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Age-related changes in reproductive effort of male bison

Christine R. Maher* and John A. Byers
Department of Biological Sciences, University of Idaho, Moscow, ID 83843, USA

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Summary. The behavior of male bison during the rut was studied, to test the prediction that reproductive effort should increase with age. Because bull bison do not show parental care, the major component of reproductive effort is competition with other bulls to obtain copulations with estrous females. Data were collected on activity budgets during the pre-rut and rut seasons, on interactions with other bulls, and on proximity to tended females during the rut. Participation in the rut started at ages 5–6. Older bulls showed greater percent time active and less percent time eating than younger bulls. The older bulls also had higher counts of dominance and fight-related interactions and lower counts for behavior associated with submission than did the younger bulls. Risk taken seemed to increase with age since bulls aged 6 to 12 participated more frequently in dangerous activities associated with fighting. Within the 6 to 12 year old group, activity patterns changed little with age. However, from the interaction information, peak ages of 8 to 11 years appeared. For the activities: back up, chase, clash, head nod, jump away, move away, run away, run toward, push heads, dominant, and risk, 11 and 12 year olds more closely resembled younger bulls. This suggests a reproductive effort curve that is flat at zero until about age 6, increases to age 8, flattens out again to around age 10, and then decreases somewhat. Reproductive effort in male bison thus generally conforms with life-history theory predictions.

Introduction

Many authors have considered reproductive value, reproductive effort, and their relationships with age (Williams 1966; Pianka and Parker 1975; Gadgil 1982; Rubenstein 1982; Clutton-Brock 1984). However, much less has been written about precise changes in behavior with age, particularly in the area of reproduction (Ryan and Dinsmore 1980; Pugesek 1981; Gadgil 1982; Rubenstein 1982; Afton 1984).

Reproductive value rises from low levels at birth to a peak at or near the first reproductive age, then declines (Emlen 1970; Pianka and Parker 1975; Gadgil 1982; Rubenstein 1982). Reproductive effort is the portion of the individual's total energy budget invested in any current reproductive acts (Pianka and Parker 1975; Clutton-Brock 1984). Generally, reproductive effort is expected to increase as residual reproductive value decreases (Williams 1966; Pianka and Parker 1975; Caswell 1982).

Despite life-history theory predicting how animals should modify behavior with age, few field tests of such predictions have been published (see Clutton-Brock 1984). Studies on birds and mammals often have not detected an increase in reproductive effort with age; however, such an increase has been reported in red deer females (Clutton-Brock 1984) and in California gulls (Pugesek 1981).

This study was conducted on male bison *(Bison bison)* which take considerable risks in rut-related fighting. Since male bison do not exhibit parental care, their investment in offspring is in terms of sperm and competition for mates. Essentially, their reproductive effort is competition for copulations. Bison have dangerous weapons and are capable of inflicting fatal injuries on each other (McHugh 1958; Lott 1974, 1979). Fighting is intense during the rut as bulls try to gain access to a receptive female. Dominance status of individuals fluctuates (Lott 1979).

This study's purpose was to ascertain if male bison show age-related changes in reproductive ef-

* *Present address:* Graduate Group in Animal Behavior and Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA

Table 1. Age distribution of 109 male bison, Fort Niobrara, Summer, 1985

Age (years)	Number
1	15
2	11
3	12
4	9
5	6
6	10
7	7
8	7
9	10
10	9
11	8
12	5

fort. Reproductive effort was measured in three ways: 1) frequency of aggressive interactions, 2) activity budgets, and, 3) proximity to estrous females. Thus, in addition to data on energy budgets, data on activities associated with risk of injury were recorded. Proximity to estrous females was measured since, intuitively, bulls closer to cows in estrus are more likely to be challenged or injured.

Methods

The study site was Fort Niobrara National Wildlife Refuge in north-central Nebraska. The bison herd there is maintained at about 225 animals. Mature male bison number about 80 (Table 1). Calves are branded on the left hip with the last digit of the year of their birth. Adults are culled when they are 12 years old. There is no supplemental feeding.

