RELATIVE ABUNDANCE OF BISON, ELK, AND PRONGHORN ON THE SOUTHERN PLAINS, 1806-1857

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James H. Shaw and Martin Lee

ABSTRACT

We searched diaries of travels over the Southern Plains from 1806-1857 for reports of bison, elk, and pronghorn. From these accounts we obtained indexes of abundance by dividing the number of days in which the animals were observed by the total number of days spent by the expeditions in each of the three prairie biomes. Organized by historical period and biome type, results show that populations of these ungulates were unstable even during the first half of the nineteenth century. The most stable populations throughout the survey period were bison on mixed-grass prairies. Bison and elk disappeared from tall-grass regions by 1833. Bison were exceptionally numerous on short-grass prairies prior to 1821 but dropped off sharply thereafter. Elk abundance was highest on tall-grass prairies during the earliest historical periods. Pronghorn were most abundant on short-grass prairies during 1806-1820 and again during the 1850s, and most abundant on mixed-grass prairies between those periods. Human influences were likely responsible for the paucity of bison on tall-grass prairies. The persistence of all three species on mixed-grass prairies was influenced by that biome's distance from centers of human populations encroaching from both east and west.

Keywords: bison; elk; pronghorn; Southern Plains; Historic period fauna

INTRODUCTION

The abundance of mammalian herbivores is important ecologically as well as anthropologically. As part of an assessment of the roles of fire and of large herbivores in shaping the southern tall-grass prairies, we devised a method of estimating the relative abundance of wild herbivores from daily accounts left by travelers through the region in the early to mid nineteenth century. We subdivided the Southern Plains into ecological types or biomes of tall-grass prairies, mixed-grass prairies, and short-grass prairies. In addition, we divided the time periods according to the type of expeditions that characterized them.

METHODS

We reviewed first-hand accounts by early explorers, surveyors, travelers, and naturalists who traveled across the Southern Plains between 1806 and 1857 (Table 1). These were years before extensive settlement by whites and before the hide hunts for bison in the 1870s. We used only accounts in which one or more persons on an expedition maintained a daily diary.

Even before the Civil War, enormous changes were underway on the Southern Plains. A brisk trade in bison robes began before the nineteenth century. Advances in firearms technology, expansion of trade, outbreaks of infectious diseases, displacement of Indians from eastern states, and encroaching white settlement all contributed to the declining stability of native wildlife populations and the ecosystems upon which they depended.

Because these changes did not all take place at once, we divided expedition accounts into four historical periods according to their primary missions. The first period, from 1806-1820, consisted

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Table 1. References consulted for historical accounts. Expedition authors are consistent with those for Figures 1-4.

Expedition	Reference
Nuttall	Nuttall 1904
Bell/James	Bell 1957; James 1905
Bell	Bell 1957
James	James 1905
Pike	Jackson 1966
Clark	Gregg 1937
Sibley	Brooks 1965; Gregg 1937, 1952
Wetmore	Hulbert 1933
Sibley/Davis	Brooks 1965
Becknell	Hulbert 1933
Fowler	Coues 1965
Marmaduke	Hulbert 1933
Latrobe	Latrobe 1832
Hammond	Hammond 1841
Boone	Fesser 1929
Magoffin	Magoffin 1962
Gibson	Gibson 1935
Woodhouse	Tomer & Brodhead1992
Wheelock/Evans	Perrine & Foreman 1925
Johnston/Edwards/ Ferguson	Johnston, Edwards, & Ferguson 1936
Stanley	Stanley & Shawver 1944
Bandel	Bandel 1932

of early explorations. The opening of the Santa Fe Trail and the resulting trading expeditions characterized the second period, from 1821-1832. Indian tribal conflicts and later the Mexican War resulted in a preponderance of military expeditions from 1833-1849. State and territorial boundary surveys typified the fourth and final period, from 1850-1857.

We traced travel routes of expeditions and plotted daily locations to the nearest contemporary county, a task usually facilitated by historians' published reviews of original accounts (Figs. 1-4). Next, we delineated tall-grass, mixed-grass, and short-grass prairies, according to generally accepted modern criteria (Brown 1985; Sims 1988; D. Engle, personal communication). Any such delineations are to some degree arbitrary, because local sites typical of short, tall, or mixed grass can be found in any of the three regions. Nonetheless, they are useful because they indicate the dominant prairie type within any region.

