Journal of Mammalogy, 2024, **105**, 1182–1189
https://doi.org/10.1093/jmammal/gyae076
Advance access publication 8 August 2024
Research Article

Research Article

Bison mother–offspring acoustic communication

Jennifer A. Clarke*

Biology Department, University of La Verne, La Verne, CA 91750, United States

*Corresponding author: Biology Department, University of La Verne, La Verne, CA 91750, United States. Email: jclarke@laverne.edu
Associate Editor was Timothy Smyser

Abstract

Mother–offspring communication is especially crucial for social species in order to synchronize activities essential for early survival including nursing, resting, maintaining proximity during group movements between food or water sources, and locating one another if separated in a large social group. One of the most social ungulate species in North America is the American Bison (*Bison bison*), formerly known as buffalo. Adult female bison associate with their young for over a year and communication between mother and offspring is likely essential for establishing and maintaining a bond upon which the life of a calf depends. One goal of this study was to quantify and compare the acoustic form of vocalizations of adult female, subadult, and calf bison and to determine how age classes differed in call structure. The other goal was to identify the contexts in which bison vocalized. Vocalizations of 101 bison (53 adult females, 15 subadults, 33 calves) in a semi-free-ranging herd in Montana were analyzed and found to be pulsatile sounds, unlike vocalizations of bison bulls or domestic cows and calves. Vocalizations of bison cows, subadults, and calves differed significantly in total duration, numbers of pulses, pulse duration, and pulse rate. Seven distinct call contexts were identified. The majority of calls were "moving-on calls" (39%), when a cow called and her calf ran to her side and the 2 moved on together, and "contact calls" (21%) when a cow called and her calf called back but neither changed their location. "Imprinting calls" and "nursing calls" were also identified. Mother–offspring acoustic communication in bison appears especially critical for coordinating movements. Understanding the role of acoustic communication in maintaining the bond between bison mothers and their offspring can contribute to the humane management and welfare of this iconic species.

Key words: age class, *Bison*, buffalo, communication, cow–calf, herd movements, imprinting, pulsatile vocalizations, welfare.

La comunicación acústica madre-cría en bisontes

Abstracto

La comunicación madre-cría es especialmente crucial para especies sociales, debido a que permite sincronizar actividades esenciales para la supervivencia temprana, como la lactancia, el descanso, el mantenimiento de proximidad durante los movimientos de los grupo entre las fuentes de alimento o agua y la localización mutua en caso de separación dentro de un grupo social grande. Una de las especies de ungulados más sociales de América del Norte es el bisonte (*Bison bison*). Las hembras adultas de bisonte se asocian con sus crías durante más de un año y la comunicación entre madre el becerro es probablemente esencial para establecer y mantener un vínculo en el que depende la vida de la cría. Uno de los objetivos de este estudio fue cuantificar y comparar la forma acústica de las vocalizaciones de hembras adultas, subadultas y crías de bisonte, y determinar cómo diferían las clases por edad en la estructura de las llamadas. Otro objetivo fue identificar los contextos en los que se emitían las vocalizaciones. Se analizaron las vocalizaciones de 101 bisontes (53 hembras adultas, 15 hembras subadultas, 33 crías) en un rebaño semi-libre en Montana. Se encontró que estas vocalizaciones eran sonidos pulsátiles, completamente diferentes a los emitidos por los bisontes machos adultos o las vacas y becerros domésticos. Las vocalizaciones diferían significativamente entre las tres clases de edad en su duración total, número de pulsos, duración de los pulsos y ritmo de los pulsos. La mayoría de las llamadas se dieron en dos contextos: "llamadas de avance" (39%), cuando una hembra adulta llamaba y su cría corría a su lado y ambas avanzaban juntas, y "llamadas de contacto" (21%), cuando una hembra adulta llamaba y su cría respondía, pero ninguna cambiaba su ubicación. También se identificaron "llamadas de impronta" y "llamadas de amamantamiento," así como otros tres contextos de llamada. La comunicación acústica madre-cría en bisontes parece especialmente crítica para coordinar los movimientos. Entender el papel de la comunicación acústica en el mantenimiento del vínculo entre las madres y sus crías puede contribuir al manejo humanitario y al bienestar de esta especie icónica. Este trabajo representa el primer estudio que investiga cuantitativamente las señales acústicas de hembras adultas, subadultas y crías de bisontes Norte Americanos mientras se desplazan en condiciones de semi-libertad.

Palabras clave: bienestar, *Bison bison*, clase por edad, comportamiento, comunicación madre-cría, improntación, movimientos del rebaño, vocalizaciones pulsátiles.

The initial and most critical communication exchange in mammals occurs between mother and offspring. The calls of a mother stimulate her offspring to come to her for nursing, protection, or to accompany her when moving to a new location. These calls are essential for mother–offspring bonding, offspring survival, and, ultimately, reproductive success (Okabe et al. 2012; Padilla de la

Received: December 5, 2023; Editorial Decision: June 26, 2024; Accepted: July 6, 2024

Torre and McElligott 2017). Mother–offspring communication is especially crucial for social species in order to synchronize activities essential for early survival (Newberry and Swanson 2008). The importance of mother–offspring acoustic signals in social mammals has been revealed in studies of pinniped species (for review, see Insley et al. 2003) and ungulates, including Fallow Deer (*Dama dama*; Torriani et al. 2006), Domestic Sheep (*Ovis aries*; Searby and Jouventin 2003; Nowak et al. 2011), Domestic Goat (*Capra hircus*; Briefer and McElligott 2011), Domestic Cow (*Bos tarus*; Padilla de la Torre et al. 2016), and feral Domestic Horse (*Equus caballus*; Nuñez and Rubenstein 2020). The majority of mother–young communication studies have focused on identifying call individuality and vocal recognition, which reduce the risk of misdirected parental care and increase reproductive success (Trivers 1972). Not surprisingly, the primary context of mother–young vocal signals in these social species has been related to nursing (e.g., Padilla de la Torre et al. 2015; Nuñez and Rubenstein 2020). Mother–young communication in social species is important in other contexts as well, particularly for species that must travel distances to find food and water while avoiding predation.

One of the most social ungulate species of North America is the American Bison (*Bison bison*). Millions of bison once grazed the plains and prairies of North America (Shaw 2000) and played a keystone role in maintaining heterogeneity in grassland ecosystems until being brought to the brink of extinction in the 1800s (Knapp et al. 1999; Lott 2002; Ratajczak et al. 2022). The North American plains bison is listed as Near Threatened due to its dependence on ongoing conservation programs to maintain populations (Aune et al. 2017). The North American plains bison also has a Species Recovery Score of 17% (Critically Depleted) because it is absent from many of its indigenous spatial units and the majority of extant herds are the result of reintroductions (Rogers et al. 2022).

