# AGE-SPECIFIC REPRODUCTIVE BEHAVIOR OF MALE AMERICAN BISON

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# PREFACE

This thesis contains four chapters written in publication format. The first two contain information on bull bison reproductive behavior; the third contains a computer model for calculating the effective population size of bison; and the fourth contains recommendations for managing bison based on the first three chapters. These chapters are written in publication format, and each contains its own acknowledgments and literature cited sections. Chapters 1 and 2 are written in *Journal of Mammalogy* format, Chapter 3 is written in *Oikos* format, and Chapter 4 is written in the format for a Fish and Wildlife Service special scientific publication.

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# CHAPTER 1

# AGE-SPECIFIC REPRODUCTIVE ACTIVITY OF MALE AMERICAN BISON

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Abstract.--Age-specific reproductive activity of male American bison (*Bison bison*) was observed at the Wichita Mountains Wildlife Refuge, Oklahoma, in the summer of 1983. The temporal distribution of calf births was determined in 1984 to estimate relative reproductive success of each age class. During peak rut (23 June to 27 July), rates of tending per male significantly increased with age of bulls. The relationship was not statistically significant, however, the mean number of estimated fertilizations by older bulls was higher than that of younger bulls. These results are consistent with data from other studies that indicate that younger bulls (less than 5 years old) are generally excluded from breeding by older, more dominant males.

Descriptive studies of reproductive behavior in bison (Egerton, 1962; Fuller, 1960; Herrig and Haugen, 1969; Lott, 1974, 1981; McHugh, 1958) have suggested that although younger bulls (less than 5 or 6 years old) are physiologically capable of breeding at 2 or 3 years of age (Fuller, 1962; Haugen, 1974; Lott, 1974; Shult, 1972), they are excluded from breeding by older, more dominant males (Egerton, 1962; Haugen, 1974; Mahan, 1978; Lott, 1974, 1981). Lott (1979, 1981) observed 38 copulations of individually-identifiable bulls at the National Bison Range and observed that the breeding bull in 37 of those copulations was between 5 and 12 years old. Questions as to which bulls actually leave progeny and whether some breed more than others are important because the rate at which a closed population loses genetic variability is a function of various factors, including variance in progeny number. Consequently, polygynous species, such as the bison, will lose more genetic variability than monogamous species if some males are excluded from breeding. The objectives of this study were to determine the relative participation of various age classes of male bison in tending cows and to estimate relative reproductive success of these age classes at the Wichita Mountains Wildife Refuge (WMWR).

## STUDY AREA

This study was conducted in the Special Use Area of WMWR, in southwest Oklahoma. The Special Use Area, which is closed to the public, contains 14,648 ha of mixed-grass prairie interspersed with post oak-blackjack oak forest and rock outcrops. The herd within this area is maintained at about 350 bison.

## METHODS

Of the 350 bison maintained in the Special Use Area of WMWR, about 50 were bulls that were 5 or more years old in the summer of 1983. During rut the herd usually split into two or three intermixing groups. The large area and the large number of mature bulls prevented observation of all of the animals simultaneously, identification of a large number of individual bulls, or observation of a large number of copulations. Therefore, I estimated reproductive success of various age classes of males on WMWR using methods similar to those used by Clutton-Brock et al. (1982) for red deer. Red deer stags monopolize breeding access to hinds by forming harems. As a crude measure of the reproductive success of stags, Clutton-Brock et al. (1982) counted the number of hinds that each stag was seen holding each day during rut. Bison do not form harems, but do form tending bonds (McHugh, 1958) that may last from a few seconds to several days. In a tending bond the bull usually stands parallel and very close to a cow, facing in the same direction. The tending bull may attempt to control the cow's movement and may isolate her from other bulls.

Direct observations of bison were made daily from 14 May to 18 August 1983 and weekly thereafter through 2 October 1983. I surveyed the Special Use Area weekly from 24 March until 24 June 1984 to determine the number of calves present and to estimate the approximate birth dates of calves born to cows of known-identity. Most observations were made from a vehicle; other researchers and refuge personnel routinely drove through this area and the bison did not appear to be disturbed by the presence of motor vehicles.

I assigned bulls to age classes based on known-age or morphological characteristics, such as body size and horn development (Allen, 1876; Hornaday, 1889--reproduced in Seton, 1909; McHugh, 1958; Lott, in litt.; Soper, 1941). Males up to 5 years old can be aged based on the shape of the horns; older bulls can be assigned to relative age classes based on body size, horn wear, and amount of hair on the head. Bull bison reach maximum size at 6 years or older (Lott, 1974). The hair on their heads continues to grow until the space between the horns is completely filled with hair at age 5 or 6 (Lott, 1974). The ages (ranging from 1 to 6 years old) of twenty-three bulls marked with numbered ear tags were known. As part of another study, these animals were either tagged as calves or aged at the time of tagging based on tooth eruption and wear (Fuller, 1959). In addition, through 1972 bison were branded with the last digit of their birth year. The youngest branded animals were 11 years old in 1983. Age Class I, II, and III males were 2 - 4, 5 - 9, and 10+ years old, respectively.

I collected data on the age composition of bull groups and mixed herds, the age class of tending bulls, and when possible, the identity of the animals observed from numbered ear tags, scars, broken horns, or other physical variations. The herd composition for bison on WMWR (Table 1) consisted of minimum estimates based on the maximum number of animals seen in a given sex/age class on a single day in 1983. The mean number of tending bonds per bull in an age class was the number of tending bonds in a given week (by bulls in a given age class) divided by the number of bulls in that age class (Table 2).

To estimate the weekly number of fertilizations achieved by each age class of bison, I multiplied the number of cows tended each week (by a given age class) by the probability that a cow would conceive during that week. The minimum probability of conception in a given week was determined by multiplying the proportion of females that conceived that year (54 calves born in 1984/122 cows in 1983) by the fraction of calves conceived (calculated by backdating one gestation length from calf birth dates) during that week (Clutton-Brock et al., 1982). Gestation length has been reported as 9 months (270 days) (Brown, 1936) and as 285 days (Haugen, 1974; Seton, 1909). I used both 271 and 285 days in my calculations.

I also calculated the number of fertilizations based only on those tending bonds in which the male performed at least one of several behaviors, such as: making a mount intention move (head is tossed toward the cow, but the front feet remain on the ground), attempting to mount (the front feet come off of the ground), chasing the female, blocking the female's path, keeping the cow on the periphery of the herd, attempting to isolate the cow, or displaying agonistic behavior such as bellowing, pawing, or wallowing. Also included in this data set were tending bonds in which there was some indication that the cow had recently been bred (e.g. holding her tail up or fresh wounds on her sides where the bull's hooves hit when he mounted her). These data comprised the "modified" tending data set. This refined approach was used to compensate for differences in the intensity of tending bonds.

## RESULTS

In 1983, peak rut occurred from 23 June to 27 July. I refer to this period throughout this paper as "rut." During this period the tending rate was at its maximum. Although tending did occur prior to and after "rut", the rates of tending (as determined by linear regression) were significantly lower ($\underline{P} = 0.0001$) than during rut (Figure 1).

The rate of tending did not differ between age classes within pre- or post-rut (Table 2). However, all three rates were significantly different ($\underline{P} < 0.01$) within rut.

There was no difference in the temporal distribution of tending among males within either Class I or Class II (Table 3 and 4); however, individual Class III males tended to fall into one of three groups (Table 5): 1) early tenders - those that tended almost equally during pre-rut and rut, (with an average of 2.7 tending bonds per male); 2) rut only tenders - those that tended during rut only (with an average of 4.6 tending bonds per male); and 3) late tenders - those that tended almost equally during rut and post-rut (with an average of 4.6 tending bonds per male). The number of tending bonds by known-identity Class III bulls on the WMWR varied from 0 - 7. "Early tenders" tended 2 - 3 cows each; "rut-only tenders" tended 2 - 7 cows each; and "late tenders" tended 2 - 6 cows each.

Weekly means of the estimated number of fertilizations per male in a given age class were calculated by dividing the number of fertilizations per age class by the number of males in that age class (Table 6) for both 271 and 285 day gestation lengths, and unmodified and modified tending data sets. Variances were not equal across age classes and, therefore, means were compared using a $\underline{t}$ test for unequal variance. In all cases Class III males had more fertilizations, but differences were not statistically significant.

Five copulations were observed (Table 7). These copulations occurred at a variety of times throughout the day and in all cases the breeding bull was in Class III.

## DISCUSSION

The rate of tending per male was significantly different between age classes during rut and this finding is consistent with those of most other researchers that breeding rate increases with age (Egerton, 1962; McHugh, 1958; Petersburg, 1973). Mahan (1978), however, believed that 7 or 8 was the "prime" age for a bull and that after that age the ability to displace other males decreased. This finding was not consistent with my results because most of the tending was done by bulls 10+ years old. The difference between the studies may be due to a slightly different herd composition. A smaller percentage of bulls in Mahan's study at Fort Niobrara were in the oldest age class than were present at WMWR (21% versus 28%); 34% of the bulls that were 2+ years old on Fort Niobrara and 18% of bulls that were 2+ years old in the WMWR were in Age Class II.

Clutton-Brock et al. (1982) pointed out that with red deer the number of hinds that a stag was able to collect in a particular season may not reflect his reproductive success because the duration of harem-holding was generally shorter than the duration of the conception peak and, therefore, some of the hinds in a stag's harem either conceived before or after his period of holding. This conclusion may also apply to bison. Bulls often tend cows that are not in estrus (Lott, 1981).

