

Scent Marking in American Bison: Morphological and Spatial Characteristics of Wallows and Rubbed Trees

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Abstract

We studied scent marking in a free-ranging population (ca. 450 animals) of American bison (*Bison bison*) in interior Alaska, USA, during rut (August 1996). Wallows averaged 2.8 m in length, 2.3 m in width, and 0.07 m in depth. Wallows were not clumped spatially, and their spatial arrangement was not correlated with their distance to the edge of the forest. Sixteen percent of these 50 wallows exhibited multiple use by bison. Bison selected fields of oats for wallowing, which had been plowed and planted in spring, over blue grass that had not been plowed recently. All sex and age classes of bison wallowed, but only large males (≥ 5 years old) wallowed more often than their proportional occurrence in the population. Bison strongly selected pole-sized black spruce (*Picea mariana*) for rubbing. Rubs averaged 50 cm in length and were centered 70 cm above the ground; rubbed spruce were located 7 m apart. No rubs were located 5 m into the forest from rubbed trees, but 80% of 60 rubbed spruce had a wallow located within 5 m of them. Bison broke the top of > 20% of the spruce they rubbed. Females rubbed trees more often than their proportional occurrence in the population. Wallowing and rubbing of trees occurred in several behavioral contexts. We hypothesize that these scent-marking behaviors are linked and may be related to the priming of estrus in females.

Key words: Alaska, American bison, *Bison bison*, rubbing, scent marking, spatial distribution, wallowing.

Introduction

Scent marking is widespread among mammals (Ewer, 1968) and has been especially well described for ungulates (Bowyer et al., 1994; Coblentz, 1976; Gosling, 1985). Some authors have considered scent marking as being synonymous with territoriality, but as Ralls (1971) noted, many nonterritorial species also scent mark. Thus, the information imparted by these displays and their

resulting marks may go well beyond the delineation of a boundary or the advertising of the presence of an animal (Leuthold, 1977). Moreover, scent-marking displays by ungulates often incorporate striking visual components that make these behaviors more obvious, and scent marking typically incorporates urine, feces, or products from scent glands as olfactory signals that accentuate the display or mark (Leuthold, 1977). The function of such displays, however, is less certain.

For American bison (*Bison bison*), at least two behavioral displays that leave behind obvious marks in the environment have been described: wallowing and the rubbing of trees (Fuller, 1960, 1961; McHugh, 1958; Meagher, 1973; Soper, 1941). Similar behaviors in other ungulates are related to scent marking (Leuthold, 1977), and we believe these displays likely perform this function in bison. In addition, we observed rubbed trees and wallows in close proximity during rut suggesting these marks may be linked behaviorally.

Our purpose was to describe wallowing and rubbing by bison during rut, quantify the morphology and spatial distribution of these marks, and to test the following null hypotheses: 1) no differences existed in the sex and age classes of bison that engaged in wallowing or rubbing; 2) no differences occurred in the social contexts in which these behaviors were performed; 3) bison did not select particular habitats in which to wallow or species or size classes of trees to rub; and 4) there was no spatial clumping of wallows and rubs, or a spatial arrangement between these marks. Finally, we discuss the potential function of wallowing and rubbing by bison during rut.

Study Area

We studied scent marking by bison on the Delta Junction Bison Range (63°50'N, 145°10'W) about 260 km southeast of Fairbanks, Alaska, USA. Most observations of bison and their scent marks were made on the Panoramic and Gerstle fields. Bison migrate to these areas in mid to late July for rut. The Delta Bison Herd, which is harvested under a permit hunt, numbers about 450 animals. This herd of plains bison (*B. b. bison*) was established in 1928 with the translocation of 23 animals from the National Bison Range in Moise, Montana (Berger, 1995). Bison occurred naturally in Alaska, however, into recent times (Guthrie, 1990).

The Delta Bison Range is managed by the Alaska Department of Fish and Game to lure bison away from nearby agricultural crops (mostly barley and oats). Thus, the fields of the bison range (ca. 6,500 ha) are plowed, planted with oats, burned, and fertilized to make these areas attractive to bison. This area is relatively level and occurs at an elevation of about 310 m. The surrounding forest is dominated by black spruce (*Picea mariana*) and aspen (*Populus tremuloides*) with an understory of willows (*Salix* sp.). Wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) both occur on the study area. The climate is typical of interior Alaska. Summers are short but temperatures may reach 30° C; winters are long (snow often persists for 8 months) and minima below -40° C are not uncommon. The mean annual temperature is -3.5° C, and the area receives 25-30 cm of precipitation annually. The area may experience high winds in any season.

