Mammal Research
https://doi.org/10.1007/s13364-019-00416-7

ORIGINAL PAPER

High society: behavioral patterns as a feedback loop to social structure in Plains bison (*Bison bison bison*)

Kelsey C. King[1] · Andrew J. Caven[1] · Katie G. Leung[1] · Dustin H. Ranglack[2] · Nico Arcilla[1]

Received: 16 November 2017 / Accepted: 24 January 2019

Abstract

Social organization as a topic has wide application often conserved across lineages and can lead to complex cultures, yet it is still not well understood in many taxa. We observed American bison (*Bison bison*) to investigate the interactions of hierarchy and behavior to elucidate patterns of social organization. Bison are highly visible animals that live in relatively accessible grasslands, and most are in semi-wild conservation herds that allows for access to low-stress observation and physiological exams. We observed behaviors in a semi-wild, reintroduced herd of 53 bison in a 140-ha prairie from April to October 2015 (165 h of observation). After establishing a linear hierarchy, we categorized individuals of each sex as high, mid-, or low ranking and then evaluated behavioral trends across rank and sex. We found that high ranking males constantly defended their linear positions and focused breeding efforts on the females with the highest productivity, consistent with disruptive sex characteristics. Intra-rank conflict focused on linear positioning likely causes the volatility in male bison hierarchy and stress of domination. Female bison, however, tend to suppress the lowest class, which likely drives their hierarchy's stability and stress of subordination. Our results show that male and female bison are impacted differently by their social rankings and show that individual aggressive actions may provide feedback loops to their social organization.

Keywords Social structure · Dominance · Class conflict · Hierarchy · Bison

Introduction

Social structure is the foundation upon which much intraspecific competition occurs, and many species in a wide swath of taxa exhibit some social structure. However, the behavioral agents driving patterns in social structure are largely unknown. Many species, especially charismatic mammals, which exhibit easily observed social behavior, are inaccessible to extensive research. These species are cryptic, far from researchers, or aquatic, and therefore typically require large investments to study (Whitehead and Rendell 2014). However, American bison (*Bison bison*) are ideal candidates to investigate social hierarchy dynamics. Nearly all Plains bison (*Bison bison bison*) herds are in some degree of captivity, under human management, and brought into holding pens annually. This allows for easy access to testing (genetic, viral, or parasite loads), and they are large and conspicuous animals, that are relatively accepting of human presence (University of Nebraska Medical Center 2016). These factors allow for humane observation and sample collection. Additionally, bison express dominance through visible aggression and appear to be influenced biologically due to their status (Fuller 1960; Lott 2003; Lott and Galland 1987; Bowyer et al. 2007; Mooring and Penedo 2014; Wolff 1998; Rutberg 1986). Finally, bison have resided in metapopulations since the late 1800s and therefore could provide useful information on cultural and genetic differences that arise when social animals are separated by some boundary or are re-integrated (Di Fiore and Rendall 1994; Whitehead and Rendell 2014).

Recent increases in the bison population and our awareness of the issues facing bison today has led to many groups

Communicated by: Karol Zub

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13364-019-00416-7) contains supplementary material, which is available to authorized users.

✉ Kelsey C. King
kelsey.king216@gmail.com

[1] Platte River Whooping Crane Maintenance Trust, Wood River, NE, USA

[2] Department of Biology, University of Nebraska – Kearney, Kearney, NE, USA

Published online: 13 February 2019

considering bison re-introductions and maintenance. However, there is still much of their natural and life history to be documented. Much of the behavioral research of the past hundred years focused on male bison during the breeding season, and therefore, we hope to detail some descriptive information on other topics to provide future studies with guidance on our methods and observations. Additionally, much of the past has focused on bison herds in massive areas that not only split off into smaller herds, which tends to reduce social stress and pressure on individuals facing aggression (Sapolsky 2005; Creel 2001), but also make identification to individuals difficult. We must recognize that the smaller the area bison groups are held in, in terms of hectare per bison, will affect the amount of visible aggression. For this study, a smaller area is ideal in that the heightened aggression could provide more data, and only changes in the abundance of aggression, not duration nor severity, have been documented (Sapolsky 2005; Creel 2001), but is a point of further research for bison. Previous research on social organization makes a few predictions on what trends we can expect to find in bison based on their social structure, but little information on the social mechanisms of hierarchy.

Studies on social hierarchy and stresses related to communal living have made some strides that can inform us on what to expect in bison society. We can predict based on their social structure and biology which individuals are most susceptible to social pressures, and it will be sexually segregated (Sapolsky 2005; Cavigelli and Caruso 2015). Male bison have a frequently shifting linear hierarchy; individuals tend to be more aggressive as they age, confront each other with physical aggression, and only large-bodied males tend to acquire mates (Lott 2003; Bowyer et al. 2007). These traits suggest that males experience stress of dominance; in other words, the highest stressed individuals are high ranking males (Sapolsky 2005), which has been suggested by one cortisol study (Mooring et al. 2006). Female bison require prime forage, are non-cooperative breeders, have stable hierarchies (when plenty of forage is available; Lott and Galland 1987), receive minimal support from kin as adults, and typically rely on non-physical intimidation (Lott 2003; Treanor et al. 2015; Rutberg 1986; Green and Rothstein 1991a, b; Hamel et al. 2012; Komers et al. 1994). Therefore, we can predict, because of these traits, that females would undergo stress of subordination (Sapolsky 2005). It is very important to understand these social pressures in bison, because it has been documented that hierarchy placement appears to be able to drastically effect health (Lott 2003; Lott and Galland 1987); however, the type of social pressure (stress of dominance or subordination) is likely leading to very different health issues and benefits (Cavigelli and Caruso 2015). If males and females in the same hierarchy position are experiencing social pressure differently, then it is certain that the care of bison must be cognizant of this.

Bison females may benefit from hierarchy-related associations with access to prime forage (Lott 2003; Rutberg 1986; Vervaecke et al. 2005). This could be reinforced by sexually dimorphic dietary needs, where females, having a smaller body size and high reproductive costs, require more micro-nutrients and more digestible food compared to males (Treanor et al. 2015). However, for males, the major benefit to higher rank is thought to be breeding access to females, resulting in the top males having more offspring (Lott 2003; Roden et al. 2003; Roden et al. 2011; Wolff 1998). These resources, forage for females and reproduction for males, can guide our predictions on the conditions around which hierarchy will become vital for resource acquisition, and what under what contexts we can expect them to change. For example, female bison tend to align their hierarchy with age, except in cases of illness or low forage availability (Lott and Galland 1987); therefore, a drought our parasite bloom should cause shifts where lower ranking females begin to push against previously high ranking females for better forage. Resources perhaps explain why female bison hierarchy in high production ecosystems may have more stability than counterparts in low production ecosystems (Lott and Galland 1987). The male hierarchy also tends to be somewhat sorted by size and/or age depending on the demographics and resources in their habitat. However, we would expect most of the aggression frequency to undergo seasonal shifts, depending on the time to breeding season, where more positions are challenged immediately prior to breeding and return to some maintenance level following breeding. However, little research has been done to track hierarchy throughout time to identify when and why deviations from age or body size occur.

