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Dominance Relations and Breeding Rate in Mature Male American Bison

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Abstract

The assumption of a linear dominance hierarchy accounted for 78 % of the outcomes of aggressive interactions in a group of 26 mature male American bison (*Bison bison*) during a breeding season. All recorded interactions between bulls were initiated aggressively, and 88 % of all interactions were won by the initiator. The dominant-subordinant roles were reversed at least once in most dyads during the three weeks. Neither age nor body weight were correlated with high social standing. Bulls with higher social standing had higher breeding rates.

Introduction

ALLEE et al. (1949) described dominance-subordination as one of the three general organizing principles of animal social systems. The tendency of certain individuals within a social group consistently to defer to certain others is a common theme in the social organization of enough species to warrant extended treatment in any general discussion of animal social behavior (WILSON 1975; BROWN 1975; BARASH 1977). Nevertheless, some very critical evaluations of the generality and utility of the concept of social dominance have developed from studies of social organization in primate groups (ROWELL 1974; BERNSTEIN 1976).

The particular form of dominant-subordinate relationships, and the way in which they affect the individuals engaged in them, will vary between species, and between age and sex classes within a species. At least some of these variations should be interpretable from knowledge of the general biology and ecology of the species, and its phylogenetic history. Our understanding of the function and selection history of this characteristic can be advanced by quantitative studies of its manifestation and consequences in a range of species.

Dominance relations in American bison (*Bison bison*) were first quantitatively studied by MCHUGH (1958). His subjects were 16 adults (including 4 bulls) living in a 152 ha enclosure in winter and 53 ha enclosure in summer.

Most of McHUGH's data were gathered in the winter. 90 % of the interactions recorded were conflicts over hay distributed in bunches as winter food. In a typical period ("the spring" of one year, not more precisely delimited) he reported only one reversal and no triangles in 726 interactions, although the gradual maturing of two young bulls over a period of years led to some triangles at other times.

Bison displace one another from naturally occurring food sources, particularly under severe snow cover feeding conditions (McHUGH 1958; MEAGHER 1973; VAN CAMP 1975) but a dominance system worked out primarily on the basis of access to bunches of hay could be distorted by the measure employed. Moreover, McHUGH's small study group was very heterogeneous with a few representatives of every age and sex class present.

EGERTON (1962) studied 25 American bison in Waterton Park. They were confined in winter to a 64 ha pasture and in summer to a 128 ha pasture, but without supplementary feeding. This group was also heterogeneous, ranging from mature bulls through mature cows to juveniles and calves. Of the 1115 interactions she observed, 94.5 % were consistent with the assumption of a linear dominance hierarchy.

A weakness that these studies share is that the relationships between any two members of the species contribute equally to the quantification of dominance as an organizational principle. Yet relationships between individuals within certain subclasses are functionally more important than are such relationships in general. For example, the special significance of the social relationships of members of certain subclasses with one another are central to understanding such commonplace phenomena as sexual dimorphism (e.g. GEIST 1974).

Mature ♂♂ constitute such a significant subclass in American bison. Bison are strongly sexually dimorphic; adult ♂♂ weigh about 900 kg and ♀♀ only about 495 kg. The ♂♂ have markedly developed fighting equipment. Mature ♂♂ constitute a natural subclass in other ways too. Except for occasional short visits, they are separate from the cow groups where the young grow up for all but a few weeks of the year. The breeding system is highly polygamous, so that even during their period of close association with groups of cows they rarely develop any lasting or consistent social relationships with them. Finally, they are competitors for a limited resource, breedable cows, which makes their relationships significant.

An obvious hypothesis about the functions of dominance relations for mature ♂♂ is that they give a breeding advantage to those with high status. This hypothesis can be examined by describing the dominance relationships in a group of mature bulls, and comparing those relationships to their breeding rate. The more closely the population and circumstances of the subjects in such a study approximate those characteristic of the species during its evolution, the more helpful the data generated will be. We do not have much certain information about naturally occurring breeding groups of bison, but the data we do have on the size and range of free ranging groups (MEAGHER 1973; FULLER 1960; LOTT 1974 a) suggest that the two mature bulls studied by McHUGH, and the four studied by EGERTON, were unnaturally small and unnaturally confined groups.

The goal of the present study was to describe and analyse dominance relations among a larger group of mature male American bison ranging over a larger area, and to correlate the observed status with the breeding rate of the individual bulls.

Methods

Study Site

The study was conducted on the National Bison Range, Moiese, Montana, where approximately 350 bison are maintained without supplemental feeding on a mildly hilly range of 7,200 ha. The herd is divided into two approximately equal populations each confined to one of 6 fenced areas averaging about 1200 ha. They are moved from one to another of these areas about every three months.

One of these populations was observed from July 18 to August 14, 1972. There were 77 breeding age (2+) cows, 22 yearling heifers, 21 yearling bulls, and 52 (2+) bulls at the beginning of the study, in a 927 ha fenced area. The number of cows, calves, and young bulls was constant throughout the study. The selected study group was the mature bulls 6 years old and older, plus one precocious five-year-old who actively participated in the social activity of the older bulls, though at a lower level than most. Initially there were 22 bulls in the study group. During the latter part of the study, 4 more bulls (numbers 23, 24, 25, and 26) entered from an adjoining area. Two of these entered the area on August 5, one on August 7, and one on August 12.