Methods

We conducted research on bison primarily during the peak of rut (8-24 August 1996). We sampled wallows on five plots that ranged from 0.42 to 1.20 ha by searching each systematically for wallows. These plots were located in fields where we had observed large groups (>50 animals) of bison previously. We measured the length, width, and maximum depth of each wallow to the nearest 1 cm and noted if more than one bison had used the wallow. We also searched a 5-m stretch at the

nearest forest edge for the presence of rubbed trees. We noted the habitat in which the wallow occurred (oats or bluegrass), the distance to the nearest wallow (an index to spatial clumping), and the distance to the edge of the forest. These spatial data also were collected for 50 random points allocated equally among our five plots.

We sampled rubbed trees along a 550-m stretch of forest edge where we previously observed bison rubbing trees. We recorded the species of tree, diameter at its base and at breast height (dbh = 137 cm), height of the first branch above the ground (all to the nearest 1 mm), and whether the tree had a broken top and was alive. We also noted if a wallow occurred within 5 m of the rubbed tree, or if another rubbed tree occurred along a 5-m transect centered on the rubbed tree, but located 5 m into the forest. We recorded data on the characteristics of the rub (length, height of the mid-point above the ground, diameter of the mid-point) to the nearest 1 mm. We also measured the distance to the nearest rubbed tree (nearest 1 cm). We collected these same spatial data for 100 trees that were not rubbed recently by bison that we selected at random along the same edge of forest. To assure trees we sampled had been rubbed recently by bison, we required that such a tree have a polished area embedded with a thin layer of dirt and have bison hair on the rubbed area.

We made behavioral observations of bison from a vehicle to avoid disturbing the animals and recorded data using an all-occurrences log (Altmann, 1974) for subsets of the herd that could be observed without having our view obscured by vegetation or topographic relief. We conducted herd composition counts and categorized bison into sex and age classes based on body size and horn conformation (Berger and Cunningham, 1994; Fuller, 1959, 1960).

We used the *G*-test for comparing behavior by bison against their proportional occurrence in the population (Sokal and Rohlf, 1969). We used the Kruskal-Wallis test (Zar, 1984) or the two-sample *Z*-test for proportions (Remington and Schork, 1970) to compare wallows and rubs with random samples. We employed simple linear regression to test for a spatial relationship between clumping of wallows and their distance to the edge of the forest (Zar, 1984).

Results

Overall, wallows were only slightly longer than wide, and were shallow (Fig. 1). The density of wallows ranged from 8 to 24/ha, with a mean of 15.4/ha ($SD = 6.3/ha$). Wallows were not located differently from random points with respect to their distance from the forest edge, or their nearest neighbor (Fig. 1).

Sixteen percent of 50 wallows exhibited evidence of use by multiple bison. These wallows were significantly ($P < 0.001$) longer ($\bar{X} = 5.2$ m, $SD = 0.8$ m) and wider ($\bar{X} = 3.9$ m, $SD = 0.4$