Hierarchy appears to be somewhat flexible; however, some individuals can be relegated to certain castes in multiple situations (Shively et al. 1997). For female monkeys, changes in the housing or individuals present led to a short period of increased aggression after which the hierarchy was determined and then aggressions settled (Shively et al. 1997); however, the strategies used by individuals or castes to ensure their rank were not followed. We are extremely interested in understanding how individuals are being affected by the strategies of groups, and what group behavioral patterns are driving the social stresses. Cavigelli and Caruso (2015) discuss a possible mechanism for the differences between stress of subordination and dominance: low versus high rates of within sex aggression lead to different stresses. However, we believe that male and female bison use differing strategies in their aggression and that the difference is not just based on the total number of incidents. In bison, female aggression is less numerous but tends to be short-lived and therefore much more difficult to detect than male aggression (Lott 2003; Lott and Galland 1987), so it is possible that rates of aggression are similar, if we account for the difference in ease of observation.

Understanding bison social hierarchy will contribute to the management of this species for genetic integrity and diversity, as well as the maintenance of natural bison relationships (Freese et al. 2007; Ballard 2013; Lott 2003). If we wish to succeed at maintaining the integrity of this species, and understand broader trends in animal behavior, we must better understand how social organizations are maintained and reinforced. We investigated trends in bison behavior to map social hierarchy and investigate behavioral feedback to those hierarchies. We expected that by mapping hierarchy and tracking certain behaviors such as courtship and challenges, we would better understand the mechanisms which form and/or maintain the hierarchy. We suspected that male and female individuals would use different mechanisms to maintain their social positions, as trends in their hierarchy are visibly different in terms of stability across years and are formed through competition over different resources (Rowell 1974; Lott and Galland 1987). Dominance, exerted through aggressive acts, occurs when members of the herd are trying to acquire resources in the presence of others (Hawley 1999), and therefore, the sum outcome of dominance interactions allowed us to map a hierarchy (Rowell 1974). Male bison typically are focused on the resource of reproductive access, and therefore, we include an investigation to courtship as well as challenging. Similarly, if we want to understand social pressures on males and females, both challenging and courtship (often harassment) are where we expected to find the most compelling trends. Finally, because linear hierarchies are tenuous, and dependent on environmental conditions (Rowell 1974; Lott and Galland 1987), we group individuals into three ranking categories. Therefore, we examine the bison by group to investigate the possibility of class suppression, jockeying for higher ranks, and courtship or challenging that is heavily tied to their society and the accompanying pressures.

Methods

Study design

We followed 53 individuals in a 140-ha fenced pasture (2.6 ha per bison) with a generally prime-aged population from April 18, 2015 to October 9, 2015. This herd contained two mature bulls (8 years old), 15 adult females (3 to 7 years old), eight young bulls (2 and 3 years old), four heifers (2 and 3 years old without offspring), 13 yearlings, and 11 calves (Fig. 1). Eleven of 15 females gave birth in the study year (Fig. 1a). Two deaths occurred in the study period, and one individual died in April of 2016. These losses had no discernible effect on other observations, and the study observations ended shortly thereafter.

The study herd is in south-central Nebraska on conservation land managed by the Platte River Whooping Crane Maintenance Trust. The herd was established February 2015 from individuals born and raised together at the Rim Rock Ranch in northwest Nebraska. Both locations contain abundant forage resources, with more biomass available at the study site. This herd continues to live together in a semi-

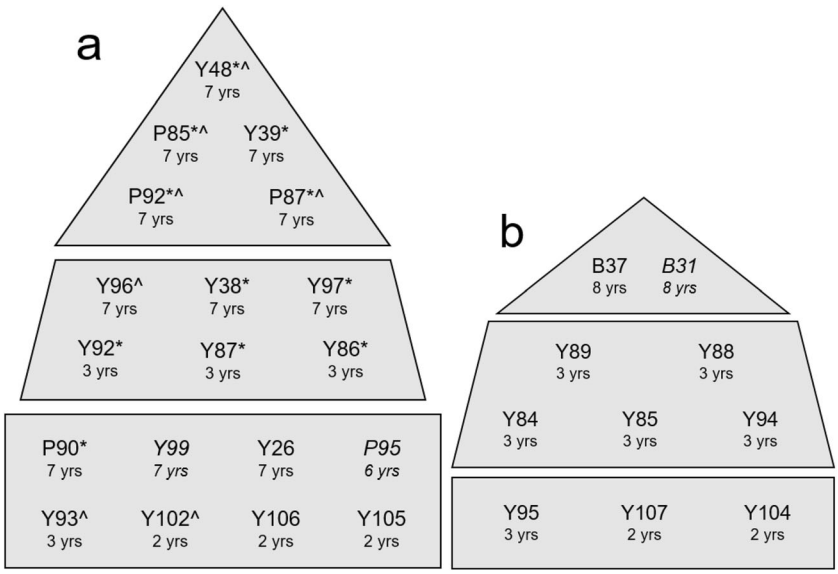

Fig. 1 Hierarchy of the study herd. **a** is the hierarchy of the females in the herd, and **b** is the males. These individuals were ranked linearly then grouped into high ranking (triangle on top), mid-ranking (trapezoid in the middle), and low ranking (the rectangle on bottom) categories. The linear ranking is approximate, and at times fluctuated within final ranking, therefore we chose to use rank categories. For each individual, the ear tag and age in the study year are listed. Asterisk indicates a calf in the study year born April to May 2015, and circumflex accent indicates a calf born in 2016. An individual in italics indicates death during or in the year following the study year. Yearlings are excluded from the figure, and all are the lowest ranked in their respective sex; there were four female yearlings and nine male yearlings in 2015

wild environment throughout their lives, with an annual working period including vaccinations, genetic, and parasite sampling. The herd had become familiar with the pasture they were observed in over approximately 3 months, with the regular amount of traffic around their pasture, with little human perturbations inside the pasture. These individuals have never been free-roaming due to fencing; therefore, we do not expect their relationships to be vastly different in the study period than from their natal grounds. During the annual working, using low-stress handling techniques, they received vaccinations against common fungal infections and deworming (see Grandin and Lanier 2015; University of Nebraska Medical Center 2016). All ages were confirmed via horn and teeth investigations (Fuller 1959; Allen 1876), and body condition was assessed using a Body Condition Scale (BCS) adapted for bison (Alberta Agricultural and Forestry 2017; Norman 2010). During annual testing, none of these bison tested positive for cattle mtDNA (see Schnabel et al. 2000; Halbert et al. 2005 for test methods).

We collected descriptive physical and behavioral data on bison from April 18, 2015 to October 9, 2015 totaling approximately 165 h of field observation and 955 individual observations of bison social behavior. It was not possible to record data blind because our methods required identification of individuals in the field. When a behavior occurred, we attempted to identify individuals involved, and described the behavior while noting the dominant/submissive behaviors and the outcome. We categorized actions by age, sex, and social ranking to investigate the process and character of hierarchy maintenance in our bison herd (Lott 2003; Bernard and Ryan 2009). The dominant and deferent behaviors were used to map the dominance by actions of individual bison in relation to the other members of the herd (see Rutberg 1986; Wolff 1998; Fuller 1960; Barroso et al. 2000; Rowell 1974; Chase 1982; Appendix 1).

