



Effects of Horning and Rubbing Behavior by Bison (*Bison bison*) on Woody Vegetation in a Tallgrass Prairie Landscape

Bryan R. Coppedge; James H. Shaw

American Midland Naturalist, Vol. 138, No. 1. (Jul., 1997), pp. 189-196.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0031%28199707%29138%3A1%3C189%3AE0HARB%3E2.0.CO%3B2-J>

American Midland Naturalist is currently published by The University of Notre Dame.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

Effects of Horning and Rubbing Behavior by Bison (*Bison bison*) on Woody Vegetation in a Tallgrass Prairie Landscape

BRYAN R. COPPEDGE AND JAMES H. SHAW

Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology,
Oklahoma State University, Stillwater 74078

ABSTRACT.—Horning and rubbing behaviors of American bison (*Bison bison*) and their effects on woody vegetation were investigated for 2 yr on a herd of 300+ animals reintroduced to a 1973-ha tallgrass prairie site in Oklahoma. Horning and rubbing activity was significantly higher in summer than in other seasons. Whether this increase was associated with rut, shedding of winter pelage, insect harassment, or a combination of these factors was unclear; however, these behaviors did have measurable impacts on the woody vegetation of the area. Bison injury to trees was minimal, although one willow (*Salix nigra*) was uprooted and killed during the study, and several other trees were seriously damaged. Bison horning had the greatest effect on saplings and shrubs, killing or severely damaging 4% of the woody plants documented within the study area and causing moderate injury to 13% and light injury to 12%. Bison showed a strong preference for small willows, killing or severely damaging 17% of the saplings and shrubs of this species during the study. Bison also used artificial, man-made objects present on the landscape such as utility poles and fenceposts. Results suggest that horning and rubbing by bison, along with fire and drought, may have influenced the historical distribution of woody vegetation in prairie environments.

INTRODUCTION

Bison (*Bison bison* L.), like many large mammals (Snyder and Janke, 1976; Inouye *et al.*, 1994), are capable of severely impacting woody vegetation. England and DeVos (1969) suggested that herds of bison in North American prairies once influenced the distribution of woody vegetation by horning, rubbing, grazing and trampling. Soper (1941) noted that wood bison (*B. b. athabascae*) destroyed trees by horning and rubbing against them to reduce insect irritation. Similar behavior has been observed in populations of plains (*B. b. bison*) bison (McHugh, 1958; Meagher, 1973). Moss (1932) and Campbell *et al.* (1994) concluded that the near extinction of bison from overhunting in the northern plains contributed to the expansion of aspen (*Populus tremuloides*) woodland into prairies during the late 1800s.

Few studies have documented quantitatively the effects of bison on woody vegetation. Edwards (1978) found that bison in private midwestern herds destroyed woody plants by horning, rubbing and feeding on bark. In one case, 15 bison in a 36-ha enclosure had debarked 80% of the 600 trees in a 1-ha grove in 1 yr, killing most by the following year. He noted that bison exhibited species preferences in their horning, rubbing and feeding activities. McHugh (1958) found that 14% of a small sample of lodgepole pines (*Pinus contorta*) horned by bison in Yellowstone National Park (YNP) were girdled and killed. Horning and rubbing of lodgepole pine by an estimated 2500 bison spending the summer of 1992 in the Hayden Valley of YNP resulted in extensive tree mortality (M. Meagher, pers. comm.).

We conducted a study of the effects of bison on woody vegetation in the Nature Conservancy's 15,342-ha Tallgrass Prairie Preserve (TPP) in Oklahoma. Bison were reintroduced to the preserve after an absence from the area of almost 140 yr (Shaw and Lee, 1995). The objectives of our research were to: (1) quantify horning and rubbing activity of bison; (2)

characterize objects selected for use by bison during these behaviors and (3) examine effects of bison horning and rubbing on woody vegetation.

