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Research article

Effects of time of day, visitor pressure and weather on the behaviour of captive American bison *Bison bison*

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Abstract

The study of bison in zoos can provide insights about the behaviour of this species with application for the management of herds held in captivity for both public display and bison farming. The aim of this study was to describe and investigate the behavioural budget of American bison in captivity, specifically focusing on how these behaviours may be influenced by time of day, visitor pressure and weather. Four bison *Bison bison* (two male and two female) at the Zoo Aquarium Madrid in Spain were video monitored for 27 days (May 2022) by three solar-powered cameras. From the footage collected, five behaviours were hourly annotated: lying, standing, moving, eating and drinking. The corresponding meteorological data (temperature, relative air humidity, temperature humidity index, wind speed, barometric pressure and solar radiation) were also measured. Data analysis examined bison behaviour and its relationship with time of day (diurnal, nocturnal), visitor pressure (low, high) and meteorological data divided in days by range of observed weather conditions (lower, upper). Bison spent most time lying, followed by standing, moving, eating and drinking. Bison spent more time lying at night and ate more during the day. The animals spent more time drinking during high visitor pressure. Behaviour was affected by weather; increased temperatures and humidity reduced movement time, while elevated barometric pressure was related with more drinking time. Lower pressure and increased solar radiation were associated with less moving/standing time and more lying time, respectively. In summary, bison behaviour was influenced by time of day, visitor pressure and weather parameters.

Introduction

American bison *Bison bison* are the largest ungulates on the North American continent and the second largest bovine in the world. Almost becoming extinct during the 19th century, the bison population has largely recovered thanks to joint efforts of both private and public initiatives, primarily through captive breeding and bison reintroduction efforts that are rapidly gaining momentum (Pejchar et al. 2021). Currently, bison populations are found in both wild and captive (farming and zoo) settings (Eisenberg 2019). Efficient monitoring of herds often requires significant labour and other resources which can often pose a logistical challenge depending on location (Jung et al. 2017, 2018). Due to their large body size, strength and reactive nature, bison handling requires specialised facilities and trained personnel (Lanier and Grandin 2015). New remote monitoring technologies could potentially provide novel solutions to identify and monitor individual bison remotely. These technologies promise to reduce animal stress while contributing to the wellbeing and safety of both animals and people (Lahoz-Monfort and Magrath 2021; Stephenson 2019). Visual surveillance methods using artificial intelligence and digital visualisation images are among the relatively new monitoring options with tested effectiveness (Busse et al. 2015; Prosekov et al. 2020) to support the monitoring of bison.

Remote monitoring under both wild and captive conditions can improve the understanding of animal responses to a diverse range of stimuli (Diana et al. 2021; Leoni et al. 2020). An important factor to be considered is the effect of meteorological variables on behaviour (Conradt et al. 2000). Fluctuations in temperature, humidity and other weather variables can affect foraging, use of shelters and reproduction, thus impacting animal populations and their ecosystem use (Allred et al. 2013; Craine 2021). Additionally, photoperiod plays an important role in biological regulation of daily activity patterns (Koop and Oster 2022; Randler 2014). In the wild, animals can often adapt their behavioural and physiological attributes according to environmental and seasonal conditions (Soravia et al. 2021). For instance, free-ranging populations may alter dispersal (Post and Forchhammer 2002), metabolism (Arnold et al. 2004) or migration (Hurlbert and Liang 2012). These behavioural and physiological adaptations are crucial to meet climate challenges and to maintain homeostasis (Mota-Rojas et al. 2021). In captivity however, animals have restricted dispersal and limited capacity to respond to changing environmental and climatic conditions, which can negatively impact their welfare (Mason et al. 2013). Even under intensive human management animals may be vulnerable to climate impacts, particularly those subjected to outdoor exposure (Mota-Rojas et al. 2022; Rioja-Lang et al. 2019).

Zoo animals face many other challenges in captive environments (Wolfensohn et al. 2018). Human presence, an intrinsic element of the zoo context, is considered an important environmental effect that influences animal behaviour (Sherwen and Hemsworth 2019). Several studies have evaluated the effect of human presence on zoo-housed animals which are reviewed elsewhere (Collins et al. 2023). In tribe Bovini (Bovidae, Bovinae), some studies have explored the effect of visitors on animal behaviour, however these findings were controversial (Edes et al. 2022; Klich et al. 2021; Sekar et al. 2008). While some authors attributed possible negative effects (e.g. stress-inducing) of visitors on the behaviour of wild cattle in captivity (Sekar et al. 2008), others have reported positive (as a kind of enrichment) or neutral (Edes et al. 2022; Klich et al. 2021) effects. Investigating this source of stimulation is important, as zoo animals spend a significant portion of their time in view by visitors which may influence their overall welfare. To the authors' knowledge, there are no studies assessing the effects of various environmental stimuli on the behaviour of zoo-housed American bison. Moreover, only one study was found that delves into the behavioural aspects of American bison in zoo settings (Robitaille and Prescott 1993), evidencing the scarcity of information about bison behaviour in captive environments.

Captive zoo settings pose many restrictive challenges for animals, such as limited space, human exposure and other external stressors. Therefore, studying these aspects is crucial for developing strategies to ensure the welfare of bison housed in zoo environments. The primary aim of this study was to describe and investigate the behavioural budget of American bison in captivity, specifically focusing on how these behaviours may be influenced by environmental factors and human presence in a zoo setting. The research sought to explore the effects of time of day, visitor pressure and weather on the behaviours of American bison during a short-term study conducted in the European spring season. This classification of visitor attendance hereafter referred to as 'visitor pressure' was used to assess the potential influence of varying visitor densities on bison behaviour throughout the study period, as the differentiation between weekdays and weekends effectively captures fluctuations in visitor numbers (Klich et al. 2021). It was hypothesized that these factors—time of day, visitor pressure and meteorological conditions—may influence the behaviour of American bison who are challenged by life in captivity where opportunities for behavioural and physiological adaptations are limited.

Materials and methods

Site, animals, enclosure and husbandry

The experiment was conducted from 5–31 May 2022 at the Zoo Aquarium Madrid, Spain (40° 40' 97.2" N, −3° 76' 39.8" W, altitude 631 m). The experiment was approved by the Animal Care Committee of the Zoo Aquarium Madrid, in accordance with the guidelines of the European Association of Zoos and Aquaria (EAZA 2022) and adhered to the legal requirements of Spain.

A herd of four captive-born American bison *Bison bison* consisting of two males (Male 1: 15 years old; Male 2: 11 months old) and two females (Female 1: 15 years old; Female 2: 10 years old) was assessed. Animals were housed together in an outdoor enclosure (Figure 1) with three zones: (1) security zone made of a water moat and lawn surrounded by wood slats separating animals and visitors (~4 m width); (2) management zone for employees, warehouse and management facility; and (3) bison zone (725 m^2, approximately 181 m^2 per animal) that consists of sandy ground, shelters and feeding troughs. The enclosure was cleaned and the troughs were filled every morning around 0900. The diet offered daily on an as-fed basis was composed of the following: 2.5 kg hay, 5 kg of chopped carrots and 5 kg of commercial cattle feed (Pasaranda, Nuter Feed S.A., Spain) per animal, in addition to mineral supplementation (Nanta sal, Nanta S.A., Spain) and fresh water supplied ad libitum. The animals had access to artificial shade provided by a cement porch (~100 m^2) and natural trees (*Morus* sp.) surrounding the enclosure. The zoo was open to visitors between 1100 and 2000, all days of the week.