Reproductive success was defined by Clutton-Brock et al. (1982) as the number of fertilizations achieved in a given year. There were no statistically significant differences between age classes in my estimates of fertilizations, but there was a tendency for older males to fertilize more cows. Estimates of fertilizations were probably not precise, however, and may not actually reflect the number of copulations. In addition, estimates of calf birth dates were based on weekly, rather than daily, calf counts and an uncertain gestation length.

Lott (1981) found that the breeding rate for mature bull bison varied substantially (0 - 4 cows bred) and that there was a tendency for individual bulls to breed over a short time period. He also believed that some males bred late in the season after other bulls were fatigued. Individual bulls in the "rut-only tenders" group had the same number of tending bonds in less than half the time as the "late tenders." No calves were conceived during post-rut, therefore "late tenders" had a lower probability of leaving offspring. If gestation is 271 days, only those bulls tending during rut would have had a chance to leave offspring. If gestation is 285 days, however, the "early tenders" may have left some offspring.

Haugen (1974) estimated breeding and calving peaks based on aged bison embryos that were collected at Fort Niobrara National Wildlife Refuge, Wind Cave National Park, and Custer State Park. To calculate these peaks he assumed that gestation was 285 days. These peaks corresponded closely to observed tending and calving peaks. Haugen (1974), thereby, concluded that the gestation period for bison is about 285 days, as reported by Seton (1929), rather than 9 months as reported by Brown (1936). If the frequency of tending is a good indication of the frequency of estrous cows, my data also indicate that gestation length is closer to 285 days than to 271 days. The peak frequency of tending by both Class II and Class III males corresponds more closely to the peak of conception with a 285-day gestation (Figure 2).

All calves born on the WMWR during 1984 were born within a 5 week span, with the majority (85%) born within 2 weeks. This observation is consistent with those of Lott (1981) who reported that 90% of the copulations on the National Bison Range occurred in 2 weeks and McHugh (1958) who reported that the greatest concentration of births in the Lamar Valley of Yellowstone National Park was within a 2-week period.

Petersburg (1973) found that older bulls left the herds during post-rut when rutting activity was at a very low level. However, on those occasions where rut activity did increase temporarily, older bulls were present. Such a behavior appeared to also occur in the WMWR herd and probably prevented younger bulls from breeding.

Herrig and Haugen (1969) believed that many of the bulls recorded as tending were only with the cows early in their oncoming estrous period. Lott (1981) also found that bulls spent a high percentage of total tending time tending cows that were not in estrus and that most of this "inappropriate" tending occurred preceeding copulation. Herrig and Haugen (1969) found that interruptions in tending bonds occurred frequently among the bison. Interruption of bonds was also observed in the WMWR herd and it is possible that a limited number of the older and more dominant bulls did most of the breeding.

## ACKNOWLEDGMENTS

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Table 1. *Herd composition of bison in the Special Use Area of the Wichita Mountains National Wildlife Refuge in 1983*.

| | |
|---|---|
| Calves | 79 |
| Yearling females | 31 |
| Cows 2+ years | 122 |
| Yearling males | 19 |
| Class I males | 62 |
| Class II males | 20 |
| Class III males | 32 |
| Total | 355 |

Table 2. *Mean number of tending bonds per male per week. Means within seasons were compared using a t test and means with the same letter in the same row are not significantly different. Comparisons of means for the entire seasons and entire age classes were made using Duncan's test and means with the same letter are not significantly different.*

| Season | Age Class | | | $\bar{X}$ ** |
|---|---|---|---|---|
| | I | II | III | |
| Pre-rut<br>(*n*=5 weeks) | 0.06 a | 0.09 a | 0.16 a | 0.10 A<br>(*n*=15) |
| Rut*<br>(*n*=5 weeks) | 0.26 a | 0.76 b | 1.68 c | 0.90 B<br>(*n*=15) |
| Post-rut<br>(*n*=8 weeks) | 0.04 a | 0.25 a | 0.28 a | 0.19 A<br>(*n*=24) |
| $\bar{X}$ ** | 0.11 A<br>(*n*=18) | 0.35 B<br>(*n*=18) | 0.64 C<br>(*n*=18) | |

* $P < 0.01$ ** $P = 0.0001$

Table 3. *Total number of observed tending bonds by known-identity Class I bulls.*

| | Male ID | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | #54 | #56 | #57 | #58 | #60 | #62 | #63 | #66 | #67 | #68 | #69 | Scar Head | Warpie |
| Pre-rut | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 |
| Rut | 1 | 2 | 1 | 4 | 4 | 1 | 3 | 1 | 1 | 0 | 2 | 0 | 0 |
| Post-rut | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| Total | 1 | 3 | 1 | 5 | 4 | 1 | 3 | 1 | 3 | 2 | 2 | 1 | 1 |

$X^2 = 30.613$, *d.f.* = 24, *P* = 0.165

Table 4. *Total number of observed tending bonds by known-identity Class II bulls.*

| | Male ID | | | |
|---|---|---|---|---|
| Season | #52 | #53 | #55 | Short right |
| Pre-rut | 1 | 0 | 2 | 0 |
| Rut | 8 | 6 | 5 | 7 |
| Post-rut | 1 | 1 | 4 | 1 |
| Total | 10 | 7 | 11 | 8 |

$X^2 = 6.546$, *d.f.* = 6, *P* = 0.365

Table 5. *Total number of observed tending bonds by known-identity Class III bulls.*

| | Male ID | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Early tenders | | | Rut-only tenders | | | | | | Late tenders | | |
| Season | #108 | 8-Brand | Jab-horn | 12-Scar | #123 | Broken right | Durante | One Horn | Stubby | Asterisk | Ringo | Shaven head |
| Pre-rut | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rut | 1 | 2 | 2 | 5 | 4 | 3 | 7 | 2 | 7 | 3 | 3 | 1 |
| Post-rut | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 1 |
| Total | 2 | 3 | 3 | 5 | 4 | 3 | 7 | 2 | 7 | 6 | 6 | 2 |

$X^2 = 37.778$, *d.f.* = 22, $P = 0.019$

Table 6. Mean estimate of the number of fertilizations per male in a given age class per week. Numbers in parentheses are variances. (See text for explanation.)

| Tending data set | Gestation length | Age class | | | P-values | | |
|---|---|---|---|---|---|---|---|
| | | I | II | III | I vs. II | II vs. III | I vs. III |
| Unmodified | 271 | 0.026<br>(0.00080) | 0.046<br>(0.00114) | 0.146<br>(0.02070) | 0.33 | 0.20 | 0.14 |
| | 285 | 0.022<br>(0.00089) | 0.098<br>(0.01727) | 0.171<br>(0.05300) | 0.27 | 0.56 | 0.22 |
| Modified | 271 | 0.009<br>(0.00015) | 0.020<br>(0.00062) | 0.077<br>(0.00984) | 0.44 | 0.28 | 0.20 |
| | 285 | 0.002<br>(0.00003) | 0.011<br>(0.00064) | 0.039<br>(0.00699) | 0.49 | 0.51 | 0.39 |

Table 7. Bison copulations observed during the 1983 rut.

| Date | Time | Age class of male |
|---|---|---|
| 16 July | 2113 | III |
| 17 July | 1300 | III (11 years old) |
| 26 July | 0845 | III |
| 28 July | 1620 | III |
| 30 July | 0832 | III |

# Figure Legends

Fig. 1.--Cumulative number of tending bonds by bulls of all ages in 1983.

Fig. 2.--Distribution of tending in relation to the conception of calves.

