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HORN GROWTH AS AN INDEX TO LEVELS OF INBREEDING IN BIGHORN SHEEP

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ABSTRACT

Horn growth of 477 rams from 17 of Montana's bighorn (*Ovis canadensis canadensis*) populations was examined. Cumulative horn volume at 3 years of age could not be related to winter range densities for either native ($r = 0.03$) or transplanted ($r = -0.12$) populations. Horn volume was not correlated with population size for transplanted populations ($r = 0.04$), though it was significantly correlated to population size for native herds ($r = 0.75$; $p < 0.01$). Cumulative horn volume was closely correlated to historic minimum population levels for native herds ($r = 0.91$; $p < 0.0005$) and historic population size was correlated to present population size for native herds ($r = 0.81$; $p < 0.005$). Thus, horn volume appears to be related to present population size for native herds because both factors are closely correlated to historic population levels. We suggest that historic population lows resulted in high rates of inbreeding that are currently being reflected in low ram horn volumes.

INTRODUCTION

Horn growth in mountain sheep is influenced by nutritional and genetic factors. Several recent studies have demonstrated the relationship between horn growth and nutrition. Geist (1971) postulated that expanding sheep populations are characterized by more rapid horn growth than sheep in stable or declining herds. Shackleton (1973) compared horn growth characteristcs of two bighorn populations and found that the higher quality population was characterized by rams with more rapid horn growth early in life. Heimer and Smith (1975) demonstrated that horn growth was inversely related to population density for the Dall's sheep (*Ovis dalli dalli*) in Alaska. Bunnell (1978) found that horn growth of Dall's sheep was related to the quality and quantity of forage which was in turn directly related to the amount of spring precipitation. This paper examines the relative importance of genetics and nutrition to horn growth in 17 bighorn sheep populations in Montana.

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METHODS

Montana Department of Fish, Wildlife and Parks has enforced a mandatory examination of all bighorn sheep harvested since 1974. Examination of ram horns by department personnel includes measurements of the length of each annual increment and the circumference at each annual ring. These data were used to calculate mathematical volume of horn grown each year of a ram's life (Heimer and Smith 1975).

Bunnell (1978) demonstrated that horn growth varied between years in Dall's sheep. To avoid possible biases of this type, a mean horn volume was calcualted for each bighorn herd based on the total number of rams measured from that population since 1974. This should prevent the data from being skewed by any one particular set of weather conditions or by unusual horn growth of any cohort.

Mean cumulative horn volume for the first four growth periods was used as a basis for comparing horn growth among the 17 populations studied. Shacketon (1973) suggested that horn growth for superior quality rams was greater than that of inferior rams for only the first 4 years of growth. He further showed that the age of social maturation is advanced among animals from high quality populations. Thus, superior quality rams become socially active early in life and must budget less energy for horn growth. Inferior quality rams, being relatively less active socially, can have larger energy budgets for horn growth and can grow larger horn segments than superior quality rams during the latter part of their lives. However, Simmons and Stewart (1979) showed that this relationship held only when comparing populations of relatively similar quality. When comparing populations of vastly different quality, horn growth was found to be greater throughout the lives of superior quality rams. In any case, when a large number of populations are compared, only the first 4 years of growth should be used.

RESULTS

Mean cumulative 3-year-old horn volumes for native populations ranged from a low of 115 to a high of 177 in^3 (Table 1), Horn volumes for all transplanted populations were larger than for any native population ranging from 184 to 285 in^3 (Table 2). Since there was such a distinct difference in horn growth between the two types of populations, we treated them separately in further analysis.

Initially, we attempted to explain differences in horn growth, particularly among native populations, by relating them to various physical

Table 1. Mean cumulative 3-year-old horn volumes, population characteristics and minimum historic population levels for native Montana bighorn herds.

Herd Name	Hunting District	Horn Volume[1]	Sample Size	Population Estimate[2]	Winter Density[3]	Historic Population Low	Historical Source
West Bitterroot	250	126	13	90	18	50[4]	Klaver (1978)
Yellowstone-Gallatin	300	150	25	150	28	75	K. Keating (Montana State University, pers. comm.)
Spanish Peaks	301	134	34	175	25	60	Couey (1950)
Hilgards	302	136	12	100	100	20	Buechner (1960)
Absaroka[5]	303	177	16	300	20	150	Buechner (1960)
Sun River	420	174	159	900	13	150	Egan (1975)
Stillwater	500	135	28	50	17	35	Stewart (1975)
West Rosebud	501	115	17	50	4	35	Couey (1950)
Hellroaring	502	122	31	75	5	50[4]	Simmons & Stewart (1977)

1 Volume in cubic inches.
2 Based on 1980-81 surveys.
3 Bighorns per square mile.
4 These populations may have actually been smaller, but data are lacking.
5 Includes portions of Yellowstone National Park.

