

American bison socioecology

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ABSTRACT

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The present species of American bison (*Bison bison*) appeared only ~5000 years before present (B.P.) as part of a relatively depauperate North American ungulate fauna. The physical and social evolution of American bison fitted it primarily to the Great Plains with their climatic seasonality and cyclicism and, to a lesser degree, to the woodland habitats elsewhere in North America. Several features of the social behavior and social systems of American bison are illuminated by this ecological–evolutionary perspective. The strong seasonality of breeding and birth appears adaptive to the seasonality of the environment, as does seasonality in the dimorphic hair displays of males. Low stability of group membership appears adaptive to the low patchiness and high cyclicism of food abundance. Flexibility in birth site selection and the determinants of dominance status among cows appears to be adaptive to the range of habitats occupied and to the fluctuations in carrying capacity associated with climatic cyclicism. The social system and ecological circumstances of the American bison probably produced an outbred species. A history of outbreeding, combined with a polygynous breeding system indicates that management goals should include relatively high effective breeding populations.

INTRODUCTION

The American bison (*Bison bison*) is the largest terrestrial animal native to North America. The modern species is the smallest of the many that evolved in North America during the last three million years (McDonald, 1981). Although some extinct species were woodland-adapted browsers, both subspecies of the present species are very much grassland-adapted grazers. The plains bison subspecies (*Bison bison bison*) inhabited the grasslands of the Great Plains and central lowlands; the wood bison (*Bison bison athabasca*) inhabited the boreal forest in the north and foraged on sedges and grasses in the meadows. Neither subspecies browses significantly.

The present species is one of the more recently evolved large mammals. It appeared only ~5000 years before present (B.P.) (McDonald, 1981). The recency of this species assures us that it underwent substantial selection following the appearance of the habitat and community structure that emerged after the most recent glaciation some 10 000 years ago.

The Great Plains and central lowlands have existed in approximately their present form since that time. They are sweeping grasslands with very few trees. Their soils are substantially glacial drift and wind-deposited loess (Hunt, 1974). These fertile soils tend to be stable for distances of many miles. The plant community they support tends to be similar for considerable distances. Consequently, food resources for bison were not patchily distributed. These plains were the areas of greatest abundance of bison, and it is reasonable to assume that these were the areas to which they were primarily adapted. However, we know that bison inhabited woodlands bordering the plains and that there were small numbers of bison as far east as Pennsylvania.

The Great Plains has a strongly seasonal climate, with a short period of high growth of grasses in spring, followed by slower growth in the summer and fall, and no growth in the winter. The amount and northerly extent of summer rainfall is largely determined by the distance north that moist air from the Gulf of Mexico penetrates. This, in turn, depends on the location of the jet stream, which can vary sharply from year to year. Therefore, the northerly extent and quantity of rainfall can vary greatly from one year to the next, sharply changing the primary productivity of the grasslands (Bryson, 1974, 1980; Bryson and Murray, 1977). This, in turn, changes the bison carrying capacity. For example, the Great Plains carrying capacity for bison probably would have declined by ~75% between 1850 and the present, with most of the decline occurring from the mid-1880s to the mid-1890s, even if Europeans had not changed the area (Bryson, 1974, 1980). Such climatic changes varied locally and quickly changed the distribution of resources on the Great Plains (Bryson and Murray, 1977). In addition to these widespread changes, rapid and profound changes in local food bases were produced by fire.

COMPETITORS

The present species of bison was selected in an environment with few competitive species. Between 10 000 and 20 000 years B.P., the large mammal fauna of North America underwent a severe depauperation. Consequently, North America has only 12 native ungulate species (Gilbert, 1978) compared to some 90 in Africa (Leuthold, 1977). Only one recent North American species, the pronghorn (*Antilocapra americana*), was a plains specialist. While pronghorns numbered in the tens of millions, they were not a serious competitor of bison. They have <10% of the body mass of bison (Yoakum, 1978). Because pronghorns are ruminants and consequently rate-limited in digestion, their much smaller body size requires a much higher quality diet. They are, therefore, very selective feeders, searching out a diet that is primarily forbs from a grassland community that is primarily grasses (Yoakum, 1978; McCullough, 1980). As bison are unselective foragers in this grassland, pronghorns represent minimal food competition for them. These circumstances

should tend to select generality and, perhaps, flexibility in bison social systems and behavior rather than strong specialization.

