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# Social behaviour of captive American bison

**Master's Thesis**

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Hereby I declare that this thesis titled “Social behaviour of captive American bison” was written just by me and that all literature sources I used are listed in References at the end of the thesis.

I agree that this thesis will be stored in the Library of Czech University of Life Sciences Prague and will be used for studying purposes.

In Prague on 27th April 2017 ………………………..…………………………

Signature

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# Abstract

**Social behaviour of captive American bison**

This master thesis reviewed the issue of the American bison (*Bison bison*) history, husbandry and behaviour, with special attention to its social behaviour. The practical part was focused on observation of the bison's herds in the individual breeding facilities and also on estimation and evaluation of the bison's hair loss degree, which was very briefly described in Vervaecke et al. (2005). The aims of the thesis were to determine and evaluate the dominance hierarchies in the individual bison's herds and to examine the connection between social rank and moulting. The research was carried out in the period from February 2016 to October 2016. In total, four American bison (*Bison bison*) herds were monitored in Ranch Gallop (n = 10), Červená ranch (n = 10), Brno zoo (n = 4) and Prague zoo (n = 6) during 180 hours. In total, 272 agonistic interactions between adult individuals were scored and used to determine the dominance ranks in the individual breeding facilities. Strong linear hierarchies were revealed in Ranch Gallop, Červená and Prague zoo, compared to Brno zoo where the perfect linear hierarchy was found. It was detected, that the degree of hair loss was significantly higher in summer and in autumn ($p < 0.05$). Social ranks were positively correlated with the degree of hair loss; higher ranking animals lost its hair earlier than lower ranking individuals. It was not proved that nursing females used higher interaction types than non-nursing ones ($p > 0.05$). This research also represents the first analysis of the difference in the degree of hair loss between individual breeding facilities. A significant difference between zoos and ranches was found ($p < 0.05$); in both zoological gardens, the animals had a significantly higher degree of hair loss compared to the animals in ranches which could be caused by the altitude in which the individual breeding facilities were located, by the ambient temperature and also by the differences in animals' nutrition.



**Keywords:** agonistic behaviour, *Bison bison*, dominance rank, hair loss, hierarchy, moulting

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## List of Abbreviations

| | |
|---|---|
| **ABS** | American Bison Society |
| **BP** | Before present |
| **CBI** | Clutton-Brock Index |
| **CULS** | Czech University of Life Sciences Prague |
| **CR** | Czech Republic |
| **DI** | Dominance index |
| **$DI_{AI}$** | Dominance index according to agonistic interactions |
| **FTA** | Faculty of Tropical AgriSciences |
| **GC** | Glucocorticoids |
| **GYA** | Greater Yellowstone Area |
| **H** | Hypothesis |
| **Ha** | Hectare |
| **RE** | Reproductive effort |
| **RHP** | Resource-holding potential |
| **USA** | The United States of America |
| **WBNP** | Wood Buffalo National Park |
| **YNP** | Yellowstone National Park |

# 1. Introduction

Before the first Anglo-Europeans settled down, there had been the largest indigenous population of the American bison (*Bison bison*), ranging from the desert grasslands of northern Mexico to the floodplain meadows of interior Alaska (Gates et al., 2010; Hidalgo et al., 2013). The American bison has lived continuously in North America for at least 300,000 years in various species during the late Pleistocene through sequential glacial and interglacial periods, then into the Holocene and present times (Gates et al., 2010).

Over the hundreds of thousands years, the American bison contributed to the coevolution of another biota, including mutualistic, trophic and commensal interrelationships, and grazing adaptations in plants. Hereby, bisons were a key component of native biodiversity of the continent and also had a significant influence on the patterns of presence, distribution and density of other species (Meffe and Carroll, 1995). At present, bisons play important ecological roles, influencing the composition, structure and stability of both plant and animal communities (Gates et al., 2010).

The social and physical evolution of the American bison fitted primarily to the Great Plains and several features of their social systems and social behaviour are explicated by this ecological-evolutionary perspective (Lott, 1991). Together with generally represented ecological factors, the dominance hierarchies, as a part of the social environment, may substantially contribute to the formation of social systems and influence the association patterns (Horová et al., 2015).

Since the 1980s, the number of the American bison raised under captive commercial husbandry has increased markedly, and nowadays they represent about 93 % of the continental population (Gates et al., 2010). The main reason for bison husbandry is bison’s meat, which is gaining increased popularity in the United States and Canada, where approximately half a million kilogrammes of bison’s meat are consumed each month (Joseph et al., 2010).

But the American bison husbandry is not popular only in the USA and Canada. Currently, several private bison ranches already exist in the Czech Republic (CR), serving for meat production, but also for landscape maintenance. Although the bison meat is not traditionally consumed in the CR, more and more Czech people are interested in the American bison husbandry and the trend is still increasing (Štěpánková, 2016).

# 2. Literature Review

## 2.1 History of American bison

The American bison (*Bison bison*) have existed in various species for more than 2,000,000 years (Danz, 1997; Gates et al., 2010). Early forms originated in South and East Asia (Krasińska and Krasiński, 2013) and appeared in Villafranchian[1] deposits of India and China and these late forms eventually gave rise to the present-day bison (Feldhamer et al., 2003; Gates et al., 2010).

The American bison's ancestors dispersed from Asia to North America (Berman, 2009) and Europe (Krasińska and Krasiński, 2013) thousands years ago (approximately 5,000 years BP), during the last Ice Age (Berman, 2009; Hidalgo et al., 2013; Lott, 1991; Rivals et al., 2007) in the middle Pleistocene (Gates et al., 2010; Krasińska and Krasiński, 2013).

During this period, the shape of the land was changed due to the glaciers and one newly exposed stretch of land crossed the Bering Strait (Berman, 2009; Krasińska and Krasiński, 2013). This narrow connected Russia to an area that is part of modern-day Alaska and the bison's ancestors were among the many animals which walked across this land bridge (Berman, 2009).

From the end of the Pleistocene until recent times, bison were the dominant ungulates of the Great Plains of North America (Freese et al., 2007; Kelliher and Clark, 2010; Lott, 1991; Mosley, 2010) and they ranged from Canada to Mexico (Clutton-Brock, 1999; Freese et al., 2007; Gates and Aune, 2008; Hidalgo et al., 2013; Mosley, 2010) as it is depicted in Appendix 1. Their eastern habitat consisted of present-day Kentucky, Ohio, Illinois, Indiana, Montana, Georgia, Mississippi, Yukon and Alaska (Davis et al., 2006; Gates et al., 2010; Miller, 2003).

However, following the arrival of Anglo-Europeans in the sixteenth century, bison became the object of hunting and slaughtering (Clutton-Brock, 1999; Mosley, 2010) for their meat supplied by market hunters and for the hides evolved from the robe trade. Other factors including impetuous hunting for recreation and sport

[1] A main division of early Pleistocene period, named for a sequence of terrestrial sediments, which were studied in the region of Villafranca d'Asti, an Italian city near Turin (Gates et al., 2010).

resulted in a dramatical decline in bison population. In addition, the environmental factors, such as regional drought, introduced bovine diseases. Moreover, competition with domestic livestock (cattle, sheep, and horses) and wild horses caused a reduction in bison population numbers (Gates et al., 2010).

In 1884, a herd of seventy-five thousand bisons was reported in eastern Montana and five thousand hide hunters had reduced their number to a few hundred within one year (Berman, 2009). By the mid-1880s the American bison was close to extinction (Binns, 2006; Herman et al., 2014).

Once the number of bison living in North America had been reduced to only a thousand of animals, the attitudes began to change (Berman, 2009; Freese et al., 2007; Miller, 2003). In the late nineteenth century, the American Bison Society (ABS) was established and also the extension of the national parks and reserve systems in Canada and in the USA did help to save the bison from extinction. Since these days, the public interest in bison conservation has begun to increase worldwide (Mosley, 2010).

The largest protected herds of American bison (4,000-5,000 animals) within their original range are in Yellowstone National Park (YNP) which was created in 1872 (Freese et al., 2007). Bison in the YNP historically occupied approximately 20,000 $km^2$ in the headwaters of the Yellowstone and Madison rivers in what is now referred to as the northern Greater Yellowstone Area (GYA), as you can see in Appendix 2 (Freese et al., 2007; Plumb et al., 2009).

In the YNP (Freese et al., 2007), Canadian Banff National Park (Ranglack et al., 2015), Custer National Park in South Dakota and the Great Slave Lake Bison Preserve in the Northwest Territories of Canada (Miller, 2003), the American bison herds are free-ranging within boundaries of the parks and nearby areas (Freese et al., 2007). Nevertheless, the majority of American bison population is located in semi-domesticated herds at present and they are raised for meat production (Miller, 2003).

Thanks to protection, numbers of American bison increased quickly, and the closeness of the extinction was averted (Freese et al., 2007). At the beginning of the twenty-first century, the population of American bison was approximately 250,000 (Miller, 2003). About 500,000 individuals live in North America at present (Freese et al., 2007; Ranglack and du Toit, 2015; Ranglack et al., 2015) and the population continues to grow.

## 2.2 Taxonomy

Despite the vast history and the symbolic and economic importance of bison to North American societies, the disagreements about bison taxonomy remain. The problem of the American bison taxonomy came into being as a consequence of a discrepancy in the historical usage of the common name as well as the scientific debate over the systematics of the genus, species and subspecies designations (Gates et al., 2010). In addition, next problems can be caused by the assignment of an animal to a genus in traditional naming schemes, which can be subjective, and changing generic names can contravene the goal of taxonomy which should stabilise nomenclature and not confuse it (Winston, 1999).

### 2.2.1 Bison or buffalo?

For many years, people called bison "buffalo" by mistake. This confusion probably started when early French explorers saw the American bison for the first time. American bison reminded the researchers their own cattle, which they called *boeufs* and the pronunciation of this French word was difficult for the British settlers (Berman, 2009). In the course of time, the word became to be pronounced "buffalo", "buffelo", "buffilo" or "buffes" (Berman, 2009; Danz, 1997; Dary, 1989; Gates et al., 2010).

Although bisons and buffalos are members of the same scientific family Bovidae, they differ from each other a lot and in spite of the confusion surrounding its name, there is no reason to interchange the American bison for buffalos as well (Berman, 2009; Feldhamer et al., 2003).

True "buffalos" are native only to Asia (*Bubalus* spp., four species of water buffalo) and Africa (*Syncerus caffer,* Cape buffalo); (Gates et al., 2010; IUCN, 2008), but that is not the only difference. The silhouette of the American bison alone distinguishes bisons from the buffalos, and what more, from any other animals (Berman, 2009).