The duration of this study was from June 6 to August 21, 1985. Total number of hours of observation was approximately 320. The early summer (June 6 to July 26) was spent in getting familiar with the animals, including finding them each day, reading the brands accurately, discovering the optimum distance for observing the bison, and recognizing their behavior patterns. The rut extends from mid to late July until late August. Observations could only be made between sunrise and sunset since the brands could not be read accurately in dim light. Bison were always observed from a vehicle. Observations were made onto a cassette recorder and transcribed later.

Focal-animal sampling was used to obtain data on sequences of activity and activity budgets. Individual bulls were selected, and each was observed for 20 min. Sampling was structured to obtain approximately equal numbers of records from each age class. The minimum number of records from any age class was 20. Also, because individuals could be recognized, they were sampled to get nearly equal numbers of records for each bull. Individual bulls were represented by at least 5 records. For the activitiy budgets, each activity was timed from start to finish, unless the 20 min ended before the activity did. These activities were drink, fight, flehmen, graze, lay, mount, run, scratch, spar, stand, walk, and wallow (see Lott 1974 for a description of these). Activity budgets were recorded during pre-rut and rut. All the times were converted to percentages except mount and flehmen, which were converted to rates.

During the rut, focal-group sampling was used to increase the number of interactions recorded. A group was selected and watched. Simultaneously, a focal bull was chosen and observed for the 20-minute session. Interactions among all bulls were recorded, including information on initiator, recipient, and the sequence of actions (after Lott 1974) performed by each. An interaction started when a bull approached within 3 m of another bull, or otherwise moved toward another bull. The interaction ended when the bulls moved apart at least 1 m and showed no signs of interacting any further. At 5-min intervals, the focal bull's location with respect of the nearest tended female was recorded.

Results

Change in activity

The rut began gradually. The bulls became increasingly restless, leaving bachelor groups and joining the cow herds, bellowing and tending cows more. For the present analysis, the day after the first observed fight was taken as the start of the rut. This cut-off classified 84.7% of observed tending bonds and all observed copulations as occurring during the rut.

Activity patterns were different between the pre-rut season and the rut. Those which increased in frequency during the rut were ($F=55.90$), walk ($F=10.22$), run ($F=8.96$), and flehmen ($F=29.37$), all $P<0.001$. Variables which decreased during the rut were lay ($F=8.43$, $P<0.001$), graze ($F=15.97$, $P<0.001$), and scratch ($F=4.93$, $P=0.03$). The following activity variables were combined: 1) percent of time spent eating was the sum of drinking and grazing time, and, 2) percent time active was the sum of wallow, walk, stand, and run. Time spent eating decreased during the rut ($F=16.47$, $P<0.001$); time spent active increased in the rut ($F=63.76$, $P<0.001$).

Age-related changes in activity budgets and interactions

An increase in time spent active was significant for 6 through 12 year olds (Fig. 1a). Ages 6, 7 and 12 all decreased eating time by a significant amount, whereas 4 year olds increased their eating time (Fig. 1b).

As with the activity budget data, the data from interactions between bulls suggested the same 1 to 5 and 6 to 12 grouping. New variables were created as combinations of original interaction variables. Submit combined backup, graze, jump away, move away, run away, swing head, turn away, turn head away, and walk away. Dominant consisted of broadside threat, chase, chin, displace bull, displace bull from cow, jump toward, mount, mounting intention movement, move toward, push