MATERIALS AND METHODS

The TPP is located ca. 25 km NW of Pawhuska in northern Oklahoma (36°50'N, 96°25'W) in the Osage Hills, an extension of the Flint Hills that lie primarily in Kansas. The Flint Hills have hilly topography and generally rocky soils that historically prevented extensive cultivation. Vegetation of the area is native grassland dominated by big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*) and little bluestem (*Schizachyrium scoparium*). Woody vegetation is limited to steep rocky slopes, some uplands, and larger drainages. The principal species are post oak (*Quercus stellata*), black-jack oak (*Q. marilandica*), green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), black walnut (*Juglans nigra*) and Kentucky coffeetree (*Gymnocladus dioica*). Black willow (*Salix nigra*), sycamore (*Platanus occidentalis*) and hackberry (*Celtis occidentalis*) are common along drainages.

Before its establishment in 1989, TPP was grazed by cattle and burned every 1–2 yr during spring. It was never plowed. A management plan was initiated in 1993 which included prescribed burning in summer, autumn and spring. About 20% of the preserve is burned annually. Three hundred bison were reintroduced into the study area, a 1973-ha part of the TPP, in October 1993. We counted and measured woody plants and other vertical objects in parallel, 10-m-wide belt transects across the study area from June to October 1993, before bison release. Surveys were conducted on foot or on an all-terrain vehicle when possible. Objects encountered during the surveys were recorded and mapped on 1:24,000 USGS topographic quadrangles with the aid of black-and-white aerial photographs taken in 1991. Existing damage to objects such as broken limbs and damage from insects, deer (*Odocoileus virginianus*) and fire were noted.

Objects were categorized as trees, small woody plants or miscellaneous objects. Trees were live woody plants ≥ 5 cm in diam at 1.4 m height and ≥ 1.8 m tall; data collected on trees included species, diameter, height to first limb, distance to the nearest tree (a measure of spatial isolation), bark texture (rough or smooth), and the presence of aromatic substances detectable by us. Small woody plants were live saplings or shrubs < 5 cm diam at 1.4 m height and ≥ 1.8 m tall; saplings were single-stemmed and shrubs were multi-stemmed. Data recorded for saplings and shrubs included species, bark texture and presence of aromatics. Miscellaneous objects were nonliving structures ≥ 0.5 m tall. Naturally occurring objects were rock outcrops, stumps and logs; artificial structures included wooden and metal poles (≥ 2 m tall), posts (< 2 m) such as fenceposts and signposts, and other items such as oil field equipment and cement bridge abutments. Data recorded for miscellaneous objects included physical descriptions and the presence or absence of detectable aromatics.

The study area was resurveyed in September and October 1995 and all objects checked for evidence of bison use. Criteria indicating bison use included the presence of shed hair; hoofprints around the base of the object; horn scratches; and broken limbs, stems or damaged bark not attributable to other causes. Bison damage to live vegetation was quantified by the area of stem girdled on trees and saplings and the percentage of shrub stems broken (light damage = 0–33%, moderate damage = 34–66%, severe damage = 67–100%). Plants killed by bison were noted. As damage to nonliving objects could not be quantified; objects were noted as being either used or unused.

We gathered data on horning and rubbing activity by observing animals under natural conditions during daylight hours from November 1993 to October 1995. Bison were observed during 194 periods totaling 331 h. Because we could not always distinguish between

TABLE 1.—Use of objects for horning and rubbing by bison as determined by (1) ground survey and (2) behavioral observations. Positive Z values indicate selection, whereas negative Z values indicate avoidance. All Z values were significant at $P < 0.001$ unless otherwise noted

Object category	% of total available objects (n = 1692)	Ground survey		Behavioral observations	
		% used by bison (n = 466)	Z value	% used by bison (n = 69)	Z value
Trees	62	37	-9.7	12	-8.3
Small woody species	24	34	4.4	12	-2.3*
Miscellaneous	14	29	7.8	76	13.8

* $P < 0.02$

horning and rubbing, we grouped horning and rubbing as a single behavior (referred to as horning) in which animals made contact with an object with parts of their head and/or neck and shoulders. Data recorded during observations included the age/sex class (bull, cow, yearling or calf) of the animal and the identity of the object horned. Data were analyzed for: (1) seasonal variation in observed horning activity (ANOVA); (2) expected distribution of horning activity by age/sex class (χ^2 goodness-of-fit test); and (3) differences in characteristics between objects used for horning and those that were not [Student's *t* test and the two sample Z test for proportions (Zar, 1984)].