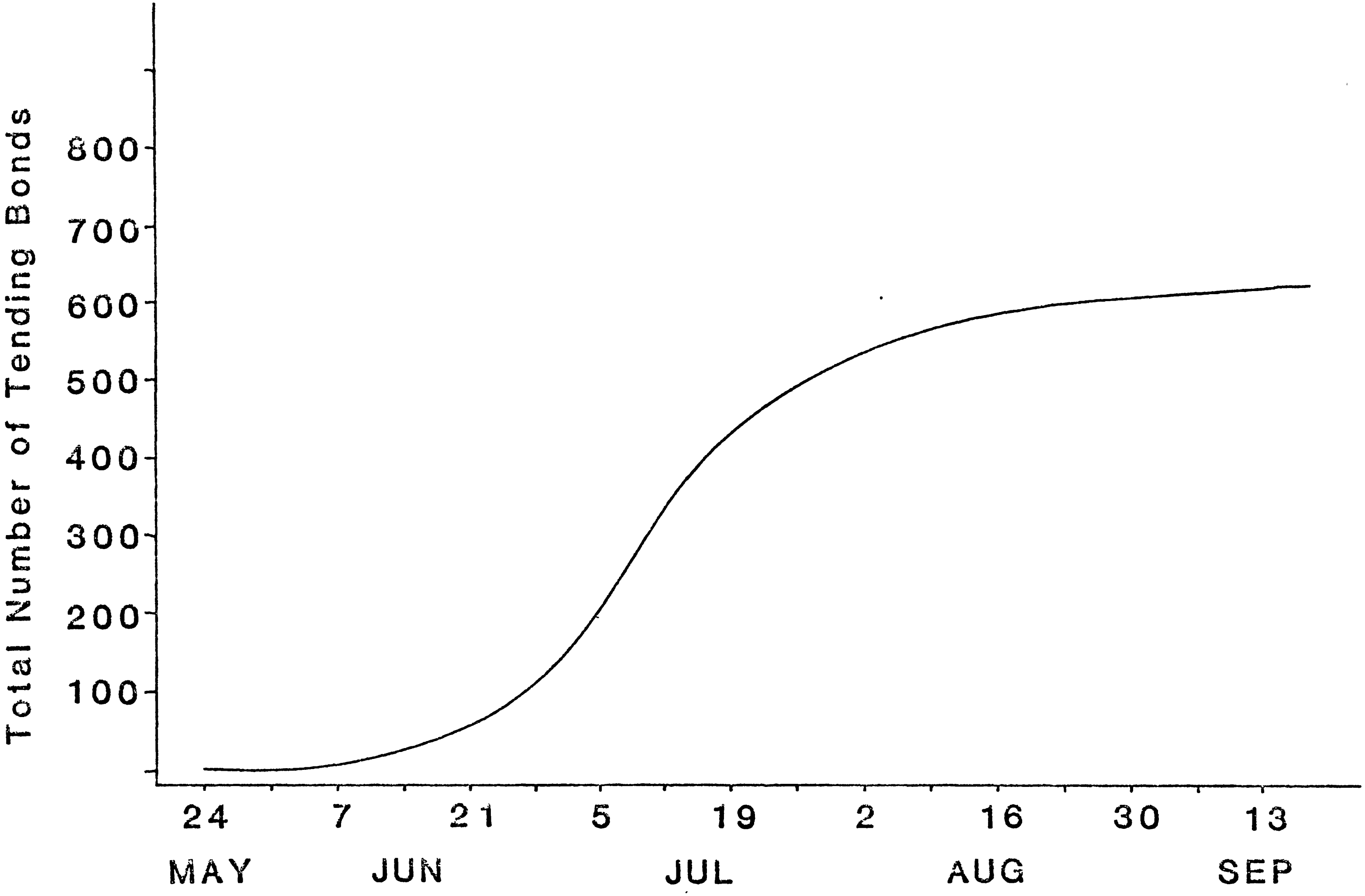

Figure 1. Cumulative number of tending bonds by bulls of all ages in 1983.

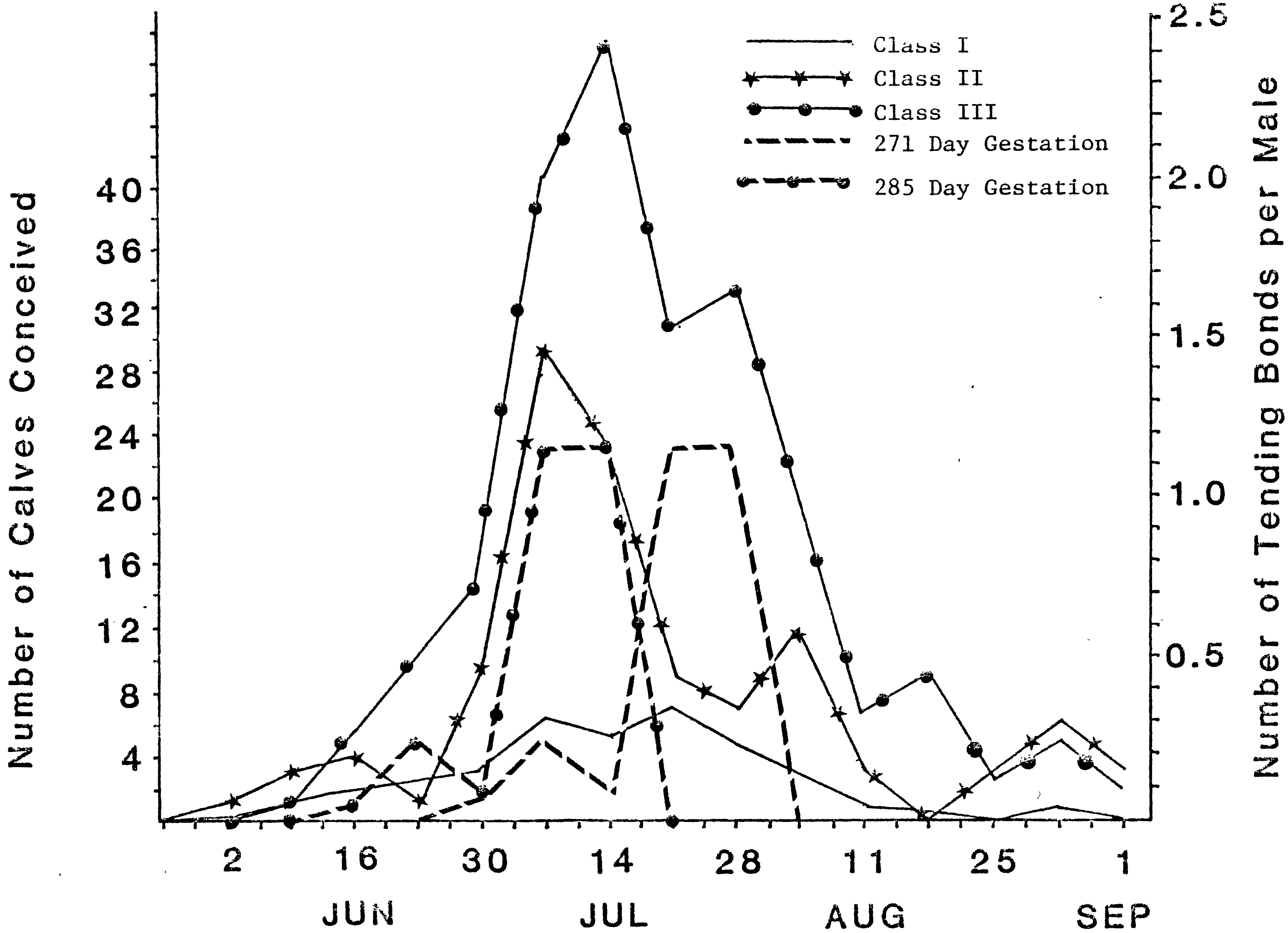

Figure 2. Distribution of tending in relation to the conception of calves.

# CHAPTER 2

# AGE-SPECIFIC REPRODUCTIVE AND AGONISTIC BEHAVIOR OF MALE AMERICAN BISON

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Abstract.--Time-budget data were collected on bull bison behavior during the 1983 reproductive season at the Wichita Mountains Wildlife Refuge, Oklahoma. Bulls were assigned to age classes based on morphological characteristics such as body size and horn development. Classes I, II, and III contained males that were 2 - 4, 5 - 9, and 10+ years old, respectively. In agonistic encounters, Class III bulls were usually initiators, and Class I and II bulls were usually recipients. Class I bulls interacted primarily with other Class I bulls and there was a tendency for their agonistic encounters to include head-butting, horning, and mount intention moves. Class III males interacted with Class III males most often and their encounters tended to involve

pawing, wallowing, bellowing, short charges, and head-on fights. Although younger males performed investigatory behaviors (such as sniffing or licking cows) as often as older males, they did not display agonistic behaviors as often. During focal animal observations, bulls younger than 5 years old were never seen in head-on fights and they never bellowed or attempted to block a cow's path. Although younger males did tend cows, this activity probably occurred prior to estrus and they were generally displaced by older, more dominant males as estrus approached.

The reproductive behavior of bison has been described by several researchers (Egerton, 1962; Fuller, 1960; Herrig and Haugen, 1969; Lott, 1974, 1981; McHugh, 1958) but quantitative time-budget studies of individual bull bison behavior are rare. In this study, I observed individual bulls and recorded various activities, with particular emphasis on agonistic and reproductive behavior.

Although bison bulls are physiologically capable of breeding by 2 or 3 years of age (Fuller, 1962; Haugen, 1974; Lott, 1974; Shult, 1972), they do not reach their maximum size until they are at least 6 years old (Lott, 1974). Most evidence indicates that younger bulls (less than 5 or 6 years old) are excluded from breeding by older, more dominant males (Egerton, 1962; Haugen, 1974; Mahan, 1978; Lott, 1974, 1981).

## STUDY AREA

This study was conducted in the Special Use Area of the Wichita Mountains Wildife Refuge (WMWR), in southwest Oklahoma. The

Special Use Area contains 14,648 ha of fenced mixed-grass prairie interspersed with post oak-blackjack oak forest and rock outcrops that is inaccessible to the general public. The refuge staff maintains a herd of about 350 bison within this area.

## MATERIALS AND METHODS

A focal animal technique (Altmann, 1974) was used wherein various activities of an individual bull, including agonistic and breeding behavior, were recorded. Behaviors were classified, with modification, according to Lott (1974). Recorded agonistic behaviors included head-butting, short charges, head-on fights, horning, facing another animal, moving toward another animal, pawing, wallowing, bellowing, broadside displays (a threat display in which the threatening animal stands broadside to the opponent with the head and body in a straight line), mount intention moves (the first stage of the copulation behavior pattern where the bull steps toward the cow and swings his head up toward her hips as if he is going to attempt to mount her), and head tosses (where one animal lowers its head and then tosses it back up). Submissive responses to agonistic encounters included walking or running away, turning away, grazing, or standing up.

I assigned bulls to age classes based on known-age or morphological characteristics such as body size and horn development (Allen, 1876; Hornaday, 1889--reproduced in Seton 1909; McHugh, 1958; Lott, in litt.; Soper, 1941). Males up to 5 years old can be aged based on the shape of the horns; older bulls can be assigned to relative age classes based on body size, horn wear, and amount of hair on the head. Bull bison reach their maximum size at 6 years old or older (Lott, 1974). The hair on their heads continues to grow until the space between the horns is completely filled with hair at age 5 or 6 (Lott, 1974). The ages (ranging from 1 to 6 years old) of twenty-three bulls marked with numbered ear tags were known. As part of another study, these animals were either tagged as calves or aged at the time of tagging based on tooth eruption and wear (Fuller, 1959). In addition, through 1972 bison were branded with the last digit of their birth year. The youngest branded animals were 11 years old in 1983. Age Classes I, II, and III contained males that were 2 - 4, 5 - 9, and 10+ years old, respectively.