Table 2. Mean cumulative 3-year-old horn volumes, population characteristics and history of transplanted Montana bighorn herds.

Herd Name	Hunting District	Horn Volume[1]	Sample Size	Population Estimate[2]	Winter Density[3]	Year(s) Trans-planted	Transplant Source
Kootenai Falls	100	188	23	150	14	1954, 1955	Wild Horse Island
Thompson Falls	121	212	42	450	38	1959	Wild Horse Island
Berray Mountain	123	194	9	125	22	1969, 1975	Sun River, Wild Horse Island
Flint Range	213	208	26	150	30	1967	Sun River
Rock Creek	216	285	4	150	25	1975	Sun River
East Bitterroot	270	221	9	60	20	1972	Sun River
Highlands	340	192	7	115	7	1967, 1969	Sun River
Wild Horse Island	--	186	22	150[4]	75	1939, 1947	Sun River

1 Volume in cubic inches.
2 Based on 1980-81 surveys.
3 Bighorns per square mile.
4 Population size from early to mid-1970's when horn volume data were collected.

habitat parameters such as soil fertility, chinook frequency on winter ranges and winter range elevation. These factors could not consistently explain differences in horn growth for Montana bighorns, though Wishart (1969) found them to be important parameters influencing horn growth in Alberta bighorns.

Bighorns from the Hellroaring, West Rosebud, Stillwater, Absaroka, Spanish Peaks and Hilgard populations occur on soils that are derived from the same geologic parent materials. Yet, horn volumes range from 177 in^3 for Absaroka rams to 115 in^3 for West Rosebud rams. Three bighorn populations are found in areas of frequent chinooks: Stillwater, Sun River and Absaroka. Again, horn volumes range from relatvely small for Stillwater rams (135 in^3) to relatively large for Absaroka rams (177 in^3). Rams that winter in alpine areas (Hellroaring and West Rosebud) consistently have small horn volumes, but they do not differ significantly from rams from low elevation winter ranges of the Stillwater, Spanish Peaks and Hilgard herds.

Since Heimer and Smith (1975) found that horn growth was correlated to population density for Alaskan Dall's sheep, we tested for a similar relationship. No significant correlation could be established when bighorn horn volumes and winter range densities for Montana's native populations were compared ($r = 0.03$). It appeared that areas capable of supporting a large bighorn population also supported rams with large horn volumes (Table 1). Population size and horn growth were significantly correlated for native populations ($r = 0.75$; $p < 0.01$) (Figure 1). It is also apparent (Table 1) that horn volume is closely related to historic minimum population levels. The correlation between these two factors is highly significant ($r = 0.91$; $p < 0.0005$) (Figure 2). Since historic minimum population levels are closely correlated with present population levels ($r = 0.81$; $p < 0.005$) (Figure 3), we assume that horn volumes are correlated with present population size only because both factors are highly correlated with minimum population levels.

Transplanted populations are all characterized by large horn volumes. As with the native herds, no significant relationship was found when horn volumes were correlated with winter density ($r = -0.12$). Unlike the native populations, no significant relationship was found between horn volumes and total population size ($r = 0.04$).

DISCUSSION

We suggest that minimum historic population size is the primary factor in determining horn growth rates for native bighorns. Those populations which at one or more times in their history dipped to 50 or 60 animals or less do not appear to be capable of supporting rams with rapid horn growth. Rams from populations that never declined to less than 125-150 animals are generally characterized by rapid horn growth and large horn volumes.