Individuals were categorized as dominant over another individual of their sex when they were dominant more than 60% of time (Rowell 1974). This gives us a reasonable guidance as to their status. However, because often there are individuals that do not consistently defer to each other and therefore are interchangeable in the linear hierarchy, we grouped the bison into high, mid-, or low ranking. This allows us to increase certainty for the rankings, decrease our error, and remove some of the issues with seasonal dominance or deference behaviors. For example, some males do not participate frequently in the hierarchy during non-breeding or are using this time to have staged fights. Generally, the cutoff between low and mid-ranking, for example, would be an area where the lowest ranking of that group are getting very high deferral rates from those next in the linear ranking (> 70% of the time). We verified the groupings with four individuals familiar with the herd to ensure the areas where groups were split were consistent across all observers of the herd.

Categorizing observations by demographic allowed us to systematically examine how challenges and breeding actions differed between demographic groups (i.e., rank, age, sex) and contexts (Bernard and Ryan 2009; Lott 2003; Rutberg 1986). Once categorized, the observations were reviewed and we further categorized based on broad themes of bison social behaviors including hierarchy (Melton et al. 1989; Dewsbury 1982; Wolff 1998; Rutberg 1986; Lott and Galland 1987), breeding (Shull 1985; Bowyer et al. 2007; Maher and Byers 1987; Lott 2003), and mothering (Green 1986; Hamel et al. 2012; Shult 1972). However, we omit observations regarding mothering from this paper and instead focus on challenges and breeding behaviors. Mothering was excluded due to the low number of observations, because this relationship does not appear to be linked to the group as a hierarchy forming relationship, and we focus on interactions that are a possible consequence of the hierarchy (Erbring and Young 1979), i.e., courtship and challenging. This analysis is not suited to behaviors involving calves for a few reasons: calves have no marking to identify them as an individual, we are not certain who their mother is when not being groomed or fed by her, and finally they do not participate in the hierarchy until the fall or winter after their birth.

Observational methods

We made three to six observations per week for periods of between 3 and 8 h in which comprehensive visual passes of the herd were made using a spotting scope and/or a pair of binoculars. We made observations behind a 2-m barbed and electric fence to avoid disturbing the bison and for the safety for the observer(s). The herd was extremely visible from an elevated road adjacent to their pasture, and this allowed us to avoid over-observation of the least wary individuals. We used modified scan sampling (Altman 1974) for observations: after an initial scan of the whole herd in which counts and foraging observations were made, the spotting scope was set on specific animals that were exhibiting social behaviors during a period where the observer would visually scan through the herd and pausing when an animal began an interaction, for example, a bison would head swing at another and the observer would record the behavior and identify the individuals involved. We focused in interactions between bison to gather enough information to map the social hierarchy evident in the results of interactions. We considered each documentation of a social interaction between two or more bison as a single observation that continued until the interaction ended. Multiple passes were completed throughout the day, from sunrise to sunset. We attempted to watch all bison equally, and observations across demographic groups (age, rank, sex) are relatively even. These methods follow established bison behavior research methods (Mooring and Penedo 2014; Shult 1972; Wolff 1998; Lott and Galland 1987). Specific information

on how bison show submission to dominant or threatening individuals is somewhat limited. Therefore, we relied heavily on descriptive resources and complied a guide for others to view (Lott 2003; Ballard 2013; see Appendix 1).

Data analysis

After aligning the bison into hierarchy group, we tabulated the frequency of challenges or courtship behaviors by sex and social rank. Challenges were tallied separately for males and females, while courtship is an interaction between males and females and therefore tallied by male courting female. We could then compare this in relation to other groups; for instance, the frequency of high ranking bull challenges to mid-ranking bulls and how it compares to the female counterparts. For example, bison 89 walked into the space of bison 88, the challenge, then it would be tabulated as a mid-rank challenge to a mid-rank male (Fig. 1). The tabulation focused on the action and not the consequence which could have led to bison 89 deferring to bison 88, despite 89 beginning the original challenge. We chose to focus on the action to more closely examine how dominance or courtship actions begin and, in general, what groups are giving or receiving the harassment of challenges or courtship. Similar methods of behavior categorization and analysis have been utilized to examine the patterns and ecological impacts of social dominance in songbirds (Marra 2000), psychological trauma and its social consequences in African elephants (Bradshaw et al. 2005; Bradshaw and Schore 2007), and the social hierarchy of female mountain goats (Fournier and Festa-Bianchet 1995).

We performed chi-squared analyses to evaluate if and how observed behaviors varied in frequency per social grouping of sex and rank. Expected values were calculated by taking the total number of behavioral observations (either courtship or challenges) and then partitioning those per group based on the proportion of the herd, by sex, that grouping represented. We examined dominance by following the challengers in terms of rank. Challenges were defined aggressive actions (of any aggression level) regardless of outcome (see Appendix 1 for detailed behavior information). This could be a step into another bison's space, a head swing, or a charge. We examined courting similarly, whereby any tending, sensing, or defending behavior counted as courtship. Only observations in which both individuals were identified to tag number/given name were included in the chi-squared analyses by rank. Note that dominant or deferent behaviors, which are utilized to construct the social hierarchy map, are not included in the analysis, only challenges. Dominance and deference are outcomes after a challenge. A challenge met with a deferral is dominant; however, there are many instances where the challenger eventually defers to the bison they challenged. Finally, to evaluate significance within the tabulated matrix, we used Bonferroni corrections as follows: $p = 0.006$ is significant (corrected 0.05 p value), $p = 0.001$ is highly significant (corrected 0.01 p value), and $p = 0.01$ is marginally significant (corrected 0.1 p value). For the ease of the reader, we report the adjusted values as equivalent to 0.001, 0.05, and 0.01 in all chi-grams.

Finally, we performed a meta-analysis to assess our arrangement of the female hierarchy by evaluating correlations between social rank and variables typically associated with physical and biological fitness (Rutberg 1986; Lott and Galland 1987). We chose the female hierarchy because the metric of fitness or reproduction is readily available without genetic testing, i.e., the number of calves across the fertile years. We utilize the ranking categories created through behavioral observations for all female bison (high, mid, and low) in combination with health metrics collected during the annual working period: body condition score (1–5), reproductive rate (0–1 calves per year), and age to conduct a Spearman rank correlation analysis (R Core Team 2015). We expect a positive relationship between the body condition score, age, reproductive rate, and our measure of rank to indicate the validity of our hierarchy mapping. Note that no female bison in our herd exceeded the age where their reproductive rates begin to decline (Green and Rothstein 1991b), so we would expect a positive relationship, as opposed to a quadratic one, between age and all other variables in this analysis.