By tracing the routes in relation to daily accounts, we were able to establish the actual number of days spent in each biome. We then searched the diary accounts for entries concerning bison, elk, or pronghorn. For entries to be counted, they had to consist of direct sightings or unequivocal observation of fresh sign, typically tracks or droppings. For bison, we established an additional category for larger herds based on the diarists' original descriptions of herd size or estimated number of animals.

The index of abundance was obtained by dividing the number of days in which bison, pronghorn, and elk were encountered by the total number of days spent in that biome type (Fig. 5) and multiplying the results by 100. We did this for each of the three species in three biomes for four historical periods. This index is a crude approximation of modern methods used to estimate abundance of large mammals in open terrain. It compares the frequency of sightings in relation to "sampling effort"; in this case, the number of days spent in each biome.

This method for estimating ungulate abundance contains potentially serious sources of error. Some chroniclers presumably were more interested in wild animals than were others. No doubt the writers varied in their thoroughness and perhaps even in accuracy. The greatest error, though, may have resulted from the changing objectives of expeditions during different historical periods. The early explorers of the first historical period may have been more inclined to record observations of wild animals, owing to their novelty. Military expeditions tended to travel hurriedly, and their pace and sense of duty may have affected their interest in recording observations of wild herds and perhaps the behavior of the wild animals themselves.

Another source of bias results from differences in travel routes. The Santa Fe trail and most other routes followed major rivers to ensure adequate water supplies for travelers and their livestock. These routes changed to some extent between historical periods. The boundary surveys of the fourth period followed east-west routes independent of major rivers.

One potential source of bias seemed serious enough to affect presentation of our results. The northern leg of the Long expedition during the first historical period was farther north than any portion of any other expedition included in our survey.