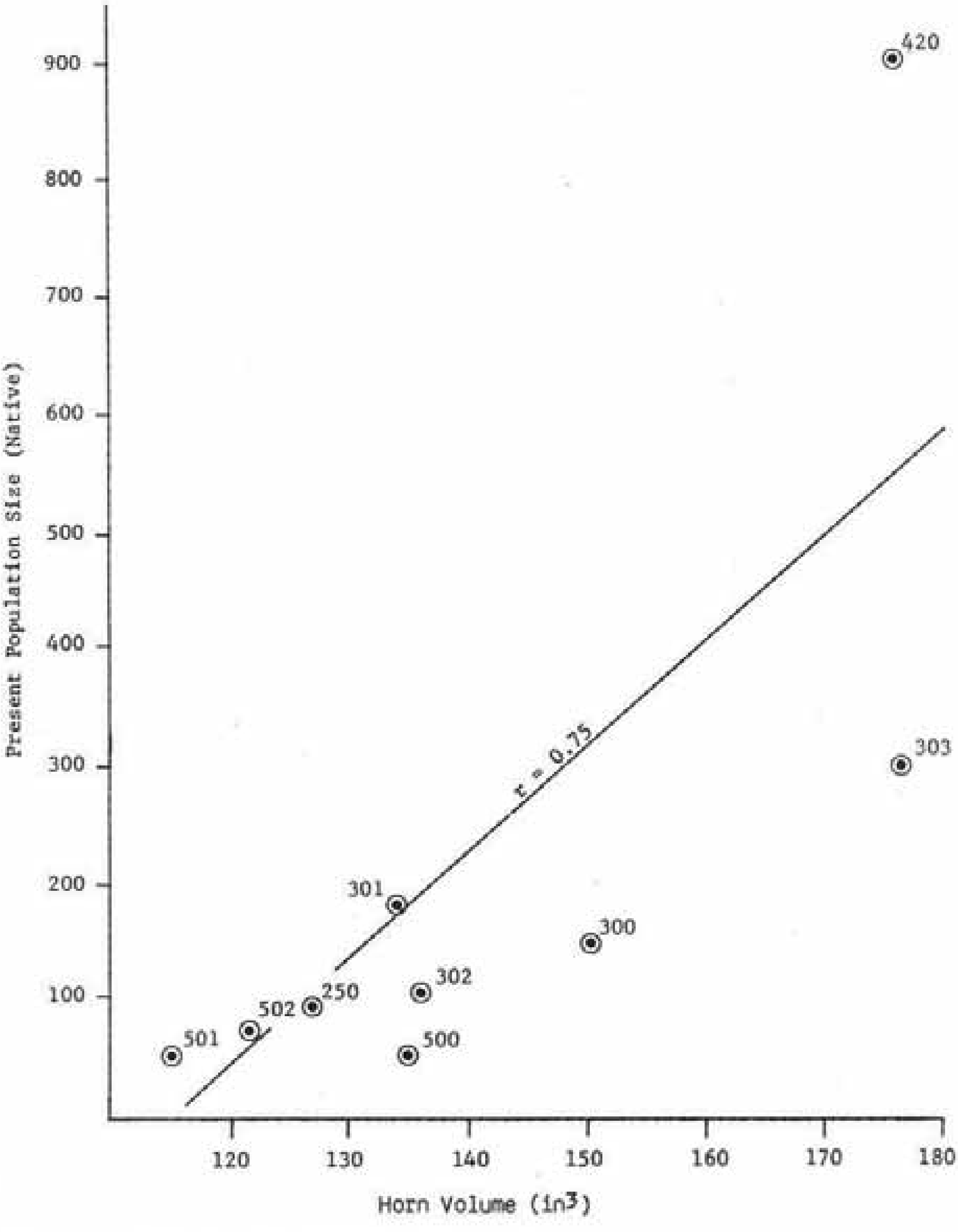

Figure 1. Relationship of horn volume and present population size for Montana's native bighorn populations.