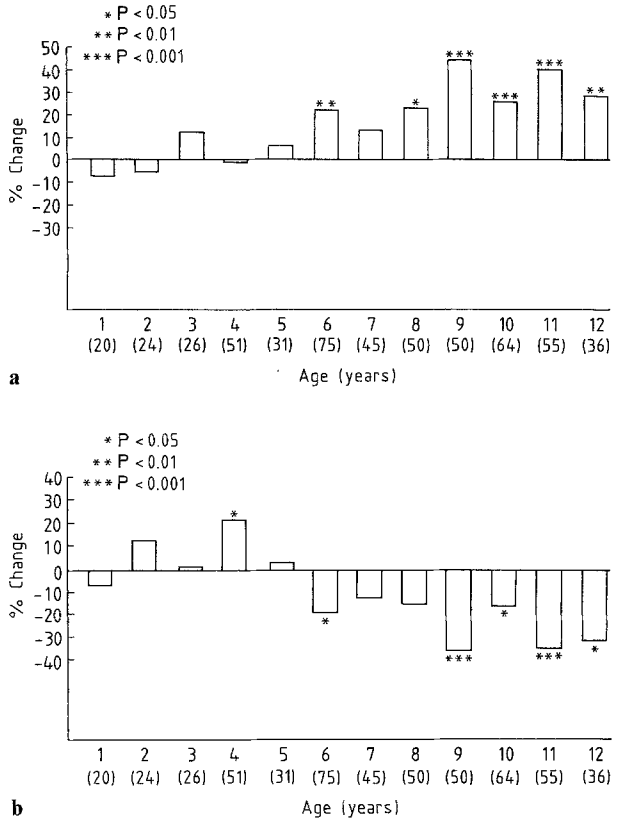

Fig. 1. **a** Percent change from pre-rut to rut for percent time active (Wallow + Stand + Walk + Run). Sample sizes are in parentheses below each age. **b** Percent change from pre-rut to rut for percent time eating (Graze + Drink). Sample sizes are in parentheses below each age

Table 2. Interaction behavior patterns that were significantly different comparing younger (ages 1–5) and older bulls (ages 6–12) (Kruskal-Wallis test, $N=1467$) (all values significant at $P<0.05$)

Behavior	χ^2
Counts greater in younger bulls than older	
Chin	52.35
Jump away	52.69
Mount	64.11
Move away	158.01
Run away	139.52
Spar	23.41
Counts greater in older bulls than younger	
Back up	395.38
Chase	115.37
Clash	44.66
Displace from cow	72.91
Fight	35.89
Head nod	30.16
Lower head	22.95
Move toward	26.26
Parallel stand	20.65
Push heads	23.43
Run toward	55.91
Swing head	24.82
Turn head toward	26.60
Walk away	24.60
Combination variables	
Dominant	269.82
Risk	81.24

back, recover cow, run toward, turn head toward, and turn toward. The new variable Risk was a combination of clash, fight, head nod, hook, lower head, push back, and push heads. Counts of single and combination interaction variables varied with age (Table 2). Younger bulls were involved more often with submission activities, mainly getting away from another bull. Older bulls, however, engaged more frequently in fight-related and dominance activities. These differences seen in activity patterns and interactions suggested a broad classification of bulls into two groups, ages 1 to 5 and ages 6 to 12.

Class 1 was defined as ages 1 to 5; class 2 was the 6 to 12 year olds. Using t-tests, significant differences were found for several activity and interaction (Fig. 2) variables. Class 1 was significantly less active ($t=-9.29$, $P<0.001$) and spent more time eating ($t=6.47$, $P<0.001$) than Class 2. For the combination variable, Submit, little difference was seen between the two classes, since all interactions had to end by one of the bulls submitting. However, the Class 2 bulls engaged in the variables, Dominant and Risk, much more frequently than did Class 1.

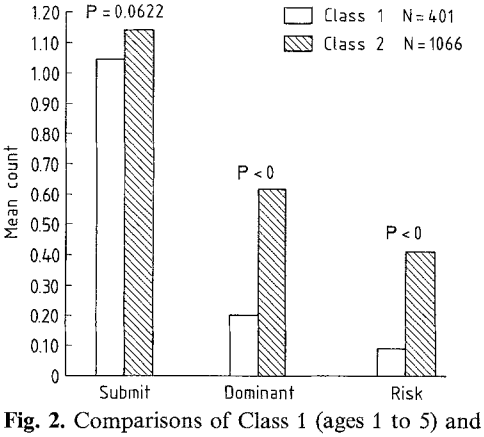

Fig. 2. Comparisons of Class 1 (ages 1 to 5) and Class 2 (ages 6 to 12) for the combination interaction variables, submit, dominant, and risk