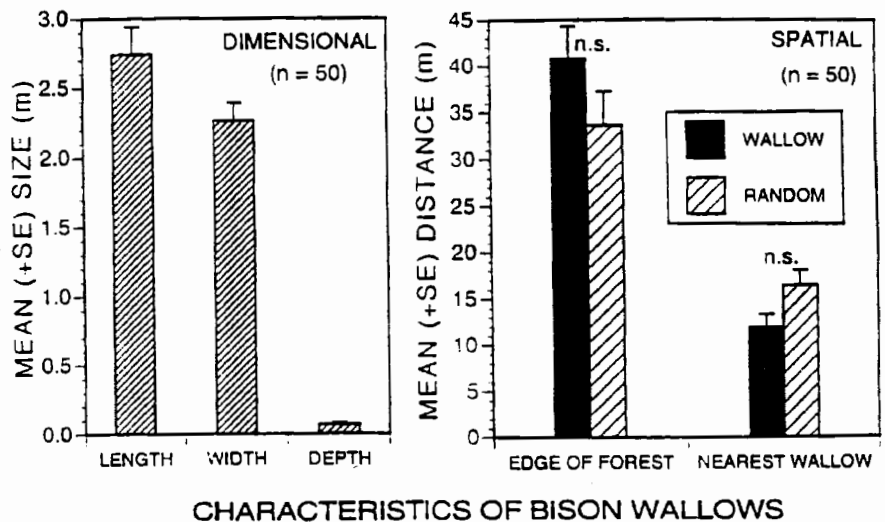


Fig. 1. Dimensional and spatial relationships of bison wallows in interior Alaska, USA, August 1996; ns = not significant ($P > 0.05$).

m), but were not deeper ($\bar{X} = 0.09$ m, $SD = 0.02$ m; $P < 0.064$) than wallows used by single bison. Wallows used by more than one bison differed, neither in their distance to the edge of the forest ($\bar{X} = 36.5$ m, $SD = 11.3$ m; $P > 0.60$) nor in their distance to their nearest neighbor ($\bar{X} = 9.6$ m, $SD = 1.9$ m; $P > 0.59$), from wallows used by single bison.

We further investigated whether the clumping of wallows, as indexed by nearest-neighbor distance, was influenced by the distance of wallows to the edge of the forest. No significant relationship existed between these variables (Fig. 2). Nonetheless, sixteen percent of 50 wallows had a rubbed tree (all black spruce) at the nearest forest edge to a wallow. Moreover, there was a significant effect of habitat on the location of wallows. Bison selected oat over bluegrass habitat for wallowing (Fig. 3). Wallowing also differed among sex and age classes of bison relative to their proportional occurrence in the population. This difference was caused mostly by large males (≥ 5 years old) wallowing more frequently than other bison (Fig. 4).

Bison wallowed in a variety of social contexts. For instance, large males urinated while wallowing on two occasions before serious fights over females. We did not observe other sex and age classes urinate in association with wallowing.

On four occasions (one large bull, one medium bull, and two females), we observed bison alternately wallow and rub trees. Twice we watched males (one large, one small) wallow nearby after smelling a tree rubbed by a female. In addition, one large male and one female

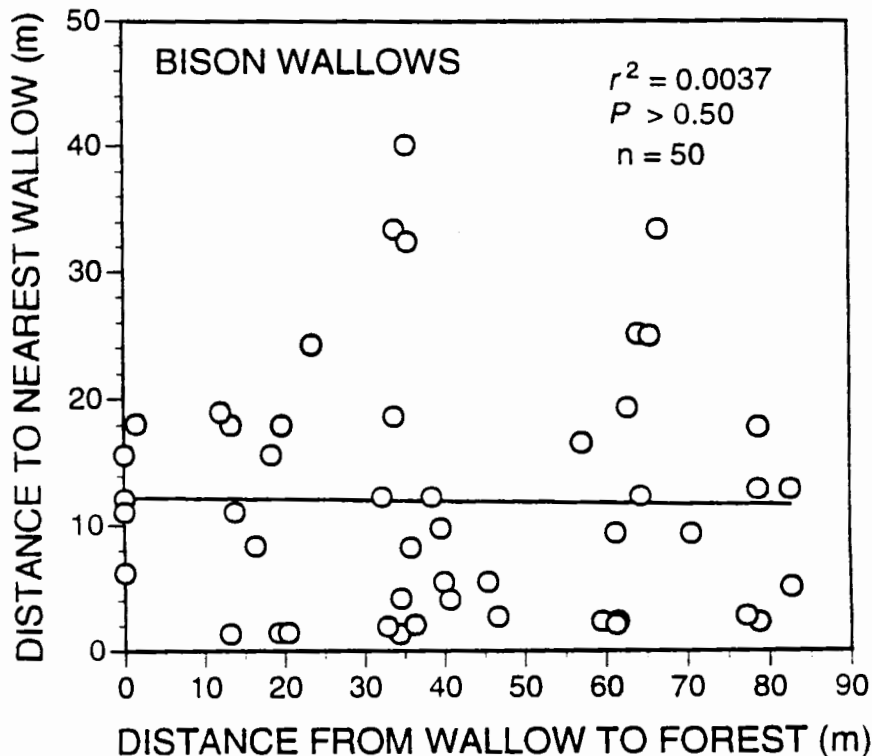


Fig. 2. Relationship of distance between bison wallows (an index to spatial clumping) and their distance to the forest edge, interior Alaska, USA, August 1996.