Behavioural observations

Three solar-powered video cameras (Reolink Argus PT, Reolink Digital Technology Co. Ltd., Hong Kong, China) with night vision capability and fixed lens (105° diagonal) were installed around the enclosure to record bison behaviours continuously (Figure 1). The four animals were individually identified by size, horn shape and individual coat patterns. Five behaviours were monitored: lying, standing, moving, eating and drinking, as described in Table 1. The behaviours were recorded and summarised hourly according to duration (minutes) and as a percentage of the total observed time. During enclosure cleaning and feeding, the bison were kept in the shelter and behaviours were not recorded. Behaviours were assessed by two observers using focal sampling and continuous observation (Bateson and Martin 2021). Six days of observation were randomly chosen and evaluated by the two observers concomitantly to determine the inter-observer error rate as proposed by Hafner et al. (1998).

Meteorological variables

According to the Köppen classification, the regional climate of the zoo is Mediterranean Csa type, with hot summers and relatively cool winters with somewhat frequent frosts. During the experimental period temperature (°C), relative air humidity (%), wind speed (m/s), barometric pressure (mb) and solar radiation (W/m^2) were collected hourly from the nearest meteorological station (40° 25' 12.0" N, 3° 45' 00.0" W) which was located 1.6 km from the bison enclosure. Based on meteorological data, the temperature humidity index (THI) was determined (Thom 1959): THI=[0.8×Temperature+(Relative Air Humidity/100)×(Temperature−14.4)+46.4].

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Statistical analysis

The data were analysed using the Statistical Analysis System (SAS®, version 9.4, Institute, Inc, Cary, NC, USA). To provide an initial overview of the data, descriptive statistics and normality tests were conducted for meteorological variables (temperature, relative air humidity, temperature humidity index, wind speed, barometric pressure and solar radiation) and behavioural data (lying, standing, moving, eating and drinking) using the UNIVARIATE procedure. Upon confirming a non-normal distribution, subsequent data analysis was conducted using appropriate tests for non-normally distributed data. A variance component analysis for inter-observer error rate was calculated using the VARCOMP procedure. The variance component for lying (0.02), moving (0.02), standing (0.02), eating (0.03) and drinking (0.001) ranged from 0.1% to 3% when comparing observers, indicating lower inter-observer error rate (≤0.05; Hafner et al. 1998). To explore relationships between different bison behaviours and understand how they might be interrelated, the CORR procedure calculated Pearson correlation coefficients among the behaviours. Subsequent analyses focused on the potential effects of time of day, visitor pressure and weather on bison behaviour. Based on the average time of sunrise and sunset over the course of the trial, two time of day periods were

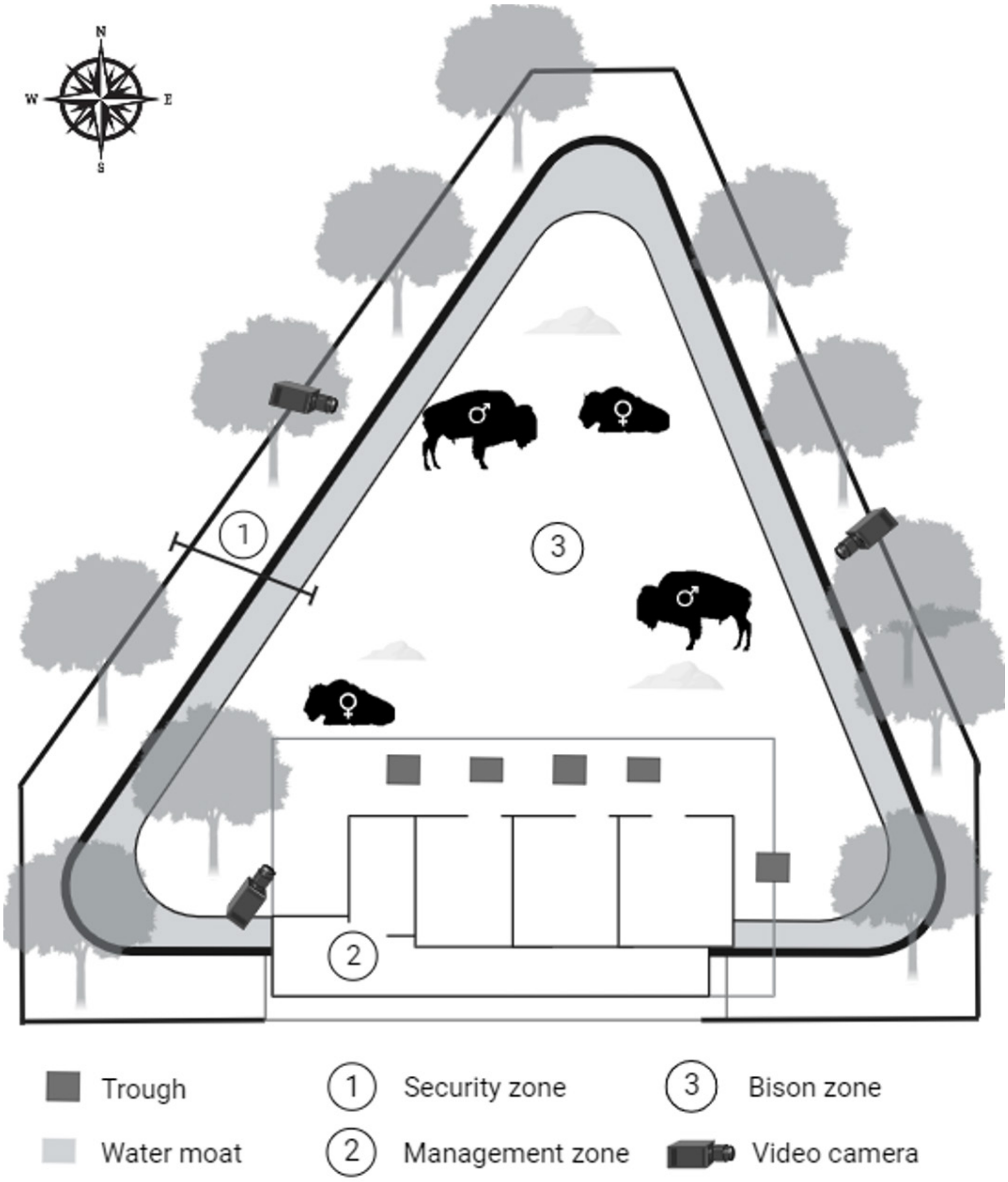

Figure 1. Sketch of the bison enclosure at the Zoo Aquarium Madrid.

Table 1. Ethogram of bison behaviours in captivity at the Zoo Aquarium Madrid.