Efforts to recover and conserve bison in North America include the establishment of bison herds in public, private, NGO, and Tribal sectors (Martin and Cammack 2022). Bison remain undomesticated and are highly valued as wildlife, as well as for their cultural significance and as a source of sustainable meat. Although the reestablishment of free-roaming herds is desired, a dominant view exists that many herds should remain fenced to reduce human–wildlife conflict (Pejchar et al. 2021). With fencing comes management and managing a wild species in which adults average 470 to 863 kg (Berger and Peacock 1988; Wyman et al. 2012) poses substantial challenges. Bison are more likely to be injured or killed while being handled than domestic cattle and highly stressed bison pose a greater threat to the safety of management personnel (Grandin 1999; Lanier et al. 1999; Duysen et al. 2017; Rioja-Lang et al. 2019).

Understanding the behavior and communication system within a bison herd would aid in animal welfare, humane management, conservation efforts of the species, and the safety of managers. Animal welfare is assessed by measuring physiological and behavioral indicators, with vocalizations being a gauge of positive welfare (Yeates and Main 2008; Laurijs et al. 2021). Vocalizations in cattle signal the physiological and emotional state of the animal calling, as determined from changes in calling rate and call structure (Watts and Stookey 2000; Marino and Allen 2017; Padilla de la Torre and McElligott 2017; Schnaider et al. 2022). Before determining how vocalizations of bison cows, subadults, and calves can be reliably used to predict behavior and assess the welfare of this species in human-caused stressful situations, the form and function of their calls must be measured and characterized in natural situations.

To date, studies of bison communication have focused on the vocalizations of male bison, termed bellows. Bellows are uttered during the breeding season in the context of male–male contests and function as intrasexual displays, encoding information about body size, physical condition, and motivation (Berger and Cunningham 1991; Wyman et al. 2008, 2012). Bison cows, subadults, and calves also vocalize as revealed in anecdotal accounts such as the description by Lott (2002:33) of cow–calf communication: "You hear their call occasionally while the animals are grazing, more frequently as a group of cows and calves walk along as they're going somewhere – say to water. You hear a lot of grunting when a herd has stampeded, separating cows and calves. Mothers and calves grunt to each other across a poststampede herd and track the right-sounding voice they hear to a reunion." The observations of Lott (2002) suggest that cow–calf vocalizations are used while moving between locations and that bison cows and calves are capable of individual vocal recognition. No study has quantitatively investigated the form and function of vocalizations of North American bison cows, subadults, and calves which numerically dominate bison herds.

One goal was to quantify and compare the form of acoustic signals used by semi-free-ranging bison cows, subadults, and calves. The results of this aspect of the study will contribute to further investigations of individual characteristics of vocalizations and individual recognition between bison cows and calves. Another goal was to identify the context of mother-to-offspring vocalizations in order to determine call function. An understanding of mother–offspring call function will enhance our knowledge of factors affecting calf survival and reproductive success and contribute to enhanced welfare.

Materials and methods.

Study area and population.

Bison vocalizations were recorded at the Flying D Ranch in Gallatin County, Montana, United States. The Flying D Ranch is a private ranch managed for the production of bison and the herds range across the 458 km^2 (~175 sq miles) property. The ranch terrain varies from rolling meadows, to steep forests and high-rolling bench topography. Natural predators of bison also inhabit the ranch, e.g., Gray Wolf (*Canis lupus*), Grizzly Bear (*Ursus arctos horribilis*), as well as natural competitors, i.e., North American Elk (*Cervus canadensis*). The bison forage over approximately 40,468 ha with multiple fenced grazing areas, each of which averages 4,856 ha. The bison are rotationally grazed between these grazing areas and, when necessary, herded with ATVs. This herd can be considered semi-free-ranging (Aune et al. 2017) because the animals roam over an immense area of natural habitat with minimal human influence on their movements, no calving support, no supplemental feed, and potential predators (wolves, bears) are present.

Sound recordings and behavioral observations were made 1 to 7 June 2020. Behavioral observations were also made 4 to 7 June 2023. The ages of the bison recorded and observed in this study ranged from newborn to 18 years old. Herd size was approximately 2,000 adult (≥3 years old) females and males. Not contributing to the count of 2000 adults, the herd also included subadult (1 to 2 years old) females and calves (≤0.5 year old). In 2023, subadult males were included in the herd. Their calls were not recorded because these subadult males remained in all-male cohort groups, with little to no interaction between them and the females and calves of the herd. Adult males grazed areas distant from the main herd and were not recorded.

Field data collection.

The observed adult female and subadult female bison had ear tags bearing a code indicating the individual and the year she was born, which allowed for identification of each animal. Recordings

and behavior observations were made from within the midst of the herd, approximately 50 m away from the nearest individual bison, and from inside or outside the field vehicle (≤2 m from the vehicle). Recordings and observations commenced 10 min after stopping the vehicle. The length of the recording/observation periods varied from 1 to 3 h depending on the behavior of the group. Recordings would continue until the herd moved to a new site to graze or when they lay down to sleep, and then a different group would be found in another part of the ranch.

A Roland R09HR recorder (Roland Corporation, Los Angeles, California) and Sennheiser microphone (Sennheiser Electronics, Wedemark, Germany) attached to a handheld shock mount and fitted with a Softie windscreen (Rycote Microphone Windshields, Ltd, Gloucestershire, United Kingdom) were used to record vocalizations (16-bit resolution, 44.1 kHz sampling rate). No recordings were made during rainy or excessively windy periods because these conditions could interfere with sound transmission (Bradbury and Vehencamp 1998). The age and identity of each adult and subadult were determined by their ear-tag numbers as well as by size, horn shape, and coloration. Calves associated closely with their mother and were unmistakable due to their small size and cinnamon brown coloration. Subadults (1- to 2-year olds) were smaller in body size and horn size compared to adults.

