlas Blizzard") that occurred in western South Dakota in 2013 against expected death losses, mortality rates, and proportional mortalities within and among cattle, sheep, horses, and bison.

Box 1. Terminology.

Observed death loss: actual count of species deaths related to a single adverse weather event.
Expected death loss: background annual mortality rates from previous reports to produce an estimate of anticipated baseline species deaths for the duration of an adverse weather event.
Mortality rate: percentage of death in relation to original species population census (can be observed or expected).
Event total death loss: sum of all species deaths resulting from the adverse weather event (can be observed or expected).
Proportional mortality: relative share of species-specific death loss as a percentage of the event total death loss (can be observed or expected).

2. Materials and Methods

2.1. Study Area

The 16 directly affected counties from Atlas Blizzard were identified from the National Oceanic and Atmospheric Administration storm events database (https://www.ncdc.noaa.gov/stormevents/eventdetails.jsp?id=480049 (accessed on 1 December 2021) and https://www.weather.gov/unr/2013-10-03_05 (accessed on 1 December 2021)). Those 16 counties (collectively and hereafter referred to as the "affected counties") include: Bennett, Butte, Corson, Custer, Dewey, Fall River, Haakon, Harding, Jackson, Lawrence, Meade, Oglala Lakota (formerly known as Shannon prior to 1 May 2015), Pennington, Perkins, Stanley, and Ziebach.

2.2. Weather Data

Weather descriptions for Atlas Blizzard are from the National Oceanic and Atmospheric Administration storm events in the aforementioned storm events database and are provided as summary statistics from their weather station networks across the affected counties.

2.3. Census Data

Affected county census of agricultural livestock populations and the number of operations specific to cattle, sheep, horse, and bison were collected from the United States Department of Agriculture livestock and animal census of 2012 for South Dakota [40]. In cases where USDA NASS may withhold disclosure of operation size because too few operations exist in a county ($n \leq 3$), species population remains undisclosed—this is especially the case for bison, in that bison operations are relatively sparse [41] compared to cattle and sheep operations. However, the number of operations remains fully disclosed by county. When the species population was missing but still had an operation count greater than zero, the data were replaced with the state average animal per operation. This was calculated by dividing the state's total number of species by the state's total number of operations. For example, the bison population in South Dakota in 2012 was 33,637 and the operation count was 104; providing an average of 323 bison per operation [42].

2.4. Mortality Data

Species-specific death loss tallies for the state of South Dakota were obtained from the South Dakota Animal Industry Board [43,44] and confirmed with the South Dakota State Veterinarian, Dr. Dustin Oedekoven (pers. comm. 2021). Note that Dr. Oedekoven stated stakeholder reporting of death loss associated with Atlas Blizzard was non-compulsory and that observed death loss reported here are estimates and likely conservative and may skew one species over another. Event total death loss was divided by the affected county sum of the animal census population and reported as a percentage of mortality rate. Average background rates of annual mortality for each species were obtained in species-specific USDA APHIS reports including cattle [34], sheep [35], horses, [36], and bison [31]. Those annual background mortality rates were used to calculate the expected weekly death loss for each species to compare with the observed death loss of each species during the Atlas Blizzard.

2.5. Computation and Statistics

All data were related, derived, calculated, and analyzed in Stata/IC (version 17.0; 64-bit; Stata, College Station, TX, USA). Standard errors are calculated ad-hoc with confidence intervals set at 95%. Data were non-normally distributed and had small sample sizes; therefore, we implement chi-squared techniques.

2.5.1. Intraspecific Death Loss: McNemar Chi-Squared Test

McNemar's chi-squared test ($M\chi^2{}_{df}$) was used to determine if the intraspecific (within species) observed death loss was significantly different from the expected death loss for the week, including the effect size as Goodman-Kruskal's gamma (γ) and odds ratio [45].