PREDATORS

Although both grizzly bears (*Ursus arctos*) and mountain lions (*Felis concolor*) are known to have killed bison (McHugh, 1958), it appears that the primary predator of bison in the past 10 000 years was the gray wolf, *Canis lupus* (Roe, 1970; Carbyn et al., 1981). This coursing predator frequently hunts in packs. Adult wolves weigh ~100 lbs and, when organized in packs, are known to kill all the large ungulates native to North America (Mech, 1970; Carbyn et al., 1981).

We have only limited understanding of the quantity and quality of wolf predation on American bison. Most bison herds have not been subject to wolf predation during the era of scientific study, and the herds that are subject to wolf predation are difficult to study. The little we do know from current studies of wolf predation indicates that wolves prefer young-of-the-year as prey and take juveniles and mature cows less frequently. Adult male bison are the least frequently attacked (Carbyn et al., 1981).

These, then, are the selective forces that have operated on the social behavior of bison. Several features of their social behavior appear to be adapted to these pressures.

STUDY SITES

Much of the most detailed knowledge of the social behavior of American bison comes from studies conducted on the National Bison Range (NBR) in western Montana, U.S.A., and on Catalina Island, California, U.S.A. The NBR is not a Great Plains habitat, but it has most of the features of one (Fig. 1). It is situated in an intermontane valley among the Rocky Mountains. While the climate and grassland community are very similar to the northern Great Plains areas, the average relief of the terrain is considerable. In addition to extensive grasslands there are sizable areas of coniferous woodlands and limited areas of riparian habitat on the NBR. The area has been divided by fences into six approximately equal areas to facilitate range management. Two herds of bison are rotated from one area to the next every 3 months.

The overwintering population is held at 350 animals divided into two herds. Some 90–100 calves are born each spring, but the population is reduced again to 350 in the fall. A small part of this reduction is due to natural mortality. Most of it is achieved through live sales of animals designated as surplus. Nearly all animals are removed and sold when they reach 10 years of age.

The whole population, except for a few recalcitrant bulls, is rounded up every year. It is driven to a central area and passed through a series of chutes



Fig. 1. American bison grazing on the National Bison Range (NBR), which is primarily a palouse prairie habitat that shares many features with the Great Plains (photograph in NBR, Montana, U.S.A., by D. Lott).

and corrals. Each calf is branded with the year of its birth. Because the brands often take poorly, they vary from animal to animal within a year class. These variations supplement natural markings to make individual recognition of most animals possible.

About 400 plains bison live on Santa Catalina Island, California, an area of 200 km². The bison have free and undisturbed access to 86% of the island, but the cows do not enter areas that are very steep, very dry, or severely damaged by goats. The climate is Mediterranean. The physiography of the island produces a repetitive series of similar microhabitats in the part frequented by bison cows. Canyons containing free water and a productive grassland community tend to be separated by steep, drier, and less productive ridges, with occasional grassy uplands interspersed. These microhabitats go through similar seasonal changes in all parts of the island.

SPACING BEHAVIOR

American bison are large and primarily adapted to grazing in an open plains environment. Their food is not patchily distributed. Food resources that are not patchily distributed are not readily defended in territories (Brown, 1964).

Moreover, the absolute costs of territorial defense increase with body size. Because larger ruminants tend to eat lower quality food, the energetic economics of territoriality make it unlikely in large ruminants (Jarman, 1974). Therefore, we would expect bison to be dominance rather than territorially organized. They seem always to be so, but their dominance relations do vary.

The dominance relations of bulls have been described only in the NBR population to date (Lott, 1979a; Rutberg, 1984). They were neither strongly linear nor particularly stable. Dominance within dyads was challenged frequently and there were many reversals as well as triangular relationships. Status was very important to bulls. The highest ranked one-third of the bulls bred two-thirds of the cows (Lott, 1979a).

Rutberg (1983) found, however, that dominance relations among cows were stable on the NBR and could be predicted solely on the basis of membership in age classes. Older cows were always dominant to younger cows; body weight was unrelated to dominance. Rutberg (1983) hypothesized that the lack of change in dominance within dyads was due to the insignificance of the dominance system in the economy of those cows. Forage was abundant. This abundance was reflected in the early age of female sexual maturity (2 years) and the very high (85–90%) calving rate in this population (McHugh, 1958; D.F. Lott, personal observations, 1966–1974).

However, there is some evidence that bison cows will challenge and change dominance relations under different circumstances. A group of cows from Catalina Island, California, that was temporarily confined to a corral and fed from a point source, expressed a dominance structure that was not strongly related to their estimated age but was very strongly related to their weight (Lott and Galland, 1987). This population differed from the one studied by Rutberg (1983, 1984) in three ways, (1) they had poorer forage, (2) they were studied in confinement, and (3) they were from a larger population that lived in smaller groups.