Instances of communication between cows, calves, and subadults were recorded ad libitum using focal-animal sampling of the group (Altman 1974). During focal-animal sampling, an individual was selected and recorded based on whether it was vocalizing and clearly visible. To determine the functions of mother-to-offspring calls, the contexts in which a bison cow or calf vocalized were identified by noting changes in the orientation and movements of the focal individual (sender) and alterations in behavior of the intended receiver. Only those instances in which the context was unquestionable were included in this analysis of bison cow–calf communication. Unquestionable contexts were defined as those that met all 3 of the following criteria: the sender was clearly identified, the receiver was clearly identified, and the resulting behavior was clearly identified. Although subadult bison are highly vocal, the context of their calls remained obscure in the majority of cases as rarely was there a clearly identifiable change in the behavior of the vocalizing subadult or the behavior of a potential receiver.

Data analyses.

A computer program for sound analysis (RAVEN PRO V1.4, Cornell University, Ithaca, New York) was used to develop spectrograms (Hamming window, 512 points, 50% overlap) and to measure 4 acoustic variables. The methods of Luis et al. (2016) were followed for quantifying pulsed signals: pulse rate, pulse duration, number of pulses per vocalization, and vocalization duration were measured and compared between adult cows, subadults, and calves. To determine statistical differences between the age classes in vocalization characteristics, comparisons were conducted of the 4 measured acoustic variables with chi-square tests and the Dunn method for multiple comparisons using rank sums (Dunn and Clark 2009) in JMP Pro 14.2 software (SAS Institute Inc., Cary, North Carolina). A discriminant function analysis using JMP Pro 14.2 software (SAS Institute Inc., Cary, North Carolina) was also conducted to reveal differences between age classes in acoustic characteristics of the vocalizations. Discriminant function analysis is a statistical procedure used to make decisions about naturally occurring group membership that classifies individuals and the probability of their classification into a certain group, in this case, age class (Ramos and Liow 2012). Significance differences were determined at the level of $P < 0.05$. Data were collected in accordance with the American Society of Mammalogists guidelines for research on live animals (Sikes et al. 2016).

Results

To investigate differences between age classes in signal characteristics, vocalizations of 101 bison were analyzed. Measurements were made of the 719 highest quality recordings using a minimum of 6 vocalization per individual of 53 adult females (446 calls), 15 subadults (87 calls), and 33 calves (186 calls).

The 4 measured variables differed significantly between the age classes (Fig. 1; Table 1). Discriminant analysis revealed differences in the acoustic structure of vocalizations between the age classes (Wilk's $\lambda = 0.10$, $F_{(8,186)} = 50.19$, $P = 0.001$; Fig. 2). Using the 4 measured acoustic variables, the discriminant function analysis allowed assigning vocalizations to the age class of the individual that produced them with a probability of 85%.

Vocalizations of calves were shorter in duration than vocalizations of subadults and adults ($z = 4.00$, $P = 0.0002$; $z = 3.55$, $P = 0.0011$; Table 1) but vocalization duration did not differ between subadults and adults ($z = 1.56$; $P = 0.35$). Vocalizations of calves and subadults exhibited higher numbers of pulses per call compared to adults ($z = 4.62$, $P < 0.0001$; $z = 3.02$; $P = 0.0076$; Table 1), but number of pulses per call of calves and subadults were similar ($z = 0.45$ $P = 1.00$). Pulse duration of calf vocalizations was significantly less than subadult and adult vocalization pulse duration ($z = 3.78$, $P = 0.0005$; $z = 8.44$, $P < 0.0001$; Table 1), and subadult vocalization pulse duration was slightly less than adult vocalization pulse duration ($z = 2.37$; $P = 0.05$). Vocalization pulse rate (pulses per second per vocalization) was significantly higher in calf vocalizations compared to subadult and adult vocalizations ($z = 3.76$, 8.47; $P < 0.001$, all cases; Fig. 3), while subadult vocalization pulse rate was only slightly higher than adult vocalization pulse rate ($z = 2.40$, $P = 0.05$).

Seven distinct contexts were identified in 164 instances in which adult female bison uttered vocalizations, based on the behavior of the sender and receiver: moving-on calls; calf contact calls; nursing calls, summons calls; imprinting calls; yearling contact calls; and seeking lost calf calls (Fig. 4). The greatest number of calls (64/164) by cows were designated "moving-on calls" and uttered by a cow immediately prior to walking to a different grazing location. In these cases, the cow would utter 1 to 4 calls in rapid succession, her calf would immediately respond by coming to her side, and they would then walk on together. The second context in which cows were most often observed to vocalize (34/164) was when a cow would utter calls and her calf would immediately respond by calling back but not joining her. There were no other changes in behavior by cow or calf in these cases of "contact calls." In 20 cases, cows uttered "nursing calls" to which her calf responded by running to her and immediately engaging in nursing. In another 20 cases, a cow uttered calls to which the calf responded by running to her but not nursing and the pair did not move on. These calls were designated "summons calls." In 17 cases the adult female bison would stand nearby or walk slowly around her newborn calf, who was lying on the ground, and she would utter repeated, soft calls. These "imprinting calls" were of extremely low intensity and repeated for extended periods of time up to 30 min. In 5 cases, adult females called back to a yearling who had vocalized, with no other change in behavior by either individual. These calls were designated "yearling contact calls." In 4 cases, adult females were observed galloping/running through the herd, alone, and repeatedly uttering extremely loud vocalizations termed "seeking lost calf calls." In these cases, the adult female exhibited signs of high stress, i.e., eyes bulging, head shaking, labored breathing, and galloping (Caven et al. 2022).