2.5.2. Interspecific Proportional Mortality: Chi-Squared Goodness-of-Fit

Event total death loss was calculated as the total sum of observed death losses during Atlas Blizzard and the same was calculated for expected death losses. These sums were then used to standardize interspecific proportional share (i.e., proportional mortality) of observed and expected total death loss as a percentage of the event total death loss; put another way, measured as the percent relative death loss over event total death loss for both observed and expected. Chi-squared goodness-of-fit ($\chi^2{}_{df\,(gof)}$) tests compare the distribution of histograms. The chi-squared goodness-of-fit test was used to determine if rank-order proportional interspecific observed death losses varied from the weekly expected death losses.

3. Results

3.1. Census, Observed and Expected Weekly Death Loss, and Observed and Expected Mortality Rates

Observed census data from the 2012 USDA national agricultural statistical service of the affected counties estimate populations (*n*) for beef cattle (557,193), sheep (120,738), horses (32,773), and bison (13,146); with the total animal census in the affected counties amounting to 723,850 (Table 1). Observed death losses (*n*) during Atlas Blizzard were reported for cattle (35,682 ± 189), sheep (6428 ± 80), horses (400 ± 20), and bison (40 ± 6); with the event total death loss amounting to 42,550 ± 206. Expected annual background mortality rates were obtained from specific USDA reports for each species, for cattle (1.5%), sheep (4.4%), horses (1.4%), and bison (2.3%; Table 1). Expected death losses for one week were calculated from the product of expected mortality rates and census numbers for cattle (161), sheep (102), horses (9), and bison (6); with expected event total death loss amounting to 278 for the week (Table 1). The expected weekly mortality rate was calculated as a percentage of expected death loss to the population census for cattle (0.03%), sheep (0.08%), horses (0.03%), and bison (0.04%; Table 1). Observed mortality rates were calculated from the observed death loss overpopulation census for cattle (6.4% ± 0.03), sheep (5.3% ± 0.07), horses (1.2% ± 0.06), and bison (0.3% ± 0.05; Table 1 and Figure 1).