Results

Hierarchy

We mapped the social hierarchy of the bison herd, placing bison into a social ranking: high, mid-, or low ranking (Fig. 1). Generally, we found that older individuals were more likely to be dominant than younger individuals (Fig. 1). The exceptions were four low ranked 7-year-old females who deferred to three mid-ranked 3-year-old bison (Fig. 1a). Two of these four individuals died before summer 2016, suggesting poor health (Fig. 1). Male challenges were often in the form of head-ups, mounting, head swinging, horning, etc. (Table 1). Females typically challenged by horning, or moving into another bison's space (Table 1). We found higher ranking older female bison tended to challenge more than lower ranking young females (Table 1). In contrast, lower ranking young male bison challenged more than older males; however, these actions were generally less aggressive in nature as compared to adult males (Table 1). Nevertheless, there was a great deal of variation between individuals, as many individuals were highly aggressive and some individuals were not recorded behaving aggressively. Hierarchy was assigned by winning an interaction and not on aggression level; therefore, because this hierarchy is not based on aggression level, we can discuss challenging frequency based on the hierarchy.

Table 1 Challenge behaviors by age and sex. Notes: Top 3 challenge behaviors utilized by each group are in *italics*. Adults indicates 3 years or older. Young indicates 2 years of age or younger. Descriptions of behaviors found in Lott (2003)

Action type	Behavior	Adult male $n = 14$	Young male $n = 79$	Adult female $n = 32$	Young female $n = 15$
Body language	Tail raise	7.1%	2.5%	0.0%	0.0%
	Back arched	*14.3%*	2.5%	0.0%	0.0%
	Broadside	0.0%	1.3%	0.0%	0.0%
	Wallow	0.0%	2.5%	3.1%	0.0%
	Pawing	0.0%	1.3%	0.0%	0.0%
	Horn display	7.1%	2.5%	0.0%	6.7%
Vocal	Bellow during attack	7.1%	0.0%	0.0%	0.0%
	Grunt growl	7.1%	1.3%	3.1%	6.7%
Low aggression	Head wrestle	*21.4%*	*26.6%*	0.0%	*13.3%*
	Mounting	7.1%	*32.9%*	0.0%	6.7%
	Claiming space	0.0%	*0.0%*	*12.5%*	33.3%
Physical aggression	Charge	*28.6%*	8.9%	*31.3%*	*13.3%*
	Chase	7.1%	2.5%	6.3%	0.0%
	Lunge	7.1%	0.0%	3.1%	0.0%
	Buck	0.0%	0.0%	3.1%	0.0%
	Head-butt/shake	0.0%	*10.1%*	37.5%	*20.0%*
	Fight	0.0%	5.1%	0.0%	0.0%

Our female bison averaged a body condition score of 3.08, suggesting the females in our herd have a natural amount of fat and are close to optimal condition on average (Table 2; Norman 2010). Additionally, these females, on average, reproduce every other year and were just over 5 years of age (Table 2). However, the highest-ranking females were the most productive in terms of total offspring (Fig. 1a). Our ranking system produced marginally significant positive correlation with body condition and significant correlations with reproductive rate and age (Table 3).

Dominance and submission

Bison showed dominance through physical, vocal, and intimidating displays, choosing different actions based on age and sex. Adult male bison rarely challenged, but when it was displayed, it was often by charging, a high-aggression maneuver (Table 1). Young males were most often observed displaying low aggression challenges including head wresting and same-sex mounting (Table 1). Same-sex mounting was typically male-on-male and specifically males of the same rank and age class, e.g., a high ranked bull mounting another high ranked bull (Table 1); however, young females and calves performed same-sex mounts as well. Adult females by contrast most often used head shaking as their aggressive behavior. Like males, the young females chose less aggressive actions than the older females by claiming space. However, this was also one of the top aggressive actions of adult females. No male bison were observed space claiming (Table 1). Higher ranking bison, regardless of sex, were generally more aggressive, likely reinforcing their rank or more confident in their challenging ability (Table 1). However, females overall tended to perform dominance behaviors that were of lower aggression and effort, than males (Table 1). For example, vocalizations were associated with moderate to high aggression and were mostly performed by males. We found that, in general, high ranked bulls most often acted aggressively to the rank just below them while tending high and mid-ranking females, while young bulls exerted dominance over each other throughout the year (Figs. 2 and 3).

Table 2 Summary statistics for female bison: body condition score, reproductive rate, and age. "BCS" refers to body condition score, which measures the amount of fat on a bison (1–5). "Reproduction" refers to the number of offspring produced per year after the age of 2 years. "Age" represents calendar years since birth

Variables	BCS	Reproduction	Age
Mean	3.08	0.53	5.32
St. dev.	0.71	0.27	2.19

Table 3 Spearman rank correlation regarding female bison: body condition, reproductive rate, and age. $n = 19$, $^{*}p < 0.10$, $^{**}p < 0.05$, $^{***}p < 0.01$

Variables	BCS	Reproduction	Age
Rank	0.42*	0.49**	0.50**
Age	0.18	0.24	
Reproduction	0.31		

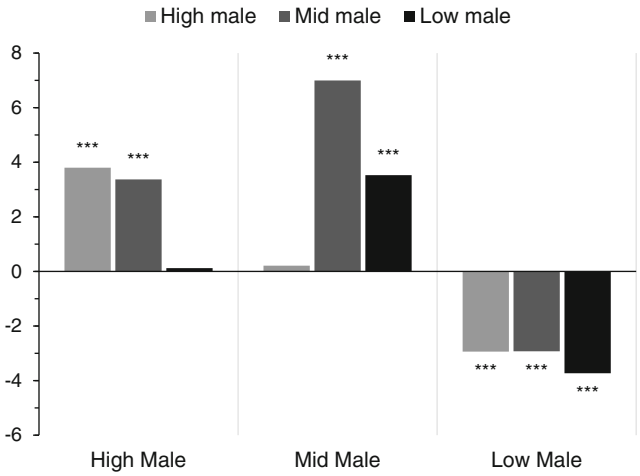

Fig. 2 Male to male challenges by hierarchy. $n = 130$, $X^2 = 118.4$, $p < 0.001$. Bonferroni corrections are shown on each comparison with equivalent p values as follows: ***$p < 0.001$, **$p < 0.05$, *$p < 0.1$. Here 0 represents expected value; a positive value is greater than expected, and a negative value is less than expected

Hierarchy influences

In this study, there were many instances of individual variation or "personality" in terms of number of challenges and who an individual preferred to challenge. Nearly 88% of challenges by low ranked males to mid-ranked males were done by Y95. He was the smallest third-year bull and was placed in the low ranked category as he rarely won a dominance interaction with any mid-ranked bull. Many of the challenges to the low ranking category in both males and females were on yearlings, the easiest individuals to exert dominance over (besides calves); however, these were not counted in Figs. 2 and 3 as the yearlings had not been ear tagged for definitive field identification.

