VARIABILITY IN PHYSICAL AND SOCIAL MATURATION BETWEEN BIGHORN SHEEP (OVIS CANADENSIS CANADENSIS SHAW) POPULATIONS

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With only rare exceptions, variation between and within population parameters has not been included in most biological models. This is in spite of the importance of such sources of variation in the theorems of population genetics (Dobzhansky 1937) and principles of taxonomy (Mayr 1969). Chitty (1955) advanced one of the first hypothesis which included population variation and the role of Natural Selection in the regulation of small rodent populations. Investigations of the postulates of this hypothesis have recently been reviewed (Krebs et al. 1973) and alternative models for small rodent populations proposed (Anderson 1970). Studies of large mammals by Klein (1964, 1965, 1969) and Nievergelt (1966) and some species of birds in Scotland (Watson and Moss 1969, Watson and Miller 1971), have revealed variation in demographical, morphological and behavioral parameters correlated with differences in environmental conditions. Whereas hypotheses concerning small rodents have stressed the importance of genotypic variation, those regarding large mammals and birds have favored phenotypic variates.

Studies of bighorn sheep (Ovis canadensis) and stone's sheep (O. dalli stonei) by Geist (1971) led him to hypothesize that observed differences in behavioral and morphological characters were the result not of specific differences but differences in the bioenergetic regimes in which the two species lived. A further study by the present author (Shackleton 1973) of expanding and stable populations of bighorn sheep supported some of the postulates proposed by Geist (1971) in his hypothesis of population quality. The purpose of this presentation is to examine some of the potential implications of such observed variability in relation to some of the problems which may be faced in the management of mountain sheep.

METHODS AND STUDY AREAS

Two populations of Rocky Mountain bighorn sheep were intensively studied during a 2½-year period. The population from the Cascade Valley, Banff National Park, Alberta, was chosen from census records because it appeared to be relatively stable in numbers and composition. The second population was located at Radium Hot Springs, Kootenay National Park, British Columbia, as records indicated this group was increasing in numbers following a decline in the mid 1960's.

Four additional populations were studied in terms of their horn and skull development and represented expanding, stable, and possibly declining populations of the same species. Their locations were: National Bison Range, Montana; Wildhorse Island, Montana; Waterton Lakes National Park, Alberta; and the East Panther River population, Banff National Park.

Records of behavioral interactions were kept during all seasons for each of the two main study populations, and details of behavior patterns performed, the age-sex class of the actors and receivers, together with other pertinent information recorded. Data on horn and skull dimensions were obtained from material found in the field or from museum collections.

Further details of the study populations and methods employed are found in Shackleton (1973).

RESULTS AND DISCUSSION

Horns and Skulls

Growth and development of sheep from the six populations were compared through measurements of annual horn sheath growth and by adult skull dimensions. Differences in annual horn sheath growth have been found between populations in different demographic states in both mountain sheep (Geist 1971) and ibex (*Capra ibex*) (Nievergelt 1966), with largest sheaths coming from expanding populations. Dimensions of annual horn sheaths were significantly larger ($p < 0.05$) initially in Kootenay National Park rams (Fig. 1) and in females. Comparisons of similar data from the four other populations showed largest dimensions in expanding populations during the first 4 years of growth.

The apparent reversal in this difference,which at first indicated that expanding populations grew shorter horn sheaths, was shown by the present author (1973) to be due to the fact that each succeeding horn sheath covered the previous years growth, so that measurements made were only of relative annual growth, and that the reversal in difference was the result of the sheep from expanding populations reaching mature, adult size at an earlier age than stable or declining populations. Because they reached mature size earlier, relative differences in annual exposed horn sheath decreased with age after maturation.

The dimensions of adult male and female sheep showed a similar relationship to demographic condition of the population from which samples were drawn. Largest skull dimensions were found in expanding populations. These results were observed between all six populations.

Differences in growth of the two main study populations were attributed in part to considerable variation between them in the extent of vertical, seasonal migration that each population could make. The arguements for this relationship between extent of seasonal, altitudinal migration and food supply, and hence growth, followed the arguements originally proposed by Klein (1964) for Alaskan deer populations.

