

ZOOL 567: Animal Behaviour: Independent Research Literature Review, Part 3

Annotated Bibliography

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The annotated bibliographies below are organized in a way so that the first article is the most relevant (being a comparative study of all hypotheses), and the 2nd, 3rd and 4th articles being of equal relevancy (the previous hypotheses in the literature). Articles 5, 6, 7, 8, and 9 are then ordered from most useful, to least useful, but are however, not as important as articles 2,3, and 4. These are articles with background information, or information on wallowing but does not focus on the primary cause of it.

Secondary Sources are indicated by a (*)

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. [https://doi.org/10.1674/0003-0031\(2000\)144\[0159:WBOABB\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2000)144[0159:WBOABB]2.0.CO;2)

Summary: This article investigated the causes of bison wallowing (“dust-bathing”) behaviour in the tall grass prairie of Kansas in 1996-1997. The authors aimed to determine the primary cause of bison wallowing based on seven previously described hypotheses in the literature. These hypotheses included grooming behaviour associated with shedding, male-male interaction, group cohesion, play behaviour, relief of skin irritations from biting insects/ectoparasites as well as thermoregulation. To explore this question, the authors first composed a year-round study. Data was collected to compare bison wallowing frequency between the months of the year. Annual wallowing frequency was measured during a 4–6-day sampling period every other week from April to September of both years, and every other month from October – March. Wallowing occurrences were determined by placing a wooden marker in the center of the wallows. Wallowing was presumed to have occurred if the stakes were knocked over or missing from their original locations. The authors also explored daily wallowing frequency by watching a random sample of bison in 2-hour intervals. The sex and age were recorded when wallowing was observed. During the annual experiment, wallowing frequency varied significantly between sampling periods, peaking in July and September. This significant difference also occurred between the two-hour intervals in the daily experiments, where wallowing occurred more frequently in the afternoon than the morning or evening. Results also showed that males wallowed more frequently than females, and that adults wallowed more frequently than yearlings. The authors suggested that wallowing was related primarily to relief from biting insects, as the circannual and circadian wallowing frequencies aligned with the annual cycles of abundance for biting insects. This study is significant because it conducted a year-round study on a bison herd with a natural sex-age distribution. Unlike older literature on the topic, the authors provided quantitative data to support observation.

Contribution: This article provides insight into the primary causes of wallowing behaviour. The research present advances the knowledge on the topic by incorporating quantitative data and statistical analysis- where older studies relied on visual observation. This article compares the previously proposed hypotheses for bison wallowing and explains why the data point to a conclusion of relief from biting insects. With these results, the article provides a new set of research topics, around testing the relief-from-biting-insect-hypothesis. This article is an excellent source for finding related articles, especially primary literature on previous hypotheses for bison wallowing.

McHugh, T. (1958). Social behavior of the American buffalo (*Bison bison bison*). *Zoologica*, 43(1), 1–40. <https://doi.org/10.5962/p.206661>

****This article is large; therefore, a brief overview is stated, and discussion focuses on parts related to wallowing behaviour****

Summary: This article investigated the social behaviours seen in the American bison (*Bison bison*) based on the observation of both free-range and confined bison herds. The author aimed to make an account of all American bison behaviours which had not been done previously in the literature. To collect data, the author completed visual observations of three bison herds in Yellowstone National Park using the naked eye and 7x50 binoculars. Telephoto lenses were used to record bison activities on motion picture film. Herd movements were noted on a map, and a hand counter was used to take a census of the herds. Bison were individually identified and aged using the physical features of the bison. The author reported observations on fundamental behaviours (feeding, grooming, vocalizations, etc.), herd coordination, herd composition, dominance hierarchies, sexual behaviour, family relations, and ecological relations. In terms of bison wallowing, the author has suggested the primary causes to be male-male interaction during the rut and play behaviour. It was stated that while observing play, wallowing occurred so frequently that it should be considered an accessory to play, or just a form of play itself. Wallowing was also stated to have increased with the onset of the rut. The author suggested that this increase was attributed to more conflict occurring as a result of breeding season, and therefore an aggressive behaviour. Overall, wallowing by bulls was attributed to the tension between bulls during the rut, occurring where bulls sensed a hostile situation. This article was significant as it was the first major account of various bison behaviours. Although extensive data analysis has not been performed, visual observation accounts are still valuable and can be used in future studies to know what behaviours to look out for.