Observation Techniques

The bison on this range are a tourist attraction, and so are well adapted to motor vehicles. Observations were made from a jeep which permitted access to nearly all frequented areas. None of the bison were disturbed at passing by the jeep or its passing by them at distances of 12 m or more. A few bulls from this population have rested in the shade cast by the jeep or scratched their flanks against it.

Observation of events and identification of individuals were aided when necessary by binoculars (10×40 and 7×35) and spotting scopes (20×). These observations were dictated to a portable tape recorder, and this dictation was transcribed for analysis.

Behavioral Events Recorded

Two general classes of behavioral events were recorded: dominant-subordinate interactions between bulls, and breeding.

Dominant-Subordinate Interactions

The most complete description of aggressive behavior patterns in bison occurs in LOTT (1972, 1974a, b). In this study the only aggressive interactions analysed were those that led to an outcome in which the loser and winner could be categorized unambiguously.

Aggressive Behavior Patterns

The following forms of aggressive behavior were recorded:

Supplanting: One bull approaching another and the other yielding and withdrawing. Such interactions were recorded only if they involved the reallocation of a limited resource, such as an opportunity to stand beside a cow or to occupy a wallow.

Head-on threats and rush threats: A mutual or unilateral approach at a walk or run (a run is extremely rare) in about the position for a straight-on attack, i. e. horns at the ready.

Broadside threats: A stereotyped threat in which the threatening animal turns broadside to his opponent and stands stiffly.

Nod threats: Bulls approach head on and stand close together raising and lowering their heads from time to time in swift, matched movements. If there is an attack it comes from the low position.

Fighting: Physical clashes in which the head and horns of one animal contact the head and horns or body of the other. Since the initiation of a fight is rarely precipitous, the first contact, at least, is nearly always head to head.

Breeding

Copulation is also described elsewhere in detail (MCHUGH 1958; LOTT 1974a, 1976). The ♂ mounts and penetrates; frequently the ♀ begins to walk or run forward. Copulation normally terminates with ejaculation, identified by a deep penetration, after which the ♂ dismounts. The pattern of copulation is very similar to that in domestic cattle (FRASER 1968) except that few bison cows stand for more than one copulation.

The sampling technique used was to survey all the available animals simultaneously, recording all events of interest and identifying the individuals involved (i.e., ad lib. sample, ALTMAN 1974). Therefore there is no way to estimate what % of the total aggressive interactions were recorded, although few were unrecorded because of inability to identify the participants. Copulation by 37 of the 77 breeding age cows in the herd was observed and recorded, and the breeding bull identified. One more cow was observed being bred, but circumstances prevented a certain identification of the bull.

The calving rate among the cows in this population is about 85 %. This implies that most of the remaining cows bred unobserved. I believe most of these cows bred when no observer was present. Our sample period did not cover all the daylight hours. In addition rutting activity continues throughout the night (LOTT unpubl. obs.).

Study Schedule and Technique

July 18 through July 24 was spent identifying individual ♂♂ in the study population, using pre-existing distinguishing features. The most important were natural morphological variations, such as scars and broken horns. In addition, each subject had been branded as a calf with a single digit indicating the year of his birth. Since several had been branded in each year, the digit alone did not distinguish individuals, but bison take brands rather poorly so individual brands of the same year varied considerably, providing further opportunities to confirm individual identities.

All these variations were noted on a set of four printed outlines representing both sides and both ends of a bull. Also, each animal was photographed from several different perspectives (including the brand on the rump) and the photographs were kept with the outlines in a looseleaf binder. This binder was available throughout the study to check on any doubtful identifications. Identification was facilitated by the observers' familiarity with bison in general, and the fact that many of the individuals were already known from previous studies.

Data recording began on 25 July. The field schedule varied slightly about a mean value of 12 h per day from about 6.30 a.m. to 6.30 p.m. Time spent locating animals averaged about one h per day. This resulted in a daily observation schedule of 11 h per day. This schedule was maintained from July 25 through August 14.

During the first two weeks the mature cows in the population were together nearly constantly, but during the final week they began to break up into the smaller groups characteristic of the rest of the year. By the last three days of observation, the largest group had declined from 150, excluding bulls, to 103. All 22 mature bulls present at the beginning were in the herd for the first week; then they began to leave for hours and days at a time. By the last four days of observation only a few were present (6, 5, 6, 5). The grouping of births each spring on this range, and the experience of following the rut through previous years, indicate that breeding is 90 % or more completed by August 14. This agreed with our observation that rutting activity had fallen to a very low ebb at this point. Accordingly the observations were terminated on that date.

Results

Description of Dominance Relations

The outcomes of the encounters were analysed by the traditional technique for describing a dominance organization (see BROWN 1975 for an exceptionally clear description of this technique). The basic strategy is to assume a dominance hierarchy exists and arrange the data to conform as closely as possible to that assumption. When properly used this approach tends to overestimate the conformity of the observations to the assumption of a dominance hierarchy by resolving all ambiguities in favor of that assumption. Therefore, these tables do not precisely represent the real world, but they are an approximation which is useful in itself, and useful for making comparisons between species and subgroups within species. Since this approach requires that each table be reordered many times, these data were manipulated by a computer, which generated Table 1.