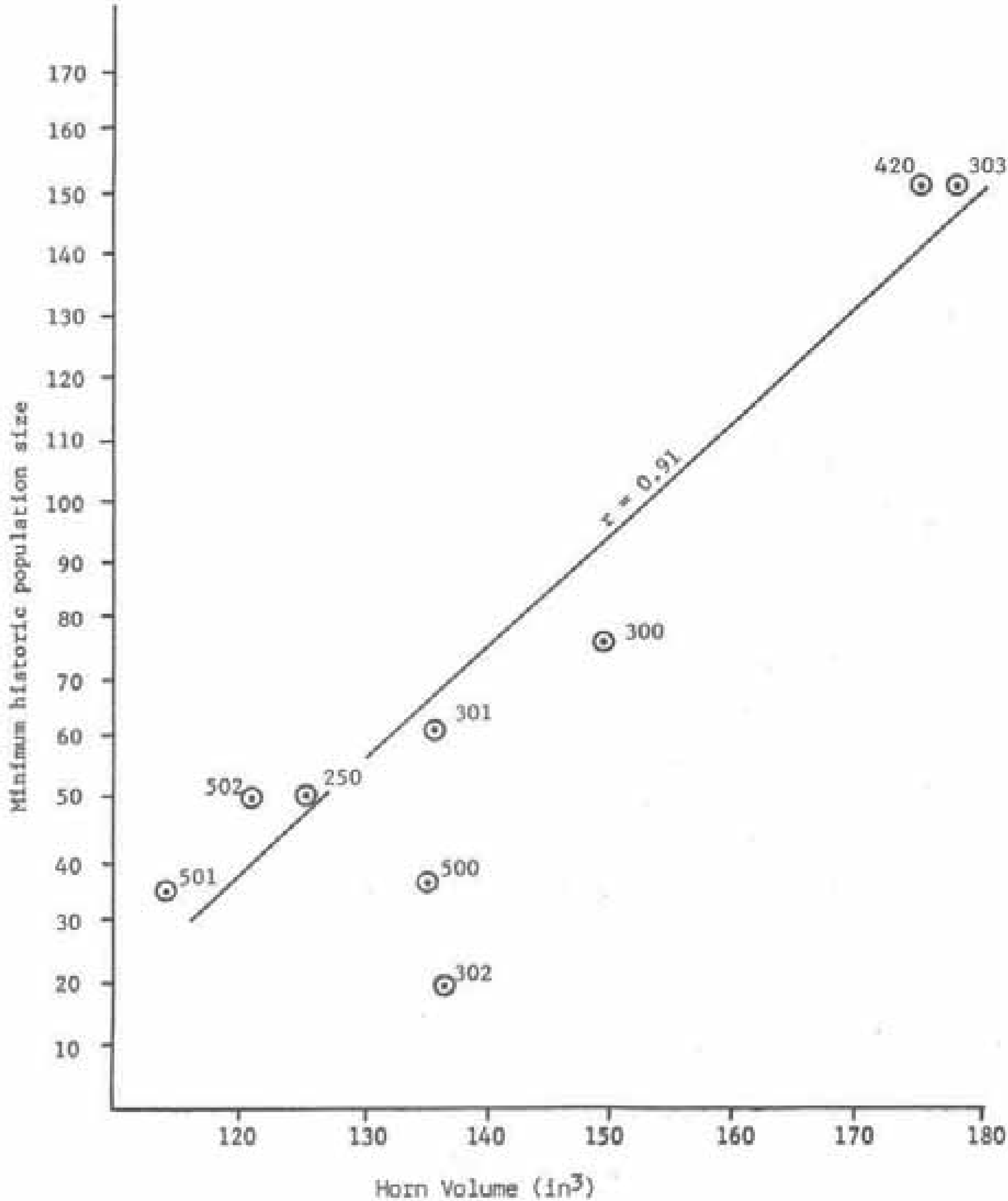

Figure 2. Relationship of horn volume and minimum historic population size for Montana's native bighorn populations.