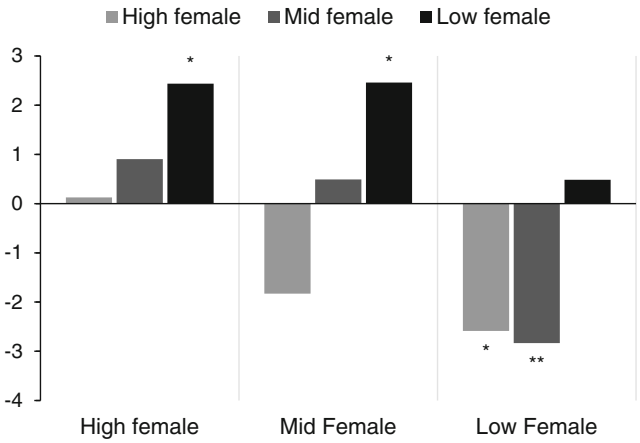

Fig. 3 Female to female challenges by hierarchy. $n = 59$, $X^2 = 31.37$, $p < 0.001$. Bonferroni corrections are shown on each comparison with equivalent p values as follows: ***$p < 0.001$, **$p < 0.05$, *$p < 0.1$. Here 0 represents expected; a positive value is greater than expected, and a negative value is less than expected. Note that the female graphs are on a different scale than the male chi-gram due to lower frequencies of challenging behaviors

For example, within high ranked females, Y48 and P85 were the most aggressive, especially to the low ranked females with all but one of the 13 observations in that category being attributable to these two, whereas P87 was not recorded aggressing, and yet did not defer to lower ranked bison females. These few individuals who challenged frequently or never did not appear to affect the analysis, and frequency did not change placement in the hierarchy.

The sexes appear to be partially dimorphic in who they challenge, outside of the low ranked individuals who tend to challenge less than expected in both sexes (Figs. 2 and 3). High or mid-ranking males frequently challenged their own rank or the rank immediately below them (Fig. 2). Male bison challenge those ranked above them less than expected (Fig. 2). Additionally, because this study took place throughout the rut, male bison challenged any other males they think they can dominate to acquire or keep a mate. We found that male aggression peaked during rut and that challenges seem to increase with rank and age of male bison. Our study found females to be generally less prone to challenging than males by more than half the total number of observations (Lott 2003; Lott and Galland 1987). For example, we found more than twice as many male challenges (130) than female challenges (59). Female intra-rank conflict is very near the expected value (Fig. 3). We found that like male bison, females tend not to challenge those above them. However, unlike male bison, females challenged those at the bottom of the hierarchy more than expected (Fig. 3).

Breeding

Observations

Demographically, members of this herd observed in courtship consisted of 10 male participants and 21 female participants. Courtship behavior, performed by males, include tending, mounting, and head-ups, as well as sniffing and/or tasting attempts of female genitalia (consistent with Lott 2003; Bowyer et al. 2007). In most cases of mounting, females moved away (41/44), and most attempted mounting was done by young bulls (39/44). In 24 observations of males searching for signs of estrus, 10 males switched the females they were examining. Females allowed the mature bulls to stay around them and tend them. In 29 accounts of female rejection of suitors (through aggression, running, or avoidance), 80% of these accounts were towards young males, 10% to multiple suitors at once, and only 10% to the mature bulls. We observed 67 tending accounts, which contained 29 instances of females running from suitors and 44 instances of males running after females or running towards competitors. Young males were typically running to females (25/28), whereas mature bulls typically were running off suitors (12/16). Females ran from young males 83% of the time and from mature bulls

only 17% of the time. One account describes a female (Y38) actively seeking out protection from a persistent young suitor (Y95) by one of the mature bulls (B37) who would not run and follow the female, but the female would do a lap away from the young suitor to return and be tended by the mature bull.

Hierarchy influences

In this study, we made 70 observations of courtship where both individuals were identified. When analyzed by hierarchy (Fig. 4) the behavior of rutting males was non-random ($p < 0.001$). High ranking males preferred high ranking females and disregarded low ranking females (Fig. 4), whereas mid- and low ranking males interacted with high ranking females less than expected (Fig. 4); though, the two low ranking male on high female observations were both by the same individual (Y104), and the four mid-male to high female courtings were all by the same individual (Y85). Mid-ranked males interacted with mid-ranked females as much as expected, but half of the mid-ranked female observations were represented by one individual female (Y38, five observations). Low ranked females are receiving the most harassment from both courting males and challenging females (Figs. 3 and 4). We found that high ranked bulls, in our case the top two, focused most their breeding efforts on the high and mid-ranked females (Fig. 4). These females produced 71% of the 2016 calves (the calving season following this rut; Fig. 1a).

Discussion

Aggregating a linear hierarchy into three groups allowed us to elucidate trends on how these groups tended to behave. We chose to examine challenges and courtship because these are the two mechanisms which can reveal and reinforce the social structure of a group, such as bison (Hawley 1999; Chase 1982; Barroso et al. 2000; Marstellar et al. 1980; Richards 1974; Rowell 1974). Also, these behaviors cause the most harassment, or are the most likely to cause observable social stress (Creel 2001; Jerry and Brown 2017; Sapolsky 2005; Barroso et al. 2000). We found that high ranking members, of both sexes, tended to challenge more, which is consistent with previous studies (Table 1; Reinhardt 1985; Lott 2003; Barroso et al. 2000). We found that high ranked male bison displayed fewer challenges per animal as compared to younger lower ranking male bison (Table 1). However, their challenges were more severe and aggressive in nature than younger male bison, including a significant amount of charging (Table 1). This may be, in part, because our herd's male social structure is very stable with only a few prime aged males (Wolff 1998). Pelletier and Festa-Bianchet (2006) documented a similar phenomenon in rocky mountain big horned sheep (*Ovis canadensis*); the stability of social relationships increased with the difference in age of individuals, but the strength of that relationship decreased with years past prime breeding age. Therefore, we expect in this herd, if no new mature males are brought in, that these two dominant bulls would persist until death or they reached 9 years of age (Lott 2003).

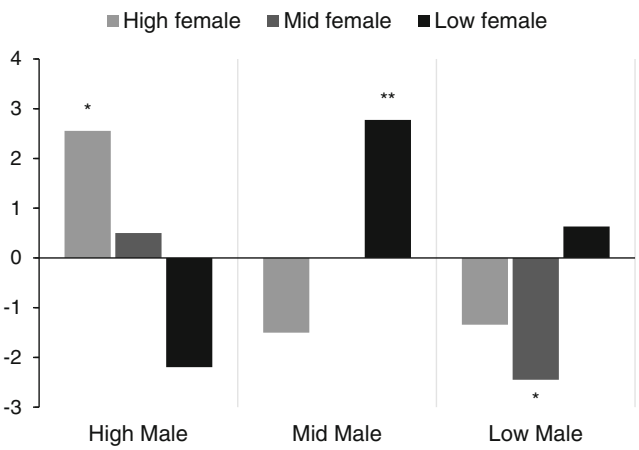

Fig. 4 Male courting behavior by hierarchy. Breeding behavior included: tending by following, mounting, or aggression by a male towards an approaching male. $n = 70$, $X^2 = 29.76$, $p < 0.001$. Bonferroni corrections are shown on each comparison with equivalent p values as follows: $***p < 0.001$, $**p < 0.05$, $*p < 0.1$

We examined our ranking system in relation to female health indicators to evaluate the relationships between these two. A Spearman rank correlation helped show the tight linkages between age, rank, and reproductive rate; agreeing with previous research (Table 3; Lott and Galland 1987; Lott 2003; Dewsbury 1982; Gauthreaux 1978). High ranked females tend to be in better body condition, have a higher reproductive rate, and are older in age than low ranking counterparts (Table 3; Vervaecke et al. 2005; Lott and Galland 1987; Lott 2003; Rutberg 1986; Shaw 2012). Body condition, which indicates current physical state, was only marginally associated with rank (Table 3), which suggests a moderate feedback loop therein (body condition increases rank or rank increases body condition). However, this statistical relationship may be weakened or partially mitigated by our finding that higher ranked bison reproduced at a higher rate, a biologically costly effort. Vervaecke et al. (2005) found that the only factor of body condition that was correlated significantly with rank was fatness, which could explain our marginally significant result. Age and reproductive rate were significantly correlated (Table 3). For example, 80% of high ranking females reproduced in both 2015 and 2016, whereas 37.5% of low ranking females reproduced only once in that 2-year period (Fig. 1). Stress of subordination may help to explain a missing factor in female reproductive rates, especially if the difference in prime forage is minimal, as stress can suppress reproductive

rates (Creel 2001). We suggest an investigation into forage quality and female rank to better elucidate the drivers of female health and reproductive rates.