RESULTS

Horning activity varied significantly by season ($F = 5.93$; $P < 0.002$). The mean (± 1 SE) number of horning incidents observed per animal per hour was highest in summer (July–September; $\bar{x} = 0.35 \pm 0.10$), intermediate in spring (April–June; $\bar{x} = 0.13 \pm 0.10$) and autumn (October–December; $\bar{x} = 0.10 \pm 0.14$) and lowest in winter (January–March; $\bar{x} = 0.04 \pm 0.15$). Observations of horning behavior were not distributed as expected across age/sex classes based on the proportion of each class in the total population ($\chi^2 = 13.5$; $P < 0.005$). Bulls, cows and yearlings performed horning behavior more than expected, while calves did so less than expected.

Bison exhibited preferences for certain objects during horning behavior. Based on the ground survey, bison preferred to use miscellaneous objects and small woody vegetation for this behavior but selected against trees (Table 1). Based on our observations of behavior, bison preferred objects in the miscellaneous category but selected against use of trees and small woody vegetation (Table 1). These conflicting results concerning small woody vegetation may have been a result of the distribution of objects on the landscape. Most woody vegetation was limited to certain topographic features such as draws, drainages and ponds, whereas miscellaneous objects were distributed at all locations within the study area. Thus, because locations for behavioral observations were made at random whenever bison were encountered, our observations may have inadvertently overrepresented bison use of miscellaneous objects but underestimated bison use of woody plants. Nevertheless, two trends in horning behavior were still apparent; bison preferred the widely available miscellaneous objects and selected against the use of trees (Table 1).

Although trees were not used in proportion to their availability among object types, bison did prefer to horn certain species. Green ash, sycamore and black willow were used significantly more than expected based on their availability on the landscape; post oak and black-jack oak were used significantly less than expected (Table 2). Bison also selected for some

TABLE 2.—Tree species used by bison for horning and rubbing. A significant positive Z value indicates selection, whereas a significant negative value indicates avoidance

Tree species	% of used trees (n = 172)	% of available trees (n = 1043)	Z value
Green ash (<i>Fraxinus pennsylvanica</i>)	36.0	21.1	4.29**
Sycamore (<i>Platanus occidentalis</i>)	20.3	10.3	3.78**
Black willow (<i>Salix nigra</i>)	19.7	9.7	3.88**
Black walnut (<i>Juglans nigra</i>)	5.8	5.8	0
American elm (<i>Ulmus americana</i>)	4.1	3.1	0.69
Post oak (<i>Quercus stellata</i>)	3.5	11.4	-3.15**
Hackberry (<i>Celtis occidentalis</i>)	2.9	5.4	-1.38
Blackjack oak (<i>Q. marilandica</i>)	1.7	21.4	-6.15**
Eastern cottonwood (<i>Populus deltoides</i>)	1.2	1.8	-0.56
Chittamwood (<i>Bumelia lanuginosa</i>)	1.2	0.5	1.10
Poplar (<i>Populus nigra</i>)	1.2	0.3	1.67*
Plum (<i>Prunus</i> sp.)	0.6	0.5	0.17
Eastern redcedar (<i>Juniperus virginiana</i>)	0.6	0.2	0.96
Bitternut hickory (<i>Carya cordiformis</i>)	0.6	0.1	1.47
Catalpa (<i>Catalpa bignonioides</i>)	0.6	0.1	1.47
Kentucky coffeetree (<i>Gymnocladus dioica</i>)	0	4.0	-2.69*
Redbud (<i>Cercis canadensis</i>)	0	1.3	-1.52
Chinkapin oak (<i>Q. muehlenbergii</i>)	0	1.2	-1.46
Persimmon (<i>Diospyros virginiana</i>)	0	0.8	-1.17
Red mulberry (<i>Morus rubra</i>)	0	0.4	-0.83
Osage orange (<i>Maclura pomifera</i>)	0	0.2	-0.54
Honeylocust (<i>Gleditsia triacanthos</i>)	0	0.2	-0.54
Dogwood (<i>Cornus drummondii</i>)	0	0.1	-0.41
Black oak (<i>Q. velutina</i>)	0	0.1	-0.41