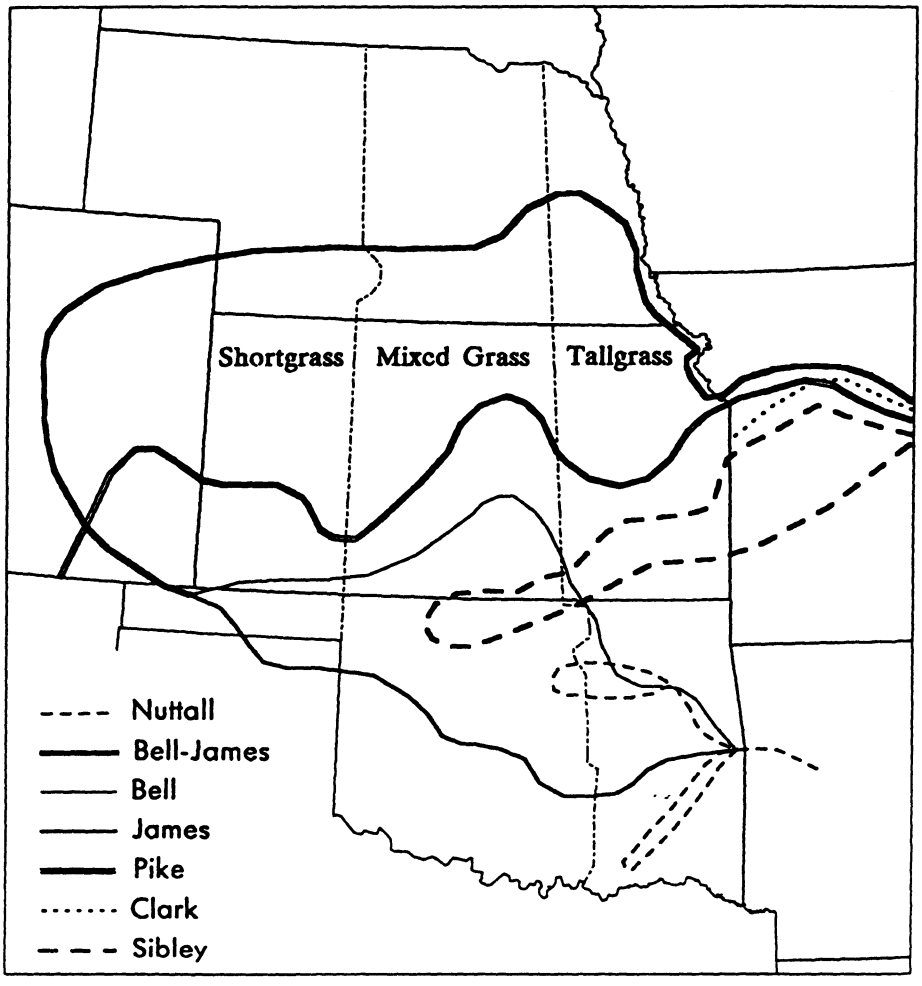

Figure 1. Travel routes of expeditions during the period of early exploration, 1806-1820.

The country through which the northern leg passed, particularly the short-grass prairie portions, is moister than short-grass prairies farther south. We thus separated the northern leg of the Long expedition for the part north of the contemporary Kansas-Nebraska border, and present results here both with and without it.

RESULTS

Bison

Index values for elk and bison are the same during the first historical period for tall grass (Fig. 6). This, of course, means that the rates of encounter were similar, not that the two species had approximately the same population densities. Herds of bison, even on tall grass, were presumably larger than herds of elk.

By the second historical period, index values for bison on tall grass dropped to less than half that of the previous period (Fig. 6). No accounts of bison on tall grass were reported during the third historical period, and only scattered ones during the fourth period.

In contrast to patterns on tall-grass prairies, bison index values on mixed-grass prairies were rather consistent throughout the four historical periods (Fig. 7).

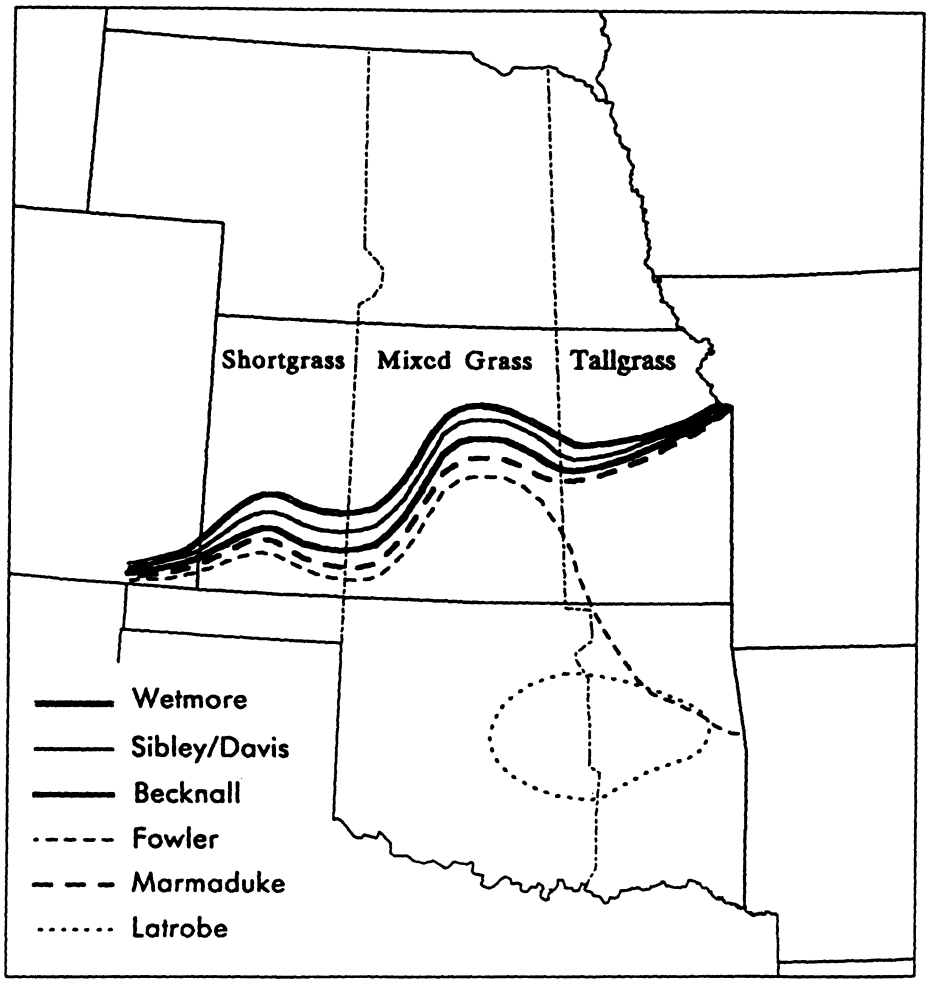

Figure 2. Travel routes of expeditions during the period of the Santa Fe trail, 1821-1832.

