Historic Bison Populations: A GIS-Based Estimate

Keith T. Weber, GIS Director, Idaho State University GIS Training and Research Center, Campus Box 8130, Pocatello, ID 83209-8130

Abstract: The number of bison (*Bos bison*) once living on the Great Plains of North America is a topic of much interest and debate. Most generally accepted estimates of historic bison populations were made around 1865-1870. Estimates range from 15 million to over 10 billion (Garretson 1938; Shaw 1995), with 65 million (Seton 1910) being the most commonly accepted number. None of these estimates, however, was made using methods that would be considered scientifically rigorous by today's standards. At best we can offer only estimations that attempt to minimize error.

This study attempts to estimate the historic bison population on the Great Plains of North America (circa 1870) using various GIS data sets that are themselves estimates of the conditions that existed or would have existed under an historic native vegetation regime. Using NRCS STATSGO soils data sets, forage productivity was estimated for native grasses under poor, normal, and favorable weather conditions. USGS 1:250,000 digital elevation models were used to account for reduced grazing capability due to slope.

Total herbage, forage demand, and stocking rate were calculated at both 50% and 100% use rates. Historic Bison carrying capacity estimates ranged from 21-88 million.

Keywords: GIS, Bison, paleoecology, STATSGO, soils, digital terrain modeling.

Introduction: Many researchers have speculated about wildlife populations prior to European settlement. Frequently we are given the impression that North America was a pristine paradise. More recent research, however, indicates that the North American ecosystem was probably not a "Garden of Eden" but may still have supported large numbers of certain wildlife species, just as it today supports large populations of humans and livestock.

Man, as part of the environment, has always had some effect on the environment. The sum of these effects has varied over time but has probably never been zero. Man has molded or changed the environment and, in so doing, has dramatically altered the population of other species. Bison (*Bos bison*) is one of those species.

While we know that bison populations probably always interfaced with humans, and that total bison population likely varied over time due to hunting, winter hardship periods, and disease, we still wonder just how many bison existed prior to contemporary times. Most estimates are given for the Post-Civil War period of 1865-1870, when many Americans decided to go west in search of fortune, freedom, and a clean start on life. Estimates of historic bison population range from 15 million (Jones *in* Roe 1970) to 10 billion animals (Garretson 1938; Shaw 1995). Most commonly accepted is the estimate by Seton (1910) who essentially used simple extrapolation to arrive at an estimated population of 65 million animals. These estimates, however, contain errors. First, the methods used to arrive at these estimates were certainly not scientifically rigorous by today's standards. Second, the observers were not biologists trained in biometry and statistics. In addition, their "sampling" included a bias, since the places traveled by early European settlers were those areas that today would be considered good or even prime habitat. The terrain and environments that made for easy overland travel also offered good bison habitat. The scenario frequently read goes like this: "observers saw 2000 bison in one day and estimated they had traveled 5 miles in that day. The observers could see bison one mile on either side of them as they traveled." Using simple mathematic extrapolation, one would calculate 2000 bison/ 10 mi^2, or 200 bison/mi^2. Taking this yet one step further, we can apply this "stocking rate" of 200 bison/mi^2 to all of western North America, giving us an estimate of historic bison population. This method is called simple extrapolation, and the problems with it are obvious.

To the author's knowledge, no estimate of bison population has ever been made using a geographic information system (GIS). Yet, the question of how many bison once existed is really a spatial analysis question that lends itself quite well to GIS. However, this research does not and cannot estimate bison population directly but rather the carrying capacity of herbivores within the estimated range of the bison herds.

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Methods: By 1870 the bison herd on the Great Plains of North America had been split into two smaller herds. The estimated range of these herds (the northern and southern herds) were "heads-up" digitized (using Albers' equal area projection) into an Arc/Info polygon coverage (figure 1). Maps from Roe (1970) were used as source data. To estimate the carrying capacity for herbivores within the northern and southern ranges, I used NRCS STATSGO (USDA 1995) data to estimate the native range condition. The Rangesite Productivity (RSPROD) table provided an estimate of native biomass produced (lbs/acre) under favorable, average (normal), and poor climatic conditions.