Peak rut occurred from 23 June to 27 July. Every 10 days, from 17 June until 5 August 1983, I observed three bulls in each of the three age classes for 15 continuous minutes during each of five time periods: 0600 - 0900, 0900 - 1200, 1200 - 1500, 1500 - 1800, and 1800 - 2100. Individually-recognizable animals were used in most cases. Occasionally an animal went out of view before the end of 15 minutes. If the animal came back in view within 30 minutes, I resumed observation.

From 6 August until 15 September 1983, focal-animal observations were limited to 10 minutes. From 6 August to 13 August 1983, two bulls from each age class were observed during each time period. From 17 August to 15 September 1983, one bull was observed from each age class during each time period every 7 days.

## RESULTS

Class III bulls were usually initiators of agonistic encounters and Class I and II males were usually recipients (Table 1). Class I males interacted primarily with other Class I males and Class II and III males interacted most often with Class III males (Table 2). All age classes had agonistic encounters with calves, yearlings, and cows.

The most common act was for one animal to move toward another one. There was a tendency for agonistic encounters involving younger males to include head-butting, horning, and mount intention moves; while those involving older males tended more to include pawing, wallowing, bellowing, short charges, and head-on fights (Table 3).

Overall, the most common response in an agonistic encounter was for the focal animal to walk away. Class I and II males tended to do this more often than Class III males, probably because they were more often recipients (Table 4). In cases involving Class III males the tendency was for the recipient to walk away, probably because Class III males were more often initiators.

An analysis of variance (AOV) showed no statistical differences (alpha = 0.05) in the frequencies of behaviors at different times of the day. The only seasonal behavioral differences occurred in post-rut when compared to rut and pre-rut and included an increased frequency of defecating, sniffing or licking cows, lip curls, sniffing the ground, and sniffing a cow's vulva (Table 5).

Younger males performed investigatory behaviors (such as sniffing or licking cows) just as frequently as older males, but Class II males displayed lip curls (Flehmen response) significantly more frequently than bulls from either of the other age classes (Table 6). Flehmen response often occurs during rut when a bull sniffs and/or licks the vulva or urine of a cow (Herrig and Haugen, 1969; Lott, 1974; Reynolds et al., 1982) and is believed to make the vomeronasal organ more effective (Estes, 1972) and to facilitate identification of females in estrus (Müller-Schwarze, 1979--cited in Lott, 1981).

Younger males did not display any of the agonistic behaviors (such as bellowing, pawing, and wallowing) as frequently as older males. Class I males never bellowed or pawed, and wallowed significantly less than Class III males (Table 6). Wallowing has a grooming function as well as an agonistic function (Reynolds et al., 1982; Shult, 1972) and may have been used in the former way by Class I males.

Older bulls spent significantly less time lying down and more time standing than younger bulls (Table 7). Bulls spent less time eating and drinking during rut and post-rut than during pre-rut (Table 8). Bulls also spent significantly less time grazing and walking and more time lying down in the afternoon, especially between 1500-1800, than at other times of the day (Table 9).

## DISCUSSION

My data indicate that bison bulls less than 6 years old are excluded from breeding by older, more dominant bulls. Younger bulls spent a lot of time investigating females but seldom displayed agonistic behavior and were recipients in the majority of cases where they were involved in agonistic encounters. Class I males interacted most often with other Class I males and their encounters tended to include head-butting, horning, and mount intention moves, described by some (Egerton, 1962; Petersburg, 1973; Reynolds et al., 1982; Shult, 1972) as "play" behavior. I never observed bulls less than 5 years old in a head-on fight. This observation is consistent with those of Lott (1974) who never observed serious fighting in bulls less than 4 years old and Petersburg (1973) who stated that most young bulls participated in little or no combat except mock battles.

The most common agonistic act was for one animal to walk toward another. The most common response was for the second animal to walk away. Lott (1974) referred to this type of response where "one bull simply yields to another without fighting or challenging" as "passive avoidance", and said that it ". . . is the behavior which is most commonly substituted for fighting." McHugh (1958) also found the majority (73%) of dominance interactions between bison to be passive.

Lott (1981) observed that bulls spend a high percentage of total tending time tending cows that are not in estrus and that most of this "inappropriate" tending occurred preceeding copulation. Much of this "early" activity may be performed by young males who are later displaced by older bulls as estrus approaches. Egerton (1962) saw 2 -5 year old bulls investigate cows but they were always interrupted and displaced by older bulls. Petersburg (1973) also stated that although young bulls investigated cows, few bellowed. This hypothesis is further supported by my data. During focal animal observations I never saw a Class I male bellow or attempt to block a female's path. Egerton (1962) believed that the investigatory behavior of younger bulls served as a "stimulus" for older bulls and Lott (1981) stated that being tended seemed to make cows attractive to bulls. My data indicate that this hypothesis may be true because the first tending bonds observed (during pre-rut) were by Class I and II males.

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Table 1. Number of times that bulls in a given age class were recipients and initiators in agonistic encounters. Numbers in parentheses are column percents.

| Age Class | Recipient | Initiator | Total |
|---|---|---|---|
| I<br>(2 - 4 years) | 92<br>(40%) | 30<br>(21%) | 122 |
| II<br>(5 - 9 years) | 94<br>(41%) | 32<br>(23%) | 126 |
| III<br>(10+ years) | 42<br>(18%) | 80<br>(56%) | 122 |
| Total | 228 | 142 | 370 |

$X^2 = 56.939$, d.f. = 2, $P = 0.0001$

Table 2. Status of the animals with which bulls in a given age class interacted agonistically. Numbers in parentheses are column percents.

| Age Class* | Other animal in agonistic encounter: Calves and Yearlings | Class I | Class II | Class III | Cows | Total |
|---|---|---|---|---|---|---|
| I | 11<br>(31%) | 53<br>(50%) | 23<br>(34%) | 45<br>(29%) | 13<br>(43%) | 145 |
| II | 9<br>(25%) | 31<br>(29%) | 23<br>(34%) | 61<br>(39%) | 6<br>(20%) | 130 |
| III | 16<br>(44%) | 23<br>(21%) | 22<br>(32%) | 50<br>(32%) | 11<br>(37%) | 122 |
| Total | 36 | 107 | 68 | 156 | 30 | 397 |

$\underline{X}^2 = 18.569$, $\underline{d.f.} = 8$, $\underline{P} = 0.0173$

* As in Table 1.

Table 3. *Age-specific frequencies of various types of agonistic encounters including: HB = Head-Butt, SC = Short Charge, BD = Broadside Display, HF = Head-on Fight, F = Faced other animal, H = Horned, MI = Mount Intention Move, MT = Moving toward, PW = Paw and Wallow, HT = Head Toss, B = Bellow. Numbers in parentheses are column percents. This table does not indicate whether the focal animal was the initiator or recipient of the action.*

| Age Class* | HB | SC | BD | HF | F | H | MI | MT | PW | HT | B | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I | 23 | 5 | 5 | 0 | 5 | 18 | 6 | 74 | 0 | 6 | 1 | 143 |
| | (82%) | (13%) | (21%) | (0%) | (20%) | (60%) | (100%) | (36%) | (0%) | (37%) | (5%) | |
| II | 4 | 12 | 14 | 1 | 10 | 8 | 0 | 66 | 0 | 7 | 8 | 130 |
| | (14%) | (32%) | (58%) | (20%) | (40%) | (27%) | (0%) | (33%) | (0%) | (44%) | (42%) | |
| III | 1 | 21 | 5 | 4 | 10 | 4 | 0 | 63 | 4 | 3 | 10 | 125 |
| | (4%) | (55%) | (21%) | (80%) | (40%) | (13%) | (0%) | (31%) | (100%) | (19%) | (53%) | |
| Total | 28 | 38 | 24 | 5 | 25 | 30 | 6 | 203 | 4 | 16 | 19 | 398 |

$X^2 = 92.010$, *d.f.* = 20, *P* = 0.0001

* As in Table 1.

Table 4. *The frequency of various responses of the recipient in agonistic encounters including: WA = Focal animal walked away, G = Graze, OWA = Other animal walked or ran away, TA = Turned away, UC = Unclear, SU = Stood up. Numbers in parentheses are column percents.*

| Age Class* | WA | G | OWA | TA | UC | SU | Total |
|---|---|---|---|---|---|---|---|
| I | 62<br>(44%) | 2<br>(29%) | 25<br>(23%) | 3<br>(7%) | 42<br>(52%) | 11<br>(65%) | 145 |
| II | 52<br>(37%) | 4<br>(57%) | 26<br>(24%) | 23<br>(50%) | 20<br>(25%) | 4<br>(23%) | 129 |
| III | 26<br>(19%) | 1<br>(14%) | 56<br>(52%) | 20<br>(43%) | 19<br>(23%) | 2<br>(12%) | 124 |
| Total | 140 | 7 | 107 | 46 | 81 | 17 | 398 |

$X^2 = 67.568$, *d.f.* = 10, *P* = 0.0001

* As in Table 1.