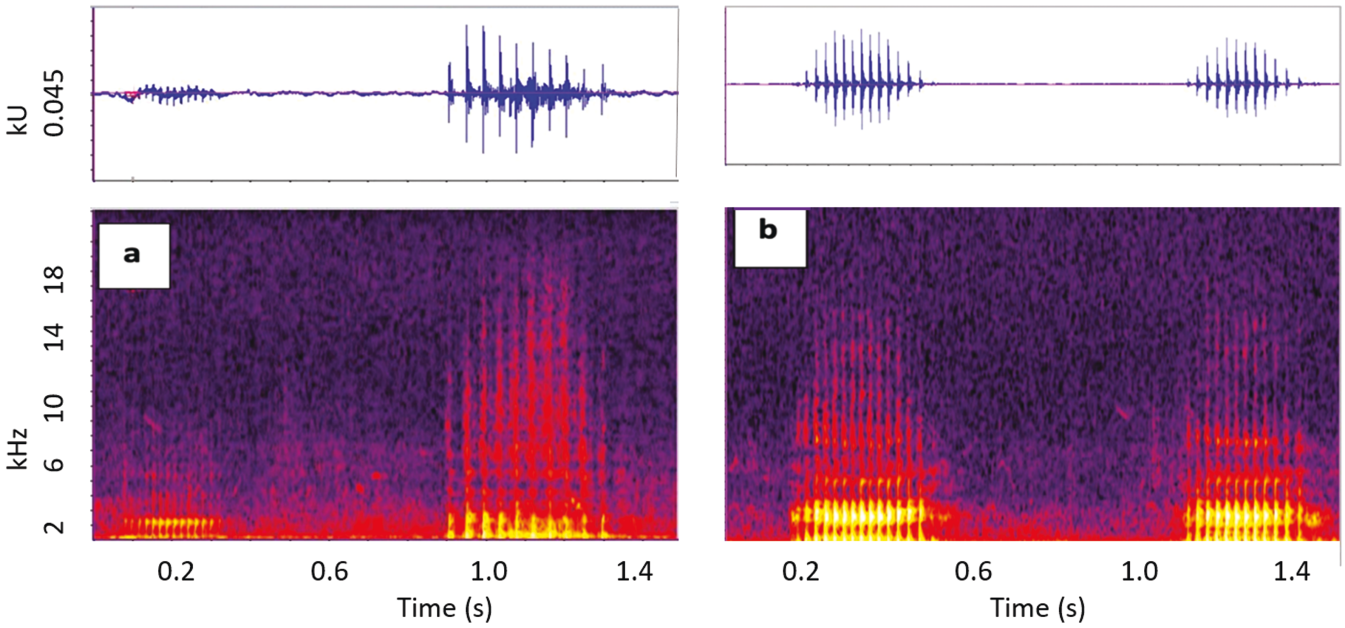

Fig. 1. Spectrograms of (a) an American Bison calf vocalization followed by that of the mother of the calf (an adult female bison) and (b) 2 vocalizations from a subadult female American Bison (2-year-old). Waveform above spectrogram also indicates pulse rate and power (energy).

Table 1. Median values and ranges of 566 calls from 101 American Bison regarding vocalization (call): duration, pulse number, pulse duration, and pulse rate for vocalizations of adult female bison (n = 53 bison, ≥3 years old); subadult female bison (n = 15 bison, 1 to 2 years old); and bison calves (n = 33 bison, ≤0.5 year old).

Acoustic measures	Adults	Subadults	Calves	$x^2_{(2,100)}$
Call duration[a]	0.31 (0.09 to 0.90)	0.38 (0.2 to 0.78)	0.25 (0.08 to 0.50)	20.1 ($P < 0.001$)
Pulse number[b]	10 (3 to 27)	13 (7 to 28)	15.50 (5 to 31)	24.5 ($P < 0.001$)
Pulse duration[a]	0.03 (0.02 to 0.05)	0.025 (0.02 to 0.04)	0.02 (0.01 to 0.02)	71.4 ($P < 0.001$)
Pulse rate[c]	33 (19 to 49)	40 (28.6 to 50)	60.87 (48.5 to8 78)	71.8 ($P < 0.001$)

Units:
[a]Seconds.
[b]Number of pulses per call.
[c]Number of pulses per second per call.

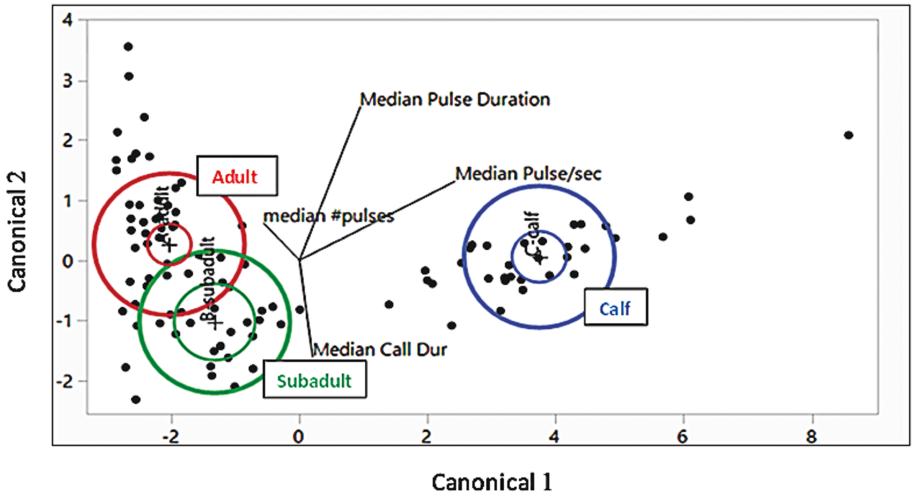

Fig. 2. Discriminant function analysis using 4 acoustic variables of vocalizations from 101 American Bison: 53 adult females (red circles), 15 subadult females (green circles), and 33 calves (blue circles) using median values for 6 calls per individual.

Discussion

This study is the first to quantify the form and identify the context of North American bison cow–calf vocalizations, although male bison bellows have been the focus of previous investigations of communication in the species (e.g., Berger and Cunningham 1991; Wyman et al. 2008, 2012; Sarno et al. 2017). The acoustic structures

of bison cow–calf vocalizations are unlike those of bull bison and unlike domestic cattle. Bull bison bellows are high amplitude, >1 s, and exhibit formants and chaos (Wyman et al. 2012). Domestic cow–calf vocalizations have clear harmonic structures and average 1.4 s (Padilla de la Torre et al. 2015). In contrast, bison cow–calf vocalizations are low amplitude, pulsatile signals that lack a harmonic structure and average a brief 0.31 s long. Bison cow–calf calls have been described as sounding like "grunts" (Lott 2002) but can be assigned to age class aurally and spectrographically. Bison cows uttered calls in 6 distinct contexts with the calf as the intended receiver, and with the calf from the prior year the intended receiver in a seventh context.

Calls of a variety of mammalian species exhibit differences between age classes in the frequency and/or time domains, including Domestic Cattle (Padilla de la Torre et al. 2015), Siberian Wapiti (*Cervus elaphus sibericus*; Volodin et al. 2016), West Indian Manatee (*Trichechus manatus manatus*; Sousa-Lima et al. 2008), Chacma Baboon (*Papio cynocephalus ursinus*; Fischer et al. 2002), Yellow-bellied Marmot (*Marmota flaviventris*; Blumstein and Munos 2005), and Leopard Seal (*Hydrurga leptonyx*; Rogers 2007). In mammalian species, differences in body size and the size of structures involved in sound production are related to vocalization frequencies, with larger size linked to the production of lower frequencies (Riede and Brown 2013). Larger size has also been linked to the ability to produce longer calls (Fischer et al. 2002). Body size can predict age in mammals and acoustic features encoding age are reasonably involved in individual discrimination (Blumstein and Munos 2005); for example, a bison cow discriminating between her new calf and her yearling offspring who often accompanies her and the calf.