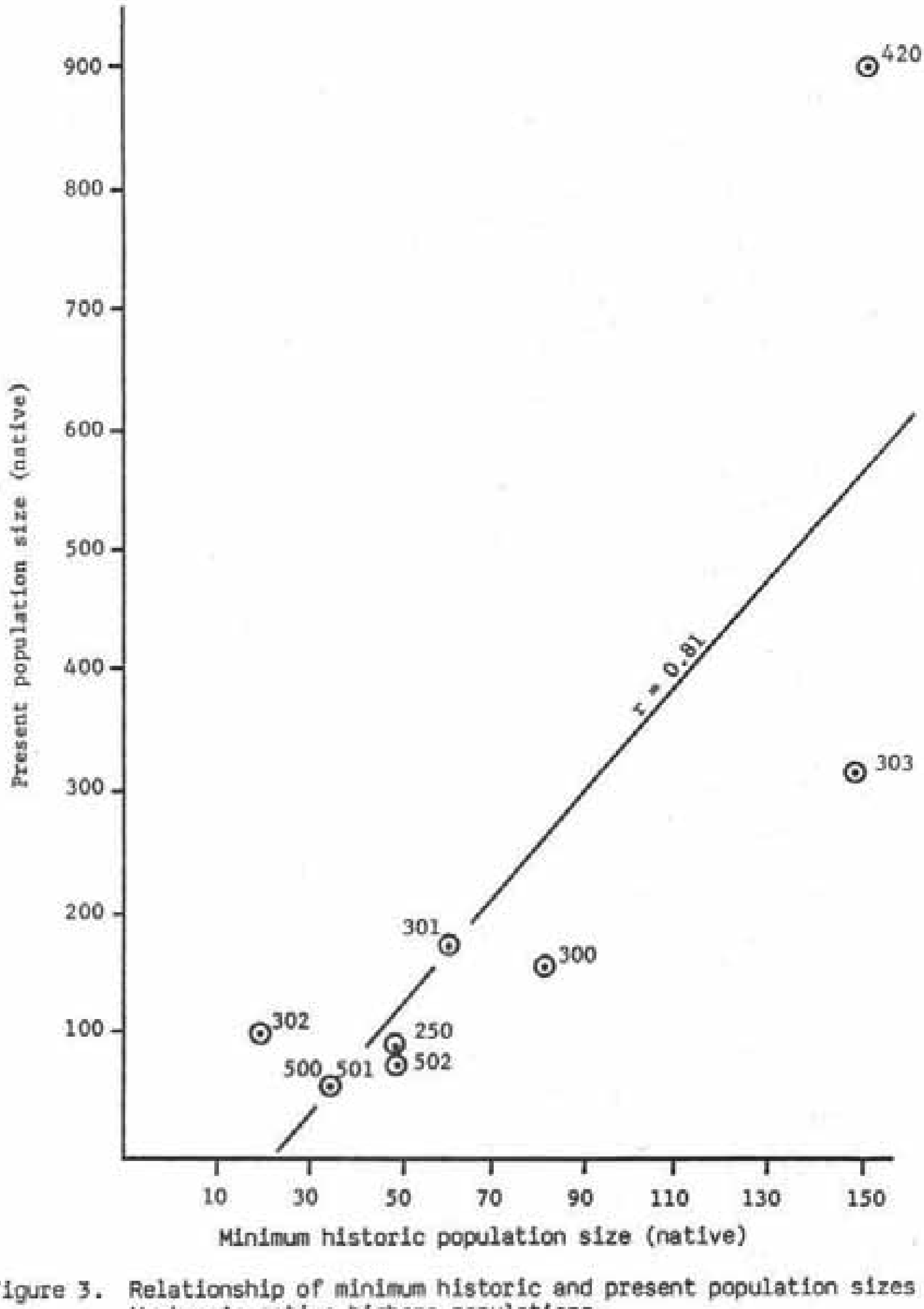

Figure 3. Relationship of minimum historic and present population sizes for Montana's native bighorn populations.

We hypothesize that differences in horn growth among native Montana bighorn populations can primarily be explained by genetics rather than nutritional differences. Most (six of nine) of these populations declined to 60 animals or less at least once during the first half of this century. During such low population periods, these herds were probably subjected to relatively high rates of inbreeding. This in turn may have affected ram horn growth in one of two ways. First, inbreeding may have reduced animal vigor which could result in decreased rates of horn growth for rams. Secondly, large horned rams may be more heterozygous than smaller horned rams. Because inbreeding increases the percentage of homozygosity, it would follow that there would be few large horned rams in an inbred population. Ryman et al. (1981) demonstrated that heterozygosity can be severely reduced in a short time in a population of 50 animals. Intensive harvest of males, such as occurred in most of these bighorn populations, would reduce the effective population size and further reduce genetic variability (Ryman et al. 1981). Population size bottlenecks have been suggested as the cause of low amounts of genetic variation in poulations of elephant seals (Mirounga angustirostris) (Bonnell and Selander 1974) and moose (Alces alces) (Ryman et al. 1977).

Native populations which have always maintained in excess of approximately 125 bighorns were probably not subject to inbreeding. Thus, a heterozygous population of relatively vigorous bighorns was maintained. These are the populations which are now characterized by rams with large horn volumes.

