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INTERIOR SHEEP STUDIES

By
Wayne E. Heimer

Final Report
Federal Aid in Wildlife Restoration
Projects W-17-8, W-17-9, W-17-11, W-21-1, and W-21-2
Job 6.12R

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FINAL REPORT (RESEARCH)

State: Alaska

Cooperator: Wayne E. Heimer

Project Nos.: W-17-8, W-17-9, W-17-11, W-21-1, W-21-2

Project Title: Big Game Investigations

Job No.: 6.12R

Job Title: Dall Sheep Body Condition and Nutritional Profile

Period Covered: July 1, 1975 through June 30, 1981

SUMMARY

A comparative study of a very high and a very low quality sheep population was conducted to test the hypothesis that the differences in quality among sheep populations result from differences in the quality of the range. Differences in population quality indicators indicated the populations are different in many respects. The hypothesis was tested by comparing the nutritive value of summer food plants, differences in plant composition of the diets of each population, the nutritive quality of rumen contents in early and late winter, and total body composition. Total body composition was measured by homogenizing the bodies of collected ewes and analyzing the homogenates to determine body percentages of fat, protein, water, and bone in the high- and low-quality groups at peak condition (before the rut) and at poorest condition (at the end of winter). It was found that diets differed between the population groups, but no differences in energy storage or utilization were discernible by the techniques applied. Consequently, the hypothesis that quality differences are caused by differences in energy availability was rejected. The simplest hypothesis consistent with observed data may involve genetic selection for differing quality groups.

Key words: body condition, Dall sheep, nutrition.

CONTENTS

BACKGROUND

In 1971, Geist proposed the "Quality Hypothesis" (now called the Dispersal Theory, Geist 1979) which formalized the common observation that not all populations of wild mountain sheep exhibit similar horn, body size, and growth rates. Wild sheep investigators have often speculated that nutrition is the primary cause for these size/age characteristics. Shackleton (1973) and Horejsi (1976) documented the phenomenon of population differences in bighorn sheep (*Ovis canadensis*), and Heimer and Smith

(1975) reported similar differences in Dall sheep (*Ovis dalli*) populations with respect to ram horn growth. Many hypotheses have been proposed to explain these differences, but nutritional considerations predominate. Simply stated, the common hypothesis is: "Since some populations of wild mountain sheep are more vigorous than others, it must be because they eat better than others." Extending this hypothesis to the classic concept of population limitation through nutritional carrying capacity, wildlife managers have commonly speculated that low-quality populations are at or above nutritional carrying capacity while those of higher quality are well below carrying capacity.

The purpose of this study was to gather comparative nutritional data from 2 Alaskan Dall sheep populations on the extreme ends of the population quality spectrum and to test the hypothesis that population quality is a function of energy availability.

OBJECTIVES

To determine the quality of forage available to, and seasonal body composition of, 2 sheep populations of greatly differing population quality.

To test the hypothesis that population quality is determined by range resource (energy) abundance.

PROCEDURES

Study Populations

Two Dall sheep population groups of vastly different quality were studied. Heimer and Smith (1975) identified a very low quality group (ARE I from Dry Creek) as well as a very high quality group (ARE III from the Tok-Robertson River area) in the eastern Alaska Range. These groups are separated by a distance of about 320 km (Fig. 1). Studies by Heimer and Smith (1975) grouped sheep by physiographic areas and ranked them according to ram horn growth, a prime characteristic of population quality (Geist 1971). Other indicators of population quality gathered included lamb production and survival, recruitment, population density, age structure, fetal weight, and suckling duration. Differences in these parameters between populations were analyzed for significance by a number of statistical tests.

Study Rationale

Energy availability, storage, and utilization were selected as indicators of range quality because they are the most suitable common denominators for comparing the food resources available to these groups of sheep. However, calorimetric analyses were not readily adaptable to this study. Amounts of energy available from forage were inferred from the range resources available to sheep and their subsequent storage as fat and protein.