Contribution: At time of publication for this article, there was no adequate scientific study of American bison social behaviour. I chose this article to then compare how far research has come in observing bison behaviour and how methods have changed over time. This paper advanced knowledge in the field of bison behaviour by outlining a good visual observation of a range of bison behaviours. This article is also a good source for finding related articles, as well as information on behaviours of similar species. Future studies could observe the same behaviours and incorporate quantitative data to support conclusions.

Reinhardt, V. (1985). Quantitative analysis of wallowing in a confined bison herd. *Acta Theriologica*, 30(7), 149–156. <https://doi.org/10.4098/AT.arch.85-7>

Summary: This article investigated a captive bison herd on the banks of the North Saskatchewan River, from 1983-1984. The authors goal was to observe American bison (*Bison bison*) wallowing behaviour and use statistical analysis, which had not been done before, to determine if there was a significant difference between the relationship of wallowing with shedding, breeding, age, sex, and dominance rank. This was done to determine what the primary cause of bison wallowing was. The herd was observed 120 hours between February 1983 and January 1984. Data collection began after sunrise, and two-hour recording sessions were made on five consecutive days each month. Behaviours were recorded simultaneously for all herd members noting the sex and age of each bison. Wallowing activity was measured as the number of occurrences observed per animal in the two-hour period. Breeding activity was also noted, and statistical analysis followed data collection. It was found that wallowing frequency was highest when shedding occurred between April and September. Dominance rank and wallowing behaviour were determined to be strongly correlated, where older dominant individuals wallowed more than younger subordinate ones. Between the age classes, adults, and sub-adults both wallowed significantly more than yearlings, and there was no significant difference in wallowing frequency between adults and sub-adults. Males and females did not differ in dominance rank or wallowing frequency. No significant correlation between wallowing, breeding or conflict behaviour was found, thus, the primary reason for wallowing was reported to be for relief of irritation from shedding, due to the higher wallowing frequency corresponding to the months shedding occurs. This study was significant because the results challenged those that had been previously reported in the literature. Incorporating statistical analysis supported the visual observations in determining the primary cause of wallowing which gained more acceptance over studies only using visual observation.

Contribution: This article was chosen as it was one of the earliest studies incorporating quantitative data to support visual observations and author's conclusions. The results did not agree with previous studies, including wallowing being a relief from insects, however this would have been difficult to observe as the herd was living in an area with minimal insects. The confined herd also had an un-natural age/sex composition, as males separate from the herd after breeding. This poses new questions such as insect influence on confined bison herds, and how significant the age/sex distribution of a herd is in regard to wallowing frequency.

Mooring, M. S., & Samuel, W. (1998). Tick defense strategies in bison: The role of grooming and hair coat. *Behaviour*, 135(6), 693–718.
<https://doi.org/10.1163/156853998792640413>

Summary: This article focused on tick defense strategies in American bison (*Bison bison*) at Elk Island National Park (EINP), Alberta, from October 1995 to June 1996 during autumn, winter, and spring when winter ticks (*Dermacentor albipictus*) are active on hosts. The authors aimed at (1) determining how bison groom and how often, (2) why bison have few ticks, and if their grooming strategies aid in this, and (3) to see if calves groom more than adults in accordance with the body size principle. To answer these questions, the authors conducted behavioural observations from a vehicle using 10x binoculars or 15-60x spotting telescope. Grooming behaviour was recorded continuously in 20-minute focal animal samples, and activity budgets were determined by instantaneous scans at 2-minute intervals within the 20-minute sampling period. The focal animal was picked at random. Grooming, recorded as an episode or bout was listed as: oral grooming, scratch grooming, rubbing, or wallowing. To analyse tick infestation, 9 hides were prepared and marked into 10x10cm squares. Random sampling was used to choose squares to analyse. A process of digestion allowed ticks to be counted, and life stages assessed. Statistical analysis followed data collection. Results showed that bison performed grooming behaviours at a high rate in October when tick larvae were looking for attachment sites. Little grooming occurred November-April when nymphal and adult ticks predominated. Newly born calves were also found to groom 15-20 times more than adults, which agrees with the body size principal prediction where smaller animals need to get rid of more ticks. Overall, programmed grooming to remove larval ticks before they attach and a bison's thick coat, are proposed major reasons that bison host few ticks. This study is significant because it suggests a reason as to why bison host less ticks than other cervids, and therefore implies ecological and evolutionary success.