Behaviour	Description
Lying	Bison lying in lateral or sternal decubitus, with legs stretched or retracted
Standing	Bison standing on all four legs without locomotion, eating or drinking
Moving	Bison walking or running
Eating	Bison with the head inside or nearby the trough chewing and ingesting food
Drinking	Bison drinking water in the trough or moat

defined: diurnal (≥0700 and ≤2100) and nocturnal (>2100 and <0700). This classification of the day into diurnal and nocturnal periods was used to assess the potential influence of day and night on bison behaviour. While bison are generally known to be diurnal, they have also been observed to be active during the night (Rutley and Hudson 2001). Additionally, as proposed by Klich et al. (2021) and zoo information (personal communication), the days were divided into two groupings according to visitor attendance: low visitor pressure on weekdays (Monday, Tuesday, Wednesday, Thursday and Friday) and high visitor pressure during weekends (Saturday and Sunday). Finally, to investigate the influence of weather on bison behaviour, the continuous meteorological dataset was transformed into two discrete groupings to represent the lower (13 days with lowest mean) and upper (14 days with highest mean) range of observed conditions within the timeframe of 1000 to 1400. To evaluate the influence of meteorological variables (lower and upper), time of day (diurnal and nocturnal) and visitor pressure (low and high) on bison behaviours, Mann-Whitney U tests were fitted using the NPAR1WAY procedure. For all analyses, $P \leq 0.05$ and $0.05 < P \leq 0.10$ were considered significant and a trend towards significance, respectively.

Results

The herd spent the most time lying (45.3%), followed by standing (24.3%), moving (17.0%), eating (11.0%) and drinking (2.4%). Similar behavioural patterns were observed in both the herd and among individuals (Figure 2). Male 1 spent more time lying than the others (Male 2, Female 1 and Female 2) and the females spent more time standing overall than the males. The behaviours were correlated to each other. Animals that spent more time lying spent less time moving (r=−0.52), standing (r=−0.59), eating (r=−0.38) and drinking (r=−0.18). Similarly, those that spent more time standing ate (r=−0.18) and drank (r=−0.09) less. Lastly, animals that moved more also consumed more water (r=0.06) but ate less (r=−0.12).

Notably, bison behaviour was influenced by the time of day and visitor pressure (Table 2). The animals spent more time eating during the diurnal period while lying behaviour was more frequent during the nocturnal period. During high visitor pressure, bison tended to drink more than during low visitor pressure.

Behaviours were influenced by weather; Table 3 presents the means of bison behaviour in relation to meteorological variables. Higher temperatures and humidity were related to less moving time. Similarly, higher barometric pressure corresponded to increased time spent drinking. Lower barometric pressure was related to reduced time spent moving. Additionally, higher solar radiation was associated with less time spent standing while lying time was increased.

Discussion

Monitoring the behaviour of wild animals in captivity through video analysis can be used as a tool in the assessment of welfare and assist in the elucidation of biological aspects that could support management decisions in zoos. Moreover, intensive investigations in captivity could support the conservation efforts of wild bison as well as support best husbandry practices in commercial livestock operations where data collection is logistically more challenging. This study examined the effects of time of day, visitor pressure and weather conditions on the behaviour of captive American bison. The behaviour of the animals was shown to be influenced by climatic and environmental variables intrinsic to the zoo, such as time of day and visitor pressure.

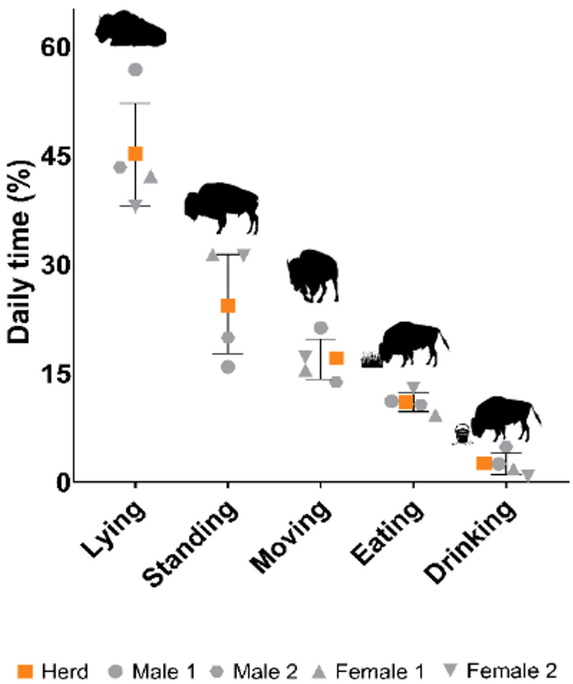

Figure 2. Relative time (%) of lying, standing, moving, eating and drinking behaviours of both the herd and individual bison

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Table 2. Means (± standard error of the mean) of bison behaviours by the time of day and visitor pressure periods.

Behaviour (%)	Time of day		Visitor pressure	
	Diurnal	Nocturnal	Low	High
Lying	74.1±1.2[B]	86.1±0.8[A]	75.4±1.4	71.7±2.3
Standing	41.3±1.2	43.1±1.4	33.0±1.6	30.5±2.1
Moving	27.4±0.9	27.2±1.3	22.8±1.1	23.48±1.8
Easting	52.9±1.4[A]	30.4±4.2[B]	54.2±1.8	49.9±2.7
Drinking	17.8±1.5	19.1±4.2	13.5±1.5[B]	20.0±3.3[A]

Different letters in the same row of each category indicate significance (A–B, P≤ 0.05) or tendency (a–b, P≤ 0.10).

Behavioural budget

The results indicated a long period of low activity (lying and standing) of the animals (~70%). This finding is more than that observed by Kohl et al. (2013) who reported low activity behaviours (bedding and standing) ranging around 62% among wild bison herds in North America. In the captive context, the results are more similar with those described by Robitaille and Prescott (1993) who studied a zoo-housed American bison herd with reported rates of 40% and 25% respectively of resting and standing during daytime hours. Overall animal activity can be influenced by several factors such as enclosure size, enrichment and climate conditions (Allred et al. 2013; Manteca et al. 2016). In the current study, the enclosure size of the bison exceeds the recommendations provided by the Association of Zoos and Aquariums' Husbandry Manual for Wild Cattle Species (~92.3 m^2/animal; Joseph 2004). However, the lack of stimuli in the enclosure may have contributed in part to the lower activity level. Strategies such as environmental enrichment can help increase activity, providing a more stimulating environment (Manteca et al. 2016; Van der Harst and Spruijt 2007). The sandy ground in the enclosure would limit the bison's natural tendency to forage while on grasslands. Brushes, like those provided to dairy cattle, could potentially be used as enrichment to encourage grooming.