Table 1 Unweighted hierarchical ordering of aggressive interaction outcomes, the number

	Losers															
Bull	01	03	04	26	02	25	06	08	24	09	05	23	10	07	12	17
01	0	8	5	0	2	0	6	11	0	3	21	0	5	7	1	3
03	0	0	4	0	0	0	4	4	0	8	12	0	12	3	2	2
04	1	1	0	0	3	0	1	4	0	4	8	0	10	1	0	1
26[3]	0	0	0	0	7	1	0	0	0	0	0	2	3	0	0	0
02	1	2	3	1	0	0	1	3	0	0	3	0	3	2	2	1
25[2]	2	0	0	0	0	0	0	0	8	12	0	1	7	0	0	0
06	1	0	0	0	0	0	0	5	0	2	6	0	5	1	2	1
08	2	0	1	0	1	0	0	0	5	11	3	6	6	0	0	4
24[1]	0	0	1	0	0	0	0	2	0	2	0	1	2	0	0	1
09	4	0	1	0	0	1	2	3	1	0	0	2	9	1	0	4
05	1	2	0	0	1	0	6	4	0	0	0	0	17	3	0	6
23[1]	2	0	0	0	1	3	0	1	0	2	0	0	1	0	0	1
10	1	1	0	0	0	0	1	2	1	2	1	0	0	6	0	3
07	3	2	0	0	0	0	0	1	0	0	2	0	0	0	3	1
12	0	0	1	0	0	0	2	0	0	0	0	0	3	0	0	0
17	1	0	0	0	0	0	0	2	0	2	2	0	1	1	0	0
18	1	0	1	0	0	0	1	5	0	6	3	0	1	1	0	1
13	1	0	0	0	0	0	2	0	0	1	2	0	2	1	2	1
14	1	0	1	0	0	0	0	0	0	0	0	2	1	0	1	4
21	0	0	0	0	0	7	0	0	1	0	0	0	2	1	0	0
19	0	0	2	0	0	0	0	0	0	2	1	0	1	4	0	1
15	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
11	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0
20	0	0	0	0	0	0	1	0	0	0	1	0	0	2	3	3
16	0	1	0	0	0	0	2	1	0	0	1	0	1	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Total Losses	22	19	20	1	16	12	29	48	16	57	67	14	94	34	16	38

* Includes two cows bred by two different bulls; [1] entered herd 5 August; [2] entered

The result produced by the minimization of the proportion of entries below the diagonal produces results that are anomalous in one respect. Some individuals are ranked below others that they have dominated in the majority of encounters (e.g. 25 won both his encounters with 01, yet is ranked below him). This is the result of treating the inter-individual relationships as subordinate to an overriding organization principle; I have designated this approach the "hierarchy-first" decision rule. To make the data in this study as comparable as possible to that of previous studies on bison I have used the "hierarchy first" decision rule in Table 1. But bulls undoubtedly behave according to their relationships to one another rather than their position in the hierarchy created by this rule. BERNSTEIN (pers. comm.) has developed a technique that restores some of the significance of relationships between individuals. He multiplies entries below the diagonal by their distance from the diagonal where distance is defined as the number of lines parallel to the diagonal from the diagonal to and including the line they fall on. The application of this rule generated Table 2. In this case the outcomes of the two approaches are nearly identical. In Table 2, 78 % of the entries are above the diagonal, and the rank orders in Table 1 and Table 2 are highly correlated ($r_s = .98$).

The most striking feature of Table 1 is that 22 % of the entries fall below the diagonal (and thus do not conform to the assumption of a dominance

of cows bred by each bull and each bull's age and (when available) body weight *Table 1*

Losers													
18	13	14	21	19	15	11	20	16	22	Total Wins	Cows Bred	Wt. (kg)	Age
5	2	3	4	2	1	0	7	0	0	96	4	758	7
7	5	1	3	4	0	0	5	1	0	77	2	-	9
4	6	0	2	2	3	1	4	0	3	59	3	810	7
0	0	0	1	1	0	0	0	0	0	15	1	-	7
3	2	4	1	1	1	0	2	0	0	36	1	-	10
0	0	8	3	3	2	0	0	0	0	46	3	-	12
1	3	1	0	1	1	0	4	0	0	34	4	790	8
2	2	1	0	6	0	1	7	1	1	60	1	-	10
0	1	3	3	2	2	0	1	0	0	21	4	771	8
0	0	2	4	4	3	0	3	2	0	46	1	866	6
5	8	0	2	5	2	1	4	0	1	68	3	884	12
0	5	3	3	1	0	0	1	0	0	24	3	907	8
4	4	7	6	4	5	0	7	2	0	57	0	765	8
2	2	3	1	1	1	0	4	1	1	28	1	850	11
1	2	0	2	0	0	0	4	0	0	15	2	799	8
8	2	2	2	3	0	0	1	0	0	27	0	801	8
0	1	1	1	1	1	0	1	0	0	26	0	772	9
1	0	3	1	3	1	1	12	1	1	36	1	808	6
0	0	0	7	3	0	0	0	1	0	21	0	774	6
0	0	1	0	5	2	1	0	1	0	21	1	801	6
0	1	1	3	0	5	1	3	0	0	25	2	770	10
1	1	0	2	0	0	0	9	2	0	16	1	-	5
0	4	0	0	0	0	0	0	1	9	0	0	821	7
0	1	2	2	1	1	0	0	0	0	17	1	-	12
1	0	0	0	0	0	0	0	0	0	7	0	-	12
0	0	0	0	0	0	0	0	0	0	1	0	-	11
45	52	46	53	53	31	6	79	12	8	888	39*		

herd 7 August; [3] entered herd 12 August.

hierarchy). Perhaps this very weak organization is due to combining into a single table data that should be considered separately. To evaluate this possibility I have sorted the data into more homogeneous sets and again attempted to order it into hierarchies.