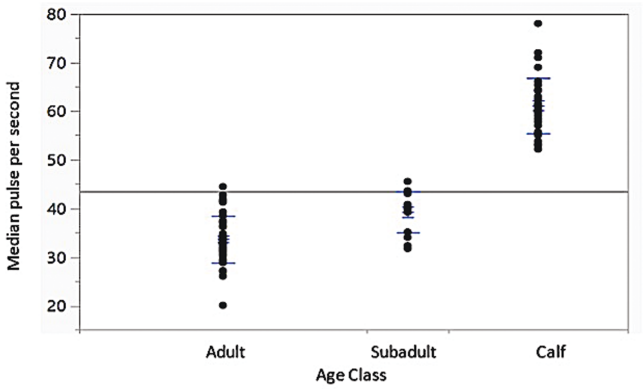

Fig. 3. Median pulse rate (pulses per second) values of vocalizations of American Bison in 3 age classes: adult females ≥ 3 years old (n = 53); subadult females 1 to 2 years old (n = 15); and ≤0.5-year-old calves (n = 33).

The lowest frequencies of the pulsatile vocalizations of bison females and their young were below 1 kHz and consistently masked in the ambient noise floor and thus did not lend themselves to valid frequency measures, similar to the grunts of Wild Boar, *Sus scrofa* (Garcia et al. 2016). However, vocalizations of adult females, subadults, and calves differed significantly in call duration, pulse duration, number of pulses, and pulse rate. Using these acoustic variables, vocalizations were correctly assigned to age class in 84% of cases. Vocalizations of bison calves differed significantly from vocalizations of subadults and adults. Calf vocalizations were shorter in total duration, with shorter pulse durations, more pulses, and a higher pulse rate than adults and subadults. Subadult vocalizations also exhibited shorter pulse durations and more pulses than adult vocalizations, to a lesser degree than calf vocalizations but contributing to a slightly higher pulse rate of subadult vocalizations compared to adult vocalizations.

The recognition process between mother and offspring in highly social mammalian species involves olfaction, audition, and vision—to varying degrees (e.g., Alexander and Shilito 1977; Jesseau et al. 2008; Sibiryakova et al. 2015; Wierucka et al. 2018). The selective pressures of a bison to identify mother and offspring in a herd are undoubtedly strong. If separated during a large-scale movement, reestablishing contact in a herd is difficult and death of the calf will result if the cow and calf are not reunited, plus the potential cost to a cow of losing a calf and misdirected care in the form of nursing an unrelated calf may be high (Clutton-Brock et al. 1989). Bison mothers and offspring typically maintained close physical proximity to one another (≤4 m), which ensured visual and olfactory contact. However, calves often wandered and interacted with other calves nearby. Although the herd was not constantly on the

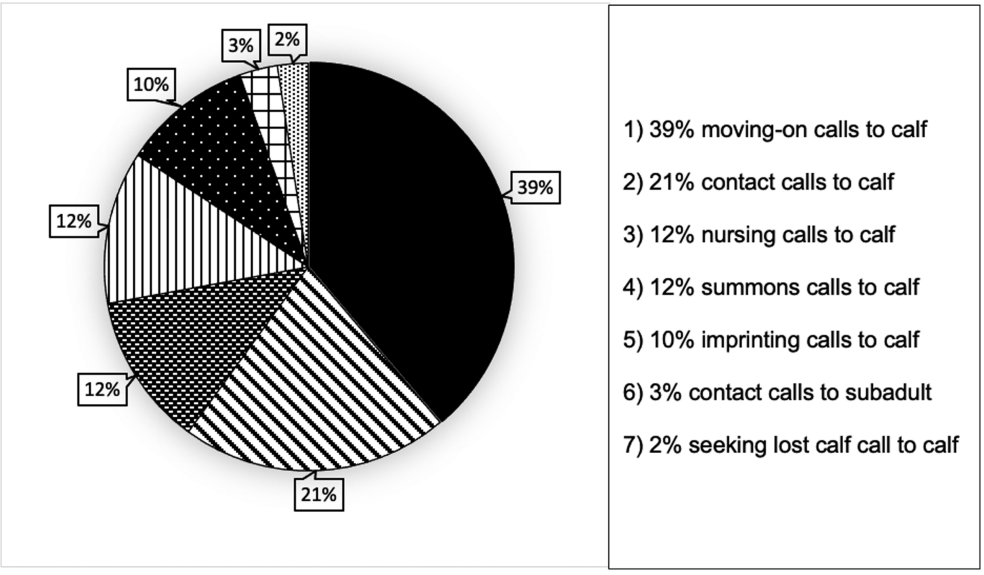

Fig. 4. Percentages of 164 calls of adult female North American bison in 7 distinct contexts, determined based on the behaviors of the sender (adult female bison) and the intended receiver (calf or subadult bison).

move, herd movements occurred daily or multiple times a day. Hours would pass with the herd remaining in 1 location, with individuals grazing or lying down, and then, one by one, females would utter "moving-on" calls, the calf would join the cow, and they would walk on together. Moving-on calls accounted for the largest category of calls (39%), emphasizing the mobile nature of a bison herd and the importance of cow–calf contact. Green (1993) proposed that high behavioral synchrony of mothers and their calves in the first month likely decreases the risks of separation and predation as well as enhancing contact maintenance and thus reducing the energetic costs of reproduction.

When a calf wandered, the mother appeared to stay visually focused on the calf. However, a calf straying in a large herd is easily obscured and out-of-sight among herd members, necessitating acoustic contact. Instances of "contact calls," the second most common call context (21%), involved the cow uttering spaced calls until the distant calf responded, usually within 5 calls by the mother. Once the calf responded, the cow would stop calling, stare fixedly in the direction of the calf (who was typically associating with another calf), and then she would resume grazing. These calls likely aided mother and young in locating one another in the event of an unexpected herd movement. Also, allowing a bison calf to wander within the herd and socialize independently may be critical for the development of social behaviors in this long-lived, gregarious species. In feral horses, mares use calls to communicate their location to their wandering foals, enabling foals to explore their environment and engage with other foals and herd members, and potentially contributing to foal survival (Nuñez and Rubenstein 2020).

