Bison West of the Rocky Mountains: An Alternative Explanation

Abstract

Although abundant on the Great Plains, bison (Bison bison) were relatively scarce west of the Rocky Mountains in the Pacific Northwest. Four explanations have been advanced to account for this low density: 1) relative inaccessibility of the area, coupled with Indian-caused mortality; 2) low protein content of forages; 3) lack of synchrony between forage plant phenology and the bison reproductive cycle; 4) periodically heavy winter snows deep enough to kill all colonizing bison. None of these explanations finds solid support in the available evidence. I propose that low bison numbers resulted from low overall forage production, and from discontinuous habitat which isolated bison populations and slowed recolonization following periodic local extinctions.

Introduction

The former distribution and extraordinary abundance of bison (Bison bison) on the Great Plains has been chronicled in detail (Roe 1970), but the occurrence of bison further west is not well known and has been a matter of considerable debate. Although bison apparently were widely distributed throughout much of the Pacific Northwest, they were abundant west of the Continental Divide only in southwestern Wyoming and southeastern Idaho. Low density of bison over most of their range west of the Divide stands in marked contrast to availability of steppe habitat which seemed capable of supporting much higher numbers. This disparity between numbers and apparent carrying capacity was noted by the earliest explorers in the area, and has stimulated much discussion since (Kingston 1932, Haines 1967, Christman 1971, Schroedl 1973, Butler 1978, Mack and Thompson 1982, Daubenmire 1985). Resolution of the problem has important implications for plant ecology and evolution (Daubenmire 1978, 1980, Mack and Thompson 1982), zoogeography (Lyman and Livingston 1983), and ethnography (Schroedl 1973, Butler 1978).

Four explanations have been proposed to account for the scarcity of bison west of the Rocky Mountains. Critical evaluation of these explanations, based on available literature, has been lacking. Because the problem is historical in nature (bison were exterminated west of the Rocky Mountains over 100 years ago), the cause of low bison numbers may never be identified conclusively; yet a considerable body of pertinent literature exists, largely overlooked by previous authors. My purpose is to examine the four explanations in light of the available evidence, then propose a new explanation.

Former Distribution of Bison

Numerous eyewitness accounts attest to the abundance of bison in southwestern Wyoming and the Snake River Plain and adjacent valleys of southeastern Idaho (e.g., Ogden 1910, Work 1913, Davis 1985, Haines 1955). There are no eyewitness accounts of bison further west and northwest, in the Pacific Northwest, but broad distribution is suggested by recovery of bison skulls and other bones from at least 44 localities in eastern Washington, eastern Oregon, and southwestern Idaho (hereafter “PNW”) (Schroedl 1973, Agenbroad 1978, Van Vuren and Bray 1985). Only one of these localities yielded evidence of more than a few individuals; hundreds of bison skulls were exposed at Malheur Lake in eastern Oregon, suggesting that bison may have been locally common there (Van Vuren and Bray 1985). Most of the 44 localities were in areas characterized by steppe vegetation which produces an appreciable biomass of graminoids, the principal forage of bison (Meagher 1973, Peden 1976, Reynolds et al. 1978, Van Vuren 1984a). Available evidence suggests that bison became extinct for uncertain reasons in eastern Oregon and Washington about 1800 (Schroedl 1973, Van Vuren and Bray 1985).

Previous Explanations

Kingston (1932) argued that physiographic barriers greatly restricted immigration of bison into the PNW, and that the few successful immigrants...
were soon killed by Indians. Archeological evidence does not support this explanation. The presence of bones of immature bison in archeological sites in southeastern Washington suggests that a breeding population inhabited the area (Osborne 1953, Schroedl 1973). A bison kill site in southwestern Idaho, in use an estimated 7000 years, incorporated 2680 m of stone fences (Agenbroad 1978); the effort for construction and the duration of use suggest that bison in the area were an established population rather than an occasional group that strayed west.

Johnson (1951), noting the apparently low densities of bison on tallgrass prairie east of the Mississippi River compared with high densities on shortgrass prairie further west, suggested that bison numbers were limited by presumed lower protein content of tallgrass species. Daubenmire (1985) interpreted this suggestion as an explanation of low bison numbers in the PNW as compared with high numbers on the Great Plains. Data on protein content of grasses do not support this interpretation. Protein content of steppe grasses in the PNW, either live (ca. 6-15% of dry weight) or cured (ca. 4-7%) (McIvain 1942, Rickard et al., Uresk and Cline 1976, Williams et al. 1981), was similar to protein content of live (ca. 6-15%) or cured (ca. 3-8%) steppe grasses east of the Rocky Mountains (Jefferies and Rice 1969, Sims et al. 1971, Willard and Schuster 1973, Goetz 1975, Cogswell and Kamstra 1976).

Mack and Thompson (1982) suggested that grass phenology in the PNW may have limited bison numbers. They noted that bison cows usually calve late April through early June and proposed that the nutritional stress of lactation coincided well with grass phenology on the Great Plains, but very poorly with phenology in the PNW, where steppe grasses are dormant during much of the summer. The underlying assumption, that the bison reproductive cycle cannot shift in response to forage availability, may not be valid. The midpoint of the breeding season of seven bison herds (McHugh 1958, Halloran and Class 1959, Fuller 1962, Meagher 1973, Petersburg 1973, Mahan 1978, Lott 1981, Lott and Galland 1985, Shall 1985) was correlated with latitude ($R^2 = 0.75, P < 0.05$). Breeding, and presumably calving, occurred up to six weeks earlier in southern herds than in northern herds, suggesting that the bison reproductive cycle can shift according to environmental conditions. Moreover, Daubenmire (1985) argued that grasses in more mesic habitats peripheral to steppe remain green throughout the summer, providing sufficient forage to sustain a substantial number of bison. The ability of bison to exploit seasonally available forage is demonstrated by the several extant herds which are migratory (Soper 1941, Meagher 1973, Van Vuren and Bray 1986).