Length of Sample Interval

Since a large part of the deviation of the data from the assumption of a linear hierarchy is due to reversals, it may be that many of the discrepancies arise from summing the relationships over time, even as short a time as three weeks. If this is so it should be revealed by describing relationships over shorter time intervals. Therefore the study period was divided approximately in half, the first 11 days separated from the second 10 days.

These data can be arranged to conform somewhat better to the assumption of a dominance hierarchy. Of the 648 encounters recorded in the first 11 days 81% fall above the diagonal, compared to 78% over the entire 21 days. So reversals are not completely random in time, but in at least some cases involve a lasting shift in the relationship between the individuals. But although dominance relations are more consistent with the assumption of a dominance hierarchy over shorter time periods, many outcomes still do not fit.

Table 2 Weighted hierarchical ordering of aggressive interaction outcomes, the number

	Losers															
Bull	0 1	0 3	0 4	2 6	0 2	0 5	0 8	2 5	2 4	0 9	0 6	2 3	1 0	0 7	1 7	1 3
01	0	8	5	0	2	21	11	0	0	3	6	0	5	7	3	2
03	0	0	4	0	0	12	4	0	0	8	4	0	12	3	2	5
04	1	1	0	0	3	8	4	0	0	4	1	0	10	1	1	6
26[3]	0	0	0	0	7	0	0	1	0	0	0	2	3	0	0	0
02	1	2	3	1	0	3	3	0	0	0	1	0	3	2	1	2
05	1	2	0	0	1	0	4	0	0	0	6	0	17	3	6	8
08	2	0	1	0	1	3	0	0	5	11	0	6	6	0	4	2
25[2]	2	0	0	0	0	0	0	0	8	12	0	1	7	0	0	0
24[1]	0	0	1	0	0	0	2	0	0	2	0	1	2	0	1	1
09	4	0	1	0	0	0	3	1	1	0	2	2	9	1	4	0
06	1	0	0	0	0	6	5	0	0	2	0	0	5	1	1	3
23[1]	2	0	0	0	1	0	1	3	0	2	0	0	1	0	1	5
10	1	1	0	0	0	1	2	0	1	2	1	0	0	6	3	4
07	3	2	0	0	0	2	1	0	0	0	0	0	0	0	1	2
17	1	0	0	0	0	2	2	0	0	2	0	0	1	1	0	2
13	1	0	0	0	0	2	0	0	0	1	2	0	2	1	1	0
18	1	0	1	0	0	3	5	0	0	6	1	0	1	1	1	1
14	1	0	1	0	0	0	0	0	0	0	0	2	1	0	4	0
12	0	0	1	0	0	0	0	0	0	0	2	0	3	0	0	2
21	0	0	0	0	0	0	0	7	1	0	0	0	2	1	0	0
19	0	0	2	0	0	1	0	0	0	2	0	0	1	4	1	1
15	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
11	0	2	0	0	1	1	0	0	0	0	0	0	0	0	0	4
20	0	0	0	0	0	1	0	0	0	0	1	0	0	2	3	1
16	0	1	0	0	0	1	1	0	0	0	2	0	1	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Total Losses	22	19	20	1	16	67	48	12	16	57	29	14	94	34	38	52

* Includes two cows bred by two different bulls; [1] entered herd 5 August; [2] entered

Situation Specificity

A second potential source of deviation of the observations from linearity is that dominance relations between the bulls were situation specific. That is, Bull A might be consistently dominant to Bull B in a specific context such as eating but consistently subordinate to Bull B in a different specific context such as tending. If this were the case, Table 1 would be reporting a melange of independent dominance hierarchies each of which was essentially linear when seen alone, but which summed up to a rather muddy picture when combined. To examine this possibility two separate dominance hierarchies were constructed: the first from encounters recorded in the single specific context of tending, and the second from encounters recorded in all other contexts combined. The hierarchy-first decision rule was used.

The results are reported in Table 3. The proportion of outcomes accounted for by the assumption of a dominance hierarchy is greater in the tending situation (81%) than in all non-tending situations combined (77%) or in tending and non-tending situations combined as they are in Table 1 (78%). The statistical reliability of these small differences can be examined by a chi-square analysis of the differences in proportions of the data accounted for. When the tending situation hierarchy is compared to the overall hierarchy, the resulting $chi^2 = 1.35$, $df = 1$, $p \simeq .25$, demonstrating that relationships in tending situa-

of cows bred by each bull and each bull's age and (when available) body weight *Table 2*