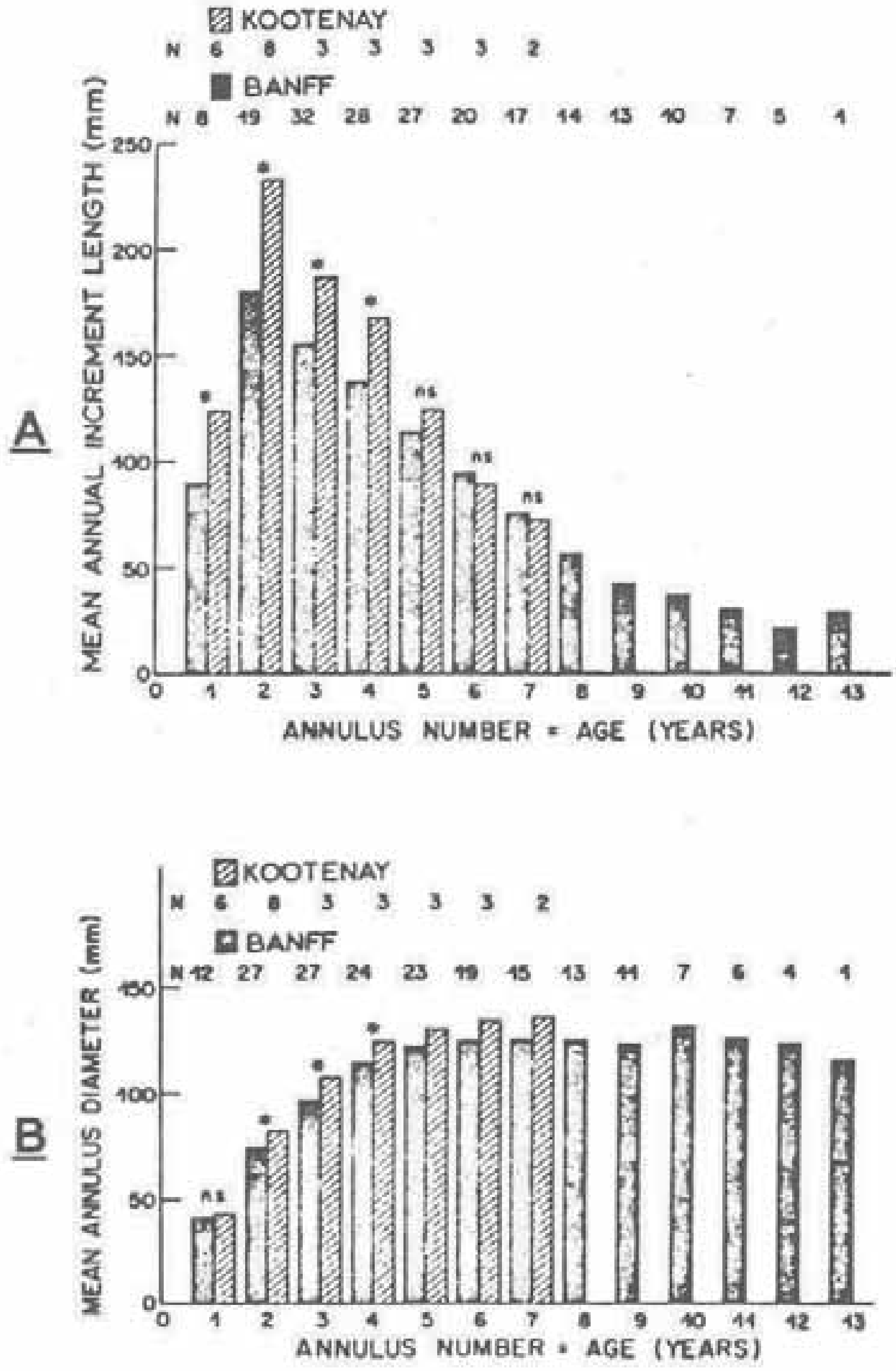

FIGURE 1. Differences in annual horn sheath dimensions for rams from Banff and Kootenay populations, showing (A) mean annual horn increment lengths, and (B) mean annual annuli diameters. Differences - (*) significant at 5% level of probability, (ns) not significant.