The time variation for which behaviours were performed by each animal may be reflective of individual needs or could be the result of herd dynamics. Male 1 numerically spent more time lying down and less time standing than all the other individuals in the herd. Although a test to assess the hierarchy ranking was not performed, based on age and size it is likely that Male 1 is the dominant animal in the group (Lott 1974; Rutberg 1986). Robitaille and Prescott (1993) studied a zoo-housed herd and reported the dominant male bison spent more time standing and moving. In wild bison herds, dominant males also spend less time lying (Melton et al. 1989). In this study Male 1 was subjected to a contraceptive method based on the gonadotropin-releasing factor (GnRF) that could explain the discrepancy in activity levels. Indeed, during observations, no indicative sexual behaviour was observed in males or females. In cattle it has been reported that GnRF vaccination decreases activity levels which may explain this observation (Janett et al. 2012; Needham et al. 2017). Female bison spent more time standing than males. The primary factor influencing these differences in standing behaviour remains undetermined. These variations may vary considerably depending on individual circumstances and needs or may diverge due to factors such as the age of Male 2 and the lower activity level of Male 1 because of the contraceptive method deployed (Janett et al. 2012; Robitaille and Prescott 1993). For most other behaviours all animals tended to maintain similar levels of activity.

The moving behaviour occupied a smaller portion of the daily time budget of the animals. In the wild, bison movement varies according to feed availability (Geremia et al. 2019; Ranglack et al. 2015), predator attacks (Carbyn 1997), human handling (Jung et al. 2019) and during the breeding season (Mooring et al. 2005). Additionally, grazing behaviour is one of the main factors affecting bison movement and displacement (Fortin et al. 2002; Kohl et al. 2013). Unlike wild populations or animals held under extensive husbandry as livestock, captive animals adjust their behaviour to cope with the limited available environment (McPhee and Carlstead 2010). Robitaille and Prescott (1993), studying zoo-housed bison, reported less movement (12.1%) for bison in a captive environment but with a greater stocking rate (109 m^2/animal) than the current study. In this case it is likely that enclosure size contributed to the more frequent moving behaviour. In the Bison genus, animals housed in larger herds and in larger enclosures also generally have a higher frequency of daily movement (Godoy 2009). Lastly, both drinking and eating comprised the smallest portion of the behavioural budget. Under free-ranging conditions, grazing behaviour usually covers 26% to 28% of the animals' daily time budget (Kohl et al. 2003). For large grazers, the ideal is to keep the environment as close to natural bison habitat as possible since it allows a greater degree of behavioural plasticity and provides a positive source of eustress (Villalba and Manteca 2019). In captivity, keeping pasture available for bison is challenging especially with a species that exhibits wallowing behaviour which directly impacts the substrate vegetation (McMillan et al. 2000). It has been suggested that wild ungulates fed with concentrates have higher rates of oral stereotypic behaviour than animals with ad libitum diets based on forage (Bashaw et al. 2001; Lewis et al. 2022). The Zoo Aquarium Madrid adopted a mixed strategy of offering concentrate with hay and vegetables that increased feeding time and occupied a significant portion of the animals' daily routine. This approach appears worthwhile as no stereotypy was noticed during observations.

The correlations observed indicate relationships between behaviours especially in relation to body posture. As expected, more time spent lying down was associated with less time standing, moving and eating. Similarly, more time standing was associated with less time eating. As discussed earlier, long periods of low activity were observed in the bison. Lastly, the more animals moved, the less time they spent eating but they did consume more water. Offering concentrate may have resulted in a shorter time eating as the nutritional density of the ration quickly met the nutritional demands of the bison (McPhee and Carlstead 2010; Pérez-Barbería 2020). Under range conditions, bison ingest most of their water through consumption of forage (McMillan et al. 2022). In the current study, the positive correlation between movement and drinking more water may be related to husbandry conditions of the bison in captivity. Although not surprising, these results help to provide a clearer understanding of how the behavioural budgets of captive bison are interconnected and how different behaviours influence one another. Future methodological approaches could further enhance understanding of captive bison behaviour by categorising behaviours into more specific groups, such as 'exploration' and 'social behaviour' and reveal their patterns and relationships with the environment and herd dynamics.

Influence of time of day, visitor pressure and weather on bison behaviours

As expected, eating behaviour was concentrated during the diurnal period of the day. Bison are diurnal animals and spend a long part of the day switching between foraging and ruminating (Fortin et al. 2002; Kohl et al. 2013). During the nocturnal period the most frequent behaviour observed was lying, which was attributed to resting and sleeping time as part of their normal circadian