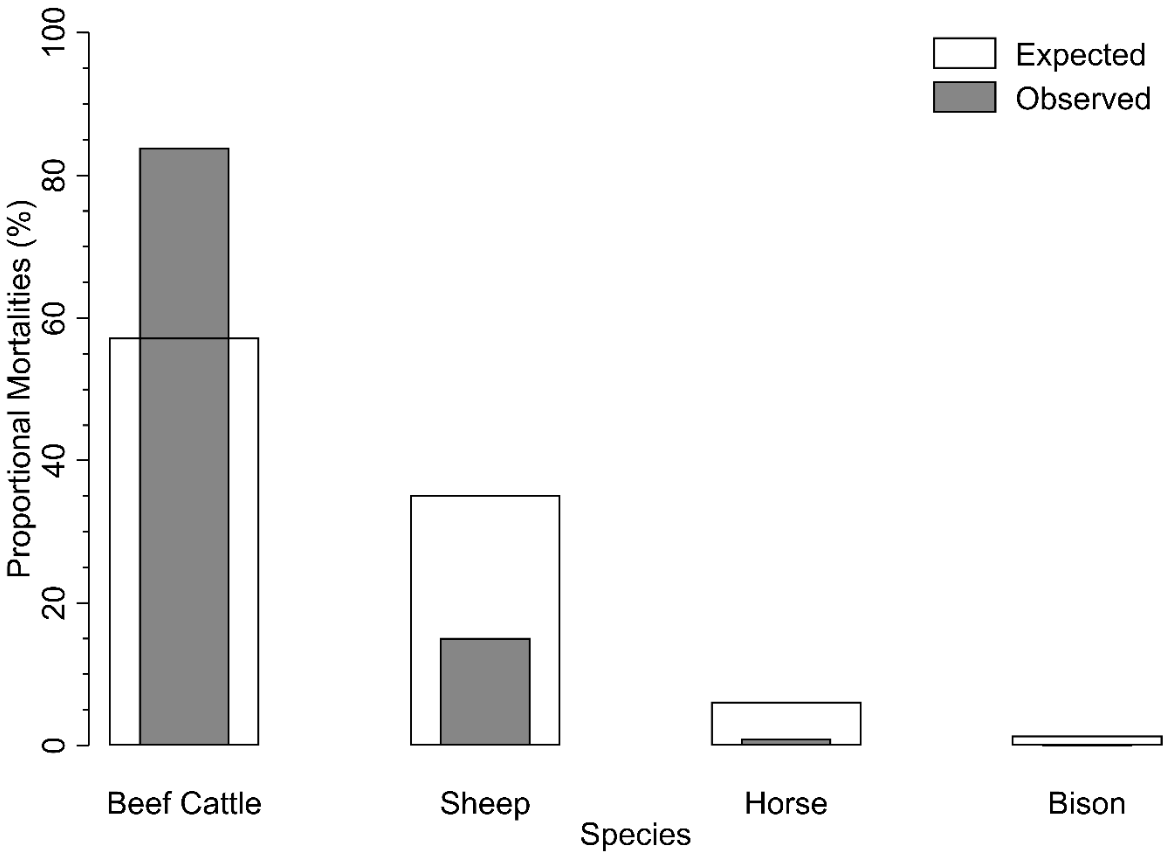

Figure 1. Histogram of expected (%; hollow fill) and observed (%; gray fill) proportional mortalities (%) of event total death loss by species including beef cattle (*Bos taurus*), sheep (*Ovis aries*), horse (*Equus caballus*), and bison (*Bison bison*) from the Atlas Blizzard affected counties in South Dakota of October 2013. Note: difference in the distribution of the expected and observed histograms is tested with $\chi^2_{(gof)}$ in Table 2.

Table 1. Livestock population census by county and by study area total, expected annual background mortality rate, expected weekly death loss, expected weekly mortality, observed death loss, and observed mortality rate for beef cattle, sheep, horse, and bison in the study area of western South Dakota. Census data derived from USDA NASS [46]. Rounding may affect some summary statistics.

County Census	Cattle	Sheep	Horse	Bison	Total
Bennett	27,496	467	924	* 970	33,049
Butte	27,911	39,626	2876	* 647	76,525
Corson	51,485	2222	1503	* 647	60,287
Custer	16,484	290	1599	2916	26,629
Dewey	41,514	2885	5021	* 647	50,987
Fall River	38,615	7202	2373	* 647	53,058
Haakon	36,775	4088	847	-	51,956
Harding	42,540	27,927	1318	2488	75,011
Jackson	33,624	606	2424	-	45,368
Lawrence	8589	535	805	* 647	10,498
Meade	70,392	15,383	4090	* 323	92,544
Oglala Lakota †	20,938	58	2181	950	25,431
Pennington	32,293	1053	1536	* 323	37,759
Perkins	56,590	15,009	2020	* 1294	79,145
Stanley	15,380	600	858	* 647	19,834
Ziebach	36,567	2787	2398	-	40,965
Summary Statistics					
Study area total population census	557,193	120,738	32,773	13,146	723,850
Expected annual background mortality rate (%)	1.5	4.4	1.4	2.3	$\bar{x}$ = 2.4
Expected background death loss in one week	161	102	9	6	Σ = 278
Expected weekly mortality rate (%)	0.03	0.08	0.03	0.04	$\bar{x}$ = 0.05
Observed death loss	35,682	6428	400	40	Σ ‡ = 42,550
Observed mortality rate (%)	6.40	5.32	1.22	0.30	$\bar{x}$ = 3.31

Symbols: (*) Estimated head count based on the number of operations listed but without a population count (to conceal privacy) multiplied by the average bison per farm in South Dakota, circa 2012 (n = 323 bison/operation). (†) Formerly Shannon County circa 2015. (‡) Event total death loss. (-) No operations reported in the county, thus a population of zero is inferred. (Σ) Row totals. ($\bar{x}$) Row means.

Table 2. Output summary table of McNemar chi-squared ($M\chi^2$) tests and Chi-squared goodness-of-fit ($\chi^2_{(gof)}$) tests comparing observed versus expected death loss of cattle, sheep, horse, bison, and across all species during Blizzard Atlas in early October 2013.