Nevertheless, the term “buffalo” has become a colloquialism commonly used in North American language and culture. Despite the persistence and acceptance of the term “buffalo”, scientific convention prescribes use designation of “bison” (Gates et al., 2010).

### 2.2.2 Genus *Bos* versus *Bison*

First to classify the American bison in 1758 in his 10th Edition of the *Systema Naturae,* was Carl Linnaeus (Gates et al., 2010; Isenberg, 2000), however, the genus *Bos* was the same genus as domestic cattle (Feldhamer et al., 2003; Wilson and Reeder, 2005).

During the 19th century, taxonomists suggested the American bison to its own genus because its anatomical distinctiveness was sufficient enough to warrant assigning. In 1827 the taxonomists assigned the subgeneric, later the generic, name *Bison* to the American and the European bison (Gates et al., 2010).

The Bison ranges among the order Cetartiodactyla (even-toed ungulates), sub-order Ruminata, family Bovidae, subfamily Bovinae and tribe Bovini, which includes four genera: *Bos* (domestic cattle and their wild relatives), *Bubalus* (Asian water buffalo), *Syncerus* (African buffalo) and *Bison* (bison) with two species: American bison (*Bison bison*) and European bison (*Bison bonasus*); (Groves and Grubb, 2011; Krasińska and Krasiński, 2013; Prusak et al., 2004; Troy, 2006).

### 2.2.3 Bison subspecies

At present, there are six bison species recognised in the Quaternary of North America, out of which five species are extinct: *Bison latifrons*, *Bison antiquus*, *Bison occidentalis*, *Bison alaskensis* and *Bison priscus.* Meanwhile *Bison bison,* which is still present in North America, is represented by two subspecies: *Bison bison bison* (the Plains or the Prairie bison) and *Bison bison athabascae* (the Wood bison); (Berman, 2009; Gates and Aune, 2008; Hidalgo et al., 2013; Meltzer, 2015). These two American bison subspecies were first distinguished by Rhoads in 1897 when the *B. bison athabascae* was formally recognised due to specific descriptions of the animal (Gates et al., 2010; Geist, 1991).

Although the subspecies differ in external and skeletal morphology and pelage characteristics (see chap. 2.3), some scientists have argued that these differences alone do not warrant subspecies designation. The issue is complicated by the human-induced hybridization between these two subspecies which started in Wood Buffalo National Park (WBNP) during the 1920s. Moreover, the concept of what represent subspecies continues to develop (Gates et al., 2010).

A similar situation occurred in European bison which is also represented by two subspecies: *Bison bonasus bonasus* (the Lowland bison) and *Bison bonasus caucasicus* (the Mountain or the Caucasian bison). The differences between these two subspecies are in the structure of the head and hoof, in hair coloration and in body size – the Lowland bison (*B. b. bonasus)* is the largest living representative of genus *Bison* (Bleyhl et al., 2015; Krasińska and Krasiński, 2013).

In general, bison is the largest native terrestrial mammal found in North America (Binns, 2006; Bowers et al., 2004; Feldhamer et al., 2003).

The classification of genus *Bison* is depicted in Figure 1 bellow.

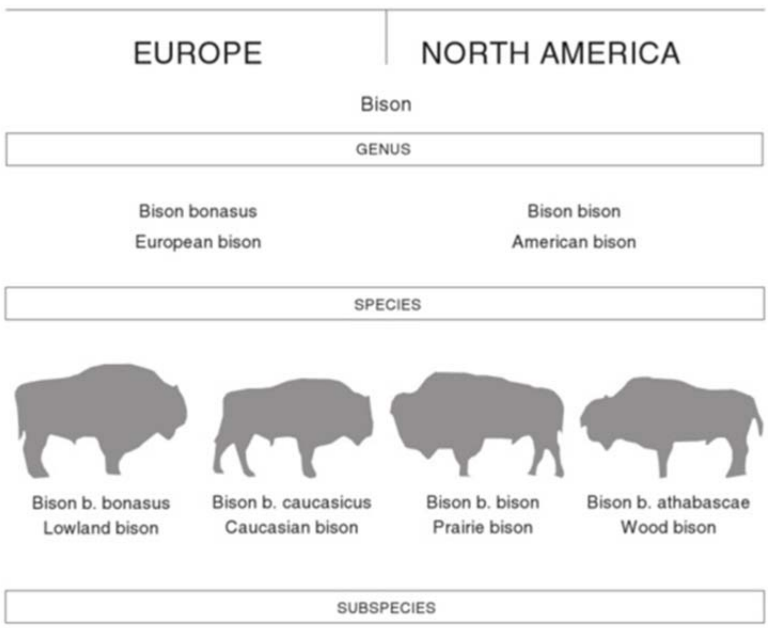


**Figure 1:** The classification of genus *Bison* (Krasińska and Krasiński, 2013)

## 2.3 American bison characteristics

### 2.3.1 Plains bison (*Bison bison bison*)

The Plains bison (*B. b. bison*), sometimes called Prairie bison, are the most recent southern variant of the North American species (Gates et al., 2010; Stephenson et al., 2001) and unlike the Wood bison (*B. b. athabascae*), this subspecies is characterized as near threatened (Gates and Aune, 2008).

In comparison with the Wood bison, *B. b. bison* have smaller and lighter body framework (within similar sex classes and age), nevertheless, the bulls can reach the weight up to 1,000 kg and stand nearly two metres at the shoulder (Fariña et al., 2013).

In contrast to the Wood bison, the Plains bison's pelage is longer with dense woolly tufts of hair between horns, its full throat mane extends below the rib cage, its beard is thicker and its hair is lighter in colour (Gates et al., 2010).

The highest point of the hump is centred over the front legs and horns are rarely extended above a mop of hair (see Appendix 3) (Pegge et al., 2011). Plains bison, as well as Wood bison, have a thick dermal shield on the forehead and between the horns and thick skin on the neck, which provides protection during fighting (Mitchell and Gates, 2002).

### 2.3.2 Wood bison (*Bison bison athabascae*)

The Wood bison (*B. b. athabascae*) is a geographic variation of the Plains bison (*Bison bison bison*) that is morphologically slightly different, but it does not genetically distinct. Historically, this species inhabited areas of northern Alaska, Yukon and Canada (Weese et al., 2014).

Like the Plains bison, the Wood bison was near to extinction in the late 1800s because of over-hunting and an only single population of about 250 animals survived (Freese et al., 2007; Steenweg et al., 2016; Strong and Gates, 2009). Therefore, *B. bison athabascae* is currently classified as a threatened (Aurini et al., 2009; Gates et al., 2001; Palomino et al., 2015) and its recovery is threatened by habitat loss and its modification, predation, loss of genetic diversity and accidental mortality (Mitchell and Gates, 2002).

In comparison with the Plains bison, *B. bison athabascae* have larger body framework (within similar sex classes and age) (Considine and Considine, 2013; Franke, 2005) and darker, heavier hair with thin beard and rudimentary throat mane (see Appendix 3) (Pegge et al., 2011). The highest point of the hump is positioned forward of the front legs. Horns are usually shorter and they extended above forelock and back from the head (Castelló, 2016; Gates et al., 2010).

## 2.4 American bison husbandry

The number of American bisons has grown rapidly over the past five decades in commercial herds (Gates et al., 2010) and the trend is still growing as well as bison production is increasing in the United States (Scanes, 2010).

This increase may reflect the advantages provided by the ecological efficiency and the adaptations of these indigenous range animals which possess several traits that can make them preferable to cattle as a range animal (Gates et al., 2010).

The feed, nutrient and mineral requirements of bison are generally similar to those for the cattle; therefore, many bison breeders apply cattle husbandry standards and practices to bison as well (Drew and Baskin, 1989; Flanders, 2011). Nevertheless, the bison has greater ability to digest poor quality forage (Gates et al., 2010; Jones, 1985) and it is more capable of surviving harsh winter conditions without any significant problems (Cavendish, 2008).

The primary aim of many commercial bison breeders is to increase profits by maximising calf production, docility, meat quality and feed-to-meat conversion efficiency, but these traits require non-random selection which leads to the animal character changes and to reducing genetic variability over time (Schneider, 1998). Furthermore, if genetically selected commercial animals would be mixed into conservation herds or could escape and join wild herds, these commercial activities could pose a threat to conservation bison populations through genetic pollution. For this reason, the most cautious action is to identify and maintain conservation bison herds and do not mix them with the commercial ones (Gates et al., 2010).

In the long term, bison industry and bison breeders could profit by supporting efforts to restore and maintain conservation bison herds because these herds secure their genome for the future producer use. This is the option not available for most other domestic animals (Gates et al., 2010).

In North America, the commercial bison population is about 400,000, divided almost equally between Canada and the USA. In conservation bison herds, the number of bisons is currently estimated at only 20,504 Plains bison and 10,871 Wood bison (Gates et al., 2010). Therefore, approximately 93 % of American bison are under commercial production and they are evincing some degree of domestication (Devine and Dikeman, 2014; Hoare, 2009).

## 2.5 Behaviour of ungulates with focus on bison

Many social ungulates, such as Barbary sheep (*Ammotragus lervia*) (Cassinello, 1995) or red deer (*Cervus elaphus*) (Bender and Haufler, 1996), are characterised by well-defined stable dominance hierarchies (Roden et al., 2005).

The hierarchical position of a definite individual can be influenced by its age, body weight, fitness, fatness (Robitaille and Prescott, 1993; Roden et al., 2005; Vervaecke et al., 2005) and it can be also associated with speed of hair loss, as it was also proved in the American bison (Vervaecke et al., 2005).

The dominance has been studied before in the American bison, but the results of different studies vary. It was found that the hierarchy in bison females in confinement, like in many other bovids such as *Bos indicus* (Chenoweth and Lorton, 2014; Orihuela and Galina, 1997) or *Bos taurus* (Roden et al., 2005), is often linear, at least stable in constant groups (Broom et al., 2009; Sneddon et al., 2005; Roden et al., 2005). On the other hand, in large wild groups of the American bison, the dominance relationships among males are unstable and non-linear (Lott, 1979).

The dominance between two bison individuals is often challenged and there are many rank reversals. Free ranging males join female herds only for reproduction during the rutting season in summer (Komers et al., 1992) and they form bachelor groups during the rest of the year. Nevertheless, these bachelor male groups are studied poorly and there is only a lack of information about their social dominance (Roden et al., 2005).