The bison cow–calf "imprinting calls" were uttered only by cows with newborn calves lying on the ground and were of low intensity and repeated for many minutes, with the cow standing beside or walking slowly around the newborn calf and with no change in behavior by the calf. Imprinting vocalizations have been documented in various mammal species and are likely crucial in facilitating mother–offspring recognition, particularly in highly mobile, social species. Domestic Sheep (*Ovis aries*) ewes exhibit a peak of vocalizations during the first 3 h after parturition and lambs can identify their mothers 48 h after birth (Sèbe et al. 2007). Bottlenose Dolphin (*Tursiops truncate*) females increase their rate of signature whistle production 5- to 10-fold immediately after the birth of their calves, which has been identified as vocal imprinting (Fripp and Tyack 2008; King et al. 2016). In colonially breeding mammals such as the Subantarctic Fur Seal (*Arctocephalus tropicalis*), pups learn to recognize the voice of their mother when they are 2 to 5 days old (Charrier et al. 2001), while Cape Fur Seal (*Arctocephalus pusillus*) pups can recognize the voice of their mother 4 to 6 h after birth, suggesting an in utero vocal imprinting in this species (Martin et al. 2022). Vocal imprinting is undoubtedly essential for a bison calf to identify, follow, and, if necessary, reunite with its mother as the herd moves between locations.

The sole call context in which bison cows uttered extremely loud calls was when they were "seeking a lost calf." During this context the bison cow exhibited signs of high stress, i.e., bulging eyes, head shaking, labored breathing, and galloping (Caven et al. 2022). Four instances of a bison cow seeking a lost calf were observed. In these cases, the cow galloped, occasionally rearing as she galloped, potentially enabling her to scan farther across the herd over the backs of herd members, calling loudly and constantly. In 2 of the 4 cases, the adult female ran back to where she had started, turned, ran in a different direction, calling loudly and constantly. In one instance, the female was identified approximately 20 min later, walking alongside her calf as they moved with the herd to a new location. The low number of observations of this context emphasizes the rarity of a bison cow becoming separated from her calf, largely attributable to their high degree of acoustic contact.

A random pattern of low amplitude calling from various individuals, namely subadult females, was maintained when a herd was grazing and relatively stationary. The intended receivers of these calls were rarely identified as there were no obvious changes in sender or potential receiver behaviors. These vocalizations may be subadult-to-subadult contact calls. Subadult females gathered in groups of 6 to 12 when they were not accompanying a cow (likely the mother) and calf. That subadults utter contact calls to one another was supported by the observation that they often traveled in relatively cohesive subadult groups during herd movements and exhibited distress (calling, galloping) if separated from their cohort.

Prior to walking to a new grazing location, vocalizations increased throughout the herd. However, in contrast, the bison were nearly silent during fast-moving herd movements. When galloping hard together as a herd, the cows, subadults, and calves uttered few calls. Calves and yearlings galloped closely alongside an adult cow, likely the mother, vocalizing only rarely as they ran. Occasionally, a calf would utter a single soft call to which the mother (presumably) would reply with a single call so quickly that her call overlapped with the conclusion of the calf's call. The lack of loud sounds, including no loud pounding of hooves due to the soft terrain, during these events was unexpected.

The findings of this study highlight the importance of mother–offspring acoustic contact in a strongly social species that moves as a large group across the landscape. The herd in this study ranges widely over one of the largest tracts of native habitat inhabited by bison in the lower 48 states with minimal human contact, no calving support, no supplemental feed, and potential predators (wolves and grizzly bears) are present. How the behavior of these bison mothers and their offspring compare to the behavior of bison cows and calves that are confined in more restrictive conditions, subjected to human hunting, or heavy predation pressure has yet to be determined.

Additional areas of investigation include identifying the specific acoustic cues used by bison calves in recognizing the calls of their mother and vice versa. Individual recognition between mothers and offspring has been the focus of numerous studies of communication among highly social and/or colonially breeding mammals (Charrier and Harcourt 2006; Charrier et al. 2010; Pitcher et al. 2010; Briefer and McElligott 2011; Padilla de la Torre et al. 2016; Green et al. 2019). Detailed investigations are needed to determine the vocalization characteristics that contribute to individual identification between bison cows and calves. This study revealed that different calls appear to serve unique functions, inspiring questions related to call structure beyond the identified differences in the temporal pattern of calling. Bison mother–offspring communication and behavior are currently critical areas of research as momentum is high regarding restoring bison to native habitat for ecological and cultural purposes, and for raising bison as a sustainable source of meat. For example, research has revealed that calves of domestic cattle that are reared with ample communication with their mothers exhibit more adaptive behaviors with conspecifics and lower cardiac stress reactions in novel situations (Buchli et al. 2017). A thorough understanding bison cow–calf communication can similarly enhance the humane management and conservation of this iconic species.

Acknowledgments

This project was possible due to the support and cooperation of Ted Turner and Family, the Turner Institute of Ecoagriculture, Carter

Kruse, Danny Johnson, Joel Lemons, and Sandy Burdette. Crockett Nash, Garett Blue, and Todd Traucht provided valuable assistance. Thanks to Holger Klinck for advice on pulsatile vocalization analysis and to Victor Carmona-Galindo for providing the Spanish translation of the abstract. The comments and suggestions of Tim Smyser and 3 anonymous reviewers greatly improved the manuscript. This work is dedicated to Val Eluding.

Funding

Funding was provided by the University of La Verne Biology Department and a University of La Verne Provost Award.

Conflict of interest

None declared.

References

Alexander G, Shilito EE. 1977. The importance of odour, appearance and voice in maternal recognition of the young in merino sheep (*Ovis aries*). Applied Animal Ethology 3(2):127–135.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49(3):227–267. https://doi.org/10.1163/156853974x00534

Aune K, Jørgensen D, Gates C. 2017. *Bison bison* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T2815A123789863. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T2815A45156541.en

Berger J, Cunningham C. 1991. Bellows, copulations, and sexual selection in bison (*Bison bison*). Behavioral Ecology 2(1):1–6. https://doi.org/10.1093/beheco/2.1.1

Berger J, Peacock M. 1988. Variability in size–weight relationships of *Bison bison*. Journal of Mammalogy 69(3):618–624. https://doi.org/10.2307/1381357

Blumstein DT, Munos O. 2005. Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Animal Behaviour 69(2):353–361. https://doi.org/10.1016/j.anbehav.2004.10.001

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland (MA, USA): Sinauer Assoc., Inc.