Social Behavior

In the general aspects of their social behavior, such as relationships of horn size and dominance status, and in choice of social partners, the two main study populations did not differ significantly. Variation did occur, however, in the age at attainment of social maturity.

Mature and juvenile behavior of rams are defined operationally by the relative performance frequencies of overt and display patterns (Geist 1971) and are illustrated in Table 1. When interacting with other rams, males from Kootenay of between 3 and 5 years of age (Class II) demonstrated a behavioral repertoire comparable to that of fully mature Banff rams aged 10 years and older (Class IV) (Table 1). On the other hand Banff rams of 3 to 5 years age (also Class II) were typically juvenile in their behavior.

During courtship of oestrus ewes during the rut, again Kootenay rams of 3 to 5 years age behaved as mature males (Table 1), instead of attempting more typical rape approaches observed in similar aged rams from Banff. In fact, only Class IV males from Banff were observed to court oestrus females, but in the case of Banff Class III rams this was probably the reduced accessibility to oestrus females due to the presence of larger Class IV's. This was not the case for juvenile Banff Class II rams.

This early attainment of social maturity on the part of young Kootenay rams was probably in part due to their advanced physical and physiological maturity over similar aged Banff males. And, secondly, to differences in population structure and composition which gave them greater access to females even during the rut and permitted them greater opportunities to develop a mature behavioral repertoire.

Life Expectancy

There were limited data from this study to suggest that mean life expectancy as measured by mean age at death of adult rams, was consistent with previous findings for mountain sheep by Geist (1971) and for ibex by Nievergelt (1966). These findings showed that in expanding populations adult males died at earlier ages than rams from stable or decling herds. Relationships between growth rates and life expectancy have been reported for a number of other vertebrate species including fish.

A mechanism involved for mountain sheep may be the energy expenditure in the rut which may deplete essential winter fat reserves that cannot be replaced after the rut. In expanding populations in which animals mature faster, they will also enter the rut at earlier ages and be exposed to this bioenergetic stress which may result in increased winter mortality. This aspect requires more detailed study.

CONCLUSIONS AND IMPLICATIONS

Taxonomy

The variability between the populations observed during this study

(TABLE a)		BANFF		KOOTENAY	
	Horn Class	IV	II	II	III
	Patterns				
MATURE	Kick	30.3*	8.6	28.3	25.2
	Twist	14.9	1.7	35.0	20.4
	Low Stretch	13.8	19.0	21.1	10.2
	Head High	6.0	15.5	3.0	3.2
	Sniff-Flehmen	4.9	0.0	1.2	3.1
	Mount	0.8	0.0	0.4	0.6
JUVENILE	Threat Jump	2.9	25.9	1.4	1.8
	Clash	2.7	8.6	3.0	4.1
	Horn Wrestle	2.6	8.6	0.0	3.2
	N!	1509	58	166	969

(TABLE b)		BANFF		KOOTENAY	
	Horn Class	III	IV	II	II
	Patterns				
RAPE	Chase-Approach	56.8	19.6	7.9	9.5
	Partial Mount	40.5	6.9	6.6	8.6
COURTSHIP	Twist	0.0	50.7	47.9	57.9
	Kick	2.7	5.4	13.2	9.1
	Sniff-Flehmen	0.0	5.1	4.8	1.4
	Mount	0.0	4.8	3.4	7.2
	Chest Push	0.0	3.5	1.3	2.3
	Bob	0.0	2.3	10.9	1.8
	Low Stretch	0.0	1.8	3.5	1.4
	N	37	969	1788	221

TABLE 1. "Mature" social behaviour of males is characterized by the performance of many display patterns, while "juvenile" behaviour consists mainly of overt patterns[1]. Pattern frequencies (percentages) performed by males a) towards males of smaller horn class size, showing differences between mature (Banff class IV) and juvenile (Banff class II) behaviour, and mature behaviour of Kootenay rams; and b) towards oestrus ewes to illustrate courtship (Banff class IV) and "rape" (Banff class II) approaches, and the mature courtship of Kootenay rams. Mountain sheep rams may be divided into 5 age-horn size classes; yearling males, and rams of horn class I (small) through to class IV's (large) as defined by their degree of horn development[27]. Due to hunting no rams of horn class IV were present at Kootenay. (*) - Percent frequencies; (!) Sample size. Note that percent frequencies do not total 100% because other pattern types were observed.