Bison abundance on short-grass prairies showed the greatest variation between historical periods for the three biomes. The highest index value for any biome during any period came from the short-grass region during the first historical period, although omission of the northern leg of the Long expedition reduces its relative value (Fig. 8). Index values for bison fell steadily on short-grass prairies with each succeeding historical period.

The ecological impact of bison is strongly influenced by group or herd size. We therefore tallied accounts in which writers specifically referred to "huge," "vast," or "large" herds. This is admittedly a less objective category than that based upon mere observation of bison or bison sign. Nonetheless, the index values for large herds largely correlated with index values for bison in general (Fig. 9).

Elk

The highest index values for elk came from tall-grass prairie regions (Fig. 6) during the first two historical periods. Elk were least abundant in short-grass regions, and intermediate in mixed-grass prairies. No accounts of elk were found on tall-grass or short-grass regions after the second historical period. In the case of tall-grass prairie,

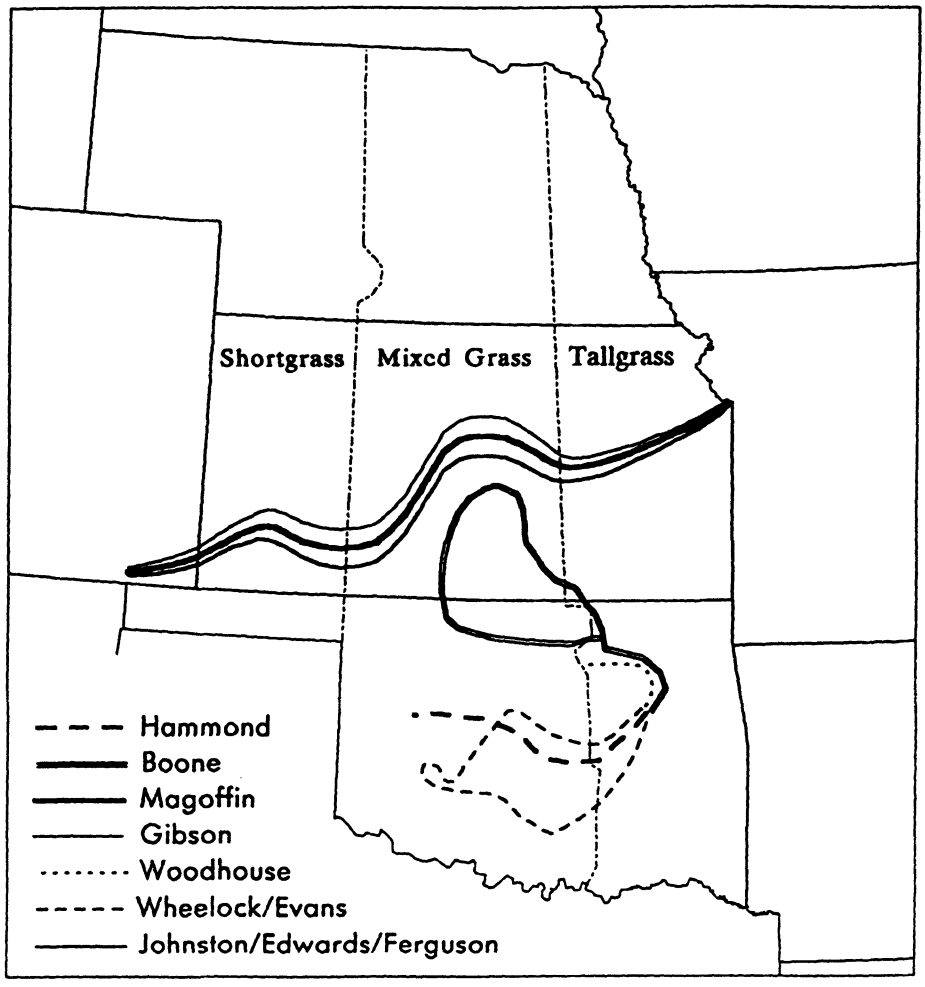

Figure 3. Travel routes of expeditions during the military period, 1833-1849.

the change in index values between the second and third historical periods was abrupt, suggesting a sudden disappearance. Elk appear to have persisted longer in mixed-grass prairies, the only biome in which they were recorded during the third and fourth historical periods.