Contribution: This study was included because as discussed in the article, grooming in bison encompasses different behaviours, one of which is wallowing. Although not focused on wallowing itself, this article provides a hypothesis that wallowing, alongside other grooming behaviours helps get rid of ticks. In the broader picture this proposes new questions about the primary causes of wallowing, and if ectoparasites are a primary cause. This study advanced knowledge in the field of livestock as it suggests a reason why bison have less ticks than other Cervids. This could lead to studies on finding ways to lower tick load in cattle.

Lott, D. F. (2002). Bull to bull and cow to bull. In D. F. Lott (Ed.), *American bison: A natural history* (pp.5-22). University of California Press. <https://doi.org/10.1525/9780520930742>

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Summary: This chapter provided details on the observation of mating behaviour of male and female American bison during the rut. Primarily focusing on finding mates and the behaviours associated with that, this chapter also discussed the role urination plays in bison wallowing. The first section provided information on male-male interactions during the rut. The actions observed between males included competitive fighting behaviours such as showing off body size, physical contact, as well as a sudden termination of a fight- suggested to occur to save valuable energy to be put towards future mating events. Urinating in a wallow before wallowing was suggested to be an example of honest chemical signaling to indicate which male had higher testosterone levels. Section two discussed the differences in energy budget allocations between old and young male bison and provided information that older bison were more likely to take risks in combat for mates as they had less to lose. Young males were more careful as they would have future opportunities to mate. The section on cow-bull relationships further explained the role of urination, and how urinating in wallows may send chemical signals to other bison. American bison have a vomeronasal organ that senses chemical cues in urine, and therefore it was suggested that males could detect whether or not a female was ovulating from her urine. It was also suggested that ovulation would be stimulated in a female by smelling a males urine. Males and females only join the same herd during mating season. The final section discussed how the competitive nature of male bison died down during the spring, and a new goal arose to graze and rest to build fat stores. This article is significant as it may suggest that bison wallow to detect the chemical/hormonal signals of the opposite sex during mating season.

Contribution: This book chapter gives a good visual overview of bison mating behaviour, that may not be described in detail in primary literature on the topic. The chapter also provides observational information about the use of wallowing during the rut and the specific behaviours seen, e.g., urination, compared to some literature that just record the number of times a bison wallows during the mating season. This chapter supports the quantitative data present in the literature, while adding a detailed description. This chapter was chosen as it gives a whole overview of bison mating, and how wallowing fits into the whole occasion.

Coppedge, B. R., & Shaw, J. H. (2000). American bison (*Bison bison*) wallowing behavior and wallow formation on tallgrass prairie. *Acta Theriologica*, 45(1), 103–110.
<https://doi.org/10.4098/AT.arch.00-10>