### 2.5.1 Social structure

Social dominance is defined as a lasting asymmetry in the outcomes in a variety of competitive interactions between specific individuals (Bernstein, 1981; Sarkar, 2003; Šárová et al., 2013), which developed in many species including mammals, fish, birds and insects (Alonso et al., 2012; Kleiman et al., 2010). Being socially dominant ensures facilitated and prior access to resources such as food, shelter and space for breeding or mating opportunities (Ceacero et al., 2012; Šárová et al., 2013).

Therefore, in comparison with subordinate individuals, social dominance can bring fitness benefits for the dominant animals, which should generally have greater reproductive and survival success (Bekoff and Byers, 1998; De Waal and Tyack, 2009). Individuals with larger resource-holding potential (RHP), which means those in ownership of phenotypic and morphological traits, such as large body size, that enable them to predominate in agonistic interactions (Favati et al., 2014), should use these traits to obtain dominance over lighter opponents. Nevertheless, various other factors, such as kinship or prior dominance experience, can also increase the probability of gaining a dominant position (Hofer and East, 2003).

Morphological characters have received much more attention than behavioural predictors of dominance, even though dominant and subdominant animals commonly differ in behaviour (Favati et al., 2014). For example, dominant individuals are often more aggressive and initiate most fights than subordinate ones (Benson and Rollin, 2008; Mills and Marchant-Forde, 2010; Nelson, 2006). Individuals, which have different social status, may also differ in behavioural responses such as explorative tendencies or boldness. In these behavioural traits, variation among individuals is often consistent through time and is used to describe an individual's personality type (Favati et al., 2014; Sih et al., 2004).

Throughout history, there were many observations of American bison herds wandering the Great Plains (Dary, 1989; Gates et al., 2010; Isenberg, 2000). Observers consistently report a definable herd structure in which cows, immature males and calves form unstable mixed-age and mixed-sex groups, and mature bulls are separated and form smaller groups throughout much of the year (Gates et al., 2010; Komers et al., 1993; Schuller et al., 2006).

Seasonal modifications in group sizes are related to landscape features, dispersion or abundance of forage (Gates et al., 2010), breeding behaviour (Komers et al., 1993) and population size (Schuller et al., 2006). The largest accumulations occur during the breeding season when mature bulls join the smaller unstable groups and show a linear dominance hierarchy. Older and heavier animals dominate over smaller and younger male individuals (Gates et al., 2010; Roden et al., 2005).

In the case of American bison females, it is evident that benefits which are related to high dominance rank can result in increased fitness, although to a lesser degree than in males. Female dominance relationships are linearly organised as well (Vervaecke et al., 2005).

### 2.5.2 Social and reproductive behaviour in males

Reproductive effort (RE), which is defined as an individual's investment in any actual reproductive act, can vary in several male ungulate species. Variation can be explained by differences in dominance, age, breeding season phase and the presence of females in oestrus (Roden et al., 2011).

The American bison is a sexually dimorphic ruminant (Berger and Peacock, 1988; Buskirk, 2016) that forms so-called "tending-bonds" in the mating system in which large-bodied and older dominant males mate more often than small-bodied and younger subdominants (Bowyer et al., 2007; Lott, 1979; Lott, 1981). During the breeding season or rut, there is behavioural evidence of polygynous mating, which is supported by genetic verification of high variability in male reproductive success, while mature males mate more often than younger counterparts (Mooring and Penedo, 2014; Willisch et al., 2012). In comparison with younger or senescent animals, male reproductive success is greater for prime-age individuals (Bowyer et al., 2007).

Most mating takes place in July and August (Lott, 1981), but it can continue till the autumn and it has been observed up to December (Mooring and Penedo, 2014). During the rut, the reproductive effort is expected to change: it will increase from early rut to peak rut and decrease in a late rut (Roden et al., 2011). During this period bison bulls attempt to keep other males away and move through the herds seeking females, which are approaching oestrus, and keep them near the edge of the herd until they accept copulation (Lott, 2002). Typical male behaviour during searching females is sniffing the anogenital region, nuzzling, face rubbing and flehmening (see Figure 2 and Figure 3) (Doty, 2012; Vandenberg, 2012; Wyatt, 2003).

Tending bulls have high dominance rank and increased levels of androgens and glucocorticoids (GC) such as cortisol as a primary response to stress because if dominant individuals are subjected to physiological and social stressors (e.g. fights at higher rates than subdominants), then the "stress of domination" hypothesis predicts higher glucocorticoids levels (Mooring et al., 2006).

Tending males are also frequently challenged by rival bulls, so-called "satellite" or "attending", which surround the tending pair and then the head-to-head fights are very common between the rivals (see Figure 4 and Figure 5) (Mooring and Penedo, 2014). The most aggressive interactions occur before copulation within 15-30 metres of the tending pair, while tending bull can be displaced by more dominant individual or lose interest in cow (Wyman et al., 2008).

The copulation is usually crepuscular or nocturnal activity (Feldhamer et al., 2003) and it is strongly seasonal; about 90 % of all copulations take place in a two week period. After copulation, which usually takes less than ten seconds, the male generally continues to tend the female for a variable length of time, from one hour to several days, before he starts to search out new mates (Lott, 1981).


**Figure 2:** Bison bull flehmening (photo: author)


**Figure 3:** Bison bull searching the female by sniffing the anogenital region (photo: author)


**Figure 4:** Rival individuals starting the fight (photo: author)


**Figure 5:** Very common aggressive interaction: head-to-head fight (photo: author)

### 2.5.3 Social and reproductive behaviour in females

Although bison females were once thought to breed only once in a season (Lott, 1981; Mooring and Penedo, 2014), they are seasonally polyestrous (Vervaecke and Schwarzenberger, 2006) and can experience up to two or three oestrous cycles per season, therefore, they can mate several times during this period. The gestation length lasts about 266 days with a single calf, occasionally twins (McDougall, 2012; Scanes, 2010). Cows give birth in brushy areas, where they are protected from predators. Calves weight from 30 to 50 lbs (13 to 23 kg) and have a reddish coat (Greenwood, 2008).

In comparison with males, females have a lower variance in reproductive success, therefore, they have been considered to be less sexually strategic. Although the full reproductive potential with all bison cows is never reached in wild conditions, the variance in the reproductive success is similar for captive and wild conditions as well (Vervaecke et al., 2005).

It is evident that selection has formed dominance hierarchies and competitive behaviour in females and it is becoming obvious that dominance relations among them also influence their fitness (Anouska et al., 2008). High social rank often results in priority of access resources, such as better quality food, water, mates and territories (Dennehy, 2001; Maestripieri and Georgiev, 2016; Shively and Day, 2015), resulting in dominants being in better condition than subordinate individuals. Unlike bulls, dominance relations among cows are stable in spring and summer and the escalated fights or reciprocated threats are rare (Rutberg, 1982).

On the other hand, lower ranking females can decrease their fitness in these opposite ways: reduce access to high-quality food and to powerful mating partners, or increase the risk of aggression resulting in injury or death (Maestripieri and Georgiev, 2016).

Overall, structured dominance hierarchies may reduce risky fights, allow individuals to retain the benefits of predator protection and provide advantages in the intergroup contest (Maestripieri and Georgiev, 2016).

### 2.5.4 Maternal behaviour

Before parturition, the behaviour of the bison females and nearby members of the herd often changes (Feldhamer et al., 2003). Cows have been described as restless and irritable (McHugh, 1958) and they usually wander away from the herd for one or more days, nevertheless, calving may occur within the herd (Gates et al., 2010). Generally, in open area, females choose a place for calving within close proximity to other herd members, while in habitat with more vegetation they usually leave (Lott, 1991).

The cow usually gives birth lying down and she often eats the placenta, amniotic membrane and portions of the umbilical cord during parturition (McHugh, 1958). After calving, the female licks the calf frequently for several hours to remove amniotic fluid from its fur and to stimulate its activity (Houpt, 2011). Licking is also necessary for drying and warming the calf and thus it reduces the stress caused by harsh climatic conditions.

A bison calf stands and suckles from thirty to eighty-five minutes after parturition, although suckling may last only ten minutes (Caboń-Raczyńska et al., 1983; Gates et al., 2010). In one or two days it follows female to re-join the herd. Calves begin grazing within a week, but still suckle several times a day for eight months. Bison females are absolutely protective (see Figure 6 and Figure 7) and thus the calves are not fully weaned until they are ten months old (McDougall, 2012). The longest contact is among cows and their female calves, which lasts through the third summer, whereas male offspring may stay with the cow through a second summer (Gates et al., 2010; Green et al., 1989). For calf-cow recognition, animals use the scent, sound and sight, but occasionally the calf can follow the wrong female (McHugh, 1958).

The other herd members may be interested in new cow-calf pair shortly after parturition and sometimes will come to lick and sniff the new-born. The adult female is still prepared to defend the calf against any threats and thus she usually tries to keep herself between her calf and other herd members. The ability of a cow defending the calf may depend on her position in the dominance hierarchy (Feldhamer et al., 2003).

Females defend their calves by quick attacks or by slow approaching the predators (Gates et al., 2010; McHugh, 1958), but the protection may be also shared by other herd members. Calves usually gather around cows, but they can tend to be positioned more toward the front half of the herd than the rear. This behaviour was suggested as reducing the probability of calf mortality (Feldhamer et al., 2003).

**Figure 6:** Bison female with her calf (photo: author)

**Figure 7:** Bison female keeping her calf outside other herd members (photo: author)

### 2.5.5 Wallowing and horning

Wallowing is common, but not the consistent behaviour of many ungulates species (McMillan et al., 2000). For example, wallowing by the Indian rhinoceros (*Rhinoceros unicornis*) and domestic pig (*Sus scrofa*) is a thermoregulatory behaviour (Davenport, 2012; Olczak et al., 2015), but wallowing by male European bison (*Bison bonasus*) and male wapiti (*Cervus elaphus*) during the rut is a conflict social behaviour (Caboń-Raczyńska et al., 1983; McMillan et al., 2000). Wallowing by European bison males and also females in another period of the year is a grooming behaviour, which can also serve as relief from biting insects (Mooring and Samuel, 1998).

All sex and age classes of American bison (*Bison* bison) also become involved in wallowing and horning (McHugh, 1958). The horning involves bison rubbing shrubs and small trees with its horns, head, neck and shoulders (see Figure 8) (Gates et al., 2010), because of the reducing insect irritation and thus the distribution of woody vegetation is influenced. During the late 1800s, near bison extinction, connected with overhunting, contributed to the expansion of aspen (*Populus tremuloides*) woodland into American prairies (Coppedge and Shaw, 1997). However, the rubbing and horning can also represent aggressive behaviour (Gates et al., 2010).