Table 5. *Mean frequencies of various behaviors (per hour) performed by bulls during different seasons including: E = Bellow, A = Attempted mount, B = Blocked female, D = Defecated, F = Sniffed or licked cow (other than the vulva), I = Mount intention move (toward a cow), L = Lip curl, M = Mount intention move (toward a male), R = Snort, P = Paw, C = Chin Rub, S = Sniffed the ground, U = Urinated, V = Sniffed cow's vulva, W = Wallow. Means with the same letter in the same column were not statistically different (alpha = 0.05).*

| | | Behavior | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Season | N | E | A | B | D | F | I | L | M |
| Pre-rut | 35 | 6.407 B | 0.000 | 0.343 | 0.571 A | 0.114 B | 1.731 | 4.931 B | 0.228 |
| Rut | 105 | 48.369 AB | 0.190 | 1.181 | 0.849 A | 0.838 B | 3.738 | 3.702 B | 0.076 |
| Post-rut | 94 | 75.655 A | 0.042 | 1.396 | 5.011 A | 3.532 A | 2.638 | 13.644 A | 0.255 |
| *P*-value * | | 0.09 | 0.15 | 0.46 | 0.03 | 0.003 | 0.59 | 0.0001 | 0.74 |

* *P*-value according to AOV

Table 5. (con.d)

| | Behavior | | | | | | |
|---|---|---|---|---|---|---|---|
| Season | R | P | C | S | U | V | W |
| Pre-rut | 0.114 | 2.900 | 2.900 | 1.714 B | 0.114 | 11.579 B | 3.507 |
| Rut | 0.724 | 2.367 | 1.206 | 6.207 B | 0.481 | 8.934 B | 3.620 |
| Post-rut | 0.894 | 4.061 | 1.149 | 16.705 A | 1.013 | 26.769 A | 4.460 |
| P-value | 0.75 | 0.49 | 0.44 | 0.0005 | 0.46 | 0.0001 | 0.83 |

Table 6. Mean frequencies of various behaviors (per hour) performed by bulls in different age classes including: E = Bellow, A = Attempted mount, B = Blocked female, D = Defecated, F = Sniffed or licked cow (other than the vulva), I = Mount intention move (toward a cow), L = Lip curl, M = Mount intention move (toward a male), R = Snort, P = Paw, C = Chin Rub, S = Sniffed the ground, U = Urinated, V = Sniffed cow's vulva, W = Wallow. Means with the same letter in the same column were not statistically different (alpha = 0.05).

| | | Behavior | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Age Class** | N | E | A | B | D | F | I | L | M |
| I | 69 | 0.00 B | 0.058 | 0.000 B | 4.315 | 1.565 | 1.928 | 4.588 B | 0.464 |
| II | 75 | 9.55 B | 0.160 | 0.907 AB | 2.593 | 2.133 | 3.467 | 12.213 A | 0.107 |
| III | 90 | 129.98 A | 0.089 | 2.214 A | 0.978 | 1.733 | 3.422 | 6.792 B | 0.000 |
| P-value * | | 0.0001 | 0.61 | 0.004 | 0.23 | 0.86 | 0.63 | 0.009 | 0.21 |

* P-value according to AOV

** As in Table 1

Table 6. (con.d)

| Age Class | Behavior | | | | | | |
|---|---|---|---|---|---|---|---|
| | R | P | C | S | U | V | W |
| I | 0.348 | 0.696 B | 0.000 B | 10.950 | 0.348 | 13.443 | 1.101 B |
| II | 0.800 | 2.094 B | 1.100 AB | 11.853 | 0.354 | 20.440 | 3.908 AB |
| III | 0.889 | 5.853 A | 2.818 A | 7.084 | 1.103 | 15.545 | 6.145 A |
| *P*-value | 0.80 | 0.003 | 0.05 | 0.37 | 0.39 | 0.20 | 0.01 |

Table 7. *Mean duration (in seconds) of various behaviors performed in a 15 minute interval by males in different age classes. Means with the same letter in the same column were not statistically different (alpha = 0.05). (Observations that were less than 15 minutes were not used in this analysis.)*

| Age Class | N | Behavior | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Graze | Lie | Stand | Walk | Run | Chase | Drink | Other |
| I | 15 | 379.54 | 329.44 A | 117.76 A | 63.19 | 0.33 | 0.15 | 0.04 A | 9.56 |
| II | 15 | 279.34 | 264.12 B | 244.29 B | 97.78 | 1.08 | 0.36 | 0.00 A | 12.66 |
| III | 15 | 304.08 | 98.80 C | 386.57 C | 93.04 | 0.23 | 0.27 | 1.37 A | 15.62 |
| *P*-value * | | 0.10 | 0.0001 | 0.0001 | 0.10 | 0.15 | 0.89 | 0.0001 | 0.39 |

* *P*-value according to AOV

Table 8. *Mean duration (in seconds) of various behaviors performed in a 15 minute interval by bulls during different seasons. Means with the same letter in the same column were not statistically different (alpha = 0.05). (Observations that were less than 15 minutes were not used in this analysis.)*

| | | Behavior | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Season | N | Graze | Lie | Stand | Walk | Run | Chase | Drink | Other |
| Pre-rut | 15 | 415.61 A | 203.41 | 204.59 | 71.49 | 0.49 | 0.00 | 1.37 A | 3.04 B |
| Rut | 15 | 301.87 AB | 211.24 | 272.07 | 93.93 | 0.70 | 0.79 | 0.04 B | 18.98 A |
| Post-rut | 15 | 245.48 B | 277.71 | 271.96 | 88.59 | 0.44 | 0.00 | 0.00 B | 15.82 A |
| *P*-value * | | 0.002 | 0.26 | 0.10 | 0.40 | 0.84 | 0.11 | 0.0001 | 0.0008 |

* *P*-value according to AOV

Table 9. *Mean duration (in seconds) of various behaviors performed in a 15 minute interval by bulls at different times of the day. Means with the same letter in the same column were not statistically different (alpha = 0.05). (Observations that were less than 15 minutes were not used in this analysis.)*

| Time Period | N | Behavior | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Graze | Lie | Stand | Walk | Run | Chase | Drink | Other |
| 0600-0900 | 9 | 401.04 A | 73.57 D | 264.74 | 139.64 A | 1.25 | 0.79 | 2.28 A | 16.70 |
| 0900-1200 | 9 | 291.44 AB | 234.00 BC | 266.38 | 95.92 A | 0.33 | 0.00 | 0.00 B | 11.93 |
| 1200-1500 | 9 | 367.16 B | 223.95 B | 251.64 | 48.63 B | 0.50 | 0.09 | 0.06 AB | 7.35 |
| 1500-1800 | 9 | 155.11 C | 469.46 A | 234.47 | 34.07 B | 0.03 | 0.26 | 0.00 B | 6.59 |
| 1800-2100 | 9 | 390.18 AB | 152.97 CD | 230.47 | 105.09 A | 0.61 | 0.17 | 0.00 B | 20.50 |
| *P*-value * | | 0.0003 | 0.0001 | 0.91 | 0.0001 | 0.36 | 0.64 | 0.0001 | 0.07 |

* *P*-value according to AOV

# CHAPTER 3

# EFFECTIVE POPULATION SIZE OF BISON ON THE WICHITA MOUNTAINS WILDLIFE REFUGE

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Abstract: POPGEN, a stochastic computer model that calculates the effective size ($N_e$) of a stable bison population, was used to examine the effects of changes in demographic parameters on $N_e$ and to analyze the genetic implications of different management strategies. With all other factors constant, an increase in either heritability of fertility or family-based mortality resulted in a decrease in $N_e$. In populations where generation interval decreased (which should lead to a decrease in $N_e$) and reproductive rates increased, the ratio of $N_e$ to N increased, indicating that reproductive rate had a stronger influence on $N_e$ than generation interval. In addition, in populations where annual recruitment of breeders decreased (which should lead to a decrease in $N_e$) and mean lifetime production increased, the ratio of $N_e$ to N increased, indicating that mean lifetime production had a stronger influence on $N_e$ than annual recruitment of breeders. Results of this study demonstrate that effective population size can be much less than

actual (8.4 to 29.6%) and that this relationship can be affected by various management practices.

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## Introduction

The detrimental consequences of decreased genetic variability, including inbreeding depression and a limited ability to adapt to a changing environment, have been widely documented and discussed. In one study done on captive ungulates, Ralls et al. (1979) found a higher juvenile mortality of inbred young than that in noninbred young in 15 of 16 species studied. Johns et al. (1977) found higher heterozygosity in deer that were carrying two fetuses than those with only one fetus.

Soulé (1980) stated that "the major goal in conservation genetics is the development of criteria for determining the population size (or minimum area) which will provide for maintenance of fitness and adaptive potential." He further noted that unless conservationists produce sound and defensible criteria for minimal population sizes there will be no rational way to counter attacks by economic and political forces that relentlessly encroach on the land and the budgets given to conservation programs. One of the first steps in developing criteria for minimum population size is deciding how much inbreeding (loss of genetic variability) is acceptable. Once this decision has been made, it can be translated into population size with the equation $1/2N_e$ = the rate of loss of heterozygosity per generation, where $N_e$ is the effective population size (Soulé 1980).

The effective population size ($N_e$) of an actual population (N) is defined as the size of an ideal population that would have the same homozygosity increase (heterozygosity decrease) as the observed population (Kimura and Crow 1963, Crow and Kimura 1970). The ideal population is one "having N constant in time, non-overlapping generations and all individuals and each sex expected to make equal contributions to the progeny" (Cavalli-Sforza and Bodmer 1971). This condition does not occur in all natural populations; therefore, actual population size may be significantly less than the effective population size.

Johns et al. (1977) have suggested that "One goal of an effective management program might be maintenance of high levels of genetic variability in local populations". Ryman et al. (1981) created a model for estimating the effective population size of hypothetical stable populations of moose (Alces alces) and white-tailed deer (Odocoileus virginianus) under various hunting regimes and used the model to compare genetic implications of different management strategies. This paper presents a similar computer modeling effort for calculating the effective population size of an actual population of bison (Bison bison) maintained at the Wichita Mountains Wildlife Refuge (WMWR). We used this model to analyze the genetic implications of different management strategies.

## Methods

POPGEN is a stochastic computer model that simulates the effective size of a bison population. We used survival and reproductive data from the bison herd on the WMWR. This model is a modification of a similar model described by Ryman et al. (1981) for calculating the effective population size ($N_e$) of moose and deer.