Due to the herds' past and present forage productive environments, and possibly the small group size, we expected females to exhibit age-based linear rankings (Lott 2003; Rutberg 1986; Melton et al. 1989; Lott and Galland 1987). Additionally, we expected the female hierarchy to remain stable over time except in the case of health problems, and males to shift, sometimes drastically, across breeding seasons or phases of the rut (Rutberg 1986; Lott and Galland 1987; Lott 2003; Vervaecke et al. 2005). Our results were generally consistent with these expectations (Fig. 1a). The four exceptions to the orderly age-hierarchy were all attributable to poor health (e.g., parasite loads, loss of a foot, poor body condition indicated by slow hair loss and a low BCS score; Lott and Galland 1987; Rutberg 1986; Vervaecke et al. 2005). However, once female (26) was placed in a herd without the dominant females, her health improved, and she became a dominant female (Caven, pers. comm 2018), therefore it is possible that the social pressure during the study time had some impact on the four mature, but low ranking, females.

We found that male bison peaked in aggression and challenges during the rut, likely elevated by female estrus, and this is consistent with previous work (Bowyer et al. 2007; Lott 2003; Mooring et al. 2004; Mooring et al. 2006). Low ranking male bison in this study were both not sexually mature, and not physically in condition to win challenges, which can explain their comparatively low challenging frequency (Fig. 2; Mooring et al. 2006; Helbig et al. 2006). This emphasizes the importance of the demographic structure of a herd and the influences on observed behaviors. However, our data suggest that male bison are forcing those ranked immediately below them to submit, while trying to raise their own linear rank via intra-rank conflict (Fig. 2). Intra-rank conflict can explain the well-established tumultuous nature of male bison rank (Lott 2003; Shult 1972; Wolff 1998). Also, we infer that intra-rank conflict is a driving factor in the stress of domination previously found in male bison (Fig. 2; Mooring et al. 2006; Sapolsky 2005). This builds on the theory described in Sapolsky (2005) who suggests that high aggression levels indicate stress of dominance. We would expect high levels of aggression when, in general, aggression is directed towards evenly matched competitors (intra-level), because linear rank is constantly changing back and forth between the pair.

Courting behaviors, as indicators of male preference, are influenced by dominance and hormonal cues in addition to female availability (Lott 2003; Maher and Byers, 1987). We hypothesize that male mate choice is based on female rank or indicators of that rank (because high ranking females were preferred). This may indicate an evolutionarily adaptive strategy where high ranking males focus breeding effort on high ranking females, who produce the most offspring, and are more sexually mature. Bulls older than six tend to be most engaged in breeding competition (Maher and Byers 1987), and the mid-ranking and low ranking bulls were all below this age. Male age and/or experience may be the most important factor explaining the low frequency of courtship behaviors in low ranked males found in our study (Maher and Byers 1987; Shull 1985; Fig. 4). Previous studies have found that young males need to learn when to tend and mate with females, possibly through social learning (Komers et al. 1994; Lott 2003), and therefore, this can explain our results. However, because females go through a synchronized estrus (Bowyer et al. 2007; Roden et al. 2011; Vervaecke and Schwarzenberger 2006), it is unlikely that one or two males could inseminate all females in a herd, especially when there are many females. This has been shown to be true in research, challenging the assumption that top bulls father all calves (Mooring and Penedo 2014; Roden et al. 2003). We found that high ranked bulls focus on high and mid-ranked females; therefore, we hypothesize that the calves of low ranked females are the most likely to be fathered by the mid-ranked bulls and suggest this for future research. If these males are ineffective in terms of maturity, via sperm or copulation, it could contribute to lower reproductive rate in low ranked females.

Unlike male bison, females aggressed year-round, equally, but with a few more instances during calving and the rut, likely their high stress periods. Like Fuller (1960), we found challenges between females to be brief and therefore comparatively difficult to detect and characterize. For this reason, our study may represent an underestimation of the frequency of female challenges, though females have been found to be less aggressive than males in all studies (Lott 2003; Lott and Galland 1987; Fuller 1960). In this study, the "toughest" female challengers focused their attention on the lowest ranking individuals, which could help explain why female rank tends to be more stable (Lott and Galland 1987; Lott 2003; Vervaecke et al. 2005; Shaw 2012; Rutberg 1986), i.e., they are not frequently challenging those near themselves in the linear hierarchy (Fig. 3). Sapolsky (2005) suggests that low aggression rates indicate stress of subordination, which could be further explained here, if low aggression rates tend to mean that unevenly matched individuals are involved in a challenge; the challenge may not be later reciprocated by the defeated, therefore aggression rates stay low.

Space claiming was a uniquely female behavior, which likely reflects the fact that females need higher quality forage than males (Treanor et al. 2015) and therefore are more benefitted by strategies that grant them access to prime forage locations. Due to the social pressure of the elite females on low ranked females, we inferred that females undergo stress of subordination (Fig. 3), from predictions based on social structure (Sapolsky 2005). Côté (2000) demonstrated that female

mountain goats' aggression towards young adult females increased with social ranking and age, while their aggression towards peers did not. Female mountain goats have a very similar social structure to bison; they exhibit a strong linear hierarchy, where the older female goats generally lead herds consisting of adult females and young of both sexes including males up to 3 years of age (Geist 1971; Côté 2000). Per Sapolsky (2005), this sort of structure predicts stress of subordination in the society, especially in groups which depend on high quality, but spatially heterogeneous forage (Edwards et al. 1996).

Male behavior may be compounding the social pressures faced by females. The bulk of male harassment, or courtship, is focused on low ranking females (Fig. 4). Avoidance of suitors has been found to determine female movements, including acquiring males to tend them and protect them from harassment (Sundaresan et al. 2007). We suspect that females, especially in cases such as this study with a low or moderate hectare per bison allotment, would attempt to secure protection from harassment because escape is unlikely. Our observations clearly show females avoiding suitors, being harassed regularly by one or more males, and even one case of a female seeking out a mature bull repeatedly during a particularly long bout of harassment. Furthermore, we found that mature bulls tend to exert more energy running off suitors (75% of the time they ran) than chasing after females (25%) during observation hours, whereas the young bulls spent their energy running after females (89% of the times they ran). The energy spent by the males during breeding may be costlier than the actual harassment experienced by females (Jerry and Brown 2017). However, the harassment is enough to drive females to stay near higher ranking males, and these males rarely need to run after females in many different locations (Lott 2003; Wolff 1998). The higher ranking males could protect from harassment, as well as provide more fit offspring, and therefore, seeking the protection of the mature bulls would be beneficial. The harassment faced by the low ranking females, by both the high ranking females (through challenges) and young males (during rut) could be very costly to their health, and perhaps contribute to their lower reproductive rates (Figs. 2 and 3; Table 3).