* P < 0.05

** P < 0.001

tree characteristics. The average (± 1 SE) diam for trees horned by bison was 25 ± 1 cm, which was significantly ($t = 2.85$; $P < 0.005$) less than the average diameter for all trees (29 ± 1 cm). Bison also selected trees with smooth bark, using them in a higher proportion than they were generally available ($Z = 3.13$; $P < 0.001$). There was no difference between trees used for horning and those generally available in either height to first limb ($P > 0.3$) or distance to the nearest tree ($P > 0.7$). The presence of odors also did not appear to influence bison choice, since trees with aromatics were not used out of proportion to their availability ($P > 0.1$).

Several trees were severely injured by bison. A moderate-sized (25-cm dbh) eastern redcedar (*Juniperus virginiana*) appeared girdled but remained alive, while a small (9 cm dbh) willow was uprooted and killed. A large, low-hanging limb on a large (41 cm dbh) blackjack oak was pushed against so hard that it broke, causing severe damage to the trunk. Several green ash trees received moderate damage to the bark. However, most trees used by bison had only light damage.

Bison horning had the most impact on small woody vegetation. Of all saplings and shrubs surveyed for this study, 4% were severely damaged, 13% had moderate damage, and 12% had light damage. Bison showed a strong preference for black willow (Table 3). Bison use

TABLE 3.—Small woody plants (saplings or shrubs) used for horning and rubbing by bison. A significant positive Z value indicates selection, whereas significant negative values indicate avoidance

Woody species	% of used plants (n = 158)	% of available plants (n = 407)	Z value
Black willow (<i>Salix nigra</i>)	60.8	28.2	7.20***
Green ash (<i>Fraxinus pennsylvanica</i>)	13.3	11.3	0.66
Sycamore (<i>Platanus occidentalis</i>)	11.4	23.0	-3.11***
Buttonbush (<i>Cephalanthus occidentalis</i>)	11.4	14.4	-0.92
Plum (<i>Prunus</i> sp.)	2.5	4.2	-0.95
False indigo (<i>Amorpha fruticosa</i>)	0.6	5.4	-2.61**
Persimmon (<i>Diospyros virginiana</i>)	0	7.6	-3.55***
Smooth sumac (<i>Rhus glabra</i>)	0	2.5	-2.09*
Osage orange (<i>Maclura pomifera</i>)	0	1.0	-0.90
American elm (<i>Ulmus americana</i>)	0	0.5	-0.79
Honeylocust (<i>Gleditsia triacanthos</i>)	0	0.5	-0.79
Post oak (<i>Quercus stellata</i>)	0	0.5	-0.79
Black walnut (<i>Juglans nigra</i>)	0	0.3	-0.71
Eastern cottonwood (<i>Populus deltoides</i>)	0	0.3	-0.71
Chittamwood (<i>Bumelia lanuginosa</i>)	0	0.3	-0.71

* P < 0.05

** P < 0.01

*** P < 0.001

of small willows was so severe that 17% of the saplings and shrubs of this species were top-killed (resulting in root-sprouting) or killed outright. Plants of sycamore, false indigo (*Amorpha fruticosa*) and persimmon (*Diospyros virginiana*) were used less than expected. There was no disproportional use of small woody vegetation based on bark texture ($P > 0.2$) or presence of aromatics ($P > 0.2$).

Bison use of items in the miscellaneous category for horning was higher than expected. Most of this use was focused on metal and wooden poles and posts (Table 4). Bison use of other miscellaneous objects, both natural and artificial, was not disproportionate to their availabilities, except for oil well rigs, which were avoided. Only wooden utility poles exhibited any detectable odors, and these were heavily used by bison ($Z = 2.95$; $P < 0.002$). In fact, horning use of a few (~5) of these poles was so severe that they were loosened from the ground and leaning, forcing local utility companies to install additional support and apply metal wire deterrents to discourage bison use.