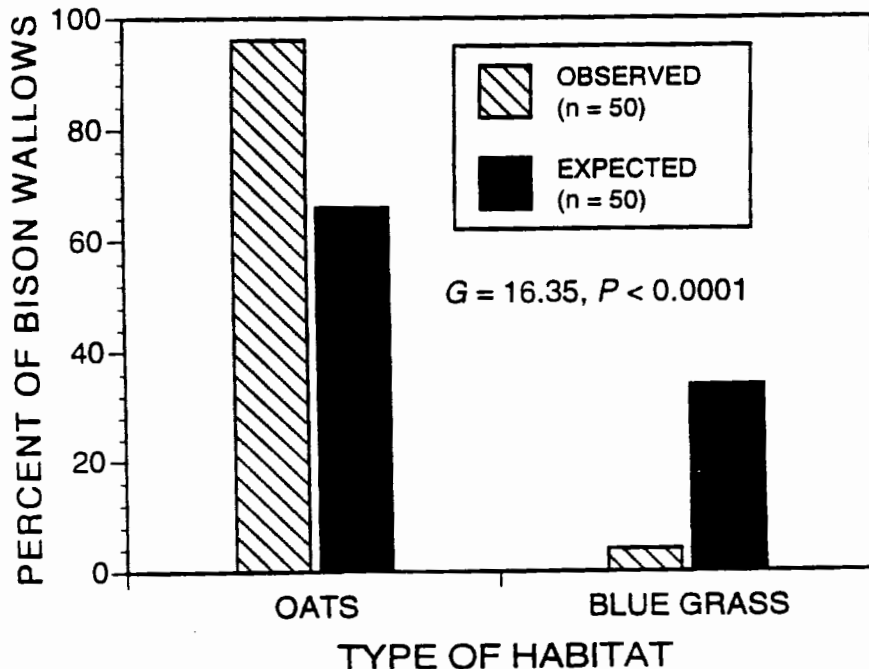


Fig. 3. Preference for wallowing by bison in oat and bluegrass habitats, interior Alaska, USA, August 1996. Oats were plowed and planted that spring, whereas blue grass had not been plowed recently.

carried the broken top from a rubbed spruce in their mouth to an existing wallow and then wallowed on top of the broken tree top. On 63% of 75 occasions, we observed wallowing by one animal trigger wallowing by other bison; 81% of 75 wallowing bouts involved both sexes.

Black spruce composed 93% of the 100 trees we sampled randomly along the edge of the forest; the remainder were willows. Only black spruce were

rubbed by bison, perhaps because willows were too small. Bison selected trees to rub that possessed a larger basal diameter and a higher first branch above the ground than were available; no difference existed in dbh between random and rubbed black spruce (Table 1). Rubs averaged > 70 cm in length and were located > 7 m apart (Fig. 5). The reason that dbh did not differ between rubbed and randomly selected trees was because bison often broke the top of spruce they rubbed, and such trees often had a dbh of zero. Over 20% of trees rubbed by bison had a broken top; bison did not select living over dead trees for rubbing (Fig. 6).