Pronghorn

Pronghorn indexes were in some respects the opposite of those for elk. The highest index values came from short-grass prairies during the fourth historical period (Fig. 8). Although never abundant in tall-grass regions, pronghorn nonetheless occurred there through the third historical period, but were not reported after 1849.

Statistical Comparisons

Statistical analysis was done through a series of 2 x 2 chi-square contingency tables, comparing adjacent historical periods and biomes. For bison, all comparisons between adjacent biomes were significant ($P < 0.05$, Table 2). Another significant difference was found between the first and second historical periods between mixed-grass and short-grass prairies. There were also significant differences between the second and third historical periods and again between the third and fourth historical periods for mixed grass versus short

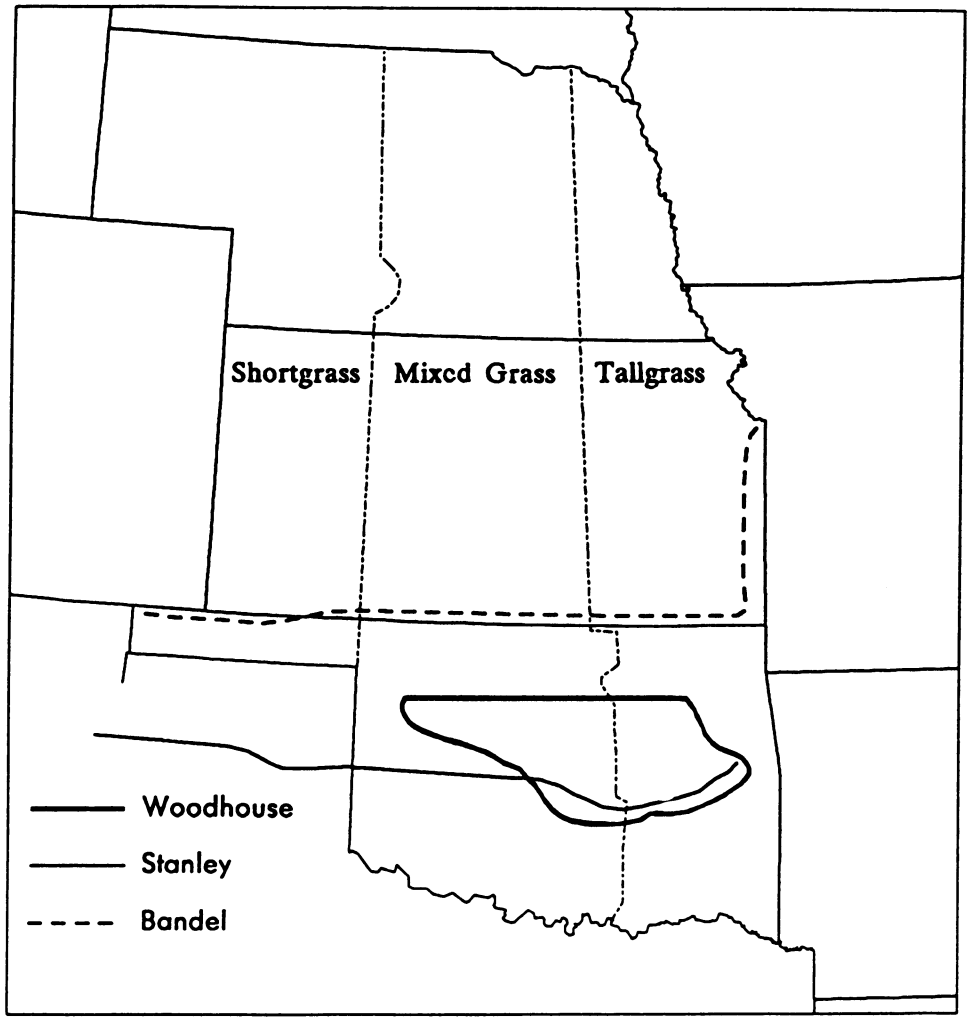

Figure 4. Travel routes of expeditions during the boundary survey period, 1850-1857.

grass (Table 2).