Summary: This article investigated the social and spatial patterns of wallowing behaviour in American bison (*Bison bison*) populations on the tall-grass prairie in Oklahoma. The authors aimed to quantify wallowing activity, and determine what landscape features bison preferred for wallowing, as a study like this had never been performed. They hypothesized that wallowing would be an adult behaviour accompanied with aggressive interactions, and that wallow formation sites would be chosen randomly on the landscape. To explore this hypothesis, the authors surveyed the study area four to twelve times a month during daylight hours to determine bison habitat use. The location, size and composition of groups were mapped onto a topographic quadrangle with the help of arial photographs. Random groups were observed during one-to-three-hour observation periods from November 1993 to October 1995. The substrate used to wallow, age/sex, and aggressive interactions associated with wallowing were recorded. To determine preferred landscape characteristics, the area was first examined to determine pre-existing soil depressions. The site was then re-surveyed bi-monthly to locate new wallows, which were mapped and used to determine elevation, slope, and aspect. Statistical analysis was performed after data collection. It was found that adults wallowed more frequently than juveniles, and aggressive interactions were rarely associated with wallowing, therefore thought to instead be a comfort or grooming behaviour. The spatial distribution of wallows was significantly different from overall bison habitat use, and bison preferred wallowing in exposed soils on level areas where fall and spring burns had occurred. This study is significant as it was the first to document specific landscape features selected by bison for the execution of wallowing behaviour. It does however present a question on whether sex distribution plays a roll in aggression as the herd composition of females to males in this study was seven to one.

Contribution: This article was chosen as it provides information on specific areas that bison target to perform wallowing activities. The majority of the results of the study aligned with previous research in the field. Data that did not proposed new questions, including how sex distribution may influence the relationship of aggression and wallowing behaviour, and what the primary causes of wallowing actually are. The article also describes how bison are able to alter the prairie landscape through wallow formation as soil disturbance sites can increase plant and habitat diversity- therefore making them a keystone species. I thought that was very interesting.

Coppedge, B. R., & Shaw, J. H. (1997). Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. *The American Midland Naturalist*, 138(1), 189–196. <https://doi.org/10.2307/2426665>

Summary: This article explored the effects of horning and rubbing behaviour by American bison (*Bison bison*) on woody vegetation in the tall-grass prairies of Oklahoma. After being re-introduced to the area after an absence of 140 years, the authors aimed to quantify horning and rubbing activity, characterize the objects selected for use by bison during these behaviours, and to examine the effect of these behaviours on the woody vegetation. From June-October 1993, the authors first counted and measured the woody plants and other vertical objects inside the study location prior to bison release which were mapped onto topographic quadrangles with help of aerial photographs. Existing damage on these plants and features were noted. Objects were categorized into three groupings including trees, small woody plants, and miscellaneous objects (wooden poles, posts, etc.). After re-introduction, the study area was re-surveyed, and objects were checked for bison use. Use was determined by presence of shed hair, hoofprints around the object, horn scratches, broken vegetation limbs, stems or bark. Live vegetation was quantified by percentage of stems broken where non-living objects were marked as used, or unused. Animals were also visually observed for horning behaviour during daylight hours from November 1993 to October 1995. Age/sex class, and objects horned were recorded. Statistical analysis followed data collection. Analysis suggested that horning and rubbing activity was significantly higher in the summer compared to other months, however, the cause for this increase was not determined. This behaviour also had measurable impacts on woody vegetation in the study area, with the greatest effect on saplings and shrubs. Bison showed a preference towards using small willows and miscellaneous man-made objects for performing horning and rubbing behaviours. This study is significant because it is one of the few studies quantitatively documenting the effects bison have on woody vegetation on the plains.

Contribution: I choose this article to further explain bison grooming behaviours and their effect on the surrounding environment. In addition, horning behaviours- like wallowing are suggested to be a socially motivated aggressive behaviour during the rut, therefore, this article can be used to compare and see if the two behaviours share a primary cause. This article advances knowledge in the field by determining what bison prefer to use for horning activities. It also presents new questions including what causes horning behaviour to be significantly higher in the summer, and what would happen if man-made objects were removed from the study area.

Mooring, M. S., Patton, M. L., Reisig, D. D., Osborne, E. R., Kanallakan, A. L., & Aubery, S. M. (2006). Sexually dimorphic grooming in bison: The influence of body size, activity budget and androgens. *Animal Behaviour*, 72(3), 737–745.