The wallowing consists of several different behaviours in the American bison (McMillan et al., 2000). Animals of both sexes and all age classes usually lie down and roll in dry, or less frequently wet, ground (see Figure 9) (Knopf and Samson, 2013), although mature bulls wallow more often during the rut. They also urinate into the wallow before rolling and pawing (McHugh, 1958). The wallowing by mature bulls can show their physical condition to other bulls and stimulate oestrus in females as well (Suthar and Dhami, 2010).

Additional behaviours associated with wallowing are lunging, neck, face and belly rubbing during lying in wallows filled with water, which can also serve for cooling the animals during hot summers (McMillan et al., 2000). Wallowing is also a social behaviour for group cohesion, while its frequency is relatively constant throughout the day and throughout the year, however, the larger frequency is at dusk, when play behaviour is most common (McHugh, 1958).

**Figure 8:** Bison horning (photo: author)

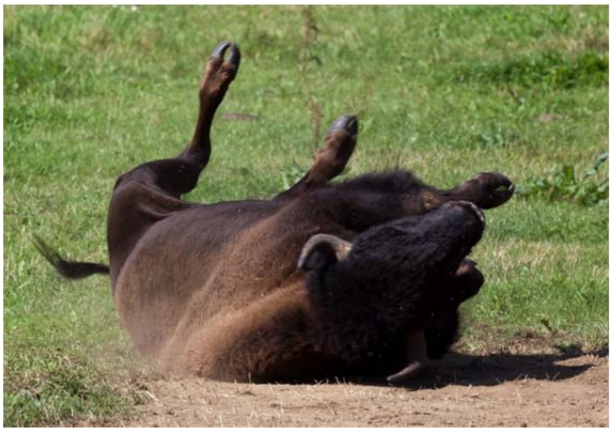

**Figure 9:** Bison wallowing (photo: author)

### 2.5.6 Vocalization

The bisons are able to produce a number of various sounds, such as roaring, snorting, tooth grinding or foot stamping (Feldhamer et al., 2003), nevertheless grunting and bellowing are considered to be the basic sounds (Gunderson and Mahan, 1980).

The snorting and roaring are made by males more frequently than by cows because they are associated with agonistic behaviour (McHugh, 1958). The snorting sound is imitated by forced air inhalation accompanied by fluttering of the soft palate. The roaring occurs any time of the year, but during the rut season, it is more intensive and more common. During the roaring the bull's tongue is protruded and the sound is produced by vigorous expiration of the air over the vocal cords (Gunderson and Mahan, 1980), whereas bawling or mooing of domestic cattle (*Bos taurus*) are produced by both inspiration and expiration of the air over the vocal cords (Colville and Bassert, 2015). Males also roar while approaching or moving through bull subgroups, while tending cows, in answer to a roar from another male or before fighting.

The females roar less often and less loudly in comparison with males. They mainly make the soft guttural grunts while protecting their newborns and they have been heard snorting while searching for lost calves (Feldhamer et al., 2003).

In comparison with adult bisons, the calves make barely audible vocalisation. They produce higher pitched grunts in response to their dams very often. Also during play fights, chases and in response to other stimuli, they usually bleat loudly. The grunting occurs throughout the year, but more often when the calves are young and then when they are leaving the dam and start forming subgroups within the herd (Gunderson and Mahan, 1980). In general, the vocalisations made by bison cows and calves are comparable in function and sound to that of domestic cattle (McHugh, 1958).

### 2.5.7 Tail posture

Bison tail posture forms a part of animal "body language" and thus it reflects its social rank within the herd. Nevertheless, it is not only this function; tail posture also serves to convey information to other herd members. It varies from holding the tail vertically or horizontally, which is a sign of sexual behaviour, aggression or danger; to tail fluttering and wagging during grazing.

During fights between males, the position of the tail upwardly is associated with dominance (Feldhamer et al., 2003), whereas tail fluttering and wagging are associated with fright and submission (Estes, 1991). Females usually hold their tail up when they are disturbed by predators and they keep it out at some angle to the body for up to several hours before copulation. In the case of bulls, the tail is held up during a sexual meeting with a cow (Feldhamer et al., 2003).

### 2.5.8 Movements and migrations

The American bison herds often migrate annually along well-established pathways when they are moving between pastures. The bisons undertake extensive seasonal movements from north to south and from east to west, searching for better food resources (Gates et al., 2010). Bisons, especially females, show very strong affinity to return to traditional winter range. Afterwards, the return usually occurs during spring. But the migration may not be only directional; in north-eastern British Columbia and in mountains areas of Wyoming, seasonal movements from higher elevations during summer and autumn to lower elevations in spring and winter are very common (Feldhamer et al., 2003). During summer, snipe flies (*Symphoromyia* sp.) can be also responsible for some elevational movements in Yellowstone bisons. Nevertheless, during this period of time, the bisons search for water resources because of that they overcome from 80 to 160 kilometres over several days (Dary, 1989; Gates et al., 2010).

During harsh conditions and inclement weather, the American bison usually head towards the blizzard, unlike domestic cattle. This behaviour is sometimes associated with the larger amount of dense and curly hair on their head and forequarters, which have good insulating properties (Lott, 2002). If the animals are unable to avoid travelling in deep snow, they form a line, in which the lead individuals plunge to create deep ditches.

Older females tend to be the most alert and they usually take the lead in sudden herd movements (McHugh, 1958). The observers described females, which are generally the leaders of the herd during movements in the Wood Buffalo National Park, although some scientists ascribed this role to the adult males (Feldhamer et al., 2003; Gates et al., 2005; Gates et al., 2010).

Disturbance of the bison herd may cause sudden movements, panic or stampedes. These animals are able to flee at speeds up to 60 km/hr (McHugh, 1958). The stampede may appear spontaneously because the initiating stimulus can be apparently insignificant. It can be caused by the sudden movement or running of one animal toward the herd, which may become after being alarmed or by any other unexpected external stimulus (Feldhamer et al., 2003).

In the Yellowstone National Park, bison migrations take place during each winter, when the extent of movements depends on the snowpack. The animals usually cross the park's western and northern borders in harsh winters, following the Yellowstone and Madison River valleys and also following the snowmobile paths on their way downhill, straying outside agreed geographical limits. All these circumstances bring the American bison into conflicts with local farmers, due to the risk of transmitting brucellosis disease to their livestock, leading to controversial culls of bisons. Nowadays, in the modern landscape, there are a lot of parcels of land owned by different interests; therefore, migratory behaviour of wild American bisons is a serious political problem (Hoare, 2009).

### 2.5.9 Moulting

Moulting commonly occurs in wild animals, as well as in animals which are kept in captivity. Nevertheless, in free-ranging mammals the hair loss is rare compared to captive individuals in whom the moulting is more frequent and extensive (Gerold et al., 1997; Steinmetz et al., 2006; Vessey and Morrison, 1970).

The American bison's thick coat of fibres serves for many purposes. In the past, it was very important mainly for native North American people, who traditionally used it for hide production, but also for textile production. But the main significance of fur is to assist bisons to withstand harsh climatic conditions (McGregor, 2012).

The winter bison's coat is very thick, with good insulating properties, which protects the animals against snow and freeze (Flanders, 2011). It has two layers. The top layer is formed of thick, dark brown hair and underneath is a layer of woolly fur, which keeps in warmth and also keeps out the damp.

The animals start to shed their winter coats in spring, and they rub their bodies against any object they can find, trying to remove it (Potts, 1999). Wallowing also helps to relieve itching skin irritations caused by the process of moulting (Knopf and Samson, 2013). The heavy fur is lost in patches (see Figure 10) and the surface of uncovered skin increases as moulting proceeds (Potts, 1999; Vervaecke et al., 2005). Nevertheless, some parts of the coat may remain on animal's legs, neck, back and hump (see Figure 11).

As spring and summer continue the new hair starts to grow. It is usually shorter and stiffer and in colour lighter brown. Thus this helps animals to stay cool on the hot summer plains. During late summer and autumn, the light summer coat gradually changes and animals start to prepare for coming winter (Potts, 1999).

Moulting may be an indicator of captive animals' overall welfare (Beisner and Isbell, 2009), and it can be also associated with the bison hierarchy. The social dominance can bring fitness benefits for the dominant individual and thus it has greater survival and reproductive success, which is also connected to its age, body weight, fatness and robe loss. For example, since barren females did not invest in gestation, their weight and body condition are superior at the end of the year and thus they can be expected to show earlier moulting and resume oestrous earlier (Vervaecke et al., 2005).

**Figure 10:** Bisons lose the winter coat in patches (photo: author)

**Figure 11:** Small part of winter coat remaining on female's neck and hump (photo: author)

# 3. Aims of the thesis

Aims of the thesis were:

1) to determine and evaluate the dominance hierarchies in captive American bison (*Bison bison*) herds in the individual breeding facilities;
2) to estimate and evaluate the changes in the degree of hair loss in captive American bison individuals;
3) to examine the connection between the social rank and moulting in bison individuals.

Hypotheses of the thesis were:

H1: the bison hierarchies will be linear in all breeding facilities;

H2: the degree of hair loss will vary among individual breeding facilities;

H3: the degree of hair loss will correlate with the social rank, where higher ranking individuals will moult earlier than the lower ranking ones;

H4: nursing females will use more intensive type of attacks than non-nursing females.

# 4. Material and Methods

The structure of the thesis was composed according to the Methodical Manual for the Writing of Master's Theses of the Faculty of Tropical AgriSciences (FTA), Czech University of Life Sciences (CULS) Prague (FTA, 2016). References were cited according to the Citation Rules of the Faculty of Tropical AgriSciences, CULS Prague (FTA, 2014).

## 4.1 Literature review

The literature review came out from the analysis of scientific publications (especially from the scientific database ScienceDirect and Web of Science) dealing with this topic. Scientific articles were searched by following keywords: agonistic behaviour, *Bison bison*, dominance rank, hair loss, hierarchy, moulting, and others.

## 4.2 Study areas and subjects

Data were collected in captive American bison (*Bison bison*) herds in two zoological gardens and two private ranches in the Czech Republic, namely in Prague zoo, Brno zoo, Ranch Gallop and Červená, in 2016. Observations were approved by head zoologists or private owners responsible for the animals in each breeding facility. No other specific permissions were required.