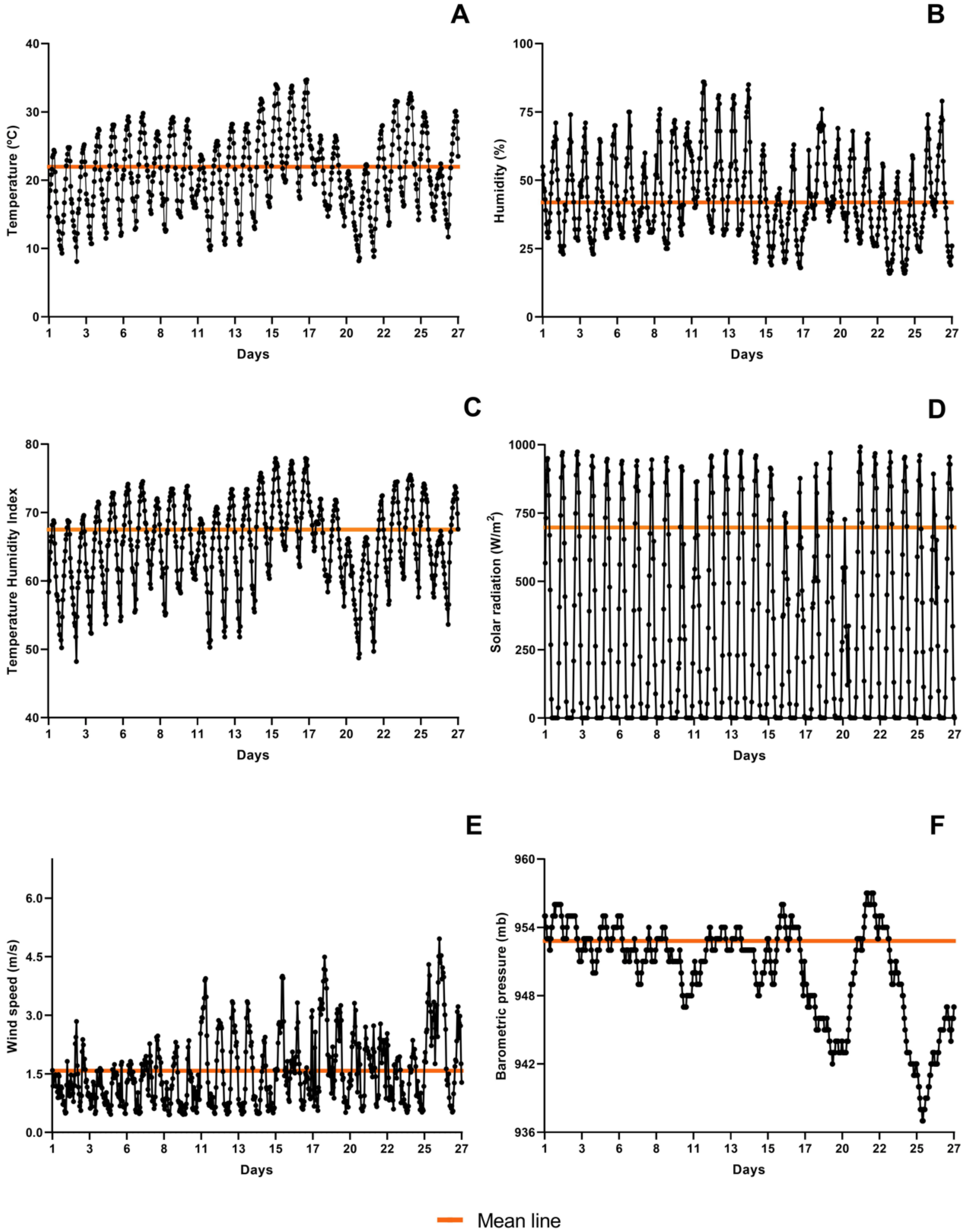

Figure 3. Hourly weather variables across the 27 days of behavioural observation: (A) temperature (range: 8.10–34.70°C), (B) relative air humidity (range: 16–86%), (C) temperature humidity index (range: 48.22–77.92), (D) solar radiation (range: 1–992 W/m2), (E) wind speed (range: 0.46–4.9 m/s) and (F) barometric pressure (range: 937–957 mb). Mean line divided lower (13 days with lowest mean) and upper (14 days with highest mean) range of observed weather conditions.

rhythm. Gübert et al. (2023) studying other zoo-housed wild Bovidae species reported that lying behaviour is most prevalent (>60%) during nocturnal periods. In general, *Bison* spp. spend most of their time resting at night (Caboń-Raczyńska et al. 1983; Den Brink 1980). The animals also seem to eat more during the diurnal period. Feeding occurred in the early morning, so it was expected that the animals would spend more time eating upon feeding (Koene 1999). Regarding visitor pressure, some studies suggest that the behaviours of zoo-housed animals are strongly influenced by the presence of visitors (Collins et al. 2023; Sherwen and Hemsworth 2019). Thompson (1989), studying 12 ungulates species in captivity, found a marked effect of visitor presence on animal behaviour. To the authors' knowledge, no studies have evaluated the effects of visitor impact on American bison but there are studies that show influences on a closely related species. In the current study comparing the two visitor pressure periods, the animals drank more during high visitor pressure (weekends) than low visitor pressure (weekdays). It was anticipated that during high visitor pressure bison would be moving more which is a possible indicator of mild distress as suggested by Sekar et al.

Table 3. Means (±standard error of the mean) and medians of the bison behaviours on lower and upper means observed meteorological variables.

Behaviours (%)	Meteorological variables	Lower		Upper	
		Mean	Median	Mean	Median
Lying	Temperature	66.2±4.2	67.6	60.6±2.6	61.8
	Humidity	59.4±3.1	61.5	65.5±3.1	66.7
	THI	63.2±4.1	66.7	61.9±2.6	62.5
	Solar radiation	57.7±3.6[b]	60.8	66.0±2.8[a]	67.4
	Wind	59.8±3.0	61.7	65.0±3.2	71.7
	Barometric pressure	60.1±3.2	60.9	64.3±3.1	72.2
Standing	Temperature	40.9±2.8	31.8	43.7±2.2	40.0
	Humidity	43.5±2.2	40.0	41.3±2.8	33.3
	THI	40.1±2.6	31.8	44.3±2.3	40.0
	Solar radiation	46.5±2.8[a]	41.7	39.6±2.1[b]	34.0
	Wind	39.7±2.3	32.7	45.7±2.6	41.7
	Barometric pressure	42.6±2.4	35.7	42.5±2.4	37.8
Moving	Temperature	25.9±1.9[a]	20.0	23.2±1.6[b]	16.0
	Humidity	27.8±1.6[A]	20.0	22.5±1.8[B]	13.9
	THI	24.4±1.7	19.0	24.2±1.6	16.5
	Solar radiation	24.5±1.9	16.7	24.1±1.5	16.7
	Wind	25.8±1.7	19.0	22.6±1.7	16.1
	Barometric pressure	19.3±1.5[B]	13.8	28.5±1.8[A]	20.0
Eating	Temperature	59.0±2.7	55.2	57.1±2.4	51.7
	Humidity	56.3±2.4	51.7	59.5±2.7	58.8
	THI	59.5±2.5	56.8	56.7±2.5	51.7
	Solar radiation	61.4±2.9	54.5	55.8±2.2	52.2
	Wind	55.9±2.4	51.7	59.8±2.6	52.9
	Barometric pressure	59.0±2.3	52.9	56.4±2.9	51.7
Drinking	Temperature	16.6±3.2	5.9	13.8±1.2	7.1
	Humidity	14.6±1.9	7.0	15.5±3.5	6.8
	THI	16.5±3.0	6.4	13.7±2.1	7.0
	Solar radiation	16.0±3.0	6.9	14.2±2.1	7.1
	Wind	18.0±2.9	7.1	11.6±1.8	5.9
	Barometric pressure	10.4±2.3[A]	5.6	18.7±2.5[B]	10.2

Different letters in the same row of each category indicate significance ([A–B], $P \le 0.05$) or tendency ([a–b], $P \le 0.10$).

(2008) but this was not the case. Among other wild cattle species, there have been conflicting results concerning the behavioural response to visitor exposure (Edes et al. 2022; Klich et al. 2021; Sekar et al. 2008). Sekar et al. (2008) reported gaurs *Bos gaurus* moved more in the presence of visitors. However, recently zoo-housed European bison *Bison bonasus* were reported to have higher levels of immunoreactive faecal cortisol (stress indicator) under lower visitor pressure (Klich et al. 2021). It has been suggested that visitor presence may have either positive or neutral effects on zoo-housed animals (Collins et al. 2017; Sherwen and Hemsworth 2019). Indeed, Edes et al. (2022) reported banteng *Bos javanicus* stayed close to visitor areas without significantly high stress signs based on the analysis of faecal glucocorticoids. These discrepancies indicate that behavioural response could vary depending on the species, individual traits and husbandry practices (Klich et al. 2021; Sherwen and Hemsworth 2019). Although physiological stress indicators (e.g. cortisol levels) were not directly measured, the results of the current study suggest that the animals might be habituated to the public's presence and visitor pressure (low or high) does not appear to have conclusively affected bison behaviour. Further research into the effects of visitors and habituation processes on animal behaviour and wellbeing could offer valuable insights, aiding zoos and parks in developing improved management and welfare policies for animals on display.