Since 1971 the bison herd on the WMWR has been managed to maintain stability in numbers and surplus bison have been auctioned each year. Detailed records have been kept on the ages of the auctioned animals and those lost to natural mortality. Natural mortality and losses to the auction represent the total mortality, and thus provide age-specific mortality ($D_X$) data. Data for 1973 to 1983 were combined to yield a $D_X$ schedule from which age-specific survival values ($P_X$) were calculated (Tables 1 and 2).

In a study of marked cows, Halloran (1968) found that the majority of cows had their first calf at three years of age; but 13% had their first calf at two years. The average reproductive rate ($F_X$) for older cows was 66.85%. In this model, we used an $F_X$ of 13% for 1 1/2 year old females (conception at one, birth at two) and two values of $F_X$, 68% and 71%, for cows 2 1/2 years and older. We used 68% because it was the lowest value that would maintain a stable population using the survival estimates that we calculated from refuge data. We then "smoothed" the $P_X$ schedule by lumping some of the older age classes that had similar $P_X$ values. Seventy-one percent was also used as an $F_X$ value with different survival schedules to determine the effects of a higher reproductive rate. Given this $F_X$ value, we systematically altered the $P_X$ values until a stable population was created. Combinations of the $P_X$ and $F_X$ values were used to create eight stable population structures (Table 3).

An $F_X$ value of 13% for 1 1/2 year old females was used in all cases. In populations I-IV, the $F_X$ value for cows 2 years and older was 71%. In populations V-VIII, $F_X$ for cows 2 years and older was 68%. To maintain the stable population when $F_X$ was decreased (in V-VIII), we increased the survival of age classes 9-16. Except for these differences in $P_x$ for age classes 9-16, the $P_x$ values for populations I and V, II and VI, III and VIII, and IV and VII were identical.

We ran simulations for age distributions and mortality estimates for the winter population, so that population size and age structure would be comparable to WMWR census data that are collected in the winter after the auction. Each simulation began with 100 newborn females. The fate of each female was determined stochastically based on the survival rate, $P_x$, for that age class. A random number between 0 and 1 was generated and if that number was less than $P_x$, the individual survived to enter the next age class. If surviving, the number of female offspring produced the following spring was determined in a similar manner based upon comparison of a random number and fecundity data. Both male and female offspring were calculated, and sex ratio at birth was assumed to be 1:1. The lifespan of bison is not well documented (Reynolds et al. 1982). The maximum lifespan of the bison was assumed to be 18 years and therefore only 19 age classes were used in these simulations.

Variability between runs was high, so we also ran the model with 1000 newborns. However, the results were almost identical to those obtained with 100 newborns (except for the smaller variability between runs). In this paper we report the results from the runs with 100 newborns because this value more realistically reflects offspring production for the WMWR population.

The model computed lifetime production (k) of each newborn female and the mean ($\overline{k}$) and variance ($V_k$) of lifetime production of those females who lived to reproductive age. Generation interval (G), defined as the "average age of the mothers of the young born during a year," (Ryman et al. 1981) and annual recruitment of breeders (M) were also calculated. Some discrepancy exists, however, in the definitions of annual recruitment of breeders used in calculating $N_e$. Ryman et al. (1981) used the number of animals born per year that would survive up to reproductive age in their calculations of $N_e$. Cavalli-Sforza and Bodmer (1971) stated that for populations with overlapping generations, the most convincing method of computing $N_e$ was one given by Nei and Imaizumi (1966) that used the number of individuals that reached the mean reproductive age (generation interval). We used this latter value in our model.

The effective number of females was then calculated using the following equation (Nei and Murata 1966--cited by Ryman et al. 1981)

$$N_e = \frac{M\,G}{(1+3h^2)\dfrac{V_{k_a}}{\bar{k}_a^2 + \dfrac{1}{\bar{k}_a}}}, \qquad (1)$$

where $h^2$ is the heritability of fertility. Heritability of fertility is believed to be low, about 10-20% (Falconer 1960). Ryman et al. (1981), used 0.10 and 0.20 in their model, whereas we used 0.0, 0.10, and 0.20.

The mean ($\bar{k}$) and variance ($V_k$) calculated in the model are of newborns. However, in a stable population the average number of <u>parents</u> born per mother ($\bar{k}_a$) must be two. To calculate variance ($V_{k_a}$) of this mean the following equation was used (Crow and Morton 1955):

$$V_{k_a} = s\,(1-s)\,\overline{k} + s^2\,V_k\,, \qquad (2)$$

where $$s = \frac{\overline{k_a}}{\overline{k}} \qquad (3)$$

and is the probability of surviving to adulthood. These equations correspond to Crow and Morton's model where survival to adulthood is random, rather than on a family basis. To account for family-based mortality, the percent mortality that is due to family ties is subtracted from $\overline{k}$. For instance, if 30% of the reduction of $\overline{k}$ down to two ($\overline{k_a}$) is assumed to be family-based (and the rest individually-based), then, if $\overline{k} = 10$, the total reduction is 8 and of this value 2.4 (30%) is family-based. Therefore, 10 is reduced to 7.6 in equation (3). If related bison tend to remain together on the refuge, then the bison rounded-up and sold at the auction ("mortality") would not be entirely random. We used 0 and 30% to examine the effect of family-based mortality.

The $N_e$ calculated in POPGEN using equation (1) is for females only. The effective population size of males was then calculated assuming that the stable population was 50% males and that the ratio of effective males to actual males was either 90% or 60% of the corresponding ratio for females. Ryman et al. (1981) used 90% in their model. However, we believed that because of the greater variability in the number of progeny produced by males and because of the exclusion of some males from breeding by more dominant males, the correct value is probably much lower; therefore, we also ran the model using 60%.

The ratio of breeding males to females further affects $N_e$ and must be taken into account when calculating the total $N_e$. In species with separate sexes, each sex makes the same contribution to the next generation; therefore, the probability that two genes in different individuals in generation t are both derived from a male in generation t-1 is 1/4 and the probability that they came from the same male is $\frac{1}{4Ne_{male}}$ (Crow and Kimura 1970). The same principle applies to females. Where the number of breeding males and females differ,

$$\frac{1}{N_e} = \frac{1}{4Ne_{male}} + \frac{1}{4Ne_{female}} \quad \text{or} \qquad (3)$$

$$N_e = \frac{4\,(Ne_{male})\,(Ne_{female})}{Ne_{male} + Ne_{female}} \qquad (4)$$

(Wright 1931--cited by Ryman et al. 1981).

## Results

We combined actual $P_x$ values from the WMWR herd (Tables 1 and 2) with $F_x$ values to create eight hypothetical, stable, bison populations (Table 3). For each population, we calculated $N_e$ for three values of heritability of fertility (H) - 0.0, 0.1, and 0.3; two values of mortality on a family basis (M) - 0.0 and 0.3; and with a ratio of $Ne_{male}/N_{male}$ (%) of both 90 and 60% of the corresponding ratio for females. We ran each of these combinations for five different sets of random numbers. Populations I, II, V, and VI have a lower yearling and higher 3 and 4 year old survival and therefore a lower annual recruitment of breeders and higher mean lifetime production than the other four populations (Table 4). Generation interval was lower in populations I-IV where survival of 9-6 year olds was lower than in the other four populations.

A direct comparison cannot be made of the $N_e$ of these populations because they were calculated for populations of different actual sizes. Therefore, we compared the percent of $N_e$ to N (Table 5). Mean percents for the five simulations ranged from 8.4 to 29.6%. The percent decreased as heritability of fertility or family-based mortality increased. The percents of $N_e$ to N were lower in populations V, VI, VII, and VIII where reproductive rates were lower and generation interval higher than in their respective pairs (I, II, IV, and III). Percents were lower in population III, IV, VII, and VIII which had a higher annual recruitment of breeders and lower mean lifetime production than the other populations.

## Discussion

When all other factors were constant, $N_e$ decreased as heritability of fertility increased. This relationship is consistent with the findings of Nei and Murata (1966) and Ryman et al. (1981). An increase in family-based mortality also resulted in a lower $N_e$, which is also consistent with Ryman et al. (1981).

Another factor that can decrease $N_e$ is overlapping generations. According to Cavalli-Sforza and Bodmer (1971) "the most convincing method of computing $N_e$ with overlapping generations among those published is the one by Nei and Imaizumi (1966). According to them,

$$N_e = t\ N_m \qquad (5)$$

where t is the mean age at reproduction (in years) and $N_m$ the number of individuals who reach the mean reproductive age per year." This equation corresponds to the top part (M x G) of equation (1) for calculating $N_e$. However, in Ryman et al. (1981) $N_m$ (annual recruitment of breeders) is defined as the number of animals of a given cohort that live to reproductive age rather than those who live to the mean reproductive age. We used the latter definition in our model.

Based on equation (5), it would appear that $N_e$ should decrease as either annual recruitment of breeders decreases or generation interval decreases. Because of the complex relationship between generation interval, annual recruitment of breeders, and age-specific survival rates this relationship does not occur in our model. The use of different age-specific survival rates made it difficult to change only one factor while keeping all others constant and thus complicated expected relationships between various factors. Although the results are not as well defined as they would have been with constant age-specific survival rates, we believe our treatment more realistically reflects the actual bison population in the WMWR.

Generation interval was lower for populations I-IV than for their respective pairs, although their respective pairs had lower ratios of $N_e$ to N. However, the reproductive rate in populations I-IV was higher than in the other groups, indicating that reproductive rate probably has a stronger influence on $N_e$ than generation interval. Unlike Ryman et al. (1981), we did not obtain a large difference in generation interval (6.46-7.03). This difference is due to smaller changes in $P_x$ values in our populations than in those used by Ryman et al. (1981).

For populations I, II, V, and VI a lower survival of yearlings, and therefore lower annual recruitment of breeders, was offset by a higher survival of 3 and 4 year olds, and therefore higher mean lifetime production. The result was larger ratios of $N_e$ to N than for the other populations.