with regard to skull dimensions used by Cowan (1940) to separate the genus Ovis, was of the magnitude normally accepted for subspeciation. There is no justification in splitting such populations as were studied into trinomial groupings. These observations of interpopulation variability are in agreement with the observations of Baker and Bradley (Baker and Bradley 1965, Bradley and Baker 1967) of variation between the desert races of bighorn sheep. Similar variability has led Cowan and McCrory (1970) to reduce the number of subspecies of mountain goat (Oreamnos americanos), and Hutton (1972) to similar conclusions regarding wapiti (Cervus elaphus canadensis). Where a race of bighorn sheep or other mountain sheep is presently warranting special treatment and expenditure of management budgets, it's taxonomic status should be established.

Maturation Rates and Their Implications

It was shown that maturation rates of both physical and behavioral characters varied between populations, with maturation being advanced in expanding populations. It is suggested that there are certain implications from such advancement in hunted populations of this species.

Consider first a previously unhunted population, containing representatives of all age and horn classes, and that the population is at or near carrying capacity. If they are now subjected to hunting in which only mature Class IV rams are harvested, this could lead to a redistribution of available energy for the hunted population. It is suggested that all members of the remaining population will benefit from this increase in available energy, and that one result may be an increase in the growth rate of young males.

If there is no response by unhunted members of the population, rams will be harvested only as they enter the legal size limits, but if there is a response then they will be entering this size limit at an earlier age than they would if the population had remained unhunted. The implications of such a response are twofold. First one begins to remove even younger animals, and secondly and perhaps more importantly, one increases bioenergetic stress on these young growing animals. Rutting stress was previously felt only by mature males whose growth had essentially ceased, but these young animals will have the energetic stresses of the rut coupled with energy requirements for growth. It is, therefore, conceivable that over-winter mortality could thereby be increased.

A third factor to consider is that although males are physiologically capable of breeding ewes as early as 18 months or perhaps earlier, the long-term effects of such a change in population composition are not known.

Another hypothetical situation also arises from considerations of the behavior of mountain sheep and is related to dispersal or the lack of it. It would appear that in a number of populations in western North America problems are encountered with areas of adjacent and apparently favorable habitat remaining unused by certain populations. No apparent barriers are observed, nor any reason for their lack of use of such apparently favorable areas. Problems are also occasionally encountered where a group of sheep are transplanted to new areas, and formation of seasonal home range patterns may require long periods of time for establishment.

Under normal circumstances the seasonal home range movements of mountain sheep, coupled with their strong attachment between years to such areas, is the very antithesis of a dispersing species, and yet this is a group which dispersed during the Ice Ages over considerable distances during relatively short periods of time. Assuming that the ability to disperse has not been lost through Natural Selection processes, studies of mammals and birds would suggest that behavioral factors would be most likely implicated as dispersal mechanisms for a species such as mountain sheep. It would be further expected that the dispersal stage would occur in young sheep rather than mature animals.

Observations of mountain sheep show that males, for example, and occasionally females do leave their maternal home range groups. Young males may then join mature male bands and take up their home ranges as discussed by Geist (1971) with reference to the role of tradition in mountain sheep society. It should be noted that young males are not "thrown" out of female groups but leave when socially dominant. But this does not answer the question as to why or what mechanisms promote them to leave.

Certainly one may suggest that the resulting separation of the sexes may reduce competition between them within a population and hence allow females access to more favorable areas during their high energetic stress periods of late gestation and lactation. But again the question must be raised as to the mechanisms involved in dispersal, i.e., what factors promote it? It would certainly seem a reasonable hypothesis to suggest that changes which are brought about in a population's composition and age structure through hunting of adult or "legal size" rams would also affect the social processes of a population. Observations of the Kootenay Park population implied that the occurrence of herding similar to harem formation and not reported in other populations was the product of the population's composition and age structure. It is, therefore, concluded that a study of dispersal mechanisms of mountain sheep may be of value to the management and conservation of this group of animals.

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