In the private ranches, outdoor enclosures differed in size (Ranch Gallop – 7.5 ha, Červená – 4.5 ha), but were similar in structure and management. The animals graze year round on meadows pastures. The area was predominantly composed of grasses, e.g. timothy grass (*Phleum pratense*), common meadow-grass (*Poa pratensis*) and orchard grass (*Dactylis glomerata*), with areas of spruces (*Picea abies*), oaks (*Quercus* L.) and birches (*Betula pendula*). The grass was abundant in summer and hay was continuously provided *ad libitum* in winter. Sources of water, as well as mineral licks, were accessible throughout the year, likewise *ad libitum*. On the other hand, in both zoos, the herds were fed by forage *ad libitum*, formed mainly by hay, throughout the year. Access to water was also provided *ad libitum*.

The zoo outdoor enclosures did not differ much in size (Prague zoo – 0.31 ha, Brno zoo – 0.25 ha), but were also similar in structure and management. Although the grass was not widespread, each enclosure was formed or surrounded with several deciduous trees, e.g. oaks (*Quercus* L.), beeches (*Fagus sylvatica*) or lime trees (*Tilia* L.).

In all zoos and ranches, indoor enclosures were absent. Only simple wooden sheds against adverse weather were available in both zoos. In the case of ranches, the shelter was provided only by trees.

Four American bison herds with 51 animals in total were included in the study. Adults, sub-adults and juveniles were present in all observed herds. Bison bulls were not separated from females, but they were present in the herds throughout the year.

Individual study areas and bison herds are described in following chapters.

### 4.2.1 Ranch Gallop

This private ranch of Mr. Jiří Votava and Mrs. Tereza Štěpánková is situated in the northeast of the Czech Republic in Vápenka near Stárkov in the Protected Landscape Area Broumovsko (50°32'26.301"N, 16°7'39.121"E) with approximately 7.5 ha of total pasture area.

The observed herd consisted of 18 American bisons in total; one male, nine females and eight offspring. Almost every individual was labelled with two ear tags, which made possible to distinguish specimens from each other flawlessly.

In this ranch, American bisons are bred mainly for landscape maintenance, but also for meat and hide production, which serves for private use only.

### 4.2.2 Červená

Bison husbandry of Mr. Radek Mach is situated in the south-west of the Czech Republic in Červená near Kašperské hory in the National Park Šumava (49°7'17.330"N, 13°34'40.004"E).

The herd of the American bison consisted of 16 animals in total with two males, eight females and six offspring.

Only nine animals were labelled with ear tags, the others were identified individually by their different morphological characteristics as body size, presence and shape of horns, physique, shape of the head, and sex.

The total area of the pasture is approximately 4.5 ha and the animals are kept there only for landscape maintenance.

#### 4.2.3 Brno zoo

Zoological garden is situated in the north-western part of Brno, in the Czech Republic (49°13'52.002"N, 16°32'5.103"E).

In total, seven American bisons are bred in the zoo with one male, three females and three offspring.

Only two individuals were labelled with ear tags, but due to the small number of animals within the herd and also small size of the enclosure, which has approximately 0.25 ha, the identification of individuals was not difficult. The animals were recognised due to different morphological characteristics (e. g. presence and shape of horns, constitution and shape of head) and sex.

#### 4.2.4 Prague zoo

Zoological garden is located in the north-western part of Prague, in the Czech Republic (50°7'0.508"N, 14°24'26.810"E).

In total, ten American bisons are bred there with one male, five females and four offspring in the area of 0.31 ha.

In comparison with Brno zoo, the animals were not labelled with ear tags; nevertheless, the identification of individuals was not problematic. The bisons were identified in the same way as in the zoo Brno.

#### 4.2.5 Bison Ranch excluded from the research

Private ranch of Mr. Dirk Van de Poel and Mrs. Eva Van de Poel is situated in the south of the Czech Republic in Rožnov near Český Rudolec (49°3'36.134"N, 15°14'0.094"E).

The herd of the American bison consisted of 46 animals in total where each individual was labelled with two ear tags. This commercial ranch serves primarily for meat production and its export.

This ranch was excluded from the research after the first observation because of a large number of animals and vast area of grasslands with approximately 50 ha of total area. Therefore, the observation was considerably problematic.

## 4.3 Data collection and observation periods

The observations were carried out between 13th February 2016 and 1st October 2016, all during daytime hours, in the course of different periods of the day. The dates of individual observations were as follows: 19/03, 30/04, 11/06, 30/07, and 11/09 in Ranch Gallop; 13/02, 26/03, 07/05, 01/07, and 14/08 in Červená; 16/04, 29/05, 09/07, 21/08, 27/08, 31/08, 01/09, and 24/09 in Brno zoo; 15/06, 08/07, 07/08, 04/09, 09/09, 17/09, 21/09, 29/09, 01/10 in Prague zoo and 02/04 in Bison Ranch, which was excluded from the research.

In Prague zoo, Brno zoo and Ranch Gallop, the animals were observed outside the herd from a safe distance, but in the case of Červená, the observer had to stay inside the enclosure several times, with owner permission. The reason was that the animals were hiding in grove amid the pasture most of the time. During these observations, the binoculars were used (see Appendix 4).

To ensure equal observation of all individuals, the observer switched position when it was necessary to cover front, mid and back positions of the herd (Vervaecke et al., 2005). The observer did not disturb the animals, did not influence their behaviour or interfere with the daily management in the enclosures. Behavioural sampling did not affect the animals in any manner (Horová et al., 2015).

In every breeding facility, behavioural interactions between animals were recorded gradually by using the Ethogram of agonistic and submissive behaviours (see Table 1) during each visit. The Ethogram was created on the basis of Vervaecke et al. (2005).

Individual agonistic encounters with submissive reactions were recorded into a loss and win table *ad libitum*. Win and loss table included information about the identity of each individual, time of the beginning and the end of the observation period, date of the observation, which animal was the winner of the encounter, which was the recipient and what type of threat it was (Horová et al., 2015). All forms of aggressive behaviour, including kicking or fighting, as well as milder forms of aggression, including threats or displacements, were recorded. The threats were described as unspecified aggression. They are summarised as non-contact aggression (Bashaw, 2011; Horová et al., 2015; Nelson, 2006).

**Table 1**: Ethogram of agonistic behaviours (based on Vervaecke et al., 2005)

| Degree of aggression | Behaviour | Clarification |
|---|---|---|
| 1 | Displacement | Approaching within one body length whereupon another individual yield |
| 2 | Threat low | Lowering the head towards an opponent |
| 3 | Threat nod | Nodding the head towards an opponent |
| 4 | Threat swing head | Swinging the head towards an opponent |
| 5 | Threat lunge | Brisk brief movement in the direction of another individual, accompanied by lowering, nodding or swinging the head |
| 6 | Brief (long) chase | Run after fleeing individual for less (more) than two body lengths |
| 7 | Thrust horn | Strong contact with the horn on or in the body of another individual |
| 8 | Butt | Lowering the head and butting another individual |
| 9 | Fight | Repeated butting and forward pushing against the other individual with lunges |
| 10 | Kick | Kicking with hind legs towards an individual |

### 4.3.1 Estimation and evaluation of the hair loss degree

For monitoring and evaluation of the degree of hair loss, each individual, including males, as well as females, was photographed during each visit in every breeding facility. The observer tried to take several pictures of each animal from different positions to be sure that the subsequent evaluation of moulting will be possible. The photographs were gradually classified, described and evaluated.

The degree of hair loss was evaluated for each individual, including males and females, as a percentage value in the range of 0 – 90 % (see Appendix 5), depending on how the areas of uncovered skin increase as moulting proceeds (Vervaecke et al., 2005).

## 4.4 Dominance hierarchy determinations

To determine the dyadic dominance relationships, all possible aggressive behaviours followed by submissive behaviours were used (Vervaecke et al., 2005; Vervaecke et al., 2000) and the data were entered into a dyadic interaction matrices (Lehner, 1996). The matrices originated from loss and win tables, which were filled in during individual observations. For each agonistic encounter, the winner and loser were recorded, allowing the calculations of wins and losses for each individual (Horová et al., 2015).

Based on the dyadic relationships between single individuals, the individual dominance indices (DIs) for all group members were calculated to evaluate the stability of hierarchy. For this step, the DIs according to the observed agonistic interactions ($DI_{AI}$) were computed, providing a measure of how dominant the individual is with regard to other group members (Langbein and Puppe, 2004), using the ratio of wins minus defeats to all decisive fights (Bowen and Brooks, 1978):

$$DI_{AI} = \sum (\text{wins} - \text{defeats}) / \sum (\text{wins} + \text{defeats})$$

A Clutton-Brock index (CBI) (Clutton-Brock et al., 1979) was also calculated for each observed member (i), of a group, providing detailed information not only about the order within the hierarchy but also about the relative distances between individuals (Horová et al., 2015). For this calculation the following formula, which was described in detail by Bang et al. (2010), was used:

$$CBI_{(i)} = (B + \sum b + 1) / (L + \sum l + 1)$$

where, *B* is the number of individuals whom the subject dominates, *b* is the number of individuals whom those dominated by the subject in turn dominate, *L* is the number of individuals who dominate the subject and *l* is the number of individuals who dominate those dominating the subject (Bang et al., 2010).

Based on wins and defeats or dominants and subordinates, respectively, the individual group members were assigned according to their $DI_{AI}$ (Langbein and Puppe, 2004; Lott, 1979; Schein and Fohrman, 1995), as well as CBI (Bang et al., 2010). The dominance hierarchies were constructed by arranging all individuals in decreasing order of their value of the indices (Bang et al., 2010). The individuals were ranked, when the top individual was assigned rank one and the lowest ranking individual rank *n*, where *n* means the total number of individuals in the herd (Vervaecke et al., 2005). When two or more individuals got the same rank, they were tied as follows. For instance, if two individuals were tied at the first position, they were both given rank 1.5 and the next individual was given rank 3 (Bang et al., 2010; Lehner, 1996).

However, it is reasonable to calculate the individual DIs for dominance hierarchies which are linear or quasi-linear (Langbein and Puppe, 2004). Therefore, Landau's index of linearity (*h*) was computed for each individual herd, providing a measure of the degree to which a dominance hierarchy is linear (Jůnková Vymyslická et al., 2015). The index was calculated using the formula:

$$h = 12 / (n^3 - n) * \sum [v_a - ½ (n-1)]^2$$

where $n$ is the total number of animals within the group and $v_a$ is the number of animals that individual '*a*' dominates. The index ranges from zero (nonlinear) to 1.0 (perfectly linear) (Lehner, 1996). The values of $h \geq 0.9$ are generally taken to indicate a strong linear hierarchy (Appleby, 1983).

## 4.5 Data analyses

The data were statistically evaluated in the StatisticaCz 12 program (StatSoft, Inc., 2013). For all calculations significance level $\alpha = 0.05$ was established. All calculated numerical values were rounded off to two decimal places.