Species	$M\chi^2$ $_{(df)}$	γ	p	OR
Cattle	35,201.89 $_{(1)}$	0.9910	<0.001	221.62
Sheep	5970.32 $_{(1)}$	0.9688	<0.001	63.02
Horse	371.49 $_{(1)}$	0.9560	<0.001	44.44
Bison	25.09 $_{(1)}$	0.7391	<0.001	6.66
All species	40,556.28 $_{(3)}$	0.9870	<0.001	153.06
$\chi^2_{(gof)}$	16.85 $_{(3)}$	–	0.0008	–

Symbols: ($M\chi^2$) McNemar's chi-squared test. ($\chi^2_{(gof)}$) Chi-squared goodness-of-fit. $_{(df)}$ Degrees of freedom. (γ) effect size as Goodman-Kruskal's gamma. (p) Significance. (OR) Odds ratio. (–) Not applicable.

3.2. Intraspecific Death Loss: McNemar Chi-Squared Test

McNemar tests ($M\chi^2$) comparing intraspecific differences of observed and expected death losses for each species (cattle, sheep, horses, and bison) showed a strong positive effect and that the observed death loss was significantly higher than expected death loss (results are summarized in Table 2). Specifically, odds ratios and effect size (γ) indicate that cattle were 221.6 times more likely to die during this blizzard than over the expected weekly background death loss; 63.0 times more likely for sheep; 44.4 times more likely for horses, and only 6.7 times more likely for bison (Table 2).

3.3. Interspecific Proportional Mortality: Chi-Squared Goodness-of-Fit

Observed proportional mortality was calculated (and shown in Figure 1) for cattle (83.9%), sheep (15.1%), horses (0.9%), and bison (0.1%). Expected proportional mortality was calculated for cattle (58.0%), sheep (36.7%), horses (3.2%), and bison (2.1%; Figure 1). Overall, a chi-squared goodness-of-fit ($\chi^2{}_{df\,(gof)}$) test showed that the distributions of the observed interspecific proportional mortality (relative share of event total death loss) were significantly different from the expected proportional mortality ($\chi^2{}_3$ = 16.85; p = 0.0008; Table 2).

4. Discussion

Weather-related death remains one of the highest non-predatory mortality causes for American cattle and sheep except for "old age" at 16% for both species, according to the USDA, essentially tied with parturition-related problems. For horses, weather-related deaths were unreported in the USDA report, but colic represented 31% of equine mortality and colic has been correlated with variable weather conditions. For bison, the USDA reports that diseases and health problems explain 61% of deaths, non-predatory injury explains 23%, and handling-related problems explain 13%, whereas weather-related death remains below 11%. However, ranching bison may offer an alternative species for red meat production for the livestock sector for the northern Great Plains (NGP) of North America, because they are native to this region [47,48] and are already a sustainable alternative meat source for tribal nations [49]. Although bison mortality appears to be less than other taxa in this study and single event, blizzards are not likely a primary contributor to bison mortality.

One aspect that may be worth exploring further, is that wet hair coats substantially reduce the insulative properties of endotherms, especially large ungulates [50]. Hypothermia in cattle may result from their single-layered hair coat structure, lacking sufficient insulative properties of winter hair coats [51–53]. Hypothermic conditions were high wind speeds, freezing precipitation, and drifting snowbanks over a 2.5-day period with windchills estimated at −12.5 °C. Yet sheep—known for their insulative woolly hair coat—also succumbed to elevated mortality rates (Table 1). High sheep mortality rates suggest that, perhaps, differences in basal metabolic rates and lower critical temperature limits between the taxa may have a role in survival to extreme cold, wet weather events. Lower critical temperature limits for each taxon with dry hair coats are as follows: cattle at −10 °C, sheep at −10 °C, horses at −8 °C [54], and bison at −30 °C [55], well beyond the lower critical temperature limit for the three former species. However, unfortunately, wet hair coats lower critical temperature limits have not been established for the species included in this study. The expected estimate of weekly death loss data from USDA for all species lacks seasonal resolution to further refine our understanding of extreme weather-related mortality events; more study is needed, especially focused on aspects of seasonality and acclimation.