The frequency with which each age class initiated interactions with all other age classes was tabulated. Following Robinson (1981), a table of expected numbers of interactions was computed

using the probability of seeing any pair-age combination interact. All encounters taken together were significant ($\chi^2 = 1068.84$, $P < 0.01$), as were encounters in which the initiator won ($\chi^2 = 1025.7$, $P < 0.01$), and in which the recipient won ($\chi^2 = 286.78$, $P < 0.01$). To determine which cells contributed to the significance, the observed value for the cell with the highest χ^2 value was replaced with the expected value for that cell, and the whole calculation repeated until the P value was greater than 0.05. Locations of significant cells are summarized as follows: ages 1 through 6 won fewer encounters than expected with ages 7 through 12. Ages 2 through 10 interacted less than expected with yearlings. This was true for all encounters and for those cases in which the initiator won the interaction. For cases in which 8 year olds were the initiator and 11 year olds the recipient, 11 year olds won more than expected. The same was true for 10 and 11 year olds, with 10 year olds initiating the sequence and 11 year olds winning. Ages 10 and 11 both won more than expected when 12 year olds initiated the encounter. When the counts of significant cells for ages 1 to 5 and 6 to 12 were compared, a significant difference was found ($\chi^2 = 12.15$, $P < 0.01$). Ages 6 to 12 won more interactions than expected by chance. When ages 6 to 12 were broken down into ages 6 to 7, 8 to 10, and 11 to 12, the counts of significant cells once again were significantly different ($\chi^2 = 10.57$, $P < 0.01$). The significance was due to the 6 and 7 year olds. They lost more than expected and won less.

Analysis of variance on activity budget variables for ages 6 to 12 revealed few differences among these ages. Only flehmen ($F = 3.41$, $P < 0.001$), lay ($F = 2.31$, $P < 0.03$), and wallow ($F = 2.41$, $P < 0.03$) were significantly different. The interaction variables gave more interesting results. Using Mann-Whitney U tests, a split within this group seemed to appear. Often 6, 7, and 12 year olds were acting more like the younger bulls, i.e., 1 through 5 year olds, participating much less in dominance and fight-related behavior patterns (Table 3). This suggests a peak of reproductive effort at ages 8–11.

Regression analyses were included to test the hypothesis that reproductive effort should steadily increase with age. Pearson correlations showed no strong correlations between the activity budget or interaction variables and age. Also, no significant relationship was found between distance to the nearest tended cow and age ($r = 0.06$, $P > 0.05$).

Multiple regression failed to show a strong correlation between activity variables and age ($r = 0.37$); for ages 6 to 12, the relationship was even weaker ($r = 0.18$). When interaction variables were used, the correlation with age was still not very strong ($r = 0.59$); for ages 6 to 12, the relationship was weak ($r = 0.34$).

Table 3. Significant ($P < 0.05$) relationships between age combinations of 6, 7, and 12 year olds with ages 6 through 12 for counts of combination interaction variables (z scores are given below the relationship; NS = not significant)

Ages	Submit	Dominant	Risk
6– 7	NS	6<7 −2.82	NS
6– 8	NS	6<8 −6.19	6<8 −2.40
6– 9	NS	6<9 −7.56	NS
6–10	NS	6<10 −7.01	6<10 −3.39
6–11	NS	6<11 −8.10	6<11 −2.41
6–12	NS	6<12 −3.94	NS
7– 8	NS	7<8 −2.45	NS
7– 9	NS	7<9 −4.10	NS
7–10	7<10 −2.03	7<10 −2.97	7<10 −2.24
7–11	NS	7<11 −3.83	NS
7–12	7<12 −2.00	NS	NS
12– 8	NS	NS	NS
12– 9	NS	12<9 −3.64	NS
12–10	NS	12<10 −2.33	12<10 −2.58
12–11	NS	12<11 −3.28	NS

Discussion

Age-changes in cost-benefit ratios for particular aspects of current reproduction, specific to both the species and the behavior under study, must be considered when predicting age-related changes in behavior. If the costs and benefits of an aggressive act which contributes to current reproduction are ignored, individuals are expected to take more and more risk with age. Theoretically, risk should increase to a value of infinity, meaning that males should participate more frequently in aggressive activities (e.g., fighting) as they get older. For a male bison, the actual cost/benefit (to current reproduction) associated with rut-related aggression likely has a U-shaped relationship with age. At

birth, the cost-benfit ratio equals infinity, since a male does not produce sperm and hence cannot reproduce. As a male approaches puberty, cost/benefit declines; fighting may be profitable in some situations. The curve flattens out during the prime years; males are likely to have reached body sizes allowing them reasonable probabilities of winning fights. As males move into old age, however, the cost-benefit ratio likely rises again, because of senile age changes which reduce fighting effectiveness. It approaches infinity as the cost approaches infinity.