These trends in social stress have implications for herd health. Our research implies that low ranking female bison, alongside high ranking males, may be the most vulnerable to disease, as high cortisol (stress hormone) levels are associated with illness and immunosuppression in mammals (Rajagopal et al. 2011; McEwen and Stellar 1993). This is consistent with the deaths in this herd: one high ranking male (undergoing stress of domination while rutting) and two low ranking females (possibly undergoing stress of subordination), supporting a sexually dimorphic stress hierarchy and associated health issues. Future research should include a cortisol study in females during the rut comparable to Mooring et al. (2006) to determine if females undergo stress of subordination as hypothesized herein.

The specific demographics, population size, and allotted habitat are all factors that could influence bison behavior or exaggerate their social hierarchy by increasing interactions (Roden et al. 2003; Dewsbury 1982). We acknowledge that social hierarchies can be exaggerated by various levels of captivity (Dewsbury 1982; Rowell 1974); however, Plains bison exist almost exclusively in captive settings (Lott 2003), and this is not likely to change. Studies have shown that the more constrained bison are, the more exaggerated the dominance of high ranking bulls (compare Roden et al. 2011 to Wolff 1998). However, there is little information on how degree of captivity affects female bison. The settings of this herd could be causing more stress to the low ranking females as there is less room to escape and thereby causing greater stress of subordination (Sapolsky 2005). Additionally, during the study period, there was an abundance of prime age females and two prime age males, which could affect the dynamics of both male and female hierarchy. Perhaps, there was an unusual amount of stress on the high ranking bull that died during the study period due to this abundance of females to defend and copulate with. However, we attempt to compensate for the demographic effects on the behavioral trends in analysis, but cannot compensate for variations in social pressures. Finally, we consider these observed behaviors as a reflection of the various strategies employed to gain resources (Hawley 1999) and therefore true to comparable situations (e.g., similar forage abundance, ha/bison, and demographics).

We found that bison society affects individuals in disparate ways based on age, sex, and rank. Male preference of females by rank appeared to be for the highest rank they can defend, which would be an effective strategy as most females reach estrus simultaneously and high ranking females are the most fecund. Additionally, our results show that male and female bison prefer to instigate conflict with differently ranked bison. Males tended to perform intra-rank challenges, focusing on linear positions, and females tended to challenge the lower ranks. This finding could explain why male hierarchy is volatile, whereas female hierarchy remains relatively stable across years (Lott 2003; Lott and Galland 1987). Our findings are parallel to the findings by Côté (2000) where the females have stable linear hierarchy in which aggression is disproportionately focused towards young females by older higher ranking females. This is predicted by the behavioral theory outlined by Sapolsky (2005), and we posit the additional factor here is the need for nutrient rich forage in a heterogeneous landscape. The social structure of bison would indicate that females should undergo stress of subordination and males stress of domination (in males this has been shown to be true see Mooring et al. 2006), and these patterns in harassment could be the force causing the dimorphic stress hierarchy. Our

observed challenging and courtship actions are a sum of all the strategies employed to gain resources; therefore, we expect flexibility across space and time and, importantly, individuals. We posit that the flexibility in intra- or inter-rank conflict will be dependent upon the resources available. If our study was to be repeated in a less productive grassland, we would expect female challenging behavior to shift from inter-rank conflict to intra-rank conflict. It would be the result of high- and mid-ranking females jockeying for increases in linear position amongst themselves and increases of lower ranking females challenging higher ranking females. Our results provide insight into the feedback loops provided by behavior that both maintain social hierarchy and provide the mechanisms for changes in hierarchy.

Acknowledgments We would like to thank many individuals that assisted with this research. This bison herd reintroduction could not have taken place without the contributions and assistance of Rim Rock Ranch and T.R. Hughes, Gilbert Butler, and J. Sandoz. We are also grateful for the work of Crane Trust staff, interns, and trustees past and present, especially M. Morten, J. Salter, A. Driver, T. Smith, and Tom Dougherty for supporting this herd in so many ways. We would also like to thank the veterinary staff at the University of Nebraska-Lincoln including Dr. C. Kelling and Dr. C. Topliff. Finally, we would like to thank the University of Nebraska Kearney collaborators past and present.

Funding Platte River Whooping Crane Trust and a Nebraska Environmental Trust Grant (number 13-171).

Compliance with ethical standards

Conflict of interest Authors King, Leung, and Caven were employed during this research with the owner of the herd: Platte River Whooping Crane Trust.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Alberta Agriculture and Forestry (2017) What's the score: Bison. Body Condition Scoring (BCS) guide. http://www1.agriculture.alberta.ca/$department/deptdocs.nsf/all/agdex9622/$FILE/bcs-bison.pdf Accessed 10 January 2017

Allen JA (1876) The American bisons, living and extinct (Vol. 10) University Press Welch, Bigelow

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Ballard J (2013) Falcon Guides: Bison. Morris Book Publishing: Falcon Guides, Helena Montana

Barroso FG, Alados CL, Boza J (2000) Social hierarchy in the domestic goat: effect on food habits and production. Appl Anim Behav Sci 69(1):35–53

Bernard HR, Ryan GW (2009) Analyzing qualitative data: systematic approaches. SAGE publications

Bowyer RT, Bleich VC, Manteca X, Whiting JC, Stewart KM (2007) Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. Ethology 113(11):1048–1060

Bradshaw GA, Schore AN, Brown JL, Poole JH, Moss CJ (2005) Elephant breakdown. Nature 433(7028):807–807

Bradshaw GA, Schore AN (2007) How elephants are opening doors: developmental neuroethology, attachment and social context. Ethology 113(5):426–436

Cavigelli SA, Caruso MJ (2015) Sex, social status and physiological stress in primates: the importance of social and glucocorticoid dynamics. Phil Trans R Soc B 370:20140103

Chase ID (1982) Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour 80(3):218–239

Côté SD (2000) Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. Behaviour 137(11): 1541–1566

Creel S (2001) Social dominance and stress hormones. Trends Ecol Evol 16(9):491–497

Dewsbury D (1982) Dominance rank, copulatory behavior, and differential reproduction. Q Rev Biol 57(2):135–159

Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proc Natl Acad Sci 91(21):9941–9945

Edwards GR, Newman JA, Parsons AJ, Krebs JR (1996) The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: an example with sheep. Appl Anim Behav Sci 50(2):147–160

Erbring L, Young AA (1979) Individuals and social structure: contextual effects as endogenous feedback. Sociol Methods Res 7(4):396–430

Fournier F, Festa-Bianchet M (1995) Social dominance in adult female mountain goats. Anim Behav 49(6):1449–1459

Freese CH, Aune KE, Boyd DP, Derr JN, Forrest SC, Gates CC, Gogan PJP, Grassel SM, Halbert ND, Kunkel K, Redford KH (2007) Second chance for the plains bison. Biol Con 136(2):175–184