<https://doi.org/10.1016/j.anbehav.2006.02.006>

Summary: This article explored the relationships of body size, breeding activity, and androgens on sexually dimorphic grooming in American bison (*Bison bison*). The authors aimed to simultaneously observe the grooming rates of male and female bison to see if body size and vigilance (alertness) had an effect on the differences between male and female grooming. Bison were studied before and during the rut (breeding season) from June-August 2002 at the National Bison Range (NBR) and from June-August 2004 at Fort Niobrara (FTN). At NBR, bison were branded with the last digit of their birth, indicating their age. As bison were not individually marked, effort was made to sample from multiple groups to avoid repeat sampling. Observations were made from vehicles using 10x binoculars and 15-60x telescopes in 20-minute sampling periods using a focal animal. Grooming behaviour was recorded continuously, and instantaneous sampling in 1-minute intervals was conducted to determine the mean percentage of time that focal animal engaged in a particular task. At FTN, bison were uniquely branded to tell them apart. Methods were the same as those at NBR except that androgen levels of these bison were measured using faecal steroid analysis. After observations were complete, statistical analysis was performed. This study found that the body size and degree of bison alertness had an effect on grooming in bison. It was also determined that male grooming was suppressed during the rut, leading to sexually dimorphic grooming, due to elevated testosterone levels. This study is significant because it provides a relationship between body size, androgen levels and grooming during the rut. Previous studies have only focused on these relationships outside the rut. This study also associated elevated androgen levels with the suppression of male grooming during breeding, while previous studies just stated that androgen levels increased during this time.

Contribution: I chose this article because it focuses on activities happening during the rut. Bison wallowing is sometimes included in grooming behaviour, and therefore this article provides information of why grooming (including wallowing) may be higher in males or females depending on time of year. This article helps achieve a better understanding of the mechanisms behind grooming, not just observations of when it happens. Bison were branded in both wildlife refuges during this study, indicating human contact. Future studies could focus on similar research questions, but in a herd not subject to human interaction to see if that has an impact.

Caboń-Raczyńska, K., Krasieńska, M., Krasieński, Z. A., & Wójcik, J. M. (1987). Rhythm of daily activity and behavior of European bison in the Białowieża forest in the period without snow cover. *Acta Theriologica*, 32(21), 335–372. <https://doi.org/10.4098/AT.arch.87-24>

Summary: This article investigated the rhythm of activity and behaviours of European bison (*Bison bonasus*) from 1982-1984 in the Białowieża Forest in Russia during the period without snow. Previous studies on European bison activity had occurred in the Prague zoo, however, these bison were not living under natural conditions. The authors aimed to explore this issue and conducted a study on a herd with a normal sex-age distribution living in their natural habitat. Activity and behaviour were analysed from both individual and group point of views, then compared to American bison (*Bison bison*). Using 7x50 binoculars, twenty daily cycles of visual observations were conducted by two observers simultaneously to determine individual behaviour. Group behaviour was observed from April-September and the duration of different activity types were noted. Forms of group activity were described in 15-minute intervals, and the percentage of bison engaging in particular activity phases were noted. The study found that the rhythm of activity occurred in many phases with group activities being highly synchronized. In terms of feeding, resting, and walking, the bison used 60.4% of the day foraging, 31.9% resting, and 7.7% for movement without foraging. A deeper look into foraging determined that bison spent 95.2% of the day grazing, 2.9% browsing, and 1.9% barking. Young calves drank milk several times a day for ~4.2minutes from May-July, and older calves drank milk ~6.7minutes from August-October. These results were similar to those observed in American bison, and slight differences were explained to be a result of the differences in habitat. Wallowing was intensified during the rut and occurred more frequently in females than males, and in adults more than juveniles. This differed from American bison as bulls wallow more frequently. This study is significant because it conducted a study on a mixed, undisturbed bison herd in their natural environment.

Contribution: I chose this article as it provides insight into the behaviour of European bison which I thought would be good to compare/contrast with the American bison. Although an older article, when published, this article advanced knowledge in the field because it focused on a mixed bison herd in periods of no snow cover, undisturbed by man. Previous studies in the area occurred during winter, where the bison were given additional food to survive. The article supports previous studies on behaviour seen in American bison, however, poses more questions of whether habitat differences are responsible for the small changes we see.