The hypothesis that horn growth differences among native populations is related more to genetic than to nutritional differences is further supported by the history of bighorns from two areas in Montana, Rock Creek and Thompson Falls. Both of these areas supported native bighorn populations that were characterized by small tightly curled horns (Berwick 1968, Brown 1974). When the native populations died out, they were replaced by bighorns from Sun River. Range conditions remained relatively unchanged. The resulting populations have rams with extremely large horn volumes (Rock Creek - 285 in^3, Thompson Falls - 212 in^3).

Geist (University of Calgary, pers. comm.) suggested that during population crashes, such as he observed in mule deer in Waterton Park, Alberta, only phenotypically inferior (i.e., small antlered) males survive. He further suggested that a similar relationship could be responsible for small horned rams occurring in Montana bighorn populations that declined to 60 or fewer animals at one or more times in their history. We do not feel that this suggestion adequately explains the phenomenon we observed for several reasons: 1) The Sun River sheep herd has probably "crashed" (declined to 150 animals) more often than any other Montana population with die-offs in 1924, 1927 and 1936 (Couey 1950). Yet horn growth for these bighorns remains excellent. 2) The surviving phenotypically inferior males would have the genetic potential that would allow their offspring to grow large horns when environmental conditions improve. Therefore, unless genetic change occurred during the crash, large horned rams would eventually reappear in the population. 3) During a mule deer population crash in Montana, nearly all bucks between the ages of 2 and 5 survived regardless of phenotypic expression (Mackie et al. 1980, R. J. Mackie, Montana State University, pers. comm.). Thus, population crashes do not always result in the loss of phenotypically superior males.

The Sun River sheep herd has ultimately been the source for all successful bighorn transplants in Montana. Thus, all transplanted populations are from what we consider to be genetically healthy stock. Since all transplanted populations are genetically similar, variation in horn growth among these populations must be related to habitat conditions.

It is not, however, surprising that winter range densities were not correlated with horn volumes for transplanted populations. Such a relationship could only be expected if all of these populations had reached equilibrium with their environments. This is generally not the case as most transplanted populations are apparently still increasing.

Among transplanted populations horn volumes are largest for the Rock Creek and the East Bitterroot herds. These are also the two most recently transplanted populations. The two oldest transplanted herds, the Wild Horse Island and Kootenai Falls populations, both have relatively small horn volumes for transplanted sheep. In fact, the mean cumulative horn volume for Wild Horse Island rams is not significantly ($p > 0.05$) different from that of Sun River rams, and the difference in horn volume between Kootenai Falls and Sun River rams is barely significant ($0.025 < p < 0.05$). It appears then that when sheep are put into a new and relatively unexploited habitat, the rate of horn growth is exceptional - far surpassing that of the parent stock. As the population expands, the rate of horn growth declines. Eventually, carrying capacity is reached and horn growth is reduced to a level similar to that of the parent stock with minor differences, due to differences in productivity between the ranges.

Horn volumes are not significantly ($p > 0.05$) different between Berray Mountain and Sun River bighorns. The Berray Mountain population is only 13 years old, yet horn volume is already similar to that of the parent stock. We speculate that because of the small size of the Berray Mountain area, as well as its relatively harsh winter conditions, carrying capacity has already been reached and the rate of horn growth has stablilized.

Apparently, transplants of 20-30 sheep can develop into genetically healthy populations because they come from heterozygous parent stock (i.e., Sun River). These sheep would have a relatively diverse genetic makeup. If conditions are such that the population can expand quickly, this diversity is maintained and a healthy population develops. If, however, the herd stagnates at only 50-60 animals, the population will eventually become more homozygous just as a native population would if it was at such a low population level for any extended period of time.

MANAGEMENT IMPLICATIONS

The genetic health of a bighorn herd is normally a factor that is not considered by a wildlife manager because data are seldom available. Yet, such information may be important to the survival of the herd as the following example illustrates.

Rock Creek, in western Montana, originally supported a native bighorn population, the history of which is well documented (Berwick 1968, Cooperrider 1969, Aderhold 1972). By the early 1900's, only eight bighorns were known to occur in the Rock Creek area. The population increased very slowly until 1965 when the herd was estimated at 175 animals. As we previously noted, rams from this herd were characterized by small tightly curled horns probably similar in volume to horns from other native populations that we have suggested were inbred. Indeed, Berwick (1968) demonstrated that the rate of inbreeding for the Rock Creek herd was relatively high. Between 1966 and 1969 this herd declined to only 10 animals and was for practical purposes extinct by 1974. Numerous reasons for the decline were cited including overgrazing by domestic stock, competition from large numbers of mule deer and encroachment on the winter range by human development. However, as we have previously mentioned, when the Rock Creek area was restocked with Sun River bighorns in 1975, the population thrived though range conditions had not improved substantially (Butts 1980). We suggest that a fundamental difference in ability to survive between the native and transplanted herds was genetically related. The inbred native population was unable to tolerate the stress of deteriorating habitat conditions, while the genetically healthy Sun River stock thrived under similar conditions.