These differences in circumstances justify at least two interpretations of the differences in behavior. First, the Catalina cows were food-limited both while free ranging and while confined. If dominance status can raise foraging success, these cows might have contested dominance status earlier and overthrown dominance relationships based on age before the cows were confined. But the dominance relations of free-ranging cows on Catalina is not known, so the dominance system observed in the corral may also have been generated there as a product of close confinement and a point source of food. However, whichever of these two factors determined the difference in social behavior, this difference occurred and this shows that bison cows will contest age-related dominance relationships in some circumstances. The third potentially significant difference is that the confined population of cows was more than twice as large as either of the NBR herds, lived in smaller groups (Lott, 1974), and ranged much more widely (Lott and Minta, 1983a). Consequently, they

interacted with other individual cows less frequently. This may have weakened dominance relations established early in life and facilitated reversals.

CALVING SEASON AND LOCATION

The sharply seasonal availability of food puts a premium on calving at the right time to take advantage of the springtime peak in high quality grass production (Rutberg, 1984). For this reason, and perhaps to gain the advantage of predator satiation that birth at a time of high calving can confer (Estes and Estes, 1979; Lott, 1981), bison calving peaks sharply, with approximately 80% of births occurring in a 3-week period (Rutberg, 1984).

As the primary adaptation of bison is to a habitat without bushy vegetation, parturition usually takes place in circumstances where a cow alone would be easily spotted. Because the group to which the female belongs represents the only available cover, it is not surprising that in open habitat cows usually give birth in or near their group. However, when living in a habitat with some trees and bushes available, most cows give birth alone under the cover of trees or shrubs (Lott and Galland, 1985). Their ability to select the birth site offering most cover, regardless of whether or not that involved proximity to other cows, may reflect the lack of competing ungulate species in North America. This lack of competition may have produced a secondary adaptation to woodland environments. This hypothetical secondary adaptation may be partly expressed through their flexibility in choice of birth sites.

BREEDING SEASON

A sharply peaked calving season means that most of the cows were bred at about the same time (Lott, 1981). Thus, many cows were in estrus during a relatively short period. This fact affects the breeding strategies of both sexes. Each estrous cow is, in effect, in competition with several others to attract the attention of breeding bulls. Their social system involves no male parental care and they breed promiscuously. Therefore, selection has probably favoured cows that bred with one of the most dominant males. With many cows in estrus at one time, cows must behave in a way that draws the attention of those bulls.

Large groups have more bulls whose attention is potentially available. The cows aggregate at the onset of the breeding season, forming the largest groups of the year in most populations (McHugh, 1958; Lott, 1974; Lott and Minta, 1983b). In addition, the cows are very restless in the early stages of estrus and repeatedly break away from the bull tending them to run through the herd, attracting the attention of other bulls (Lott, 1981).

For the bulls, the peaking of the breeding season puts a premium on making a maximum effort in minimum time. This has consequences for both the relationships among bulls and their interactions with cows. The short breeding

season appears to intensify dominance interactions among the bulls. Higher status bulls have substantially higher breeding success. Because the breeding season is very short, bulls that are of lower status at the beginning of the season must raise their status quickly if the change is to benefit them. Therefore, status is challenged frequently and intensely. The result is that there are many reversals in status, and status contests frequently escalate into fights (Lott, 1979a).

The breeding strategy also seems to be influenced by the shortness of the season. Because most breeding takes place in a few days, bulls follow a strategy that appears to risk the certainty of fertilizing 1 cow in order to have the chance of fertilizing others. Bulls frequently break off tending a cow that is not yet fully receptive to test the receptivity of others. Also, their post-copulatory sequestering of cows is brief and sometimes does not occur at all (Lott, 1981).

GROUPED VERSUS SOLITARY

Group membership provides some protection against predation (Hamilton, 1971; Bertram, 1978), especially from coursing predators such as wolves. Therefore, those bison most at risk should tend to form groups. We find that cows, presumably for their own sakes and that of their calves, tend to be in groups of 24–40 individuals, whereas mature bulls tend to be solitary or with 1 or 2 others except during the breeding season (McHugh, 1958; Lott, 1974; Meagher, 1973).

The lower gregariousness of mature bulls presumably reflects their lesser vulnerability to predation. Their foraging and social behavior outside the breeding season reflects the seasonality both of breeding and of availability of food. They spend most of the year acquiring and conserving energy in the form of fat, which is consumed rapidly during the breeding season. Mature bulls lose a minimum of 10% of their body weight during the rut owing to a combination of sharply reduced feeding and sharply increased, energy-costly social interactions (Lott, 1979a).