Briefer E, McElligott AG. 2011. Mutual mother–offspring vocal recognition in an ungulate hider species (*Capra hircus*). Animal Cognition 14(4):585–598. https://doi.org/10.1007/s10071-011-0396-3

Buchli C, Raselli A, Bruckmaier R, Hillmann E. 2017. Contact with cows during the young age increases social competence and lowers the cardiac stress reaction in dairy calves. Applied Animal Behaviour Science 187:1–7. https://doi.org/10.1016/j.applanim.2016.12.002

Caven AJ, Leung KG, Vinton C, Krohn B, Wiese JD, Salter J, Ranglack DH. 2022. A behavioral index for assessing bison stress level during handling and demographic predictors of stress response. Journal of Applied Animal Welfare Science 25(1):41–53. https://doi.org/10.1080/10888705.2021.1963250

Charrier I, Aubin T, Mathevon N. 2010. Mother–calf vocal communication in Atlantic walrus: a first field experimental study. Animal Cognition 13(3):471–482. https://doi.org/10.1007/s10071-009-0298-9

Charrier I, Harcourt RG. 2006. Individual vocal identity in mother and pup Australian sea lions (*Neophoca cinerea*). Journal of Mammalogy 87(5):929–938. https://doi.org/10.1644/05-mamm-a-344r3.1

Charrier I, Mathevon N, Jouventin P. 2001. Mother's voice recognition by seal pups. Nature 412(6850):873–873. https://doi.org/10.1038/35091136

Clutton-Brock TH, Albon SD, Guinness FE. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337(6204):260–262. https://doi.org/10.1038/337260a0

Dunn OJ, Clark VA. 2009. Basic statistics: a primer for the biomedical sciences. Hoboken (NJ, USA): John Wiley and Sons.

Duysen E, Irvine K, Yoder A, Topliff C, Kelling C, Rajaram S. 2017. Assessment of tribal bison worker hazards using trusted research facilitators. Journal of Agromedicine 22(4):337–346. https://doi.org/10.1080/1059924X.2017.1353937

Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM. 2002. Acoustic features of male baboon loud calls: influences of context, age, and individuality. The Journal of the Acoustical Society of America 111(3):1465–1474. https://doi.org/10.1121/1.1433807

Fripp D, Tyack P. 2008. Postpartum whistle production in bottlenose dolphins. *Marine Mammal Science* 24(3):479–502.

Garcia M, Gingras B, Bowling DL, Herbst CT, Boeckle M, Locatelli Y, Fitch WT. 2016. Structural classification of wild boar (*Sus scrofa*) vocalizations. Ethology 122(4):329–342. https://doi.org/10.1111/eth.12472

Grandin T. 1999. Habituating antelope and bison to cooperate with veterinary procedures. Journal of Applied Animal Welfare Science 3(3):253–261. https://doi.org/10.1207/s15327604jaws0303_6

Green A, Clark C, Favaro L, Lomax S, Reby D. 2019. Vocal individuality of Holstein-Friesian cattle is maintained across putatively positive and negative farming contexts. Scientific Reports 9(1):18468. https://doi.org/10.1038/s41598-019-54968-4

Green WC. 1993. Social effects of maternal age and experience in bison: pre- and post-weaning contact maintenance with daughters. Ethology 93(2):146–160. https://doi.org/10.1111/j.1439-0310.1993.tb00985.x

Insley S, Phillips AV, Charrier I. 2003. A review of social recognition in pinnipeds. Aquatic Mammals 29(2):181–201.

Jesseau SA, Holmes WG, Lee TM. 2008. Mother–offspring recognition in communally nesting degus, *Octodon degus*. Animal Behaviour 75(2):573–582. https://doi.org/10.1016/j.anbehav.2007.06.015

King S, Guarino E, Donegan K, Hecksher J, Jaakkola K. 2016. Further insights into postpartum signature whistle use in bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science. https://doi.org/10.1111/mms.12317

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie: bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49(1):39–50. https://doi.org/10.2307/1313492

Lanier J, Grandin T, Chaffin A, Chaffin T. 1999. Training American bison (*Bison bison*) calves. In: National Bison Association, editor. Bison World. Fort Collins (CO, USA): Colorado State University; p. 94–99.

Laurijs KA, Briefer EF, Reimert I, Webb LE. 2021. Vocalisations in farm animals: a step towards positive welfare assessment. Applied Animal Behaviour Science 236:105264. https://doi.org/10.1016/j.applanim.2021.105264

Lott DF. 2002. American bison: a natural history (vol. 6). Oakland (CA, USA): University of California Press.

Luis AR, Couchinho MN, Dos Santos ME. 2016. A quantitative analysis of pulsed signals emitted by wild bottlenose dolphins. PLoS One 11(7):e0157781. https://doi.org/10.1371/journal.pone.0157781

Martin JM, Cammack KM. 2022. The North American bison management system: reintroduction of a species with ecological, economic, and cultural roles in a changing climate. Journal of Animal Science 100(Supplement_3):78–78. https://doi.org/10.1093/jas/skac247.153

Martin M, Gridley T, Elwen S, Charrier I. 2022. Early onset of postnatal individual vocal recognition in a highly colonial mammal species.

Proceedings of the Royal Society of London, B: Biological Sciences 289(1988):20221769. https://doi.org/10.1098/rspb.2022.1769

Marino L, Allen K. 2017. The psychology of cows. Animal Behavior and Cognition 4(4):474–498. https://doi.org/10.26451/abc.04.04.06.2017

Newberry RC, Swanson JC. 2008. Implications of breaking mother–young social bonds. Applied Animal Behaviour Science 110(1–2):3–23. https://doi.org/10.1016/j.applanim.2007.03.021

Nowak R, Kelle M, Lévy F. 2011. Mother–young relationships in sheep: a model for a multidisciplinary approach of the study of attachment in mammals. Journal of Neuroendocrinology 23(11):1042–1053. https://doi.org/10.1111/j.1365-2826.2011.02205.x

Nuñez CM, Rubenstein DI. 2020. Communication is key: mother–offspring signaling can affect behavioral responses and offspring survival in feral horses (*Equus caballus*). PLoS One 15(4):e0231343. https://doi.org/10.1371/journal.pone.0231343

Okabe S, Nagasawa M, Mogi K, Kikusui T. 2012. The importance of mother–infant communication for social bond formation in mammals. Animal Science Journal 83(6):446–452. https://doi.org/10.1111/j.1740-0929.2012.01014.x