Predictions of behavior can be made based on the cost-benefit ratio for current reproduction. At young ages, when the actual ratio exceeds the optimum, the risk taken to reproduce should be rare or absent. Onset of reproductive effort should be abrupt, reflecting the age at which the actual cost-benefit ratio for risky acts associated with current reproduction has declined to intersect the reproductive value-defined optimum cost-benefit ratio curve. For middle ages, when the actual cost-benefit ratio is equal to or less than the optimum level as defined by reproductive value, the behavior should be frequent and increasing with age. At older ages, however, both the actual and optimal ratios are increasing, and predicting increasing or decreasing amounts of effort depends on the rate of increase of the cost-benefit ratios. Conformity to predicted behavior is more likely to vary and behavior becomes harder to predict.

The change in activity patterns between the pre-rut and rut was significant only for certain ages of male bison. Older bulls reduced their energy intake, presumably to be more active, tending cows. Therefore, the older bulls traded the chance to store more energy for winter for the opportunity to reproduce. Despite sexual maturity at age 3, the decreased eating and increased activity tradeoff did not appear until age 6. These older bulls appeared to take higher risk than the younger ones to acquire matings. Interaction analysis seemed to show the same division between groups of bulls aged 1 to 5 and 6 to 12. The older bulls interacted much more aggressively with each other.

The χ^2 analysis of wins and losses for each age again showed the differences between the two groups of male bison. Younger bulls did not take the risk of opposing older, heavier, and more experienced bulls. Very old bulls, i.e., 12 year olds, theoretically should take more risks in fighting because of lower reproductive value. However, they did not appear to be doing this. The old bulls either were not able to win because of physical condition or submitted for some other reason.

These data suggest an increase in reproductive effort beginning around age 6, contrasted with sexual maturation which occurs at age 3. Male bison are not the only ungulates to postpone reproduction past the age of sexual maturity. Usually the young males cannot compete with older ones for terrritories, harems, or tended females (Struhsaker 1967; Clutton-Brock et al. 1982; Geist 1971; Kitchen 1974; Byers and Kitchen 1987; Rubenstein 1982).

The life history theory predicting an increase in reproductive effort with age (Williams 1966; Pianka and Parker 1975; Caswell 1982) seems generally to be true for male bison. Young immature bulls, for which reproduction-related activities hold a high cost, are not participating in the rut. Once a bull has attained a particular size and level of strength (around age 5 or 6), he then changes his activity patterns. However, the level of interactions with other bulls is still lower than older bulls. Reproductive effort is increasing but is not at its highest point. Effort seems to reach a maximum between ages 8 to around 11. By the age of 12, some other changes are occurring. Old males of other species of ungulates may stop reproduction. They often are solitary or stay in bachelor herds and are in poor physical condition (Bergerud 1974; Sinclair 1974; Jarman 1979; Clutton-Brock et al. 1982). Although the activity patterns are not very different from younger bulls, the interaction counts and win/loss counts change. These bulls win less, even when they initiate an interaction. They fight less and submit to younger bulls more. They appear to take less risk than slightly younger bulls.

These results suggest the shape of the reproductive effort versus age curve for male bison. It is flat at zero from birth until about age 5. It then begins to increase until around age 8. At this point, it starts to flatten out and levels off until about age 11. Then it begins to decline. Unfortunately, what happens from this point on is unknown. Bulls older than 12 years were not present in this study. Because of the increasing actual and optimum cost-benefit ratios, the amount of risk taken probably becomes more variable. Also, since natural selection would be acting on fewer animals in these older age classes, increased variation is again expected.

The problem of what happens past age 12 is a difficult one to answer. For those bison herds with accurate age information, culling at a certain age is routine. Studies of other long-lived polygynous mammals seem warranted, to ascertain if increased variance of reproductive effort is common at old ages.

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