Losers													
1 8	1 4	1 2	2 1	1 9	1 5	1 1	2 0	1 6	2 2	Total Wins	Cows Bred	Body Wt. (kg)	Age
5	3	1	4	2	1	0	7	0	0	96	4	758	7
7	1	2	3	4	0	0	5	1	0	77	2	-	9
4	0	0	2	2	3	1	4	0	3	59	3	810	7
0	0	0	1	1	0	0	0	0	0	15	1	-	7
3	4	2	1	1	1	0	2	0	0	36	1	-	10
5	0	0	2	5	2	1	4	0	1	68	3	884	12
2	1	0	0	6	0	1	7	1	1	60	1	-	10
0	8	0	3	3	2	0	0	0	0	46	3	-	12
0	3	0	3	2	2	0	1	0	0	21	4	771	8
0	2	0	4	4	3	0	3	2	0	46	1	866	6
1	1	2	0	1	1	0	4	0	0	34	4	790	8
0	3	0	3	1	0	0	1	0	0	24	3	907	8
4	7	0	6	4	5	0	7	2	0	57	0	765	8
2	3	3	1	1	1	0	4	1	1	28	1	850	11
8	2	0	2	3	0	0	1	0	0	27	0	801	8
1	3	2	1	3	1	1	12	1	1	36	1	808	6
0	1	0	1	1	1	0	1	0	0	26	0	772	9
0	0	1	7	3	0	0	0	1	0	21	0	774	6
1	0	0	2	0	0	0	4	0	0	15	2	779	8
0	1	0	0	5	2	1	0	1	0	21	1	801	6
0	1	0	3	0	5	1	3	0	0	25	2	770	10
1	0	0	2	0	0	0	9	2	0	16	1	-	5
0	0	0	0	0	0	0	0	0	1	9	0	821	7
0	2	3	2	1	1	0	0	0	0	17	1	-	12
1	0	0	0	0	0	0	0	0	0	7	0	-	12
0	0	0	0	0	0	0	0	0	0	1	0	-	11
45	46	16	53	53	31	6	79	12	8	888	39*		

herd 7 August; [3] entered herd 12 August.

tions considered alone are not reliably more consistent than relationships overall. The chi-square value of the difference in proportions accounted for in tending and non-tending hierarchies is 1.70 ($df = 1$, $p \simeq .20$). Therefore, the relationships between bulls in the single situation of tending are not reliably more consistent than in the non-tending situations combined.

It is also clear from inspection of the table that the ranking of bulls in the tending situation differs from their ranking in the non-tending situations. Yet these rankings are by no means independent. The Spearman rank correlation (r_s) between the tending ranking and the non-tending ranking is .81. This is a statistically significant correlation ($z = 4.03$, $p < .001$) and accounts for 66 % of the total variance. Thus the rankings of the bulls are somewhat situation specific, but most of the ranking is determined by some feature of the individual bulls that transcends particular situations.

It appears that these data cannot be arranged in a matrix that meets the expectations created by the word "hierarchy". That word suggests some overall organizational structure which would result in many more of the outcomes falling above the diagonal. On the other hand the data clearly deviates from randomness. Observation of the animals and inspection of the data both suggest that the only operating level of organization is the dyad. That is, however, a significant level of organization. Individuals do dominate other in-

Table 3: Comparison of tending and not-tending ranks

Tending Rank				Not Tending Rank			
Bull	Cows Bred	Wt. (kg)	Age	Bull	Cows Bred	Wt. (kg)	Age
01	4	758	7	26	1	-	7
03	2	-	9	25	3	-	12
04	3	810	7	01	4	758	7
06	4	790	8	02	1	-	10
08	1	-	10	03	2	-	9
05	3	884	12	04	3	810	7
26	1	-	7	05	3	884	12
23	3	907	8	06	4	790	8
02	1	-	10	10	0	765	8
25	3	-	12	24	4	771	8
09	1	866	6	17	0	801	8
10	0	765	8	13	1	808	6
07	1	850	11	18	0	772	9
24	4	771	8	08	1	-	10
13	1	808	6	09	1	866	6
19	2	770	10	07	1	850	11
15	1	-	5	14	0	774	6
17	0	801	8	23	3	907	8
12	2	799	8	12	2	799	8
18	0	772	9	15	1	-	5
20	1	-	12	19	2	770	10
14	0	774	6	20	1	-	12
21	1	801	6	21	1	801	6
11	0	821	7	16	0	-	12
16	0	-	12	11	0	821	7
22	0	-	11	22	0	-	11

dividuals; moreover, some individuals dominate more other individuals more of the time, which makes it possible to order their wins and losses. The resulting ranking probably should not be called a hierarchy, but it does represent a loose social standing which may have some significance to the bulls. The remainder of this section is devoted to a description of these dyadic relationships, an analysis of their determinants and an examination of the consequences of the social standing produced by the summation of these dyadic relationships.

Reversals

Most of the entries that fall below the diagonal record outcomes between pairs in which there were also opposite outcomes, i.e. reversals. To further determine the contribution of reversals to the deviation of the results from a linear hierarchy, all the pairs of bulls that interacted more than once were tracked. Of the 154 pairs of bulls with more than one interaction, only 68 pairs retained a consistent dominant-subordinant relationship for the entire three week study period. 49 pairs switched roles between the beginning and the end of the study, and 37 pairs switched roles and then switched back to the original relationship one or more times.