Padilla de La Torre MP, Briefer EF, Ochocki BM, McElligott AG, Reader T. 2016. Mother–offspring recognition via contact calls in cattle, *Bos taurus*. Animal Behaviour 114:147–154. https://doi.org/10.1016/j.anbehav.2016.02.004

Padilla de la Torre MP, Briefer EF, Reader T, McElligott AG. 2015. Acoustic analysis of cattle (*Bos taurus*) mother–offspring contact calls from a source–filter theory perspective. Applied Animal Behaviour Science 163:58–68. https://doi.org/10.1016/j.applanim.2014.11.017

Padilla de la Torre MP, McElligott AG. 2017. Vocal communication and the importance of mother–offspring relations in cattle: commentary on Marino and Allen (2017) The psychology of cows. Animal Behavior and Cognition 4(4):522–525. https://doi.org/10.26451/abc.04.04.13.2017

Pejchar L, Medrano L, Niemiec RM, Barfield JP, Davidson A, Hartway C. 2021. Challenges and opportunities for cross-jurisdictional bison conservation in North America. Biological Conservation 256:109029. https://doi.org/10.1016/j.biocon.2021.109029

Pitcher BJ, Harcourt RG, Charrier I. 2010. Rapid onset of maternal vocal recognition in a colonially breeding mammal, the Australian sea lion. PLoS One 5(8):e12195. https://doi.org/10.1371/journal.pone.0012195

Ramos SDS, Liow SR. 2012. Discriminant function analysis. In: Chapelle C, editor. The encyclopedia of applied linguistics. New York (NY, USA): Blackwell Publishing.

Ratajczak Z, Collins SL, Blair JM, Koerner SE, Louthan AM, Smith MD, Taylor JH, Nippert JB. 2022. Reintroducing bison results in long-running and resilient increases in grassland diversity. Proceedings of the National Academy of Sciences of the United States of America 119(36):e2210433119. https://doi.org/10.1073/pnas.2210433119

Riede T, Brown C. 2013. Body size, vocal fold length, and fundamental frequency—implications for mammal vocal communication. Nova Acta Leopoldina NF 111(380):1–20.

Rioja-Lang FC, Galbraith JK, McCorkell RB, Spooner JM, Church JS. 2019. Review of priority welfare issues of commercially raised bison in North America. Applied Animal Behaviour Science 210:1–8. https://doi.org/10.1016/j.applanim.2018.10.014

Rogers LR, Ranglack DH, Plumb G. 2022. *Bison bison* (Green Status assessment). The IUCN Red List of Threatened Species 2022: e.T2815A281520221.

Rogers TL. 2007. Age-related differences in the acoustic characteristics of male leopard seals, *Hydrurga leptonyx*. The Journal of the Acoustical Society of America 122(1):596–605. https://doi.org/10.1121/1.2736976

Sarno RJ, Grigione MM, Hig A, Childers E, Ecoffey T. 2017. The association between continual, year-round hunting and bellowing rate of bison bulls during the rut. PeerJ 5:e3153. https://doi.org/10.7717/peerj.3153

Schnaider MA, Heidemann MS, Silva AHP, Taconeli CA, Molento CFM. 2022. Vocalization and other behaviors as indicators of emotional valence: the case of cow–calf separation and reunion in beef cattle. Journal of Veterinary Behavior 49:28–35. https://doi.org/10.1016/j.jveb.2021.11.011

Searby A, Jouventin P. 2003. Mother–lamb acoustic recognition in sheep: a frequency coding. Proceedings of the Royal Society of London, B: Biological Sciences 270(1526):1765–1771. https://doi.org/10.1098/rspb.2003.2442

Sèbe F, Nowak R, Poindron P, Aubin T. 2007. Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Developmental Psychobiology 49(4):375–386. https://doi.org/10.1002/dev.20218

Shaw JH. 2000. How many bison originally populated western rangelands? Bison World 25:38–41.

Sibiryakova OV, Volodin IA, Matrosova VA, Volodina EV, Garcia AJ, Gallego L, Landete-Castillejos T. 2015. The power of oral and nasal calls to discriminate individual mothers and offspring in red deer, *Cervus elaphus*. Frontiers in Zoology 12(1):1–13. https://doi.org/10.1186/s12983-014-0094-5

Sikes RS, The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97(3):663–688. https://doi.org/10.1093/jmammal/gyw078

Sousa-Lima RS, Paglia AP, da Fonseca GA. 2008. Gender, age, and identity in the isolation calls of Antillean manatees (*Trichechus manatus manatus*). Aquatic Mammals 34(1):109–122.

Torriani MV, Vannoni E, McElligott AG. 2006. Mother–young recognition in an ungulate hider species: a unidirectional process. The American Naturalist 168(3):412–420. https://doi.org/10.1086/506971

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago (IL, USA): Aldine Publishing Company; p. 136–179.

Volodin IA, Sibiryakova OV, Volodina EV. 2016. Sex and age-class differences in calls of Siberian wapiti *Cervus elaphus sibiricus*. Mammalian Biology 81(1):10–20. https://doi.org/10.1016/j.mambio.2015.09.002

Watts JM, Stookey JM. 2000. Vocal behaviour in cattle: the animal's commentary on its biological processes and welfare. Applied Animal Behaviour Science 67(1-2):15–33. https://doi.org/10.1016/s0168-1591(99)00108-2

Wierucka K, Pitcher BJ, Harcourt R, Charrier I. 2018. Multimodal mother–offspring recognition: the relative importance of sensory cues in a colonial mammal. Animal Behaviour 146:135–142. https://doi.org/10.1016/j.anbehav.2018.10.019

Wyman MT, Mooring MS, McCowan B, Penedo MCT, Hart LA. 2008. Amplitude of bison bellows reflects male quality, physical condition and motivation. Animal Behaviour 76(5):1625–1639. https://doi.org/10.1016/j.anbehav.2008.05.032

Wyman MT, Mooring MS, McCowan B, Penedo MCT, Reby D, Hart LA. 2012. Acoustic cues to size and quality in the vocalizations of male North American bison, *Bison bison*. Animal Behaviour 84(6):1381–1391. https://doi.org/10.1016/j.anbehav.2012.08.037

Yeates JW, Main DC. 2008. Assessment of positive welfare: a review. Veterinary Journal 175(3):293–300. https://doi.org/10.1016/j.tvjl.2007.05.009