DISCUSSION

Bison at the TPP had measurable effects on only a few trees, but significantly affected shrubs and saplings (especially willows). Willows (*Salix*) are a major diet component for some populations of bison (Waggoner and Hinkes, 1986); however, our preliminary studies of diets show that willows are not a major food component for this population. Because willows and most of the woody vegetation in the study area were adjacent to water, we did not attempt to assess the importance of distance to water as a factor in bison use of an object. However, woody vegetation near water bodies were most affected by bison in other studies (McHugh, 1958; England and DeVos, 1969). Unfortunately, our study area also contained numerous man-made objects that were readily used for horning, especially utility

TABLE 4.—Use of miscellaneous objects for horning and rubbing by bison. Significant positive Z values indicate selection, whereas significant negative Z values indicate avoidance

Category & description	% of used objects (n = 136)	% of available objects (n = 242)	Z value
Natural			
Rock outcrops	10.3	9.5	0.25
Stumps & logs	3.7	3.7	0
Artificial			
Wooden poles & posts	29.4	19.0	2.31*
Metal poles & posts	41.9	30.6	2.21*
Oil well rigs	0	19.8	-5.54**
Other	14.7	17.4	-0.68

* P < 0.02

** P < 0.001

poles. This preference is consistent with historical accounts that mention bison rubbing and toppling of telegraph poles (McHugh, 1972). The presence of these objects undoubtedly affected the level of use and overall impact bison had on the naturally occurring woody vegetation in our study area. Removal of these artificial objects might substantially increase bison use of woody vegetation and thereby more closely restore presettlement conditions and associated biotic interactions.

Results from previous studies (McHugh, 1958; Meagher, 1973; Edwards, 1978) indicate that bison prefer to horn aromatic species such as cedars and pines. Although we found no bison selection for trees that we detected as aromatic, bison in our study horned (and nearly killed) a single large eastern redcedar tree and horned treated utility poles that were aromatic. Thus, bison appear to prefer aromatic objects as horning stations. Presumably these aromatic substances have insecticidal or repellent properties desired by the animals to provide relief from insect harassment. The increased rate of horning in summer when insects are most prevalent lends support to this idea, as do Soper's (1941) observations that insect harassment of bison was often followed by horning and rubbing behaviors. Many woody species that have invaded prairie sites such as pines (Steinauer and Bragg, 1987) and eastern redcedar (Blewett, 1986) have aromatics. Although the invasion of these species is attributed to fire suppression (Arend, 1950), they also may have been used by bison as horning and rubbing stations.

McHugh (1958) postulated that horning was a socially motivated aggressive behavior similar to wallowing during the rut. Reinhardt (1985) reported that wallowing was associated only with shedding and not with insect harassment or rutting behavior. Shedding, rut and insect harassment all occur simultaneously in summer; therefore, it may be a combination of these factors that result in horning and wallowing behaviors. Carefully designed studies would be needed to distinguish among these possible causes.

High moisture requirements (Abrams, 1986; Steinauer and Bragg, 1987; Knight *et al.*, 1994), droughts (Albertson and Weaver, 1945) and fire (Briggs and Gibson, 1992; Grimm, 1984) are all known to affect tree distribution in prairies. The lack of fire allows woody plant invasion of prairie sites (Bragg and Hulbert, 1976; Anderson and Schwegman, 1991), and most studies attribute the cause of invasion only to fire suppression (Abrams, 1986; Steinauer and Bragg, 1987; Briggs and Gibson, 1992). As burning has been a part of the

management practices of our study site during most of this century, bison effects on woody vegetation appear to complement those of fire. With estimates of historic populations ranging in the tens of millions (Shaw, 1995), roaming herds of bison could have caused extensive damage and mortality to woody vegetation. We concur with earlier studies (Edwards, 1978; Campbell *et al.*, 1994) that suggest that bison, in conjunction with other factors such as fire and drought, significantly limited the historic distribution of woody vegetation in the Great Plains.

Acknowledgments.—Financial and logistical support for this study was provided by The Nature Conservancy and the Oklahoma Cooperative Fish and Wildlife Research Unit (U. S. National Biological Service, Oklahoma Department of Wildlife Conservation, Oklahoma State University, and Wildlife Management Institute, cooperating). We thank D. M. Leslie, Jr., D. M. Engle, T. S. Carter and M. Meagher for constructive comments on an earlier manuscript draft.