Normality analyses (Kolmogorov-Smirnov test) were performed prior to applying appropriate statistical tests. The data did not show the normal distribution (Kolmogorov-Smirnov, $p < 0.05$); therefore, following non-parametric tests were used for the next data analyses: Kruskal-Wallis test, Mann-Whitney U test, Pearson's chi-squared test, Spearman's correlation and Multiple comparison of p-values.

The individual agonistic encounters were recorded in all herd members, but afterwards, calves, as well as juveniles, it means animals younger than two years, were excluded from the statistical evaluation. Only the interactions between adult males and adult females, that mean 30 animals in total, were statistically assessed.

For further data evaluation, the differences of the hair loss degree of the winner and hair loss degree of the recipient were also calculated. The individual observations were sorted according to the seasons, where March, April and May are considered as spring; June, July and August as summer; September, October and November as autumn; and December, January and February as winter (Barnett and Dobson, 2010; Fedorova et al., 2015). However, winter was not included in the statistical assessments because the data from this season came only from one breeding facility.

# 5. Results

## 5.1 Dominance hierarchy analyses

The data were collected within 180 total hours of observation time, concretely 53 hours in Ranch Gallop, 48 hours in Červená, 39 hours in Brno zoo and 40 hours in Prague zoo. In total, 272 agonistic interactions between adult individuals were recorded (see Table 2), but according to the Ethogram of agonistic behaviours (see Table 1), not all agonistic encounters among animals were scored.

The most common interaction types were “displacement” and “threat low”, the less frequent interaction was “threat swing head” and rarely observed interactions were “threat lunge” and “thrust horn”. The other interactions were not scored. The percentages of the individual interactions, which were recorded, are depicted in Figure 12 below. The animals, that attacked the other individuals, have always been victorious.

During each aggressive contact or display, the loser apparently avoided the winner with the submissive behaviour, such as walk away from approaching individual well before it is within one body length, jump or flee and not return to the conflict (similarly as in Vervaecke et al., 2005).

**Table 2:** Detailed information about the data collection. M = male, F = female

| Locality | Season | Total number of individuals[1] | Herd structure[2] | Number of interactions[3] | Observed hours |
|---|---|---|---|---|---|
| Ranch Gallop | 2016 | 18 | 1M, 9F | 102 | 53 |
| Červená | 2016 | 16 | 2M, 8F | 75 | 48 |
| Brno zoo | 2016 | 7 | 1M, 3F | 44 | 39 |
| Prague zoo | 2016 | 10 | 1M, 5F | 51 | 40 |

[1] Including calves and juveniles

[2] Number of adult individuals only

[3] Number of interactions between adult animals only

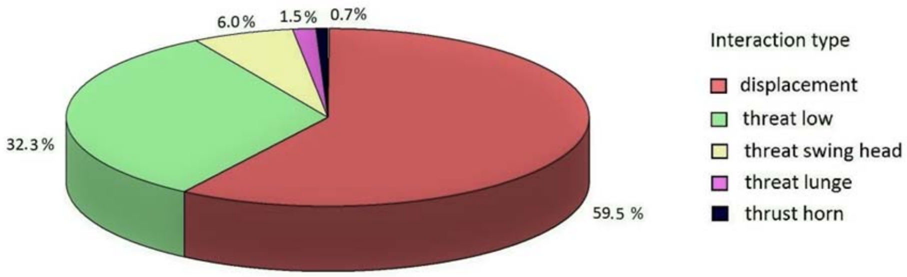


**Figure 12:** Percentages of individual interaction types, which were scored

According to both counted dominance indices ($DI_{AI}$ and CBI), the hierarchies were well determined, and the relationships were transitive. The individual dominance matrices of herds in Ranch Gallop, Červená and Prague zoo showed a strong linear hierarchy and even perfect linear hierarchy was found in Brno zoo (see Table 3 below).

**Table 3:** Analyses of linearity in all studied American bison herds

| Locality | Season | Number of adult animals | Landau's index (*h*) | p - value | Hierarchy |
|---|---|---|---|---|---|
| Ranch Gallop | 2016 | 10 | 0.96 | p < 0.05 | Strong linearity |
| Červená | 2016 | 10 | 0.98 | p < 0.05 | Strong linearity |
| Brno zoo | 2016 | 4 | 1.00 | p < 0.05 | Perfect linearity |
| Prague zoo | 2016 | 6 | 0.97 | p < 0.05 | Strong linearity |

## 5.2 Dominance rank and the degree of hair loss

In total, 3,148 photographs were taken in all breeding facilities, enabling the estimation and evaluation of the degree of hair loss.

The differences of the hair loss degree of the winner and hair loss degree of the recipient varied according to the season (Kruskal-Wallis test: $H (3, N = 272) = 36.36$, $p = 0.0001$), where the difference was significantly higher in summer and in autumn in comparison with spring (Multiple comparison of p-values, $p = 0.0001$).

There was no significant correlation between the differences of the winner's moulting and moulting of the recipient and the interaction types ($r_s = -0.03$, N = 272, p = 0.66) during individual seasons ($p > 0.05$).

A significant correlation between the difference of moulting of the winner and moulting of the recipient and $DI_{AI}$ rank was found in spring ($r_s = -0.30$, N = 60, p = 0.02) and in summer ($r_s = -0.20$, N = 149, p = 0.02). On the other hand, there was a negative correlation between the difference of moulting of the winner and moulting of the recipient and CBI rank ($r_s = -0.21$, N = 272, p = 0.83), regardless of the season.

A significant difference in the degree of hair loss was found between zoos and ranches (Mann-Whitney U test: U = 1051.50, Z = 5.63, p = 0.0001). This difference occurred during summer (Mann-Whitney U test: U = 228.00, Z = 4.18, p = 0.0001), where the animals in zoological gardens had a higher degree of moulting in comparison with the individuals in ranches.

During summer, it was proved that the animals in Prague zoo and in Brno zoo had significantly higher degree of hair loss than the animals in Ranch Gallop and Červená (Kruskal-Wallis test: H (3, N = 150) = 39.77, p = 0.0001 and Multiple comparison of p-values, p = 0.0004), as depicted in Figure 13 below.

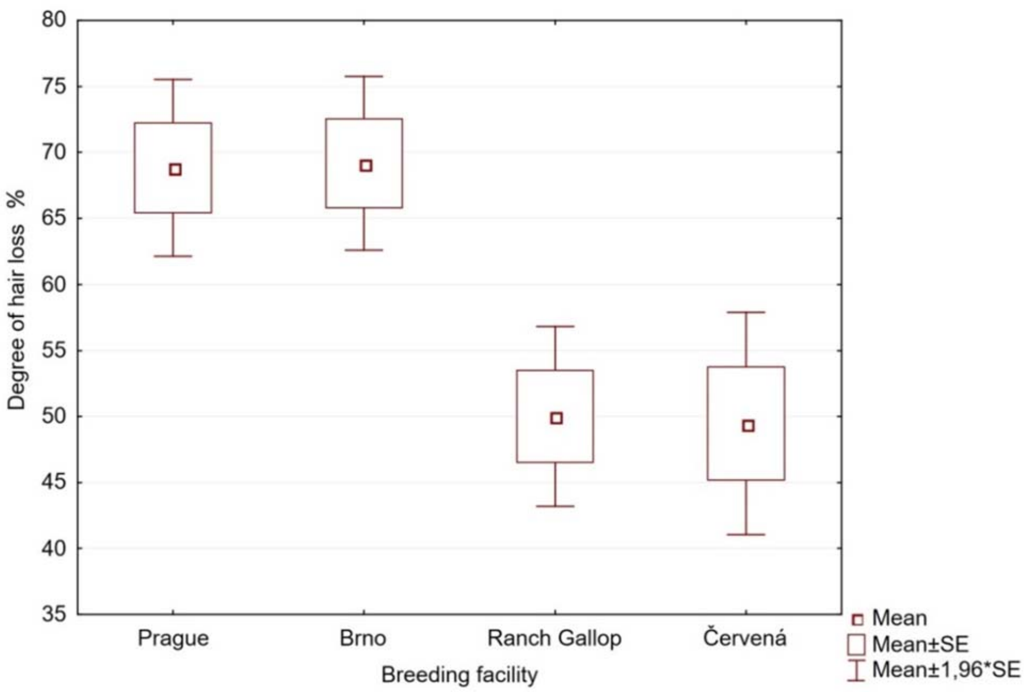


**Figure 13:** Differences in the degree of hair loss among the individual breeding facilities during summer

It was found that the rank of the animals counted by $DI_{AI}$ and CBI significantly correlated with a degree of hair loss (Spearman's correlation, rs = -0.21, N = 150, p = 0.01 and rs = -0.17, N = 150, p = 0.04, respectively).

It was not proved that nursing females used higher interaction types (see Table 1) than non-nursing females (Pearson's chi-squared test: $\chi^2 = 0.88$, df = 2, p = 0.64). It was not also proved that nursing had an effect on the nursing females' hair loss degree (Mann-Whitney U test: U = 1739.00, Z = 1.03, p = 0.30).

# 6. Discussion

## 6.1 Herd structures and observation methods

In this research, bison bulls were not assembled in bachelor groups outside of the breeding season (non-rut) and they were not divided over different female herds during the rut as it was in the study of Roden et al. (2005). Contrarily, the bulls were present within the female herds all year-round in all breeding facilities and they were included in the observations, unlike in Vervaecke et al. (2005). Calves, as well as juveniles, were also included in the observation methods, same as in Vervaecke et al. (2005) research, but unlike that, they were not included in the statistical assessment.

In most cases, the animals were observed outside the enclosures, but Roden et al. (2005), Vervaecke et al. (2005) and Bowyer et al. (2007) monitored the bison herds from a four-wheel drive vehicle within the herd, which the animals were habituated to.

## 6.2 Dominance hierarchy analyses

This study represents the analyses of the dominance hierarchies in the captive American bison herds, which included both cows and bulls together, compared to other studies. This situation is uncommon because only Reinhardt (1985) studied social behaviour in a confined bison males and females together.

On the other hand, Krasiński and Raczyński (1967), Lott (1974, 1981, and 1991) and Roden et al. (2005) investigated the behaviour of bulls and Lott and Galland (1987), Rutberg (1982) and Vervaecke et al. (2005) discussed factors that influence dominance relationships between bison cows. McHugh (1958) made the first systematic assessment describing all behavioural patterns of free-ranging bison and Lott (1979) examined the dominance hierarchy in the wild American bison bulls. However, Roden et al. (2005) claimed, that this problematic is poorly studied and therefore there is a lack of information about wild bison social dominance.