The behavioural activity patterns of ungulates are entwined with their physiological rhythms and environmental conditions. Research has shown that weather parameters (wind speed, relative humidity, temperature, solar radiation and rainfall) all affect behaviours of free-ranging bison (Martin and Barboza 2020; McMillan et al. 2021, 2022). In captivity, even with the availability of shelters and resting areas, animals may be more susceptible to the effects of weather, especially those which are exposed outdoors (Domínguez-Oliva et al. 2022; Mota-Rojas et al. 2022). Higher temperatures were reported to increase lying behaviours of zoo-housed giraffes *Giraffa camelopardalis,* zebras *Equus zebra* and elands *Taurotragus oryx* (Jenssen 2023). However, the current results show that in bison, higher temperatures and humidity were related only with moving time. Animals from temperate climates have different physiological and metabolic adaptations compared to animals from tropical climates that may explain the differences between the captive species (Trudgill et al. 2005). In domestic cattle *Bos taurus,* higher temperature and THI also decreases animal activity (Herbut et al. 2018). Changes in these behaviours occur as a result of how the thermoregulatory mechanism adjusts the energy exchange dynamics between the animal's body and the environment (Finch 1986). Bison and cattle are phylogenetically related and this may be a common strategy employed by both species for body heat regulation (Kohl et al. 2013; McMillan et al. 2000). Among meteorological variables measured, solar radiation and barometric pressure also impacted the recorded behaviours. It is known that solar radiation affects cattle behaviour, mainly European breeds *Bos taurus taurus* that are less heat tolerant than zebu breeds *Bos taurus indicus* (Chan et al. 2010; Schütz et al. 2009). Cows spend less time lying and more time standing during higher solar radiation incidence (Schütz et al. 2011). In cattle, Legates et al. (1991) reported that in field studies both radiation and pressure may impact physiological and behavioural measures. Despite bison having greater heat tolerance than cattle, solar radiation still seems to affect their behaviour (Allred et al. 2013). In this study, data collection occurred during the spring under relatively mild weather conditions. Climatic variables still exerted some influence on bison behaviour and this may not be of a magnitude that could conclusively alter the behaviour observed (Table 2). Another plausible explanation is that solar radiation influenced bison behaviour through solar loading, influencing the circadian rhythm through solar light more so than as a climate variable in and of itself. Understanding the influence of these climate variables on bison behaviour is important for effective facility management and assertive decision-making. Animals in confinement such as in enclosures could particularly benefit from strategies aimed at enhancing their thermal comfort and supporting the expression of their natural behaviours.

Limitations and future directions

While the documented results herein suggest a causal relationship between the influence of environmental effects on bison behaviour, this study had some limitations. First, the sample size was very small which likely alters bison herd dynamics. Second, the herd sex ratio was unbalanced in relation to bison held in more wild conditions which may have further influenced the behavioural results. Additionally, the data were collected during a single season (spring) in a European zoo, so gathering more data over multiple seasons would help to better understand the phenomena studied. The provision of rigorous information about the influence of time of day, visitor pressure and weather on bison behaviour and general activity levels has the potential to assist with decision-making on husbandry practices in other zoo settings and could be extrapolated to commercial bison farming, especially when the herds are very small. This study demonstrates the value of continuous monitoring of behavioural measures to assess bison welfare and demonstrates the need for more automation in behavioural assessments. Future captive bison research efforts should utilise the extensive annotation done in this study with a goal towards the development of more automated image analysis using artificial intelligence and deep learning to improve bison welfare under intensive captivity conditions.

Conclusions

Time of day and weather substantially influenced bison behaviour. There were individual behavioural differences observed between animals, mainly in lying and standing behaviours. Bison spent more time lying at night and ate more during the day. Visitor pressure does not appear to have conclusively affected bison behaviour. Additionally, higher temperatures and humidity were related to reduced moving time, while higher barometric pressure was associated with increased time spent drinking. Lastly, lower barometric pressure and higher solar radiation were related with less time spent moving and standing, respectively, while lying time increased.

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References

Allred B.W., Fuhlendorf S.D., Hovick T.J., Dwayne E.R., Engle D.M., Joern A. (2013) Conservation implications of native and introduced ungulates in a changing climate. *Global Change Biology* 19(6): 1875–1883. doi:10.1111/gcb.12183

Arnold W., Ruf T., Reimoser S., Tataruch F., Onderscheka K., Schober, F. (2004) Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 286(1): R174–R181.

Bashaw M.J., Tarou L.R., Maki T.S., Maple T.L. (2001) A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science* 73(3): 235–247.

Bateson M., Martin P. (eds.). (2021) *Measuring Behaviour: An Introductory Guide 4th Ed*. Cambridge, UK: Cambridge University Press.

Busse M., Schwerdtner W., Siebert R., Doernberg A., Kuntosch A., König B., Bokelmann W. (2015) Analysis of animal monitoring technologies in Germany from an innovation system perspective. *Agricultural Systems* 138: 55–65. doi:10.1016/j.agsy.2015.05.009

Caboń-Raczyńska K., Krasińska M., Krasiński Z. (1983) Behaviour and daily activity rhythm of European bison in winter. *Acta Theriologica* 28(18): 273–299.

Carbyn L.N. (1997) Unusual movement by bison, *Bison bison*, in response to wolf, Canis lupus, predation. *The Canadian Field-Naturalist* 111(96): 307–311.

Chan E.K.F., Nagaraj S.H., Reverter A. (2010) The evolution of tropical adaptation: Comparing taurine and zebu cattle. *Animal Genetics* 41(5): 467–477. doi:10.1111/j.1365-2052.2010.02053.x

Collins C., Corkery I., Haigh A., McKeown S., Quirke T., O'Riordan R. (2017). The effects of environmental and visitor variables on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) in captivity. *Zoo Biology* 36(4): 250–260. doi: 10.1002/zoo.21370

Collins C., McKeown S.O., Riordan R. (2023) A comprehensive investigation of negative visitor behaviour in the zoo setting and captive animals' behavioural response. *Heliyon* 9(6): e16879. doi:10.1016/j.heliyon.2023.e16879

Conradt L., Clutton-Brock T.H., Guinness, F.E. (2000) Sex differences in weather sensitivity can cause habitat segregation: Red deer as an example. *Animal Behaviour* 59(5): 1049–1060. doi:10.1006/anbe.2000.1409

Craine J.M. (2021) Seasonal patterns of bison diet across climate gradients in North America. *Scientific Reports* 11(1): 6829. doi:10.1038/s41598-021-86260-9

Diana A., Salas M., Pereboom Z., Mendl M., Norton T. (2021) A systematic review of the use of technology to monitor welfare in zoo animals: Is there space for improvement? *Animals* 11(11): 3048. doi:10.3390/ani11113048

Den Brink W.J.V. (1980) The behaviour of wisent and bison in larger enclosures. *Acta Theriologica* 25: 115–130.

Domínguez-Oliva A., Ghezzi M.D., Mora-Medina P., Hernández-Ávalos I., Jacome J., Castellón A., Falcón I., Reséndiz F., Romero N., Ponce R., Mota-Rojas D. (2022) Anatomical, physiological, and behavioral mechanisms of thermoregulation in elephants. *Journal of Animal Behaviour and Biometeorology* 10(4): 2233. doi:10.31893/jabb.22033

Edes A.N., Liu N.C., Baskir E., Bauman K.L., Kozlowski C.P., Clawitter H.L., Powell D.M. (2022) Comparing space use and fecal glucocorticoid concentrations during and after the COVID-19 closure to investigate visitor effects in multiple species. *Journal of Zoological and Botanical Gardens* 3(3): 328–348. doi:10.3390/jzbg3030026

Eisenberg C., Aune K., Plumb G. (2019) Saving the American bison: How an iconic keystone species is shaping modern wildlife conservation. *Bulletin of the Ecological Society of America*, 100(4): 1–3. doi:10.1002/bes2.1584

European Association of Zoos and Aquaria (2022) *EAZA Research Standards.* https://www.eaza.net/assets/Uploads/EAZA-Documents-2022/2022-04-EAZA-Research-Standards.pdf

Finch V.A. (1986) Body temperature in beef cattle: Its control and relevance to production in the tropics. *Journal of Animal Science* 62(2): 531–542.