Thus, inbred populations must be managed much more carefully than other bighorn herds. All efforts must be directed at minimizng stress for these populations whether that stress be from competition with native or domestic ungulates, or from human related activites such as mining, subdivisions, or even intensive studies by well-meaning biologists. We also suggest that horn growth can be used as one of the best indicators of when a tranplanted bighorn population reaches equilibrium with its forage base (i.e., reaches carrying capacity) by comparing horn growth of the transplanted herd to that of the parent stock. Of course, this comparison is only valid if range conditions for the two populations are reasonably similar.

We are presently planning to further test the hypothesis presented in this paper by introducing rams from a high quality population into a low quality herd - probably the Stillwater herd. Horn growth will continue to be monitored to determine the effects of this action. A better approach to determining the horn growth potential of various populations would be to keep captive rams on a high quality diet. If our hypothesis is correct, rams from the populations that are thought to be inbred would continue to grow smaller horns than rams from populations thought to be more heterozygous. Unfortunately, budget limitations will undoubtedly prohibit this approach.

LITERATURE CITED

Aderhold, M. W. 1972. The history, winter range, and current status of the Rock Creek, Montana bighorn sheep herd. Unpub. M.S. thesis. Univ. Montana, Missoula. 104pp.

Berwick, S. H. 1968. Observations on the decline of the Rock Creek, Montana, population of bighorn sheep. Unpub. M.S. thesis. Univ. Montana, Missoula. 245pp.

Bonnell, M. L. and R. K. Selander. 1974. Elephant seals: genetic variation and near extinction. Science 184:908-909.

Brown, G. W. 1974. Distribution and population characteristics of bighorn sheep near Thompson Falls in northwestern Montana. Unpub. M.S. thesis, Univ. Montana, Misssoula. 134pp.

Buechner, H. K. 1960. The bighorn sheep in the United States; its past, present and future. Wildl. Monogr. 4. 174pp.

Bunnell, F. L. 1978. Horn growth of Dall sheep. J. Wildl. Mgmt. 42(4): 764-775.

Butts, T. W. 1980. Population characteristics, movements and distribution patterns of the upper Rock Creek bighorn sheep. Unpub. M.S. thesis. Univ. Montana, Missoula. 120pp.

Cooperrider, A. Y. 1969. Competition between mule deer and bighorn sheep on Rock Creek winter range, Montana. Unpub. M.S. thesis. Univ. Montana, Missoula. 92pp.

Couey, F. M. 1950. Rocky Mountain bighorn sheep of Montana. Montana Fish and Game Comm. Bull. 2:1-90.

Egan, J. L. 1975. Montana's Rocky Mountain bighorn sheep. Montana Dept. of Fish and Game, Game Mgmt. Div., Helena. Mult. 68pp.

Geist, V. 1971. Montana sheep: a study in behavior and evolution. Univ. Chicago Press, Chicago. 383pp.

Heimer, W. E. and A. C. Smith. 1975. Ram horn growth and population quality, their significance to Dall sheep management in Alaska. Alaska Dept. of Fish and Game. Wildl. Tech. Bull. 5:1-41.

Klaver, R. W. 1978. A management oriented study of the ecology of bighorn sheep in the Bitterroot Mountains, Montana and Idaho. Unpub. M.S. thesis. Univ. Montana, Missoula. 112pp.

Mackie, R. J., D. F. Pac and H. E. Jorgensen. 1980. Population ecology and habitat relationships of mule deer in the Bridger Mountains, Montana. in Montana Deer Studies, Job. Prog. Rept., Montana Department of Fish and Game Fed. Aid Proj. W-120-R-11. Mult. pp. 96-139.

Ryman, N., R. Baccus, C. Reuterwall and M. H. Smith. 1981. Effective population size, generation interval and potential loss of genetic variability in game species under different hunting regimes. Oikos 36:257-266.