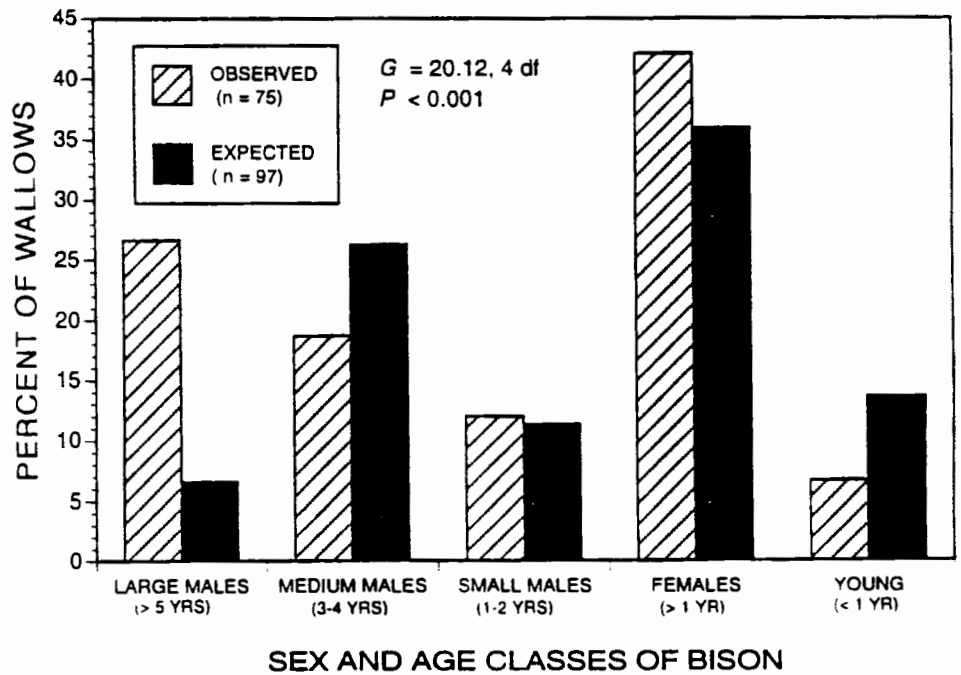


Fig. 4. Wallowing by sex and age classes of bison relative to their proportional occurrence in rutting groups, interior Alaska, USA, August, 1996.

Table 1. Characteristics of black spruce that were rubbed by bison compared with randomly selected spruce in interior Alaska, U.S.A., August 1996.

Characteristic	Rubbed (n = 60)			Random (n = 93)			P-value ^a
	\bar{X}	SE	Range	\bar{X}	SE	Range	
Diameter at base (cm)	15.6	1.1	4.8 - 60.9	12.6	0.9	2 - 38.2	<0.05
Diameter at breast height (cm)	7.9	1.2	0 - 45.0	6.9	0.9	0 - 31.0	n.s.
Height of 1 st branch above ground (cm)	59.2	6.2	2.0 - 212.0	31.6	2.8	1 - 124.0	<0.01

^aP-values from Kruskal-Wallis test; ns = not significant

No rubbed trees were located by searching a 5-m transect parallel to the forest edge 5 m into the forest from each rubbed tree; rubs were confined to the edge of the forest. Eighty percent of 60 rubbed spruce had a wallow located within 5 m of a rub. Although all sex and age classes of bison except young rubbed trees, females rubbed trees disproportionately more often than did other bison (Fig. 7).

Discussion

Both wallowing and rubbing of trees clearly constitute scent-marking behavior by bison. Scent urination among ungulates is a common form of such marking (Coblentz, 1976), and the association of urinating and wallowing by large male bison fits this common pattern. For instance, elk (*Cervus elaphus*) typically thrash-urinate prior to aggressive interactions between large males during rut (Bowler and Kitchen, 1987; McCullough, 1969). Likewise, moose (*Alces alces*) urinate in rutting pits; ostensibly to attract females during the mating season (Miquelle, 1991). Coblentz (1976) provides an extensive review of this behavior in bovids and other ungulates.

Coblentz (1976) noted that scent urination may have a dual function. First, this behavior may serve to advertise the physical condition of males via the odor of byproducts of metabolism contained in their urine, as proposed initially by McCullough (1969) for elk. Thus, dominant individuals in good physical condition could intimidate potential rivals by a urine odor that signaled their status without engaging in dangerous combat. The potential shortcomings of males adopting such a strategy when in poor condition or in attempting to mask declining physical condition have been discussed by Coblentz (1976) and Bowyer and Kitchen (1987) and will not be reiterated here.

A second function of scent urination involves the priming of estrus in females (Coblentz, 1976). Large males mate more often than smaller subordinates in bison (Berger and Cunningham, 1994; Lott, 1974, 1979, 1981), and reproductive effort increases as males age (Maher and Byers, 1987). Coblentz (1976) provides an extensive review documenting that the presence of a dominant, rutting male can hasten the onset of estrus in both bovids and cervids. In many species, late-born young are at a selective disadvantage (Clutton-Brock et al., 1987), thereby conferring benefits to females with young conceived earlier in the mating season. Moreover, advantages relative to predation may accrue to young that are born synchronously (Estes, 1976). Indeed, bison in northern environments are preyed upon by wolves and bears (Carbyn and Trotter, 1987), but variation in birth synchrony