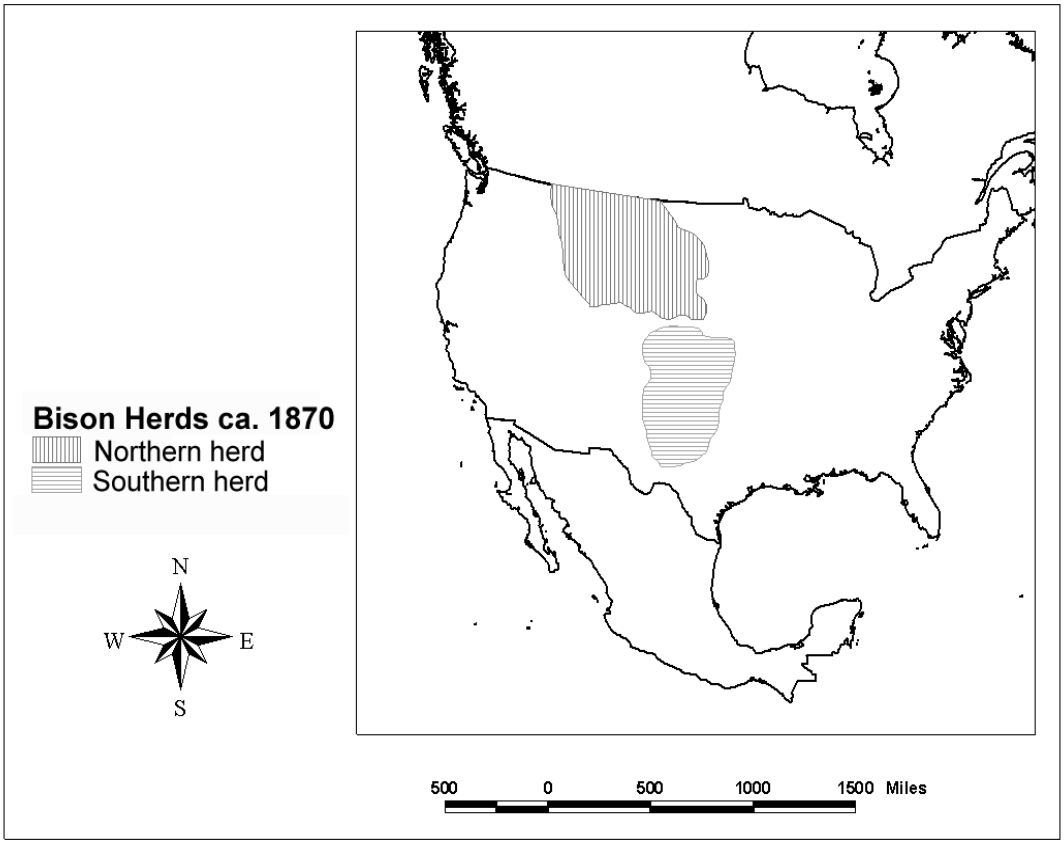

Figure 1: Historic bison herd ranges used in this study.

The effect of topography on bison is similar to its effect on domestic cattle (National Bison Association 1997). I used guidelines prepared by Holecheck et. al. (2001) to calculate carrying capacity reductions due to topography (table 1). Topography (specifically slope) was calculated for the study using 1:250,000 USGS DEM's that were mosaiced together using Arc/Info. Slope was calculated in percent using Arc/Info.

Carrying capacity estimates were made based on both a 50% and 100% use of available biomass. In addition, I used two animal unit calculations since reports of the amount of forage required by bison daily vary in the literature (50.4 lbs [Pyle and Johnson, 1997]; 36 lbs [Holecheck et. al, 2001]). Forage demand estimates vary with Pyle and Johnson's inclusion of trampling, dunging, and other waste of forage not directly consumed by grazers. The animal units used have been adjusted to represent bison units.

To help validate these methods, I examined the Konza prairie of Kansas where bison graze under essentially native range conditions. I estimated carrying capacity for the Konza prairie using these same methods, and then compared these results to actual population figures.

Percent Slope	Stocking rate adjustment
<10	No reduction
10.0-30.0	-30%
30.1-60.0	-60%
>60	No use

Table 1 : Effect of slope on rangeland stocking rate.

Results: The carrying capacity for both northern and southern herds, following Pyle and Johnson's forage demand guidelines, slightly exceeds 60 million animal units under average climatic conditions. In comparison, the carrying capacity, following Holecheck et. al., is nearly 70 million animal units (table 2) under otherwise identical scenarios.

Carrying capacity at 100% use			
Climatic condition	Forage requirement guidelines	Northern herd	Southern herd
Favorable	Pyle and Johnson	29,054,379	47,504,159
	Holecheck	33,432,436	54,662,319
Average	Pyle and Johnson	24,139,105	36,043,389
	Holecheck	27,776,505	41,474,585
Poor	Pyle and Johnson	18,294,134	24,535,800
	Holecheck	21,050,784	28,232,975

Table 2: Herbivore carrying capacity on historic bison range under varying climatic conditions.

Since most literature regarding historic bison herds indicates that bison were migratory (Hornaday 1889; Seton 1910; Roe 1970), it seems that 100% use of available biomass may not be realistic. In addition, 100% use of herbage biomass is rarely, if ever, seen in nature except perhaps under extreme stress conditions (e.g., prolonged drought or containment). Further, since bison are considered primarily gramivores (Steuter and Hidinger 1999) and rangeland biomass includes non-grassy species, setting the carrying capacity to 50% use may present a more realistic figure. Under this scenario, nearly 35 million animal units are available for bison (table 3).