Reversals were not restricted to bulls of generally low social standing or low breeding rates. For example, the three highest standing bulls, numbers 1, 3 and 4, had a total of 32 reversals among their 61 losses.

Relation of Initiation of Encounter to Winning the Encounter

It was not possible to determine which animal initiated 111 of the encounters. Of the 777 encounters in which the initiator was known, 688 were won by the initiator and 89 were won by the recipient. As Table 4 illustrates, the proportion of encounters in which the initiator dominated was less when the recipient was tending than when neither animal was tending. The chi-square value of these proportions ($chi^2 = 3.04$, $df = 1$, $p = .08$) suggests that this is probably a reliable difference. Apparently then, either the tending bulls have a higher motivational level and so successfully resist bulls that would otherwise dominate them, or the non-tending bulls were more likely to challenge a bull dominant to them when that bull was tending than when he was not. Of course it is not necessary to choose between these two factors; both might be involved, even in single encounters.

Table 4: Number of encounters in which the initiator dominated as a function of whether or not the recipient was tending

	Recipient Tending	Neither Bull Tending
Initiator Win	365	273
Recipient Win	57	27

When the interaction progressed beyond threats to fighting, initiators were no more likely to win than recipients. Table 5 reports the outcomes of fighting versus threat encounters. The differences in proportions reported in Table 5 are statistically reliable ($chi^2 = 72.03$, $df = 1$, $p < .0001$).

Table 5: Comparison of the number of encounters in which the initiator dominated as a function of whether or not the encounter became a fight

	Initiator Win	Recipient Win
Fight	26	25
Not Fight	662	64

Fights were more likely to be the occasions for a reversal than were threat interactions. Table 6 reports the relation between fight and threat interactions and the occurrence of reversals. When a chi-square test is applied to Table 6 the resulting value is $chi^2 = 32.35$, $df = 1$, $p < .001$.

Table 6: The number of interactions leading to a reversal as a function of whether or not the interaction became a fight

	Reversal	Not Reversal
Fight	44	79
Not Fight	110	655

Determinants of Social Standing

Weight and age have proven to be determinants of status in dairy cattle (Schein and Fohrman 1955; Beilharz et al. 1966; Bouissou 1972). Weight was determined after rather than before or during the rut. The limitations of this timing are obvious and should be recalled in evaluating the results. Moreover, it was possible to obtain weights on only 16 bulls. The Spearman rank correlation between weight and overall rank (Table 1) is positive but small

(.11) and not statistically reliable ($z = .42$, $p = .34$). This correlation, if it were statistically reliable, would account for only 1 % of the total variance.

Age was unambiguously recorded from the age brands. Inspection of Table 1 suggests that there is no relationship between age and status. The r_s value of .07 is small and not statistically reliable ($z = .36$, $p = .36$), confirming this impression.

Level of aggression has been described as the determinant of status among dairy cows of similar age and size (COLLIS 1976). As an index of level of aggression COLLIS used the number of interactions initiated. When the bulls in this study are ranked by the number of interactions initiated and this rank is correlated with overall dominance rank as described in Table 1, the resulting Spearman rank correlation (.68) is statistically significant ($z = 3.40$, $p < .001$) and accounts for 46 % of the variance.

The interpretation of this correlation is very unclear. It might be that high aggressiveness leads to both high social standing and the initiation of many encounters. On the other hand it might be that animals having high social standing initiate many encounters as they displace lower standing animals from limited resources. The more individuals an animal dominates, the more such encounters it will initiate. In that case a high level of initiation of aggressive encounters would be a consequence of high social standing rather than a cause of it.

Relationship of Social Standing to Breeding Rate

Tables 1, 2 and 3 reveal a general tendency for higher social standing to be associated with higher rates of breeding. The chi square values of differences in breeding rate between the 13 bulls with the highest social standing compared to that of the 13 remaining bulls is $chi^2 = 3.92$, $df = 1$, $p < .05$ in Table 1, and $chi^2 = 3.92$, $df = 1$, $p < .05$ in Table 2. Both higher and lower chi-square values can be obtained by categorizing more or fewer bulls as high or low social standing, but this analysis demonstrates that the apparent breeding advantage to high standing bulls is statistically reliable.

Discussion

The dominance structure described here contrasts sharply with that described by previous studies of dominance relationships in bison (MCHUGH 1958; EGERTON 1962). The greatest contrast is in the degree of conformity of the hierarchically arranged relationships to the assumption of a linear hierarchy. While both MCHUGH and EGERTON found that over 94 % of the encounters they observed could be arranged to fit that assumption, only 78 % of the encounters observed in this study could be so arranged.

Each of the three social organizations studied had about the same number of members. The differences observed were due to differences in composition of social organizations. Dominance relationships among the mature bulls are much looser and more transitory than those among the mixed groups. Several differences in group composition seem likely to be the causes of these differences. 1) The several km^2 of range available on the National Bison Range, and the generally asocial behavior of mature ♂♂, produces few contacts outside the breeding season. 2) In contrast to MCHUGH's bison, this population had no supplemental feeding, which causes crowding and competition over a limited resource and thus exacerbates dominance relationships. 3) All the animals in this study were in a single age-sex class; consequently there were

more of the very small differences in size, strength, experience and aggressiveness that lead to reversals.