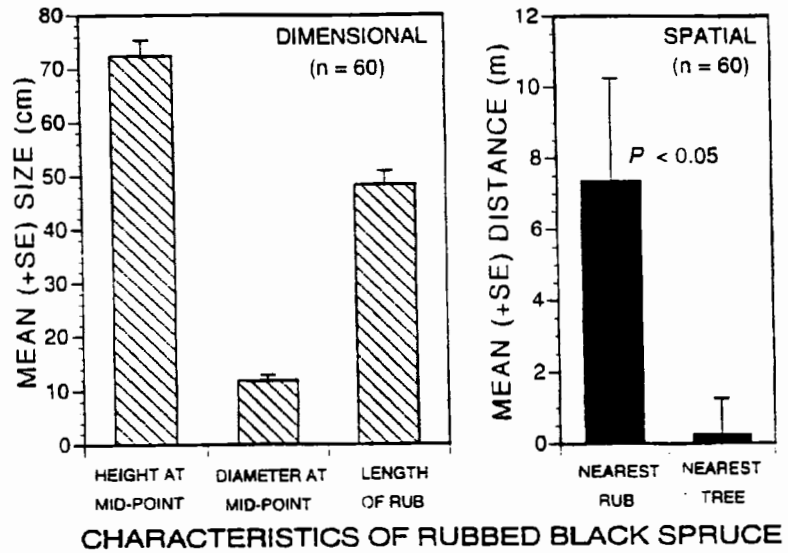


Fig. 5. Dimensional and spatial relationships of black spruce rubbed by bison, interior Alaska, USA, August 1996.

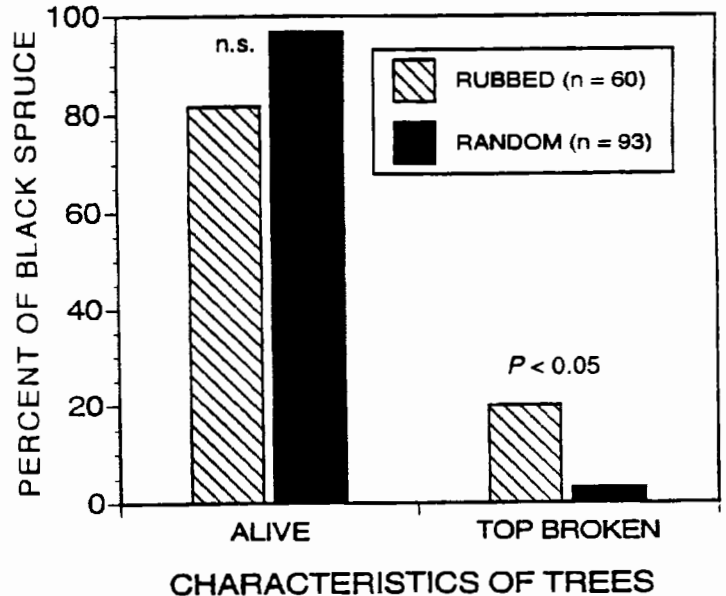


Fig. 6. A comparison of black spruce rubbed by bison with randomly selected spruce, interior Alaska, USA, August 1996.



Fig. 7. Rubbing of black spruce by sex and age classes of bison relative to their proportional occurrence in rutting groups, interior Alaska, USA, August 1996.

occurs among populations of bison (Green and Rothstein, 1993; Rutberg, 1984; Shaw and Carter, 1984). Moreover, bison (Berger, 1992) and other ungulates (Rachlow and Bowyer, 1991) likely have the ability to adjust gestation length, but such adjustments would not likely compensate completely for a failure to conceive at an optimal time. These two hypotheses for scent urination are not mutually exclusive, however, and wallowing by male bison may serve both functions (dominance signaling and priming of estrus in females) because this behavior occurred in both male-male and male-female contexts.