Carrying capacity at 50% use			
Climatic condition	Forage requirement guidelines	Northern herd	Southern herd
Favorable	Pyle and Johnson	14,527,189	23,752,064
	Holecheck	16,716,218	27,331,159
Average	Pyle and Johnson	12,069,552	18,021,694
	Holecheck	13,888,252	20,737,293
Poor	Pyle and Johnson	9,147,067	12,267,900
	Holecheck	10,525,392	14,116,488

Table 3: Herbivore carrying capacity on historic bison range under varying climatic conditions.

The same techniques described above were applied to the Konza prairie (Kansas) where the controlled bison population is based on 25% use with bison grazing limited to about 28% of the prairie. The population on the Konza prairie is maintained at 225 bison.

The author's model estimates a carrying capacity of 226 AU (under average conditions) based on 25% use of 28% of the area.

Discussion: Under all scenarios, the estimated carrying capacity for both northern and southern herds ranges from 24-88 million animals units. As mentioned earlier, these figures assume that all rangeland biomass is suitable forage for bison. Further, we must realize that the carrying capacity estimates presented here are really carrying capacities and not specifically population estimates. Hence, the bison carrying capacity must be reduced to accommodate other forms of herbivory (other wildlife species, insects, etc.) and vegetation loss, specifically wildfires that would have temporarily altered the carrying capacity of the range. Bearing this in mind, it seems likely that this model may overestimate the population of bison historically supported, and that the real population may have been fairly smaller. Similarly, McHugh (1972) calculated carrying capacity at 30 million using average carrying capacity of western ranges and extrapolating this figure over the entire historic bison range.

Records of animals killed and of bison hides shipped between 1870-1874 offer some validation of these estimates. According to Hornaday (1889), approximately 3.1 million bison were killed during that time period. Interestingly, I found no record of kills that would indicate that the population ever exceeded 30 or even 24 million animals.

Could bison have achieved or maintained a population of 60-65 million (Seton 1910 and 1929) ecologically? Certainly, bison populations could have and probably did exceed the carrying capacity of their habitat occasionally over time. But for such a large population to be maintained over extended time periods seems unlikely. Based on this model, bison use rates of available biomass would need to have been at or very near 100% for extended time periods to achieve and maintain a population of 60-65 million animals.

In speculation, let's say that the bison population in the mid-late 1800's was at 60-65 million animals. We should then realize that the population must have been grazing at or near 100% use under average or, more likely, favorable climatic conditions. If a period of drought followed, this would induce a dramatic decline in the herd's population. Coupled with high kill rates from a previously unknown predator (European settlers), this could have brought the bison to near- extinction.

Some recent research questions whether bison herds really were migratory (Hart 2001). If not, local populations or meta-populations could not have grazed at 100% use for extended time periods, but perhaps 50% use could have been supported with even lower use rates in the more xeric parts of the bison's range.

It seems very unlikely and ecologically unfeasible that the historic bison herds once numbered 65 million animals (and used 100% of the herbage biomass) based on this model. It is more likely that bison used perhaps 50% of the biomass, with residual biomass used by other herbivores. Even 50% use may be a generous overestimate.

Assessment of Error and Bias: One assumption of the model is that all biomass is bison forage. This is certainly not true. Hence, all estimates made using this model over-estimate bison carrying capacity. In addition, one must remember that these estimates are of carrying capacity and not actual population. Based on our knowledge of how populations vary around their carrying capacity, one can feel relatively confident that the true population did not

substantially exceed the carrying capacity for extended periods of time. It is more likely, however, that a population is maintained at less than carrying capacity (Brewer 1988). However, the accuracy of this model's carrying capacity estimate has not been validated for range conditions in the late 1800's. The Konza prairie case study used in this research only validates the model in the late 1900's, a full century too late. A good deal of research has already been completed regarding the condition of native prairie (Shantz 1923; Weaver and Clements 1938; Weaver 1954; Weaver and Albertson 1956; Kuchler 1964; Dodd 1979; Lauenroth et. al. 1999). However, the fact remains that the true condition of native prairie will never be known for certain. In addition, the carrying capacity estimate given here is not specific to bison but rather to all herbivores in that area. In essence, all herbivores would be sharing the available biomass.

Another error influencing the accuracy and validity of this research is the lack of data for the historic bison range in Canada. This omission tends to under-estimate the population and offers a more conservative estimate. In addition, I should point out that the extent of bison range used in this research (figure 1) is itself an estimate. The edge of the range was not a barrier to the bison but was a constraining limit to the geographic information system.

The STATSGO data used to estimate biomass are also imperfect, primarily due to the coarseness of the source data. This data were then generalized as described earlier (Joao 1998). Other errors that propagated (Heuvelink 1998) through this research included elevation data errors, again due primarily to the coarseness of the 1:250,000 data.

Conclusions: Each of the more rigorous estimates of carrying capacity and population presented here indicate that the historic bison population probably was not 65 million but more likely 20-44 million. Even these more conservative estimates lead one to believe that historic bison populations were truly large and certainly a magnificent sight to behold. The tragedy that over-harvest brought such a large population to near-extinction is not diminished by these data.

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