The distribution of fighting through time is another probable source of reversals and triangular relationships. Fights tend to occur in bursts ("fighting storms", LOTT 1974 a). In a typical 22 min storm the most active bull was in 10 fights. He won the first several, but as he tired began to lose, sometimes to bulls he had beaten earlier. If dominance relations established through wins and losses are only occasionally challenged, the degree of randomness introduced into fighting by temporary determinants of fighting ability such as fatigue or injury during fighting storms would tend to disorganize the hierarchy.

In fact, as I have already noted, the resulting ranking probably should not be called a hierarchy. Not calling it a hierarchy implies use of a formal definition or set of criteria by which a ranking can be determined to be hierarchical or not. I am not aware of any such definition or criteria, and I do not offer any now. One of the major values of these data is to identify the necessity to consider useful ways to conceptualize variations in dominance-organized societies. I believe, however, that this issue will be more usefully addressed after a comparative data base has been established which describes dominance relations in a broader range of species studied in circumstances relevant to their evolution.

As WADE (1978) has observed, dominance relations may occur at more than one level of organization. In the case of bison bulls there seems to be no reason to suppose a higher level of organization than the dyad. Reports of dominance-organized species operating at this low level of organization are uncommon in the literature, but that does not necessarily mean that this level of organization is uncommon among the animals. When more kinds of animals have been studied under more biologically relevant circumstances this pattern may be observed frequently.

However common or uncommon the pattern eventually proves to be it is an important characteristic of bison, and the fact that the level of organization is low does not make it insignificant. It is important to recognize that some bulls dominate more individuals more of the time and therefore the bulls in an area can be arranged in a loose ranking. Consequently I have chosen the phrase "social standing" to recognize the rough ranking that exists among bison without implying the level of structure that "hierarchy" connotes.

While both age and (by inference) weight were strongly correlated with status in the earlier studies, they were not in this study. The weight data are ambiguous. Since they were collected after the rut it is possible that the greatest losses during the rut were sustained by the bulls with the highest social standing, an interpretation that is generally consistent with the fact that more encounters were generally recorded for high standing bulls than for low standing bulls. On the other hand, most encounters do not really consume much energy and the limited data on pre and post breeding season weights of bulls in this age range suggests that all bulls may lose about the same amount of weight. Mature bulls from this population weighed immediately before and 6 weeks after the 1963 breeding season lost an average of 91 kg.

The lack of any relationship between age and social standing suggests that mature bulls reach some sort of plateau that extends at least across the years represented here. This in turn implies that each individual bull does not have one or two peak years at a prime age, but rather achieves a certain relative breeding potential upon maturity and maintains it for much of the rest of his life.

Comparison with Baboon Social Organizations

Dominance organizations and their reproductive consequences have been well described in *Papio cynocephalus* (HAUSFATER 1975) and *Papio anubis* (DEVORE 1965; BERNSTEIN 1976). These species' dominance relations take place in a different biological context than those of bison, and hence have instructive similarities and differences corresponding to their different phylogenetic histories and ecological circumstances.

An important similarity is that reproductive advantage is conferred by dominant social standing or status among ♂♂. Not all the variance in reproductive rate is explained by dominance relations, but dominant ♂♂ generally sire more offspring than subordinate ♂♂, just as they do among bison.

But because of certain features of the biology of bison which contrast with those of social primates, several aspects of the dominance relations which underlie this fundamental similarity are sharply different.

Initiation of Dominant-Subordinant Interactions

The baboons live in stable and persistent groups. Group membership is essential to the long-term survival of each individual, and the individual relationships that maintain that group cohesion are important to both parties to each relationship. So it is not surprising that social primates have available and use behavior by which a subordinate can initiate an interaction with a dominant *as a subordinate.* ROWELL (1974) and others have pointed out that many dominant-subordinate interactions are initiated by the subordinate in the form of signals of subordinate status.

The contrast to bison is very revealing. Group membership in itself confers little, if any, advantage to mature ♂♂. Their relationships serve primarily to reduce the energetic costs and risks of injury that fighting imposes. That is probably why none of the recorded dominant-subordinate interactions were initiated with a behavior that signaled the subordinate status of the initiator. In fact this age and sex class seems to lack such signals. All my observations suggest that when a subordinate mature male bison initiates an interaction he does it with an aggressive signal and he initiates it to attempt dominance rather than to confirm subordination.

Stability of Dominant-Subordinate Relations

Another contrast in the manifestation of dominance relations between mature male bison and baboons is the much lower degree of stability in the relationships between individuals. The number of reversals recorded between bison in only three weeks would be without parallel in a natural group of either *Papio cynocephalus* or *Papio anubis.* There are several reasons for this. One is that there are many more mature ♂♂ in most natural breeding groups of American bison, so that a number of animals are close to one another in each of the features that lead to status differences and so are in a position quickly to surpass one another as a result of minor changes in physical prowess.

Also, breeding season in bison, unlike that in baboons, is sharply peaked. The bulk of the copulations occur in a two week period. Reversals must happen soon if they are to confer any reproductive advantage in a given year. Thus it is adaptive for the bulls to make a maximum effort to obtain or maintain social standing and the breeding advantages it confers during that time. Much of the year's total energy budget might be spent during that time and the weight study cited earlier shows that seems to be so.