LITERATURE CITED

- ABRAMS, M. D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio*, **65**: 29–37.
- ALBERTSON, F. W. AND J. E. WEAVER. 1945. Injury and death or recovery of trees in prairie climate. *Ecol. Monogr.*, **15**: 393–433.
- ANDERSON, R. C. AND J. E. SCHWEGMAN. 1991. Twenty years of vegetational change on a southern Illinois (USA) barren. *Nat. Areas J.*, **11**: 100–107.
- AREND, J. L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. *J. For.*, **48**: 129–130.
- BLEWETT, T. J. 1986. Eastern redcedar's (*Juniperus virginiana* L.) expanded role in the prairie-forest border region, p. 122–125. *In*: G. K. Clambey and R. H. Pemble (eds.). Proceedings 9th North American Prairie Conference. North Dakota State University, Fargo.
- BRAGG, T. B. AND L. C. HULBERT. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.*, **29**: 19–24.
- BRIGGS, J. M. AND D. J. GIBSON. 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. *Bull. Torrey. Bot. Club.*, **119**: 300–307.
- CAMPBELL, C., I. D. CAMPBELL, C. B. BLYTH AND J. H. MCANDREWS. 1994. Bison extirpation may have caused aspen expansion in western Canada. *Ecography*, **17**: 360–362.
- EDWARDS, T. 1978. Buffalo and prairie ecology, p. 110–112. *In*: D. C. Glenn-Lewin and R. Q. Landers, Jr. (eds.). Fifth Midwest Prairie Conference Proceedings. Iowa State University, Ames.
- ENGLAND, R. E. AND A. DEVOS. 1969. Influence of animals on pristine conditions on the Canadian grasslands. *J. Range Manage.*, **22**: 87–94.
- GRIMM, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.*, **54**: 291–311.
- INOUE, R. S., T. D. ALLISON AND N. C. JOHNSON. 1994. Old field succession on a Minnesota sand plain: effects of deer and other factors on invasion by trees. *Bull. Torrey. Bot. Club.*, **121**: 266–276.
- KNIGHT, C. L., J. M. BRIGGS AND M. D. NELLIS. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. *Landscape Ecol.*, **9**: 117–125.
- McHUGH, T. 1958. Social behavior of the American Buffalo (*Bison bison bison*). *Zoologica*, **43**: 1–54.
- . 1972. The time of the buffalo. A. A. Knopf, New York. 339 p.
- MEAGHER, M. M. 1973. The bison of Yellowstone National Park. *Natl. Park. Serv. Sci. Monogr. Ser.*, **1**: 1–161.
- MOSS, E. H. 1932. The vegetation of Alberta. IV. The poplar association and related vegetation of central Alberta. *J. Ecol.*, **20**: 380–415.
- REINHARDT, V. 1985. Quantitative analysis of wallowing in a confined bison herd. *Acta Theriol.*, **30**: 149–156.
- SHAW, J. H. 1995. How many bison originally populated western rangelands? *Rangelands*, **17**: 148–150.
- AND M. LEE. 1995. Ecological interpretation of historical accounts of bison and fire on the

southern plains with emphasis on tallgrass prairie. Final Report to the Nature Conservancy. 75 p.

- SNYDER, J. D. AND R. A. JANKE. 1976. Impact of moose browsing on boreal-type forests on Isle Royale National Park. *Am. Midl. Nat.*, **95**: 79-92.
- SOPER, J. D. 1941. History, range, and home life of the northern bison. *Ecol. Monogr.*, **11**: 349-412.
- STEINAUER, E. M. AND T. B. BRAGG. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska sandhills prairie. *Am. Midl. Nat.*, **118**: 358-365.
- WAGGONER, V. AND M. HINKES. 1986. Summer and fall browse utilization by an Alaskan bison herd. *J. Wildl. manage.*, **50**: 322-324.
- ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, N.J. 718 p.

SUBMITTED 18 APRIL 1996

ACCEPTED 2 OCTOBER 1996