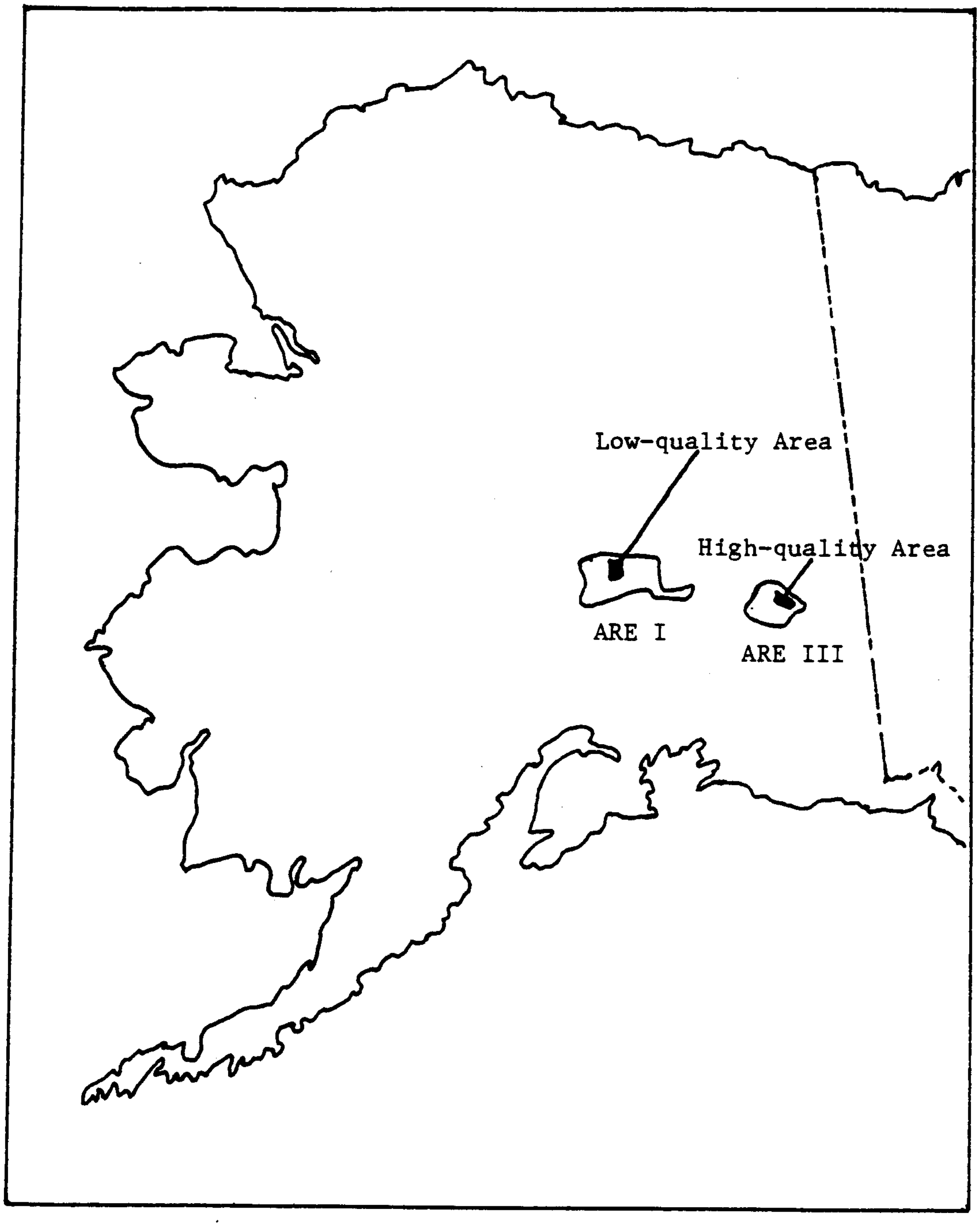

Fig. 1. Study area location within Alaska. Outlined areas are from Heimer and Smith (1975) horn growth work. Shaded areas are study units where data were gathered and ewes were collected.

Range Resources

Species Composition of Diets:

Washed rumen contents were sorted into identifiable plant groups to characterize the winter and spring diets of both populations. After washing, plant fragments were separated by plant group, and the percentage volume of each group determined by water displacement. The following plant groups were classified: grass and sedge leaves and stems, woody stems and associated green leaves, leaves of *Dryas octopetala* and *Salix* spp., lichen and moss, and the base parts of *Oxytropis* spp. Differences in utilization of plant groups between populations were tested using Student's *t* test for unpaired means where variance is unknown (Zar 1974).