Fortin D., Fryxell J.M., Pilote R. (2002) The temporal scale of foraging decisions in bison. *Ecology* 83(4): 970–982. doi:10.1890/0012-9658

Geremia C., Merkle J.A., Eacker D.R., Wallen R.L., White P.J., Hebblewhite M., Kauffman M.J. (2019) Migrating bison engineer the green wave. *Proceedings of the National Academy of Sciences* 116(51): 25707–25713. doi:10.1073/pnas.1913783116

Godoy E. (2009) Effects of the Captive Environment and Enrichment on the Daily Activity of European Bison (*Bison bonasus*). Linköping, Sweden: Master Dissertation, Linköping University. https://urn.kb.se/resolve?urn=urn:nbn:se:liu:diva-19925

Gübert J., Hahn-Klimroth M., Dierkes P.W. (2023) A large-scale study on the nocturnal behavior of African ungulates in zoos and its influencing factor. *bioRxiv* 2023.06.13.544771. doi:10.1101/2023.06.13.544771

Hafner E., Philipp T., Schuchter K., Dillinger-Paller B., Philipp K., Bauer P. (1998) Second-trimester measurements of placental volume by three-dimensional ultrasound to predict small-for-gestational-age infants. *Ultrasound in Obstetrics and Gynecology* 12(2): 97–102. doi:10.1046/j.1469-0705.1998.12020097.x

Herbut P., Angrecka S. (2018) Relationship between THI level and dairy cows' behaviour during summer period. *Italian Journal of Animal Science* 17(1): 226–233. doi:10.1080/1828051X.2017.1333892

Hurlbert A.H., Liang Z. (2012) Spatiotemporal variation in avian migration phenology: Citizen science reveals effects of climate change. PLoS ONE 7(2): e31662. doi:10.1371/journal.pone.0031662

Janett F., Gerig T., Tschuor A.C., Amatayakul-Chantler S., Walker J., Howard R., Bollwein H., Thun R. (2012) Vaccination against gonadotropin-releasing factor (GnRF) with bopriva significantly decreases testicular development, serum testosterone levels and physical activity in pubertal bulls. *Theriogenology* 78(1): 182–188. doi:10.1016/j.theriogenology.2012.01.035

Jenssen I.C.Ø. (2023) Behaviour of Animals in a Mixedspecies African Savannah Zoo Exhibit Related to Expansion of the Enclosure, Visitor Numbers and Weather Effects. Ås, Norway: Master Thesis, Norwegian University of Life Sciences. https://hdl.handle.net/11250/3077706

Joseph S. (ed.). (2004) *Husbandry Manual for Wild Cattle Species*. Silver Spring, Maryland: Association of Zoo and Aquariums Bison, Buffalo & Cattle Advisory Group. Available online: http://www.azaungulates.org/husbandry-manuals

Jung T.S., Larter N.C. (2017) Observations of long-distance post-release dispersal by reintroduced bison (*Bison bison*). *The Canadian Field-Naturalist* 131(3): 221–224. doi:10.22621/cfn.v131i3.1825

Jung T.S., Hegel T.M., Bentzen T.W., Egli K., Jessup L., Kienzler M., Kuba K., Kukka P.M., Russell K., Suitor M.P., Tatsumi K. (2018) Accuracy and performance of low-feature GPS collars deployed on bison *Bison bison* and caribou *Rangifer tarandus. Wildlife Biology* 2018(1): 1–11. doi:10.2981/wlb.00404

Jung T.S., Konkolics S.M., Kukka P.M., Majchrzak Y.N., Menzies A.K., Oakley M.P., Peers M.J.L., Studd E.K. (2019) Short-term effect of helicopter-based capture on movements of a social ungulate. *The Journal of Wildlife Management* 83(4): 830–837. doi:10.1002/jwmg.21640

Klich D., Łopucki R., Gałązka M., Ścibior A., Gołębiowska D., Brzezińska R., Kruszewski B., Kaleta T., Olech W. (2021) Stress hormone level and the welfare of captive European bison (*Bison bonasus*): The effects of visitor pressure and the social structure of herds. *Acta Veterinaria Scandinavica* 63(1): 24. doi:10.1186/s13028-021-00589-9

Koene P. (1999) *When feeding is just eating: How do farm and zoo animals use their spare time? Regulation of feed intake*. Proceedings 5th Zodiac Symposium, Wageningen, Netherlands. CABI Publishing, 13–19.

Kohl M.T., Krausman P.R., Kunkel K., Williams D.M. (2013) Bison versus cattle: Are they ecologically synonymous? *Rangeland Ecology and Management* 66(6): 721–731. doi:10.2111/REM-D-12-00113.1

Koop S., Oster H. (2022) Eat, sleep, repeat – endocrine regulation of behavioural circadian rhythms. *The FEBS journal* 289(21): 6543–6558. doi:10.1111/febs.16109

Lahoz-Monfort J.J., Magrath M.J.L. (2021) A comprehensive overview of technologies for species and habitat monitoring and conservation. *BioScience* 71(10): 1038–1062. doi:10.1093/biosci/biab073

Lanier J.L., Grandin T. (2015) The calming of American bison (*Bison bison*) during routine handling. Colorado State University Libraries.

Legates J.E., Farthing B.R., Casady R.B., Barrada M.S. (1991) Body temperature and respiratory rate of lactating dairy cattle under field and chamber conditions. *Journal of Dairy Science* 74(8): 2491–2500. doi:10.3168/jds.S0022-0302(91)78426-9

Leoni J., Tanelli M., Strada S.C., Berger-Wolf T. (2020) Ethogram-based automatic wild animal monitoring through inertial sensors and GPS data. *Ecological Informatics* 59: 101112. doi:10.1016/j.ecoinf.2020.101112

Lewis K., Parker M.O., Proops L., McBride S.D. (2022) Risk factors for stereotypic behaviour in captive ungulates. *Proceedings of the Royal Society B* 289(1983): 20221311. doi:10.1098/rspb.2022.1311

Lott D.F. (1974) Sexual and aggressive behavior of adult male American bison (*Bison bison*). *International Union for Conservation of Nature - IUCN Publications New Series* 1(24): 382–394.