### 6.2.1 Agonistic interactions

According to the Ethogram of agonistic behaviours (see Table 1), not all agonistic encounters among individuals were scored in this research in contrast with Roden et al. (2005), Vervaecke et al. (2005) and Coppedge et al. (1997). The most common interaction types, observed in both males and females, were “displacement” and “threat low”, the less frequent interaction was “threat swing head” and rarely observed interactions were “threat lunge” and “thrust horn”. Nevertheless, Rutberg (1982) mentioned that during spring and summer, the dominance relations among bison cows are stable and reciprocated threats or escalated fights are rare. This situation is sharply in contrast with the aggressive behaviour of bison bulls, especially during the mating season which takes place in July and August, as Lott (1979; 1981) described. Rutberg (1982) suggested that these differences occur because the fitness benefits of aggression are much lower to females than to males. But in this thesis, the aggression among bison bulls, in the form of serious fighting, was not scored in the individual breeding facilities except Bison Ranch, which was excluded from the research. During one day of observation in Bison Ranch the aggressive encounters, such as “thrust horn” and “fight”, among bulls were scored. According to the opinion of the author of this study, the animals could be more aggressive due to the high number of individuals within the herd, where 46 bisons were present, including more than two bulls.

However, all submissive behaviours such as walk away, jump or flee, were recorded, similarly as in Vervaecke et al. (2005). The animals, which were attacked by the other individuals, adopted a submissive posture and never reciprocated any attacks. These situations demonstrate that the submissive animals accepted their subordinate positions.

Although it is known that cows usually defend their calves by more aggressive attacks (Gates et al., 2010; McHugh, 1958), the fourth hypothesis of this thesis was rejected because it was not proved that nursing bison cows used more intensive type of attacks than non-nursing individuals. This discrepancy probably arose due to the predominance of mild agonistic interactions among individuals.

### 6.2.2 Linearity and dominance indices

In this study, the results of the linearity did not differ from the other mentioned studies (Roden et al., 2005; Rutberg, 1982; Vervaecke et al., 2005); the dominance hierarchies were linear in all cases. However, the calculation method for linearity determination differed little. In this case, the Landau's indices of linearity (*h*) were computed, similarly as Roden et al. (2005) and Vervaecke et al. (2005) did, but subsequently these authors used the improved index of linearity (*h´*), according to De Vries (1995), in case of unknown relationships. The unknown relationships could reduce the Landau's index (*h*) and significance of linearity could be underestimated (Hohmann et al., 2012). Since the degree of linearity was highly significant in this research, using the Landau's index (*h*), there was no need to use the improved linearity index (*h´*).

The individual dominance indices ($DI_{AI}$ and CBI) were not counted in any study examining the bison hierarchies. Roden et al. (2005) mentioned the use of some dominance indices but did not specify which ones. For instance, the other authors rather used the I&SI method (De Vries, 1998; Vervaecke et al., 2005). Nevertheless, CBI was computed in the other studies focusing on the ungulates hierarchies (Clutton-Brock et al., 1979; Horová et al., 2015; Jůnková Vymyslická et al., 2015).

However, $DI_{AI}$ may be especially useful when only a few unknown relationships occur and nearly all of the animals within a herd are involved in a similar number of agonistic interactions (Langbein and Puppe, 2004). Therefore, the CBI was also calculated because it remains a suitable index for societies in which multiple interactions are uncommon (Bang et al., 2010; Clutton-Brock et al., 1979).

The dominance hierarchies may change during the year and therefore it would be more advantageous to calculate the individual dominance indices for each season separately but in general, due to the small number of interactions, it was not possible to realize it in this study.

## 6.3 Degree of hair loss and associated analyses

This research also represents the analysis of the connection between the hierarchy and the bison hair loss degree, which was very briefly described in Vervaecke et al. (2005). The hair loss degree was also investigated with other factors such as season and nursing, which have not been explored yet in any other study focusing on bison's problematic. A very important part of this thesis was also to compare the degree of moulting among zoos and ranches, which has not been studied before as well.

According to my best knowledge, the other studies focusing on connection between the ungulates' hierarchy and moulting do not exist. Nevertheless, there have been a lot of studies focusing on factors which influence hair loss in other mammals, especially in rhesus macaques (*Macaca mulatta*) (Beisner and Isbell, 2008 & 2009; Honess et al., 2005; Vessey and Morrison, 1970).

### 6.3.1 Monitoring and evaluation of moulting

In this study, the degree of hair loss was recorded gradually during the whole observation period from February 2016 to October 2016 in comparison with Vervaecke et al. (2005), who monitored the moulting only during one day, on 6$^{th}$ June. After that, they made a second evaluation after checking the herd in the reverse order to correct for fluctuation of observer's criteria during the evaluation. However, the observation and evaluation of moulting only during one day are inadequate. In this study, the bisons were not moulted completely on 6$^{th}$ June and the ranges of values were approximately 30 - 50 % of the robe loss. According to the statistical assessment, the highest percentage of exposed skin was observable during August, September and October; in summer and autumn respectively (Barnett and Dobson, 2010) in all breeding facilities. These periods were the most suitable for the evaluation of moulting.

Another fact was also that Vervaecke et al. (2005) monitored the American bison herd in the Belgian Ardennes, where the altitude was approximately 500 metres above sea level (Destain et al., 1996). Thus, the altitude did not differ much from this research, where Ranch Gallop was situated approximately 450 metres above sea level (Štěpánková, 2016) and Červená was located approximately 700 metres above sea level (Mach, 2016). Therefore, there was a low probability that the percentages of moulting in this research differed from Vervaecke et al. (2005) significantly in the course of the same observation period.

All males and females were included in moulting estimation and statistical evaluation unlike Vervaecke et al. (2005), who excluded barren females from the statistical evaluation because they were supposed to be in better body condition and therefore they might lose their hair earlier, compared with females which were pregnant. These authors also did not include any males into the investigation.

### 6.3.2 Difference in moulting among zoos and ranches

The degree of hair loss differed between zoos and ranches. In Prague zoo and Brno zoo the animals showed a bigger hair loss degree than the animals in Ranch Gallop and Červená. The difference was most evident in summer when the differences in moulting were most evident. The author of this thesis suggested that this result could be related to the altitude in which the individual breeding facilities were located. Both zoological gardens were placed in lowland regions, whereas both ranches were placed at higher altitudes, as it was mentioned above in the text. Of course, the environmental temperature as well as other factors were related to the altitude and thus it could be also related to moulting.

Another factor, which could be related to this result, was nutrition of the animals. In both ranches, bisons predominantly grazed on grasslands, whereas in both zoos the animals were fed predominantly by hay. This fact could also affect animals' health condition because the bisons in both ranches often suffered from diarrhoea, caused just by fresh grass (Mach, 2016; Štěpánková, 2016). In the past, even liver flukes (*Fasciola hepatica*) were found in liver biopsy after slaughtering in Ranch Gallop, where a natural water resource could probably be a source of infection (Štěpánková, 2016).

Summarised, it is known that animals, which are not in a good physical condition and which are suffering from diseases, usually have the residues of their hair longer than healthy individuals (Vervaecke et al., 2005). All mentioned factors could affect the results of the statistical assessments.

### 6.3.3 Dominance rank and the degree of hair loss

Despite the fact that the observation periods and evaluations of moulting in this research differed from Vervaecke et al. (2005), the results of correlations did not differ much. In both studies, it was proved that the hierarchical position of the animals had an effect on the hair loss degree. This fact was again associated with many factors, such as animals' body condition, age, weight and others because higher ranking individuals were supposed to be younger, heavier and healthier. Therefore, it was expected that these animals lost its hair earlier than the lower ranking individuals. A more detailed description of these mentioned factors associated with dominance rank was described in chapter 6.4 below.

Langbein and Puppe (2004) mentioned that when using the $DI_{AI}$ for the hierarchy determination, the results could be confusing since an individual which was dominant over only a few herd members but achieved a high number of successful agonistic interactions could get a higher $DI_{AI}$ than the individual which is dominant over many group members but achieved only a lower number of successful agonistic interactions. Despite this, the results of correlations did not differ much, using $DI_{AI}$ ranks, as well as CBI ranks in this study.

In this thesis, it was not proved that nursing had an effect on the degree of hair loss, however, it should be evident. Since females invested their energy in gestation and lactation, they were expected to show later hair loss because they were not in such a good physical condition, compared to barren females, similarly as Vervaecke et al. (2005) described.

## 6.4 Dominance rank and other individual attributes

In past studies focusing on social dominance in ungulates, the researchers could analyse the connection between the dominance rank and the other individual attributes, such as weight, age and fatness because these data were available, compared to this study. Unfortunately, these attributes were not possible to obtain and explore further. Nevertheless, the results of individual studies vary.

In studies focusing on bisons, as well as on other ungulates, the dominance rank has been positively correlated with age (Horová et al., 2015; Jůnková Vymyslická et al., 2015, Rutberg, 1982), where older individuals often occupied the top hierarchical positions within the herds (Horová et al., 2015; Pluháček et al., 2006; Roden et al., 2005). The bison's dominance rank has been positively correlated also with body weight (Lott and Galland, 1987; Green and Rothstein, 1991; Roden et al., 2005; Vervaecke et al., 205), which is generally used as a reliable indicator of animal's quality (Vervaecke et al., 2005). The results differed in the study of Rutberg (1982) who did not find the relationship between dominance rank and body weight. In Lott (1979) study neither age nor weight correlated with the dominance status.

Two causal explanations can be suggested for this association. Weight can affect fighting ability (Lott and Galland, 1987) and thus result in high dominance rank and/or high dominance rank can improve feeding access and thus ensure higher weight (Vervaecke et al., 2005).

Another factor, which was examined by Vervaecke et al. (2005), is fatness, which also correlated significantly with bison's dominance rank. According to this author, the fatness, as a condition parameter, can actually be a better measure than weight because the result of the correlation between rank and fatness was the most robust. Nevertheless, the significant correlation between fatness and weight was overridden by their mutual association with dominance rank. Comparing the animals with similar weight (and age), heavier but thin animals were likely to be lower ranking than less heavy individuals with bigger fat deposits (Vervaecke et al., 2005).

Vervaecke et al. (2005) also observed, that ownership of horns can be important in rank acquisition and its maintenance in bisons, as well as in cattle (Bouissou, 1972) because over the course of the year, a top ranking bison female dropped to bottom rank after losing its horns during a fight with another individual (Vervaecke et al., 2005).