Fuller WA (1959) The horns and teeth as indicators of age in bison. J Wildl Manag 23(3):342–344

Fuller WA (1960) Behavior and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic 13(1):2–19

Gauthreaux Jr SA (1978) The ecological significance of behavioral dominance. In: Bateson PPG, Klopfer PH (eds) Social Behavior, Springer, Boston, pp 17–54

Geist V (1971) Mountain sheep. A study in behavior and evolution. University of Chicago Press

Grandin T, Lanier JL (2015) The calming of American bison (Bison bison) during routine handling. Department of Animal Sciences, Colorado State University, Ft. Collins, CO at http://www.grandin.com/references/bison.paper.html Accessed 15 April 2015

Green WC (1986) Age-related differences in nursing behavior among American bison cows (*Bison bison*). J of Mammal 67(4):739–741

Green WC, Rothstein A (1991a) Sex bias or equal opportunity? Patterns of maternal Investment in Bison. Behav Ecol Sociobiol 29(5):373–384

Green WC, Rothstein A (1991b) Trade-offs between growth and reproduction in female bison. Oecologia 86(4):521–527

Halbert ND, Ward TJ, Schnabel RD, Taylor JF, Derr JN (2005) Conservation genomics: disequilibrium mapping of domestic cattle chromosomal segments in North American bison populations. Mol Ecol 14(8):2343–2362

Hamel S, Craine JM, Towne E (2012) Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. Ecol Appl 22(5):1628–1639

Hawley PH (1999) The ontogenesis of social dominance: a strategy-based evolutionary perspective. Dev Rev 19(1):97–132

Helbig L, Woodbury MR, Haigh JC, Barth AD (2006) The onset of puberty in North American bison (*Bison bison*) bulls. Anim Repro Sci 97(1):12–24

Jerry M, Brown C (2017) Fitness costs of sexual harassment—the Price of persuasion. Ethology 123(3):242–250

Komers PE, Messier F, Flood PF, Gates CC (1994) Reproductive behavior of male wood bison in relation to progesterone level in females. J Mammal 75(3):757–765

Lott DE (2003) American Bison: a natural history. University of California Press, Berkeley, CA

Lott D, Galland J (1987) Body mass as a factor influencing dominance status in American bison cows. J Mammal 68(3):683–685

Maher CR, Byers JA (1987) Age-related changes in reproductive effort of male bison. Behav Ecol Sociobiol 21(2):91–96

Marra PP (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behav Ecol 11(3):299–308

Marsteller FA, Siegel PB, Gross WB (1980) Agonistic behavior, the development of the social hierarchy and stress in genetically diverse flocks of chickens. Behav Process 5(4):339–354

McEwen BS, Stellar E (1993) Stress and the individual: mechanisms leading to disease. Arch Intern Med 153(18):2093–2101

Melton DA, Larter NC, Gates CC, Virgl JA (1989) Bisoniana 102. The influence of rut and environmental factors on the behavior of wood bison. Acta Theriol 34(12):179–193

Mooring MS, Patton ML, Lance VA, Hall BM, Schaad EW, Fortin SS, Jella JE, McPeak KM (2004) Fecal androgens of bison bulls during the rut. Horm Behav 46(4):392–398

Mooring MS, Patton ML, Lance VA, Hall BM, Schaad EW, Fetter GA, Fortin SS, McPeak KM (2006) Glucocorticoids of bison bulls in relation to social status. Horm Behav 49(3):369–375

Mooring MS, Penedo MCT (2014) Behavioral versus genetic measures of fitness in bison bulls (*Bison bison*). J Mammal 95(5):913–924

Norman A (2010) Bison body condition: management tool to monitor the nutritional status of the bison cow. Texas A&M University https://cnrit.tamu.edu/ganlab/filecabinet/19 Accessed 10 January 2017

Pelletier F, Festa-Bianchet M (2006) Sexual selection and social rank in bighorn rams. Anim Behav 71(3):649–655

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org Accessed 10 Dec 2015

Rajagopal T, Archunan G, Sekar M (2011) Impact of zoo visitors on the fecal cortisol levels and behavior of an endangered species: Indian blackbuck (Antelope cervicapra L.). J Appl Anim Welf Sci 14(1):18–32

Reinhardt V (1985) Social behavior in a confined bison herd. Behaviour 92(4):209–226

Richards SM (1974) The concept of dominance and methods of assessment. Anim Behav 22:914–930

Roden C, Hilde V, Guy M (2003) Reproductive success of bison bulls (*Bison bison bison*) in semi-natural conditions. Anim Repro Sci 79(1):33–43

Roden C, Stevens JM, Vervaecke H, Van Elsacker L (2011) Reproductive effort of bison bulls (*Bison bison*) in semi-natural conditions. J Ethol 29(2):285–291

Rowell TE (1974) The concept of social dominance. Behav Biol 11(2):131–154

Rutberg AT (1986) Dominance and its fitness consequences in American bison cows. Behaviour 96(1):62–91

Sapolsky RM (2005) The influence of social hierarchy on primate health. Science 308(5722):648–652

Schnabel RD, Ward TJ, Derr JN (2000) Validation of 15 microsatellites for parentage testing in north American bison, *Bison bison* and domestic cattle. Anim Genet 31(6):360–366

Shaw RA (2012) Social organization and decision making in North American bison: implications for management. Dissertation, Utah State University

Shively CA, Laber-Laird K, Anton RF (1997) Behavior and physiology of social stress and depression in female cynomolgus monkeys. Biol Psychiatry 41(8):871–882

Shull AM (1985) Age-specific reproductive behavior of male American bison dissertation. In: Oklahoma State University

Shult MJ (1972) American bison behavior patterns at Wind Cave National Park. Dissertation, Iowa State University

Sundaresan SR, Fischhoff IR, Rubenstein DI (2007) Male harassment influences female movements and associations in Grevy's zebra (*Equus grevyi*). Behav Ecol 18(5):860–865

Treanor JJ, Richards JM, Schneider DR (2015) Nutritional ecology. In: White PJ, Wallen RL, Hallac DE, Jerrett JA (eds) Yellowstone bison: conserving an American icon in modern society. Yellowstone Association, Mammoth, Wyoming pp 97–105

University of Nebraska Medical Center (2016) Bison handler tailgate training safety manual 1. Center for Agricultural Safety and Health. University of Nebraska Medical Center. https://www.unmc.edu/publichealth/cscash/_documents/Bison%20Handler%20Tailgate%20Training%20Safety%20Manual%20V1_2016.pdf Accessed 15 January 2017

Vervaecke H, Roden C, de Vries H (2005) Dominance, fatness and fitness in female American bison, *Bison bison*. Anim Behav 70(4):763–770

Vervaecke H, Schwarzenberger F (2006) Endocrine and behavioral observations during transition of non-breeding into breeding season in female American bison (*Bison bison*). Theriogenology 66(5):1107–1114

Whitehead H, Rendell L (2014) The cultural lives of whales and dolphins. University of Chicago Press

Wolff JO (1998) Breeding strategies, mate choice, and reproductive success in American bison. Oikos 83(3):529–544