The peaking of breeding in bison that creates this urgency is an adaptation to very strong seasonality in the availability of energy in temperate zones. Hence a principal determinant of the differences in social organization of bison and baboons is the difference in the annual distribution of incident solar energy.

Summary

Like many age and sex classes of many species, mature male American bison are characterized by dominant-subordinate relationships, but these relationships do not conform very closely to the model of a linear hierarchy. They are often inconsistent and transitory. Nevertheless they confer significant breeding advantage on individuals with higher social standing.

These bulls are in unstable groups that have little biological value for them. Consequently, in contrast to many primates, they lack behavior that promotes group cohesion and social stability. Their repertoire functions primarily to maximize individual social standing while minimizing individual costs during the period of physical proximity forced by the temporary aggregation of breedable cows.

Zusammenfassung

Wie Alters- und Geschlechtsgruppen vieler Arten sind auch die des erwachsenen männlichen Amerikanischen Bisons durch eine Rangordnung gekennzeichnet, die aber nicht streng linear ist. Die Dominanzbeziehungen sind oft unbeständig. In der Rangordnung höher stehende Tiere haben einen deutlichen Vorteil bei der Fortpflanzung. Die Bullen leben in unbeständigen Gruppen, deren biologischer Wert für sie nur klein ist. Folglich fehlen ihnen im Gegensatz zu den Primaten Verhaltensweisen, die den Gruppenzusammenhalt und die soziale Stabilität fördern. Ihr Repertoire an Verhaltensweisen zielt auf Maximierung des eigenen sozialen Status und auf Minimierung der Kosten während der Fortpflanzungszeit, in der die Nähe zu anderen Bullen durch die zeitweilige Ansammlung von Kühen erzwungen wird.

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Literature cited

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK and K. P. SCHMEDT (1949): Principles of animal ecology. Saunders, Philadelphia • ALTMAN, J. (1974): Observational study of behavior: sampling methods. Behaviour 49, 227—268.

BARASH, D. P. (1977): Sociobiology and behavior. Elsevier, New York • BEILHARZ, R. G., D. F. BUTCHER and A. E. FREEMAN (1966): Social dominance and milk production in Holsteins. J. Dairy Sci. 49, 887—892 • BERNSTEIN, I. S. (1976): Dominance, aggression and reproduction in primate societies. J. Theor. Biol. 60, 459—472 • BOUISSOU, M. F. (1972): Influence of body weight and presence of horns on social rank in domestic cattle. Anim. Behav. 20, 474—477 • BROWN, J. L. (1975): The Evolution of Behavior. W. W. Norton, New York.

Collis, K. A. (1976): An investigation of factors related to the dominance order of a herd of dairy cows of similar age and breed. Appl. Anim. Ethol. **2**, 167—173.

DeVore, I. (1965): Male dominance and mating behavior in baboons. In: Sex and Behavior. (Beach, F. A., ed.) J. Wiley and Sons, New York.

Egerton, P. J. M. (1962): The cow-calf relationship and rutting behavior in American bison. Unpubl. M. S. thesis, Univ. of Alberta.

Fraser, A. F. (1968): Reproductive Behavior in Ungulates. Acad. Press, New York • Fuller, A. W. A. (1960): Behavioral and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic **13**, 3—19.

Geist, V. (1974): On the relationship of social evolution and ecology in ungulates. Am. Zool. **14**, 205—220.

Hausfater, G. (1975): Dominance and reproduction in baboons (*Papio cynocephalus*). Contributions to Primatology Vol. **7**. S. Karger, New York.

Lott, D. F. (1972): Bison would rather breed than fight. Nat. Hist. Aug.—Sept. **8**, 40—45 • Lott, D. F. (1974a): Sexual and aggressive behavior of mature male American bison. In: Behavior in Ungulates and its Relation to Management. (Geist, V., and F. Walther, eds.) IUCN, Morges, Switzerland, **1**, 382—394 • Lott, D. F. (1974b): Aggressive behavior in mature male American bison (film). Psychol. Cin. Reg., Pennsylvania State Univ., 12 min • Lott, D. F. (1976): Sexual behavior of the American bison (film). Psychol. Cin. Reg., Pennsylvania State Univ., 9 min.

McHugh, T. (1958): Social behavior of the American buffalo (*Bison bison bison*). Zoologica **43**, 1—40 • Meagher, M. M. (1973): The bison of Yellowstone National Park. Nat. Park Serv. Sci. Monog. Ser., No. **1**, Gov. Printing Office, Washington D. C.

Rowell, T. A. (1966): Hierarchy in the organization of a captive baboon troop. Anim. Behav. **14**, 430—443 • Rowell, T. A. (1974): The concept of social dominance. Behav. Biol. **11**, 131—154.

Schein, M. W., and M. H. Fohrman (1955): Social dominance relationships in a herd of dairy cattle. Anim. Behav. **3**, 45—55.

Van Camp, J. (1975): Snow conditions and the winter feeding behaviour of *Bison bison* in Elk Island National Park. Canadian Wildl. Serv. Parks Advisory Report.

Wade, T. D. (1978): Status and hierarchy in nonhuman primate societies. In: Perspectives in Ethology. (Bateson, P. P. G., and P. H. Klopfer, eds.) Plenum Press, New York • Wilson, E. O. (1975): Sociobiology. Belknap, Cambridge.

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