For elk, significant differences occurred between mixed-grass and short-grass prairies for the first two historical periods, if the northern leg of the Long expedition is excluded, and between tall-grass and mixed-grass prairies for the second versus the third historical period (Table 3).

There was a significant difference in pronghorn indexes between the first and second historical periods for tall-grass versus mixed-grass prairies if the northern leg of the Long expedition is included (Table 4). Significant differences were also found between the first and second periods for mixed grass compared with short grass (Table 4). Tall-grass versus mixed-grass prairie indexes differed significantly between the second and third historical periods and between the third and fourth historical periods (Table 4). The third and fourth historical periods showed significant differences for mixed-grass versus short-grass prairies.

DISCUSSION

While the indexes reported above may contain serious biases, they probably represent the best measurement of the relative abundance of bison, elk, and pronghorn that we will ever have for the Southern Plains during the first half of the nineteenth century. These results indicate that bi-

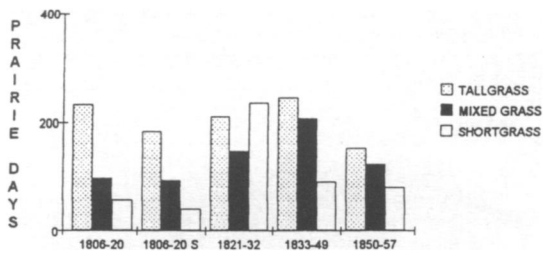

Figure 5. Prairie days by period and biome. "S" omits the north leg of the Long Expedition.

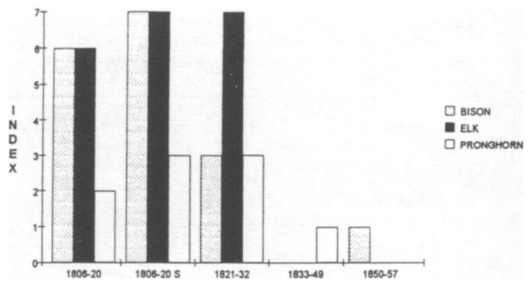

Figure 6. Abundance of ungulates on tall grass. "S" omits the north leg of the Long Expedition.

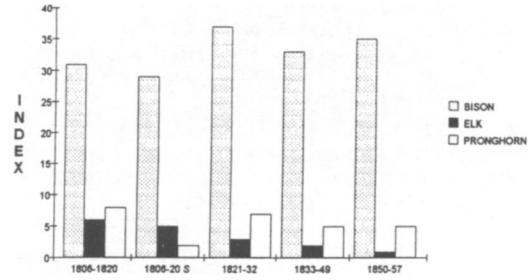

Figure 7. Abundance of ungulates on mixed grass. "S" omits the north leg of the Long Expedition.

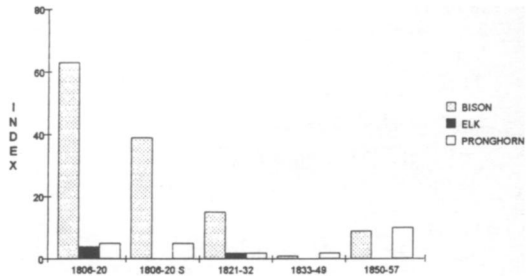

Figure 8. Abundance of ungulates on short grass. "S" omits the north leg of the Long Expedition.