Ryman, N., C. Beckman, G. Bruun-Petersen and C. Reuterwall. 1977. Variability of red cell enzymes and genetic implications of management policies in Scandinavian moose (*Alces alces*). Hereditas 85:157-162.

Shackleton, D. M. 1973. Population quality and bighorn sheep (*Ovis canadensis canadensis* shaw). Ph.D thesis. Univ. Calgary. 226pp.

Simmons, C. A. and S. T. Stewart. 1977. Special big game surveys and inventory - Region 5. Job Prog. Rept., Montana Dept. of Fish and Game Fed. Aid Proj. W-130-R-8. Mult. 54pp.

_________. 1979. Special big game surveys and inventory - Region 5. Job Prog. Rept., Montana Dept. of Fish and Game Fed. Aid Proj. W-130-R-10. Mult. 96pp.

Stewart, S. T. 1975. Ecology of the West Rosebud and Stillwater bighorn sheep herds, Beartooth Mountains, Montana. Unpub. M.S. thesis. Montana State Univ., Bozeman. 130pp.

Wishart, W. 1969. Bighorns and little horns. Alberta Lands and Forests 12(3):4-10.

CONFERENCE DISCUSSION

Q. I have a comment. Have you ever seen what happens when a population crashes?

Ans. Not really.

Q. I've had the "good luck." Not with mountain sheep but with deer. I think it is revelant to this discussion; because you are suggesting that it may be inbreeding effects. I suggest that there is an alternate explanation and I will describe it for you and then you can judge for yourself. I studied deer in Waterton Park, Canada. My concern was, at that time, to find some sort of explanation for the great diversity in the phenotypes of bucks we have, some enormous monsters walking around, which of course, at the time I studied them during a population high, were the breeding bucks. Very, very busy, very actively engaged. I have the data on how long they lived subsequent to becoming breeding bucks. But during this study, which lasted 8 years, we had a number of serious winters and, lo and behold, we had a crash. At that time something became very apparent that previously I had not really noticed. I had noticed a large number of old bucks which were very small in body size and antler size. After the crash, there were no big bucks around except for one and he was a special case. After the crash what we had, and breeding, in that population when the population was at the absolute minimum, were the small-antlered, poorly grown individuals. In other words, we're talking here about natural selection. If the population crashes often enough, what you are going to have is, very frequently, the breeding of genotypes that are relatvely slow growing that produce slow growing individuals with relatively small horns. That's a possible explanation for what you have seen as well.

Ans. That would seem to be a possibility. Another thing I neglected to mention, as you talked about earlier, these small populations have been hunted since the middle 50's so not only are they small populations but we are constantly selecting against the larger males in these populatons. However, only small populations now have small horned rams despite some exceedingly heavy huntng pressure in larger populations.

Q. It sounds to me like you probably have two factors working here. These transplant areas are chosen because of the quality of their range. So the transplanted sheep could be showing large horn growth due to nutritional factors, whereas you might have some genetic factors in the native herds.

Ans. I'm sorry if I have confused you. My point was that the source of all transplanted populations, was from what we consider to be a genetically healthy population, i.e. Sun River. Any variation that we see in horn growth among them is forage-related or nutritionally related. It is only in the native populations that I feel that we really have any genetic changes. So we are talking about two different factors in the two types of populations. Horn growth in transplanted populations appears to be primarily nutritionally controlled while in native populations horn growth is probably more genetically controlled.

Q. Is horn growth for all transplanted herds greater than that of the herd they were transplanted from?

Ans. Except for the old transplants: Horn growth for the longest-term transplants is not statistically different from that of the source herd. The two oldest transplants are Wildhorse Island and Kootenai Falls.

Q. Sun River has some of your biggest rams. Aren't they natives?

Ans. Sun River and the northern end of Yellowstone National Park have the largest horn growth of our native herds.

Q. So they have a tremendous potential to get even bigger when they are moved out.

Ans. That's exactly right.

Q. Why, then, does horn growth vary among transplanted populations.

Ans. Capacities may be different in different areas. What I'm suggesting is that you can use horn size on these transplanted populations as an indicator of when you are reaching their carrying capacities. When the transplant first occurs horn growth is tremendous. But as the population grows toward the capacity of the range horn growth declines until eventually it is similar to that of the source herd.