Manteca X., Amat M., Salas M., Temple D. (2016) Animal-based indicators to assess welfare in zoo animals. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 11. doi:10.1079/PAVSNNR201611010

Martin J.M., Barboza P.S. (2020) Decadal heat and drought drive body size of North American bison (*Bison bison*) along the great plains. *Ecology and Evolution* 10(1): 336–349. doi:10.1002/ece3.5898

Mason G., Burn C.C., Dallaire J.A., Kroshko J., McDonald Kinkaid H., Jeschke J.M. (2013) Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour* 85(5): 1113–1126. doi:10.1016/j.anbehav.2013.02.002

McMillan B.R., Cottam M.R., Kaufman D.W. (2000) Wallowing behavior of American bison (*Bos bison*) in tallgrass prairie: An examination of alternate explanations. *The American Midland Naturalist* 144(1): 159–167. doi:10.1674/0003-0031(2000)144[0159:WBOABB]2.0.CO;2

McMillan N.A., Fuhlendorf S.D., Luttbeg B., Goodman L.E., Davis C.A., Allred B.W., Hamilton R.G. (2021) Are bison movements dependent on season and time of day? Investigating movement across two complex grasslands. *Ecosphere* 12(1): e03317. doi:10.1002/ecs2.3317

McMillan N.A., Fuhlendorf S.D., Luttbeg B., Goodman L.E., Davis C.A., Allred B.W., Hamilton R.G. (2022) Bison movements change with weather: Implications for their continued conservation in the Anthropocene. *Ecology and Evolution* 12(12): e9586. doi:10.1002/ece3.9586

McPhee M.E., Carlstead K. (2010) The importance of maintaining natural behaviors in captive mammals. In: Kleiman D.G., Thompson K.V., Baer C.K. (eds.). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management.* Chicago, Illinois: The University of Chicago Press, 303–313.

Melton D.A., Larter N.C., Gates C.C., Virgl J.A. (1989) Bisoniana 102. The influence of rut and environmental factors on the behaviour of wood bison. *Acta Theriologica* 34(12): 179–193. doi:10.4098/AT.arch.89-21

Mooring M.S., Reisig D.D., Osborne E.R., Kanallakan A.L., Hall B.M., Schaad E.W., Wiseman D.S., Huber R.R. (2005) Sexual segregation in bison: A test of multiple hypotheses. *Behaviour* 142(7): 897–927. doi:10.1163/1568539055010110

Mota-Rojas D., Pereira A.M.F., Martínez-Burnes J., Domínguez-Oliva A., Mora-Medina P., Casas-Alvarado A., Rios-Sandoval J., de Mira Geraldo A., Wang D. (2022) Thermal imaging to assess the health status in wildlife animals under human care: Limitations and perspectives. *Animals* 12(24): 3558. doi:10.3390/ani12243558

Mota-Rojas D., Titto C.G., Orihuela A., Martínez-Burnes J., Gómez-Prado J., Torres-Bernal F., Flores-Padilla K., Carvajal-de la Fuente V., Wang D. (2021) Physiological and behavioral mechanisms of thermoregulation in mammals. *Animals* 11(6): 1733. doi:10.3390/ani11061733

Needham T., Lambrechts H., Hoffman L. (2017) Castration of male livestock and the potential of immunocastration to improve animal welfare and production traits. *South African Journal of Animal Science* 47(6): 731–742. doi:10.4314/sajas.v47i6.1

Pejchar L., Medrano L., Niemiec R.M., Barfield J.P., Davidson A., Hartway C. (2021) Challenges and opportunities for cross-jurisdictional bison conservation in North America. *Biological Conservation* 256: 109029. doi:10.1016/j.biocon.2021.109029

Pérez-Barbería F.J. (2020) The ruminant: Life history and digestive physiology of a symbiotic animal. In: García-Yuste S. (ed.). *Sustainable and Environmentally Friendly Dairy Farms*. Cham, Switzerland: Springer International Publishing, 19–45.

Post E., Forchhammer M.C (2002) Synchronization of animal population dynamics by large-scale climate. *Nature* 420(6912): 168–171. doi:10.1038/nature01064

Prosekov A., Kuznetsov A., Rada A., Ivanova S. (2020) Methods for monitoring large terrestrial animals in the wild. *Forests* 11(8): 808. doi:10.3390/f11080808

Randler C. (2014) Sleep, sleep timing and chronotype in animal behaviour. *Animal Behaviour* 94: 161–166. doi:10.1016/j.anbehav.2014.05.001

Ranglack D.H., du Toit J.T. (2015) Habitat selection by free-ranging bison in a mixed grazing system on public land. *Rangeland Ecology and Management* 68(4): 349–353. doi:10.1016/j.rama.2015.05.008

Rioja-Lang F.C., Galbraith J.K., McCorkell R.B., Spooner J.M., Church J.S. (2019) Review of priority welfare issues of commercially raised bison in North America. *Applied Animal Behaviour Science* 210: 1–8. doi:10.1016/j.applanim.2018.10.014

Robitaille J.F., Prescott J. (1993) Use of space and activity budgets in relation to age and social status in a captive herd of American bison, *Bison bison. Zoo Biology* 12(4): 367–379. doi:10.1002/zoo.1430120407

Rutberg A.T. (1986) Dominance and its fitness consequences in American bison cows. *Behaviour* 96(1–2): 62–91. doi:10.1163/156853986X00225

Rutley B.D., Hudson R.J. (2001) Activity budgets and foraging behavior of bison on seeded pastures. *Journal of Range Management* 54(3): 218–225. doi:10.2307/4003237

Schütz K.E., Rogers A.R., Cox N.R., Tucker C.B. (2009) Dairy cows prefer shade that offers greater protection against solar radiation in summer: Shade use, behaviour, and body temperature. *Applied Animal Behaviour Science* 116(1): 28–34. doi:10.1016/j.applanim.2008.07.005

Schütz K.E., Rogers A.R., Cox N.R., Webster J.R., Tucker C.B. (2011) Dairy cattle prefer shade over sprinklers: Effects on behavior and physiology. *Journal of Dairy Science* 94(1): 273–283. doi:10.3168/jds.2010-3608

Sekar M., Rajagopal T., Archunan G. (2008) Influence of zoo visitor presence on the behavior of captive Indian gaur (*Bos gaurus gaurus*) in a zoological park. *Journal of Applied Animal Welfare Science* 11(4): 352–357. doi:10.1080/10888700802330093

Sherwen S.L., Hemsworth P.H. (2019) The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals* 9(6): 366. doi:10.3390/ani9060366

Soravia C., Ashton B.J., Thornton A., Ridley A.R. (2021) The impacts of heat stress on animal cognition: Implications for adaptation to a changing climate. *WIREs Climate Change* 12(4): e713. doi:10.1002/wcc.713

Stephenson P.J. (2019) Integrating remote sensing into wildlife monitoring for conservation. *Environmental Conservation* 46(3): 181–183. doi:10.1017/S0376892919000092.

Thom E.C. (1959) The discomfort index. *Weatherwise* 12(2): 57–61. doi:10 .1080/00431672.1959.9926960

Thompson V.D. (1989) Behavioral response of 12 ungulate species in captivity to the presence of humans. *Zoo Biology* 8(3): 275–297. doi:10.1002/zoo.1430080308

Trudgill D.L., Honek A., Li D., Van Straalen N.M. (2005) Thermal time – concepts and utility. *Annals of Applied Biology* 146(1): 1–14. doi:10.1111/j.1744-7348.2005.04088.x

Van der Harst J.E., Spruijt B.M. (2007) Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare* 16(1): 67–73. doi:10.1017/S0962728600031742

Villalba J.J., Manteca X. (2019) A case for eustress in grazing animals. *Frontiers in Veterinary Science* 6: 303. doi:10.3389/fvets.2019.00303

Wolfensohn S., Shotton J., Bowley H., Davies S., Thompson S., Justice W.S.M. (2018) Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals* 8(7): 110. doi:10.3390/ani8070110