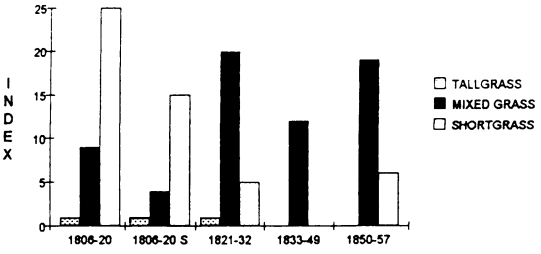

Figure 9. Large herds of bison. "S" omits the north leg of the Long Expedition.

son were far less abundant on tall-grass prairie than on mixed-grass or short-grass prairie. All of the expeditions began in tall-grass regions and headed west. It is a reasonable presumption that writers would have recorded most conscientiously their first contacts with bison, particularly the larger herds. Any bias in these accounts would thus have likely overestimated bison in tall-grass regions.

The most common explanation for the paucity of bison in tall-grass regions is insufficient nutritional quality during winter. Forage production in tall grass, of course, averages higher than for prairies farther west. Cattlemen have long noted that tall-grass species do not cure well in their above ground portions and thus they provide supplemental feed during winter. Supplementation does not raise carrying capacity for cattle but it does ensure a higher and more reliable rate of calf production, making it cost-effective (T. McCollum, personal communication).

Bison, however, can digest rough forage better than can cattle (Plumb and Dodd 1993), and may therefore be able to subsist over winter in tall-grass regions. The latest census and calving figures for bison on tall grass at Konza Prairie in Kansas indicate that bison can reach population densities of one per eight acres and maintain calving rates of 80-90% in the absence of supplementation (E. Finck, personal communication).

Some tall-grass species, most notably big bluestem (*Andropogon gerardii*), show relatively low growth rates following grazing (Wallace

Table 2. Chi-square comparisons of bison indexes by adjacent historical periods and adjacent biomes. TGP = tall-grass prairie; MGP = mixed-grass prairie; SGP = short-grass prairie.

Comparison	df	χ^2	P
1806-20, 1821-32, TGP, MGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	1.53	0.216
TGP vs MGP	1	45.79	<0.0001
1806-20, 1821-32, TGP, MGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	2.57	0.110
TGP vs MGP	1	42.34	<0.0001
1806-20, 1821-32, MGP, SGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	30.07	<0.0001
MGP vs SGP	1	20.20	<0.0001
1806-20, 1821-32, MGP, SGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	11.64	<0.0006
MGP vs SGP	1	10.78	<0.001
1821-32, 1833-49, TGP, MGP			
1821-32 vs 1833-49	1	3.23	0.072
TGP vs MGP	1	61.90	<0.0001
1821-32, 1833-49, MGP, SGP			
1821-32 vs 1833-49	1	12.48	0.0004
MGP vs SGP	1	39.43	<0.0001
1833-49, 1850-57, TGP, MGP			
1833-49 vs 1850-57	1	1.23	0.268
TGP vs MGP	1	67.11	<0.0001
1833-49, 1850-57, MGP, SGP			
1833-49 vs 1850-57	1	6.63	0.01
MGP vs SGP	1	47.16	<0.0001

Table 3. Chi-square comparisons of elk indexes by adjacent historical periods and adjacent biomes. TGP = tall-grass prairie; MGP = mixed-grass prairie; SGP = short-grass prairie.

Comparison	df	χ^2	P
1806-21, 1821-32, TGP, MGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	1.08	0.299
TGP vs MGP	1	1.60	0.206
1806-20, 1821-32, TGP, MGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	0.50	0.470
TGP vs MGP	1	1.93	0.164
1806-20, 1821-32, MGP, SGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	1.67	0.197
MGP vs SGP	1	0.60	0.439
1806-20, 1821-32, MGP, SGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	2.50	0.114
MGP vs SGP	1	5.20	0.023
1821-32, 1833-49, TGP, SGP			
1821-32 vs 1833-49	1	7.20	0.007
TGP vs MGP	1	3.60	0.058
1821-32, 1833-49, MGP, SGP			
1821-32 vs 1833-49	1	2.20	0.138
MGP vs SGP	1	2.20	0.138
1833-49, 1850-57, TGP, MGP			
1833-49 vs 1850-57	1	0.00	0.000
TGP vs SGP	1	0.00	0.000
1833-49, 1850-57, MGP, SGP			
1833-49 vs 1850-57	1	0.00	0.000
MGP vs SGP	1	0.00	0.000

1987; Vinton and Hartnett 1992), although the complex interaction between fires, microsite, and grazing remains poorly understood (Vinton and Hartnett 1992). This lack of resistance to repeated grazing episodes has been cited as evidence that tall-grass prairie is not well adapted to intensive or prolonged bison grazing (L. Wallace, personal communication).