Non-provisioning production livestock (i.e., horses) might have artificially low death loss because of different husbandry practices that keep them closer to ranch headquarters and in protective facilities (e.g., barns and stables). Provisioning livestock species (i.e., meat and wool provided from cattle, sheep, and bison) would be in summer grazing pastures in early October, often far away from ranch headquarters [56]. Many of the cattle that perished during the Atlas Blizzard suffered from suffocation under snow drifts or hypothermia-induced congestive heart failure [43], whereas the cause of death in the other species was not explicitly reported (D. Oedekoven, South Dakota State Animal Industry Board Veterinarian, pers. comm., 2018 and 2021).

Climate resiliency is multifaceted, especially for primary producers such as foresters, fisherman, ranchers, and farmers, but here we focus on the ecological and physiological resiliency of bison, cattle, sheep, and horses. The bison management system (BMS) is different from conventional livestock agriculture or wildlife conservation [32]. The BMS is multisectoral, comprising four major sectors [32], including: (1) nonprofit NGOs, (2) tribal nations, (3) private agricultural production, and (4) public agency wildlife conservation. The BMS multisector system, while moderately vulnerable to climate change [32]—less so than their cattle rancher counterparts [57,58], intrinsically has diverse strategies to manage population demographics and densities, and herd health and animal welfare to meet goals and overarching mandates. These diverse management strategies, nevertheless, serve as problem-solving innovations to multifaceted issues regarding climate change and climate variability—species selection is one of those management strategies that may determine climate resilience capacity.

Climate variability is expected to increase through the 21st century in the NGP of North America with more frequent and intense weather events including blizzards, droughts, and floods [33,59,60]. Increased variability decreases the productivity of plants and animals [61–64] and may threaten the sustainable production of certain crops and livestock in the NGP [65]. Transitioning agricultural lands of the NGP—a region of which 90% is privately owned and mostly in the agriculture sector [32,66]—into climate-resilient types of production is reliant upon the adoption of climate-resilient crop and livestock production. The bison market, however, has its own challenges: the market is slower than the cattle market in that there are fewer processing plants, bison take longer to achieve target slaughter weight, and there are high costs of entry into the bison industry because of higher value per animal. Although there is a delayed rate of bison maturation and a later target market weight, the climate-resiliency of the species appears to be greater than cattle under extreme winter weather conditions. What remains unknown, and should be explored further, if possible, are death rates for other wildlife ungulate species found in this region during Atlas Blizzard, including pronghorn antelope (*Antilocapra americana*), elk (*Cervus canadensis*), deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Ecologically, maintaining variable-weather-resilient large-bodied ungulate wildlife species (*sensu lato* species that are physiologically resilient to variable and extreme weather [67–69]) is critical to sustaining ecosystem resiliency [17]. Therefore, the loss of physiologically resilient ungulates to impending climate change and climate variability will decrease holistic ecosystem function and ecological services, including provisioning ecosystem services such as meat, fiber, and hide production [70].

5. Conclusions

An expected 50% increase in blizzards per season will increasingly threaten some large ungulate populations in the NGP, requiring adaptive and resilient management strategies for well-balanced and integrated wildlife conservation and livestock production. A combination of husbandry, animal behavior, and baseline physiology may explain the inequitable death loss of the studied species during the Atlas Blizzard of 2013 in western South Dakota. Moreover, management strategies that limit the effect of blizzards on bison are considerably reduced compared to those recommended for cattle [71], in that no additional management strategies are suggested prior to, during, or post blizzards because bison appear to be relatively, naturally unaffected by blizzards. Yet more research needs to be conducted on bison regarding extreme summer weather conditions such as heat waves, heat stress, and drought. Ranching bison, which have lower mortality rates in extreme weather events such as blizzards, may provide a ranch-scale alternative pathway for increasing individual operation and livestock sector climate resiliency.

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Data Availability Statement: All data used here are reported in Table 1.

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