# 7. Conclusions

This research demonstrated that clear linear dominance hierarchies existed in captive American bison herds, where the relationships were transitive in all breeding facilities. Hereby the first hypothesis of this thesis was accepted.

The second hypothesis of the thesis has never been determined and evaluated before in other studies focusing on bison problematic. However, this hypothesis was also accepted because a significant difference in the degree of hair loss was detected between zoos and ranches, where the bisons in Prague zoo and Brno zoo had a higher degree of hair loss compared to individuals in Ranch Gallop and Červená.

In the case of the correlation between the individuals' dominance ranks and the hair loss degree, it was found out that the hierarchical animal status was connected with moulting. Thus it was proved that higher ranking animals lost its hair earlier than lower ranking individuals. This result accepted the third hypothesis.

The fourth hypothesis was rejected because it was not proved that nursing females used more intensive type of attacks during individual agonistic encounters than non-nursing females. As well as the connection between the nursing and the degree of hair loss was not found.

This master's thesis brought new hypothesis with its statistical analysis and consequently it is also providing an opportunity to other scientists to continue in examining this issue more deeply and subsequently to compare their results with this study. Nevertheless, this problematic cannot be further examined in the Czech Republic because there are only two zoological gardens, in particular Prague zoo and Brno zoo, where the American bison are held.

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# Appendices

<u>List of Appendices:</u>

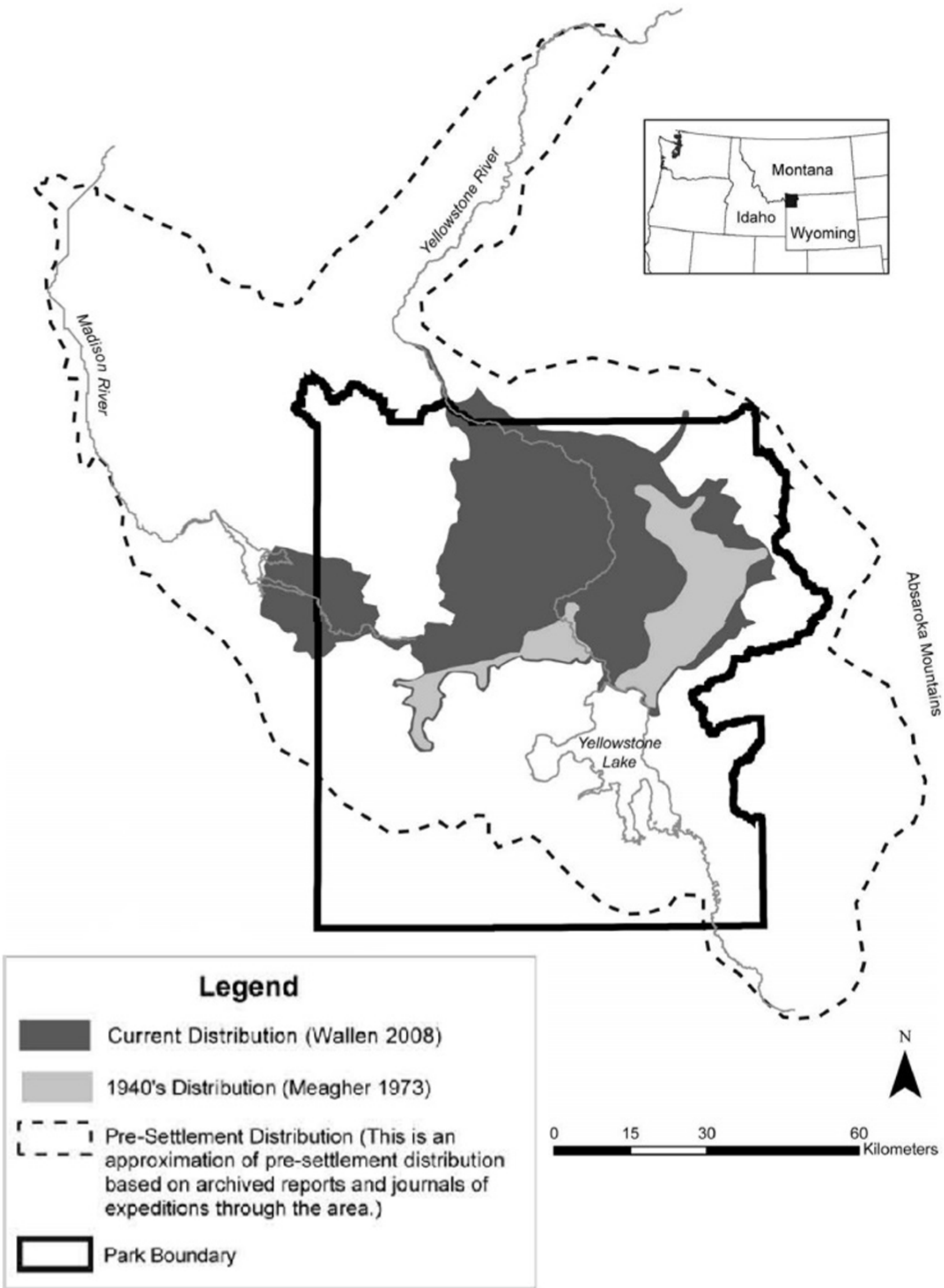
# Appendix 1

**The current and historical range of American bison (*Bison bison*) in North America:**


Source: Berman (2009)

## Appendix 2

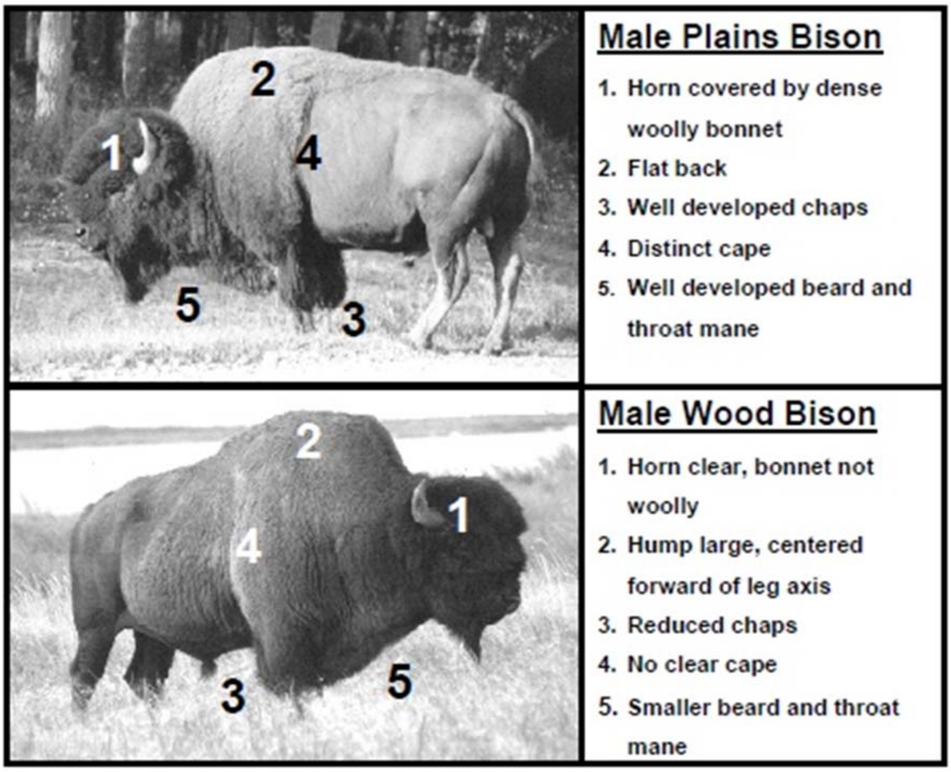
**Yellowstone National Park and the pre-settlement, mid-20$^{th}$ century, and present distribution of Yellowstone bison:**



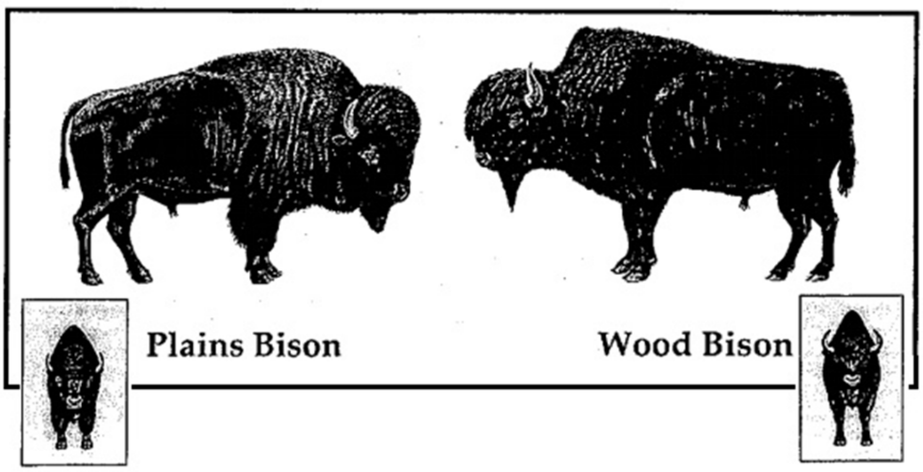

Source: Plumb et al. (2009)

## Appendix 3

**Physical differences of the American bison; comparison of morphological, structural and pelage characteristics between woods and plains bison:**




Source: Mitchell and Gates (2002)




Source: Stephenson et al. (2001)

# Appendix 4

**Demonstration of the observation methods:**

Not only in the case of Červená the binoculars had to be used, sometimes it was necessary to use it in Ranch Gallop as well because of the vast pasture area.

Photo: Vladimír Novák

Sometimes the observer was lucky to monitor the animals from a very close distance; nevertheless, behavioural sampling did not affect the animals in any manner.

Photo: Martin Franc

## Appendix 5

**Examples of evaluation of the degree of hair loss:**

For this appendix, the mixtures of the best quality photographs were selected from all breeding facilities to demonstrate individual stages of moulting. The estimated percentages of hair loss are written under the following figures.

The set percentage of moulting: 0 % (photo: author)

The set percentage of moulting: 10 % (photo: author)

The set percentage of moulting: 20 % (photo: author)


The set percentage of moulting: 30 % (photo: author)


The set percentage of moulting: 40 % (photo: author)

The set percentage of moulting: 50 % (photo: author)

The set percentage of moulting: 60 % (photo: author)

The set percentage of moulting: 70 % (photo: author)

The set percentage of moulting: 80 % (photo: author)


The set percentage of moulting: 90 % (photo: author)