But the grazing response hypothesis only indicates that bison did not occur in tall grass in large numbers by the time the first historical accounts were recorded, a conclusion entirely consistent with the direct observations that we reviewed. Had bison exploited tall-grass prairies more thoroughly and in larger numbers, they might have shifted the vegetation away from such species as big bluestem and more toward forbs and mixed or even short-grass species. Yet, such vegetative composition was not reported for tall-grass regions.

Perhaps a more likely explanation for the shortage of bison on tall grass was the presence of large numbers of Indians dependent to a substantial extent upon agrarian practices. The trend among anthropologists in recent years has been to revise upward the numbers of Indians that lived in the Americas before extensive white settlement. Thornton (1987) estimated that at least 72 million people lived in the Americas at the time of first

Table 4. Chi-square comparisons of pronghorn indexes by adjacent historical periods and adjacent biomes. TGP = tall-grass prairie; MGP = mixed-grass prairie; SGP = short-grass prairie.

Comparison	df	χ^2	P
1806-20, 1821-32, TGP, MGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	0.27	0.606
TGP vs MGP	1	5.50	0.023
1806-20, 1821-32, TGP, MGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	2.78	0.096
TGP vs MGP	1	1.80	0.180
1806-20, 1821-32, MGP, SGP, including N. leg Long Expedition			
1806-20 vs 1821-32	1	4.52	0.033
MGP vs SGP	1	2.84	0.092
1806-20, 1821-32, MGP, SGP, excluding N. leg Long Expedition			
1806-20 vs 1821-32	1	4.06	0.044
MGP vs SGP	1	4.06	0.044
1821-32, 1833-49, TGP, MGP			
1821-32 vs 1833-49	1	1.33	0.248
TGP vs MGP	1	4.27	0.039
1821-32, 1833-49, MGP, SGP			
1821-32 vs 1833-49	1	0.33	0.564
MGP vs SGP	1	4.06	0.044
1833-49, 1850-57, TGP, MGP			
1833-49 vs 1850-57	1	1.00	0.317
TGP vs MGP	1	7.67	0.005
1833-49, 1850-57, MGP, SGP			
1833-49 vs 1850-57	1	5.33	0.021
MGP vs SGP	1	2.95	0.086

contact. At least five million of these lived in what is now the continental United States. Numbers of Indians declined following contact and that trend continued into the nineteenth century. One authority tracked the decline of North American Indians from an estimated 1,052,000 in 1800 to 771,000 in 1850, a decline of roughly 27% (Ubelaker 1992).

If North American Indians had had the numbers and the organization to repel bison from tall-grass (agrarian) areas, they would certainly have had the motives for doing so. The prospect of tens of thousands of bison trampling crops just before harvest would have provided strong incentives.

Whatever the original reasons for low numbers of bison in tall-grass regions, our review suggests that they, along with elk and pronghorn, disappeared from tall-grass prairies decades before the hide hunts that ended the days of free-ranging herds. The robe trade, with its emphasis on hides from female bison, may have contributed to this early decline, though many of the robes reaching eastern markets came down the Missouri River, presumably from northern short-grass prairies (Roe 1970).

The sudden drop in bison numbers on southern short-grass prairies after 1821 may have been due to two forces. Dendrochronological records (Stahle and Cleveland 1988; Stahle and Hehr 1984) indicate that a severe drought struck the Southern Plains in the early 1820s, presumably either starving bison in short-grass regions or else forcing them to move farther east. In addition, the Santa Fe Trail opened in 1821. Wagons heading east from Santa Fe frequently carried bison robes (Roe 1970), so any bison ranging near the growing settlement of Santa Fe would have come under increasing hunting pressure.

The fact that bison, elk, and to some extent even pronghorn seemed to have persisted longest on mixed-grass prairies may have had more to do with geography than with habitat quality. Oklahoma and portions of central Kansas were among the last regions settled by whites. That settlement pattern, along with distance from markets, may have been major reasons for the persistence of large wild ungulates in mixed-grass prairies.

Acknowledgments

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