Hypotheses concerning scent urination, however, will not explain why female bison wallow. One explanation is that wallowing is merely comfort behavior to help reduce ectoparasites. For instance, wallowing in captive bison was confined to the period in which they were shedding hair, and all sex and age classes of bison wallowed (Reinhardt, 1985). We cannot discount that some of the wallowing we observed was comfort behavior, but several lines of reasoning make it unlikely that this was the only function of this behavior. We confined our sampling to the peak of rut, where the social role for wallowing should be most important if this behavior relates to dominance interactions or reproductive status. Clearly, the behavioral significance of wallowing for males (i.e., scent-urination) and its link with aggressive behavior in large bulls (Lott, 1974, 1979, 1981) argues against the exclusive use of wallowing as a comfort behavior. Likewise, differential amounts of wallowing by the sex and age classes of bison (Fig. 4) suggests a social function for wallowing. Synchrony in wallowing also suggests a social role for this behavior. Reinhardt (1985) reported that 61% of 264 wallowing bouts involved two or more bison; we observed multiple bison wallowing in 63% of 75 wallows. We know of no evidence for social facilitation in grooming behaviors or what the adaptive

significance of synchronized comfort behaviors might be. Finally, the behavioral and spatial relationships between wallowing and rubbing indicates these behaviors have a social significance to bison. None of these observations can be explained solely as an outcome of comfort behavior.

We hypothesize that wallowing by females is a return signal to males that advertises the presence of a female near estrus. Rutting groups we observed moved several kilometers during a day, and wallowing by females would leave behind a visual and likely an olfactory signal that could attract large males. These large males make extensive movements during rut in search of estrous females, and females would likely benefit from attracting large, dominant males for mating. Moreover, bison males may be choosy in selecting a female with which to mate (Berger, 1989), providing another reason for females to advertise their reproductive status; not all females may be receptive each year (Lott, 1985). In addition, we hypothesize that females may come in contact with pheromones that prime estrus by wallowing where males have wallowed previously; 81% of 75 wallowing bouts involved both sexes. The advantages of synchronized reproduction to females already have been noted. Obviously, more research is needed to critically test these ideas, but our observations are consistent with these potential functions for wallowing.

Rubbing of trees is a common scent-marking behavior of ungulates, especially among cervids. For instance, mule deer (*Odocoileus hemionus*, Bowyer, 1986), white-tailed deer (*O. virginianus*; Benner and Bowyer, 1988; Marchington and Hirth and, 1984; Oehler et al., 1995) elk (Bowyer and Kitchen, 1987) moose (Bowyer et al., 1994), roe deer (*Capreolus capreolus*, Johanson et al., 1995), and many other species all rub trees in a social context, although the function of this behavior likely varies among species.

We hypothesize that female bison rub trees to advertise estrus, as Bowyer et al. (1994) suggested for the function of this behavior in moose. Rubbed trees would provide a less ephemeral mark than a wallow and would aid large males searching for potential mates. Of course, the return signal from males (i.e., the presence of a potential mate) likewise would be advantageous for both sexes. Females rubbing more often than other bison (Fig. 6), however, suggests the function of this behavior relates primarily to the reproductive status of females during rut. The behavioral association between wallowing and rubbing by bison indicates a similar function for these behaviors. Although more data are needed to test this hypothesis, our data are consistent with this interpretation.

Why trees are an important component of scent marking in a species adapted to a grassland environment is uncertain. Certainly, bison would have encountered scattered trees in the prairies (Higgins, 1986), and perhaps the rarity of trees help to further attract the attention of conspecifics to the mark. Oehler et al. (1995) have documented the importance of trees to white-tailed deer in a prairie environment.

Finally, the absence of a spatial clumping of wallows likely relates to the many behavioral contexts in which wallowing occurred. If wallowing serves a social function other than territoriality, there is no obvious benefit to a clumped spatial distribution; bison are not territorial (Lott, 1974). The absence of a spatial relationship between the distribution of wallows and distance to the edge of the forest (Fig. 2) indicates it is not the edge of the forest alone that is important. Rather, the link between rubbing of particular trees (Table 1) and the presence of nearby wallows indicate the similar nature of these scent marks. Selection for a particular habitat for wallowing, however, may concentrate wallows in some areas (Fig. 3). We believe that selection for oat habitat for wallowing was

more likely related to this habitat being plowed than to the type of vegetation, thereby creating a more favorable substrate for wallowing.

Clearly, the reasons underlying why bison wallow and rub trees and the functions of these behaviors are complex and require further study. We hope, however, that our data and the hypotheses we forwarded will provide the necessary first steps in understanding scent marking in this unique ungulate.

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