Daubenmire (1985) proposed that occasionally heavy snowfall west of the Rocky Mountains, held in place by shrubs, was sufficient to kill any bison that crossed the Continental Divide. Telfer and Kelsall (1984) reported that bison seemed less efficient than several other native North American ungulates at coping with deep snow, but it is unknown if this relative inefficiency translated into an absolute inability to survive in the PNW. There is a crucial difference between snowfall sufficient to cause local mortality in bison, which has been documented (Meagher 1973), and snowfall periodically so severe that a vast area was rendered entirely uninhabitable. Daubenmire derives support for his explanation largely from historical accounts of domestic livestock encountering difficulty with deep snow. The underlying assumption, that bison and livestock are ecologically similar, is probably invalid (e.g., Peden et al. 1974; Christopherson et al. 1978; Schwartz and Ellis 1981; Van Vuren 1982, 1984a; Van Vuren and Bray 1983). Moreover, there are numerous reliable descriptions from the 1800's of factors such as drowning, fire, and quicksand killing large numbers of bison, but none of mass mortality due to deep snow (Roe 1970). Indeed, historical accounts indicate bison were not greatly affected by snow (Roe 1970, 203).

Any explanation for low bison numbers in the PNW should also account for the disappearance of bison in the area about 1800. Christman (1971) suggested that this extinction, which occurred shortly after local Indians acquired the horse, resulted from the increased efficiency and mobility of mounted hunters. The preference of Indians for bison is demonstrated by numerous accounts of PNW tribes making trips of 500 km or more on horseback to hunt bison east of the Continental Divide (e.g., Ogden 1910, Stewart 1938). Daubenmire (1985), however, argued that Christman's suggestion was inconsistent with
Schroedl's (1973) conclusion that bison numbers in eastern Washington were seemingly in decline long before introduction of the horse. Schroedl's conclusion was based on a temporal decline in numbers of archeological sites in which bison have been found and in numbers of bison bone fragments per site. This evidence is questionable. The decline in number of sites containing bison, from nine (2500-1500 BP) to six (500-200 BP), is unconvincing. Schroedl did not compare the number of sites in which bison were found with the number in which they were not found; a higher number of older sites containing bison could simply reflect a higher number of such sites being excavated. The temporal decrease in bison bone fragments resulted entirely from the disproportionate influence of one of the 22 sites excavated; this site was among the oldest and contained 74% of all bison bone fragments recovered. Moreover, Butler (1978) noted that changes in number of bison bone fragments found in archeological sites could be more a reflection of changes in local hunting patterns than of trends in bison numbers. The data are inadequate for any conclusion about pre-extirption changes in bison numbers; hence, increased hunting efficiency of mounted Indians remains a valid explanation of extinction of bison in the PNW.

A New Explanation

I propose that low bison numbers in the PNW resulted from low carrying capacity and from periodic local extinctions followed by slow rates of recolonization. This theory hinges on two heretofore unconsidered differences in steppe vegetation and physiography east and west of the Rocky Mountains. First, production of herbaceous vegetation in steppe communities was much lower in the PNW than in the Great Plains. Herbaceous biomass production in ungrazed PNW steppes was ca. 400-1500 kg/ha (Daubenmire 1970, Rumsey 1971, Rickard 1985), compared with ca. 1500-3500 kg/ha or more in the Great Plains (Dix 1960, Hulett and Tomanek 1969, Shiflet and Dietz 1974). Densities of bison were lower west of the Rocky Mountains than east simply because of lower carrying capacity. Early dormancy of steppe vegetation may have further reduced carrying capacity (Mack and Thompson 1982).

Second, vegetation east of the Rocky Mountains consisted of nearly continuous grassland, virtually all of it suitable bison habitat. Any area suffering a local population reduction or extinction of bison could be recolonized quickly by adjacent herds. In contrast, much of the terrain west of the Rocky Mountains was a mosaic of habitats, many of them unsuitable for bison. Distribution of bison probably was disjunct, with physiographic barriers such as mountains, deserts, or deep canyons hindering movement of individuals between many populations. McDonald (1981, 227) found a high incidence of dental anomalies among bison skulls recovered from Malheur Lake and suggested they were from an isolated, inbred population. Dental anomalies have been associated with small initial size and potential inbreeding in other bison populations (Van Vuren 1984b). Periodically, deep snow (Daubenmire 1975), concerted hunting effort by pre-horse Indians (Kingston 1932), or other mortality factors may have caused local extinctions. Slow immigration rates probably left such areas vacant of bison for many years, serving to further reduce overall numbers in the PNW. The large number of bison skulls found at the bottom of Malheur Lake may represent a herd that mired in the mud during summer or broke through the ice during winter and drowned. Both events were important causes of mass mortality of bison on the Great Plains (Roe 1970).

Acquisition of the horse by Indians probably led to increased hunting mortality of bison; 1000 were killed by a band of Indians in southeastern Idaho in one day, without firearms (Haines 1955, 36). On the Great Plains, continuous, productive habitat permitted rapid recolonization by adjacent herds. In the PNW, however, low densities throughout the area and slow recolonization resulted in rapid extinction.

Acknowledgments

I thank K. B. Armitage, B. E. Coblentz, R. S. Hoffmann, and C. E. Martin for critically reviewing the manuscript.

Bison West of the Rocky Mountains 67
Literature Cited


Received 24 October 1986
Accepted for publication 12 January 1987

Bison West of the Rocky Mountains 69