Another factor that affects $N_e$ is the ratio of breeding males to breeding females. When the number of breeding males equals the number of breeding females, $N_e$ is the sum of $Ne_{male}$ and $Ne_{female}$. Where $Ne_{male}$ is not equal to $Ne_{female}$, $N_e$ is less than the sum of the two and is more strongly influenced by the smaller of the two values.

Due to a lack of age-specific data on reproductive rates of male bison, calculations of $N_e$ for males were not possible. Ratios of $N_e$ to N for males were calculated using both 90% and 60% of the corresponding ratio for females. This value may be very conservative, however, especially in polygynous species such as bison where $N_e/N$ may be lower due to exclusion of some males from breeding. Depending on the degree of this exclusion of breeders, the total effective size of the population could be lower than that predicted by the model. To get a more accurate estimate of the effective number of males, we need detailed information on age-specific reproductive rates of individual males.

Family-based survival also affects $N_e$. Ryman et al. (1981) believe that "profound family survival is not likely to occur in moose and white-tailed deer," so they chose a value of 10% for family-based mortality. They do state, however, that "spatial variation in hunting intensities might easily result in pronounced family survival." At the

WMWR, bison are rounded-up every fall for auction. If bison tend to remain in herds with closely related individuals, then "survival" may, in part, be on a family basis. Therefore, we chose a higher value (30%) than Ryman et al. (1981) for family-based mortality. As family-based mortality increased (from 0-30%) $N_e$ decreased.

The model demonstrates that effective population size can be much less than actual population size. The percent of effective to actual population size ranged from 8.4 to 29.6% in our model. Ryman et al. (1981) obtained a percent of $N_e$ to N of approximately 20-40% for moose and 35-40% for white-tailed deer.

Many of the basic biological factors that affect $N_e$, such as heritability of fertility and reproductive rates, can either be controlled very little or not at all through management. One factor that can be managed to increase effective population size, however, is actual population size over time. The smaller the fluctuation in population size over time, the greater $N_e$ will be. The WMWR is already trying to maintain a stable population of bison.

In addition, the more equal the ratio of $Ne_{male}$ to $Ne_{female}$ the higher the total $N_e$ will be. The actual sex ratio of bison in the WMWR is close to 1:1. However, $Ne_{male}$ is probably much less than $Ne_{female}$ because of breeding exclusion of males and a larger variance in progeny number for males and therefore the actual number of males may need to be maintained at a higher level.

Another factor that can be controlled through management and may have a significant effect on $N_e$ is family-based mortality. Preliminary analysis shows that during the fall (when round-up occurs) the probability of finding a cow and her yearling in the same group is roughly 50% (Shaw and Carter 1985). To maximize $N_e$, bison should be rounded-up and auctioned in a way that would minimize the loss of groups of closely-related individuals. One way of accomplishing this might be to sell only yearlings from one group and only adults from another group.

The effect of manipulating various factors to increase $N_e$ may not be apparent. For instance, if the number of animals in each age class that are sold each fall could be manipulated to maintain a stable population with as much genetic variability as possible, an attempt could be made to increase annual recruitment of breeders by selling fewer yearlings. However, if the number of three and four year olds sold was increased to maintain a stable population, the mean lifetime production would drop. For this particular population, this drop would cause a decrease in $N_e/N$ according to our model.

Of the age structures we created, V or VI maximizes $N_e$ for the WMWR population. Although $N_e/N$ was higher for population I and II the reproductive rate necessary for these populations is probably higher than that which exists on the WMWR since the reproductive rate on the WMWR is probably close to 68% (Halloran 1968) (populations V-VIII) and since more recent unpublished data indicate that no cows on the WMWR produce calves as 2 year olds. Populations V and VI differ from VII and VIII in that the former have lower survival rates for yearlings and higher survival rates for 3 and 4 year olds.

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Tab. 1. Age-specific mortality rates ($D_x$) calculated from records of natural mortality and auction sales of bison cows on the Wichita Mountains National Wildlife Refuge.

| Age | Year | | | | | | | | | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (years) | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | $D_x$ | Lx | $P_x$ |
| | | | | | | | | | | | | | 655 | |
| 0 | 2 | 1 | 2 | 2 | 3 | 3 | 2 | 1 | 1 | 2 | 4 | 23 | 632 | 0.96 |
| 1 | 22 | 26 | 15 | 25 | 18 | 22 | 30 | 29 | 29 | 34 | 32 | 282 | 350 | 0.55 |
| 2 | 27 | 7 | 2 | 6 | 9 | 7 | 6 | 2 | 4 | 7 | 8 | 85 | 265 | 0.76 |
| 3 | - | - | 1 | 1 | - | 1 | 1 | 4 | 5 | 11 | 6 | 30 | 235 | 0.89 |
| 4 | 1 | 1 | 1 | 1 | - | - | - | 1 | 2 | - | 4 | 11 | 224 | 0.95 |
| 5 | - | - | - | 6 | 1 | 6 | 4 | 4 | 1 | 1 | 1 | 24 | 200 | 0.89 |
| 6 | 3 | 1 | 1 | - | - | 9 | 3 | 5 | 1 | 4 | 2 | 29 | 171 | 0.86 |
| 7 | - | 7 | - | - | 1 | - | 1 | 1 | 3 | 1 | 2 | 16 | 155 | 0.91 |
| 8 | 1 | 6 | - | 1 | - | 3 | - | 3 | 2 | 4 | - | 20 | 135 | 0.87 |
| 9 | - | 2 | 5 | 9 | 6 | - | 4 | 1 | 4 | 1 | - | 32 | 103 | 0.76 |
| 10 | - | 2 | 4 | - | 2 | - | - | 3 | 3 | 3 | 2 | 19 | 84 | 0.82 |
| 11 | 1 | 1 | 3 | - | 2 | 3 | 2 | - | 4 | 1 | 2 | 19 | 65 | 0.77 |
| 12 | - | - | 7 | 2 | - | 9 | 2 | 3 | 2 | 3 | 2 | 30 | 35 | 0.54 |
| 13 | 1 | - | 1 | 1 | 2 | 6 | 1 | - | 2 | - | 1 | 15 | 20 | 0.57 |
| 14 | - | - | 1 | - | 1 | 4 | - | 1 | 2 | - | - | 9 | 11 | 0.55 |
| 15 | - | - | - | - | 1 | 3 | - | - | - | - | - | 4 | 7 | 0.64 |
| 16 | - | - | - | 1 | - | 1 | - | - | - | - | 1 | 3 | 4 | 0.57 |
| 17 | - | - | - | - | - | - | - | - | - | - | - | 0 | 4 | 1.00 |
| 18 | - | - | - | - | 1 | 1 | - | - | - | - | - | 2 | 2 | 0.50 |
| 19 | - | - | - | - | - | - | - | - | - | - | - | 0 | 2 | 1.00 |
| 20 | - | - | - | - | 1 | 1 | - | - | - | - | - | 2 | 0 | 0.00 |

Tab. 2. Age-specific mortality rates ($D_x$) calculated from records of natural mortality and auction sales of bison bulls on the Wichita Mountains National Wildlife Refuge.

| Age | Year | | | | | | | | | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (years) | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | $D_x$ | Lx | $P_x$ |
| | | | | | | | | | | | | | 610 | |
| 0 | - | 2 | 1 | 1 | 2 | 2 | 2 | - | 1 | 1 | 4 | 16 | 594 | 0.97 |
| 1 | 10 | 11 | 12 | 21 | 21 | 24 | 24 | 23 | 31 | 40 | 34 | 251 | 343 | 0.58 |
| 2 | 35 | 6 | 2 | 6 | 9 | 12 | 8 | 10 | - | 7 | 8 | 105 | 238 | 0.69 |
| 3 | 1 | 5 | 5 | 4 | 4 | 22 | - | 20 | 2 | 51 | 11 | 41 | 197 | 0.83 |
| 4 | 2 | 1 | 1 | 2 | 1 | - | - | - | 4 | 4 | 1 | 17 | 180 | 0.91 |
| 5 | 2 | 1 | - | 4 | - | 4 | 1 | - | 4 | 6 | 5 | 32 | 148 | 0.82 |
| 6 | 1 | 1 | 1 | - | - | 1 | 4 | - | 3 | - | 2 | 13 | 135 | 0.91 |
| 7 | 1 | - | 1 | 1 | - | 5 | 5 | - | 2 | 4 | 2 | 22 | 113 | 0.84 |
| 8 | 2 | - | 1 | - | 1 | 2 | 3 | - | 5 | 2 | 2 | 18 | 95 | 0.84 |
| 9 | - | - | 2 | 4 | 2 | - | 1 | - | 2 | 1 | 1 | 12 | 83 | 0.87 |
| 10 | 1 | - | 1 | 2 | 6 | 1 | 3 | - | 2 | - | 0 | 17 | 66 | 0.80 |
| 11 | 1 | - | 4 | 1 | 7 | 4 | 1 | - | 2 | - | 1 | 21 | 45 | 0.68 |
| 12 | 1 | - | 1 | 3 | 7 | 2 | 1 | - | - | - | 1 | 16 | 29 | 0.64 |
| 13 | - | - | - | 3 | 3 | 2 | 1 | - | - | - | 1 | 10 | 19 | 0.66 |
| 14 | - | - | - | 1 | 1 | 4 | - | - | - | - | - | 6 | 13 | 0.68 |
| 15 | 1 | - | - | - | - | - | - | - | 1 | - | 2 | 4 | 9 | 0.69 |
| 16 | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 8 | 0.89 |
| 17 | - | - | 1 | - | - | - | - | - | - | - | - | 1 | 7 | 0.88 |
| 18 | - | - | - | - | - | - | 1 | - | 1 | - | - | 2 | 5 | 0.71 |
| 19 | - | - | - | - | - | - | - | - | - | - | - | 0 | 5 | 1.00 |
| 20 | - | - | - | - | - | - | - | - | 1 | - | - | 1 | 0 | 0.00 |