At the end of the rut, in mid- to late summer, males re-establish their solitary pattern. The reduction in aggressive interaction that their dispersion produces is reinforced by the loss of their sexually dimorphic hair displays, which probably decreases each bull's effectiveness as a stimulus for aggression by other bulls (Lott, 1979b).

UNSTABLE ASSOCIATIONS

American bison females and their calves were sometimes thought to live in stable matriarchal groups, with daughters staying with their mothers whilst sons drift off to disperse (Seton, 1929; Soper, 1941). This hypothesis was

tested on a population of ~400 bison on Catalina Island (Lott and Minta, 1983b). A sample of cows were marked and followed for 5 years. During these years, 8 calves were born to our marked group. Mature cows associated with one another randomly. In fact, a truncated binomial distribution generated by random association of dyads plotted exactly over a curve of their associations (Lott and Minta, 1983b). Cows and their young calves were, of course, different. The 4 male and 4 female calves stayed with their mothers for an average of 9 and 14 months, respectively; well past weaning age. However, when they ended their association, the cows and calves moved immediately to a random level of association, just as though they had never had any special relationship.

In other populations, at least some cases of mother–daughter associations last longer than those observed on Catalina (W. Green, personal communication, 1988; Shaw, 1990). This difference opens the door to some intriguing analyses of the ecological determinants of each pattern and the proximate mechanisms that produce them. However, there are no reports of other stable associations, and group stability is clearly typically low. Selection may have favored this pattern of behavior because the ecology of bison seems likely to favor ready dispersers. The patchiness of the forage is very low. Therefore, suitable habitat should exist in most directions for any individual. There is little to be gained from exploiting the older individuals' knowledge of foraging areas as there is, for example, in Mountain sheep (Geist, 1971). Moreover, the strong year-to-year fluctuation of the Great Plains climate makes the amount and quality of forage available in any one general area vary sharply from year to year. Thus, there is no substantial risk to dispersal, and there may be a considerable advantage. It seems likely that the lack of stable social group membership in bison was selected to facilitate dispersal in a non-patchy, fluctuating environment.

HOME RANGES

If American bison have been selected for ready dispersal, it might be expected that they would have large home ranges. The available information indicates that this is so, but it also indicates that their home range behavior adjusts to their local ecology.

In the terminology of Baker (1978), bison were probably neither nomadic (i.e. having no apparent fixed pattern of directions) nor long distance movers. More likely, plains bison typically circulated within a home range depending on local conditions (water, forage phenology, salt, wallows, and insects) (Roe, 1970). This type of movement has been called "seasonal latitudinal return migration" (Baker, 1978).

Frequently a migratory animal may have two distinct home ranges (the total fraction of the familiar area physically visited by an animal in a given

time interval); for example, a summer and a winter home range. Meagher (1973) described a clear example of a seasonal latitudinal return migration for female bison in Yellowstone National Park, Montana and Wyoming, U.S.A. Several rather distinct bison sub-populations move from traditional winter ranges to traditional summer ranges and back, generally along traditional routes.

Meagher views the occurrence of these movements, the routes used, and the destinations as products of environmental heterogeneity. Much of Yellowstone Park is forested. The preferred bison habitat is in the interspersed meadows. Seasonal changes in snow depth, temperature, presence of biting insects, and the annual cycle of the plant community create strong contrasts between areas situated at different elevations. These contrasts seem to determine the movements she observed.

On the other hand, it was found that plains bison on Catalina Island ranged widely despite low habitat variation (Lott and Minta, 1983a). Sixteen marked cows were located an average of 48.1 times over 44 months. The subjects were found in nearly every part of the available and suitable areas of the island. The mean area of the home ranges was 56.1 km².

Large ungulates do not necessarily have large home ranges. Except for migratory movements, nearly all species of African ungulates have much smaller home ranges than those of bison on Catalina or in Yellowstone Park (Leuthold, 1977). Water buffalo in Australia have home ranges of < 3 km², only about 5% the size of bison home ranges on Catalina, even during severe drought (Tulloch, 1978).

Perhaps the unstable climate of the North American Plains and the varying resource distribution it produced, selected for the bison cows' propensity to explore. Whatever the reason, bison seem predisposed to range more widely than most other large ungulates. At the same time, Meagher's (1973) data make it clear that loyalty to a large traditional home range is an important feature of the Yellowstone population. How this ranging propensity manifests itself apparently depends on the particular environmental pressures on a particular population. In recent years the growing Yellowstone population has extended its winter range to previously unoccupied areas both inside the park and outside of it (M. Meagher, personal communication, 1987).

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