Tab. 3. Age-specific survival rates ($P_x$) for eight hypothetical stable bison populations.

| Age (years) | Populations I | II | III | IV | V | VI | VII | VIII |
|---|---|---|---|---|---|---|---|---|
| 0 | 0.96 | 0.96 | 0.96 | 0.96 | 0.96 | 0.96 | 0.96 | 0.96 |
| 1 | 0.60 | 0.60 | 0.75 | 0.75 | 0.60 | 0.60 | 0.75 | 0.75 |
| 2 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |
| 3 | 0.91 | 0.89 | 0.80 | 0.78 | 0.91 | 0.89 | 0.78 | 0.80 |
| 4 | 0.91 | 0.93 | 0.75 | 0.77 | 0.91 | 0.93 | 0.78 | 0.75 |
| 5 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 |
| 6 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 |
| 7 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 |
| 8 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 |
| 9 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 10 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 11 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 12 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 13 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 14 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 15 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 16 | 0.70 | 0.70 | 0.70 | 0.70 | 0.75 | 0.75 | 0.75 | 0.75 |
| 17 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 |
| 18 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 |

Tab. 4. Mean values of five simulations of eight bison populations.

| Population | Annual Recruitment of Breeders | Mean Lifetime Production | Variance in Lifetime Production | Generation Interval | Actual No. of Females |
|---|---|---|---|---|---|
| I | 59.8 | 3.47 | 10.52 | 6.67 | 425 |
| II | 59.2 | 3.54 | 10.67 | 6.74 | 424 |
| III | 73.6 | 2.74 | 10.03 | 6.51 | 437 |
| IV | 73.8 | 2.73 | 9.76 | 6.46 | 436 |
| V | 59.6 | 3.54 | 11.69 | 6.98 | 437 |
| VI | 58.0 | 3.50 | 11.98 | 7.03 | 436 |
| VII | 74.0 | 2.70 | 10.42 | 6.75 | 449 |
| VIII | 73.8 | 2.70 | 10.47 | 6.78 | 447 |

Tab. 5. Mean percents of $N_e$ to N in hypothetical stable bison populations.

| | H= 0 | | | | 0.1 | | | | 0.2 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M= 0 | | 0.3 | | 0 | | 0.3 | | 0 | | 0.3 | | |
| Population | %=0.9 | 0.6 | 0.9 | 0.6 | 0.9 | 0.6 | 0.9 | 0.6 | 0.9 | 0.6 | 0.9 | 0.6 | $\bar{X}$ |
| I | 28.4 | 22.4 | 24.6 | 19.2 | 23.4 | 18.8 | 20.2 | 16.2 | 20.2 | 16.0 | 17.6 | 13.8 | 20.07 |
| II | 29.6 | 23.4 | 25.2 | 20.4 | 24.8 | 19.8 | 21.0 | 16.8 | 21.2 | 16.6 | 17.8 | 14.2 | 20.90 |
| III | 19.0 | 14.8 | 17.2 | 13.2 | 15.6 | 12.4 | 14.2 | 10.8 | 13.2 | 10.6 | 11.8 | 9.2 | 13.50 |
| IV | 18.8 | 14.6 | 17.0 | 13.4 | 15.6 | 12.4 | 13.8 | 10.8 | 13.2 | 10.2 | 11.8 | 9.4 | 13.42 |
| V | 26.4 | 21.0 | 22.6 | 18.0 | 21.8 | 17.4 | 18.4 | 14.4 | 18.6 | 14.8 | 15.6 | 12.2 | 18.43 |
| VI | 24.4 | 19.6 | 19.8 | 17.4 | 20.6 | 16.0 | 17.0 | 13.4 | 17.4 | 13.8 | 14.6 | 11.6 | 17.13 |
| VII | 17.2 | 13.8 | 15.4 | 12.4 | 14.0 | 11.2 | 12.4 | 10.0 | 11.8 | 9.6 | 10.6 | 8.4 | 12.23 |
| VIII | 17.6 | 14.2 | 16.0 | 12.6 | 14.4 | 11.4 | 13.0 | 10.0 | 12.2 | 9.6 | 11.0 | 8.6 | 12.55 |

# CHAPTER 4

# RECOMMENDATIONS FOR BISON MANAGEMENT ON THE WICHITA MOUNTAINS WILDLIFE REFUGE

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The consequences of decreased genetic variability have been widely documented. These consequences include inbreeding depression and a limited ability to adapt to a changing environment. As Johns et al. (1977:171) suggested, ". . . one goal of an effective management program, might be the maintenance of high levels of genetic variability in local populations."

The following recommendations are based on data collected on the Wichita Mountains Wildlife Refuge (WMWR) bison herd and a computer model for calculating the effective population size ($N_e$) of this population. $N_e$ is a relative measure of the amount of genetic variability being lost in a population and is defined as the size of an ideal population that would have the same homozygosity increase (heterozygosity decrease) as the actual population (Crow and Kimura 1970, Kimura and Crow 1963). The ideal population is one ". . . having N constant in time, non-overlapping generations and all individuals and each sex expected to make equal contributions to the progeny" (Cavalli-Sforza and Bodmer 1971:416).

## Population Size Over Time

The larger the fluctuation in population size over time, the larger the loss of genetic variability will be. The WMWR has been trying to maintain a stable number of bison by annually auctioning surplus animals and continuation of this practice is beneficial.

## Sex Ratio

When the effective number of males ($Ne_m$) equals the effective number of females ($Ne_f$), $N_e$ equals the sum of $Ne_m$ and $Ne_f$. Where the effective sex ratio is not equal, $N_e$ is less than the sum of the two and is more strongly influenced by the smaller of the two values. Because of the breeding exclusion of some males and the larger variance in progeny number for males than for females, it may be beneficial to maintain a larger actual number of males than females to obtain an equal sex ratio of effective males to female.

In addition, Lott (1979:429) found that where there was a large number of mature male bison ". . . there were more of the very small differences in size, strength, experience and aggressiveness . . ." that lead to changes in social status. It is possible, therefore, that in a population with many males there will be more closely-ranked individuals and therefore more shifts in social standing, which is correlated with breeding rate (Lott 1979). Therefore, a larger proportion of breeding males may result from maintaining a larger number of breeding age males.

In addition, because the breeding season is sharply peaked (85% of calves were born within 2 weeks in 1983) and because a bull can only tend one cow at a time, it seems likely that with a large number of mature bulls, breeding might be distributed more evenly.

## Selective Removal of Non-related Individuals

As family-based mortality increases, the amount of genetic variability that is lost increases. The auction acts as a major source of "mortality" on the bison and care should be taken to minimize the sale of closely-related individuals. Shaw and Carter (1985) say that "Cow-calf groups are made up of associations between adult cows and offspring of various ages and are not essentially random association . . .". They have found that during fall, when round-up occurs, the probability of capturing a cow and her yearling within the same group is roughly 50%. The refuge staff, therefore, may want to consider randomly selecting individuals for sale from several groups rather than rounding-up entire groups of bison or selling only yearlings from one group and only adults from another group.

## Age Structure

Of those age structures examined the best one for maintenance of genetic diversity for the WMWR herd is the one that resulted with the recommended survival rates given in Table 1. These survival rates correspond very closely to the average actual survival rates of bison on the WMWR from 1973-1983 (Table 1). A slight increase in the number of younger animals sold and a decrease in the number of older animals sold would result in removal rates that would conform more closely to the recommended rates. The resulting shift to a slightly older age structure should lead to an increased mean lifetime production and an increased generation interval, both of which should increase $N_e$.

## General Management Practices

Some of the recommendations given rely on the ability to age individuals accurately. Bulls can be accurately aged to the year class up to 5 years and cows up to 2 or 3 years based on the shape of the horns. One practice that could be used to allow more accurate age determination is branding. Branding was used at the WMWR until 1972 and is still used in some other managed bison herds. If calves are branded each year with the last digit of that year (and branding is switched to the opposite hip every 10 years) then much of the uncertainty in aging bison would be removed.

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Table 1. Survival rates recommended on the basis of a computer model, and actual average survival rates of bison on the Wichita Mountains Wildlife Refuge from 1973 - 1983.

| Age | Recommended Survival Rates | Actual Female Survival Rates | Actual Male Survival Rates |
|---|---|---|---|
| Calf | 0.96 | 0.96 | 0.97 |
| 1 | 0.60 | 0.55 | 0.58 |
| 2 | 0.75 | 0.76 | 0.69 |
| 3 | 0.91 | 0.89 | 0.83 |
| 4 | 0.91 | 0.95 | 0.91 |
| 5 | 0.88 | 0.89 | 0.82 |
| 6 | 0.88 | 0.86 | 0.91 |
| 7 | 0.88 | 0.91 | 0.84 |
| 8 | 0.88 | 0.87 | 0.84 |
| 9 | 0.75 | 0.76 | 0.87 |
| 10 | 0.75 | 0.82 | 0.80 |
| 11 | 0.75 | 0.77 | 0.68 |
| 12 | 0.75 | 0.54 | 0.64 |
| 13 | 0.75 | 0.57 | 0.66 |
| 14 | 0.75 | 0.55 | 0.68 |
| 15 | 0.75 | 0.64 | 0.69 |
| 16 | 0.75 | 0.57 | 0.89 |
| 17 | 0.66 | 1.00 | 0.88 |
| 18 + | 0.66 | 0.50 | 0.57 |

# VITA

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