Nutritive Quality of Summer Food Plants:

Relative amounts of energy available on summer range were inferred from previous studies of nutritive quality of selected food plants gathered on a low-quality area near ARE I (Whitten 1975) and a high-quality area in ARE III (Winters 1980).

Protein and Fiber Content of Washed Rumen Contents:

Another way of estimating the relative energy available to each group studied was analysis of the nutritive quality of food plants selected by the sheep on each range. This was done by analyzing rumen samples from Dall ewes collected in early November just before the rut and in early April. Rumen samples were mixed, washed, oven-dried at 65 C for 24 hours, and proximate analyses of nutrients were performed using Van Soest's method (1963).

Body Composition

Sampling Intensity:

In the low-quality group, 9 ewes (3.6%) were collected from an estimated population of 250 ewes for the early winter sample, and 13 (5.4%) ewes were collected from the same population in spring.

In the high-quality population, sampling intensity was 15 of 500 ewes (3%) in early winter and 12 of 485 (2.5%) in spring.

Collection and Preparation:

Ewes were shot at random and transported by helicopter to the laboratory where contour length, girth, and height at the shoulder were measured. Animals were then weighed, necropsied, examined to estimate age, and prepared for gross body composition determinations. Viscera were removed, weighed, frozen, and then stored for later analysis. Each carcass was divided into halves by median sagittal section with a carpenter's saw. One half was weighed and frozen for subsequent fat, water, and protein determinations; the other half was weighed and boned to determine skeletal weight. Bones were either cleaned and dried, or boiled, cleaned, and dried before weighing. Hooves and horns were not included.

Frozen carcass halves and viscera were ground separately using an Autio 801 B grinder provided by the reindeer research group at the University of Alaska. Excluding horns and hooves, these halves were cut into small chunks approximately 15 cm across with a band saw. Pieces were then randomly mixed and fed through the large grinder, using a cutting head with 2 cm openings. Ground material was then mixed by hand and run twice through the large grinder. A high-speed chopper with cutting head openings of 0.7 cm was then used to complete homogenization. The homogenate was run through this machine, mixed by hand, and again passed through the machine. Five subsamples (approximately 50 gm each) were then randomly selected from the homogenate as it was stirred to form a composite carcass sample of about 250 gm. Visceral organs and fetuses were homogenized by 3 passes through the high-speed chopper with hand mixing between each pass. Visceral composite samples were taken in the same manner as carcass homogenates.

Analysis:

Homogenized samples were then sent to a commercial laboratory for analyses of protein, fat, and water content. Crude protein was determined from Kjeldahl total nitrogen, lipids were gravimetrically determined by ether extraction, and water by evaporation. Composition of body components was calculated as follows using female No. 4565 as an example.

Calculations:

Basic Data

Accession No. 4565 female, age 18 months, collected 10/29/76

Total live mass - 42.70 kg
Rumen-Reticulum fill - 5.68 kg
Other gut contents - 0.75 kg
One-half carcass at analysis - 14.10 kg
One-half carcass fresh weight - 16.40 kg
Bones in one-half carcass - 1.94 kg
Visceral mass (exclusive of alimentary contents) - 3.46 kg
Visceral homogenate composition - 54% water, 22% fat, 22.5% protein
Carcass homogenate composition - 15.2% fat, 11.1% protein, 33.8% water

Calculations

14.10 kg carcass at analysis x 0.152	=	2.14 kg fat
14.10 kg carcass at analysis x 0.111	=	1.57 kg protein
One-half total bone mass	=	1.94 kg bone
		5.65 kg nonwater materials

5.65 kg of nonwater material subtracted from the fresh carcass weight of 16.4 leaves 10.75 kg water or 65% water in the fresh carcass

Likewise:	3.46 kg viscera x 0.540	=	1.87 kg H_2O
	3.46 kg viscera x 0.214	=	0.74 kg fat
	3.46 kg protein x 0.225	=	0.78 kg protein

Summing up:	Sampled body mass	=	36.19 kg as below
	2 x 10.75 kg H_2O	=	21.50 kg in carcass
	2 x 2.2 kg fat	=	4.28 kg in carcass
	2 x 1.57 kg protein	=	3.14 kg in carcass
	2 x 1.94 kg (1/2 bones)	=	3.88 kg bones
	1.87 kg H_2O in viscera		
	0.74 kg fat in viscera		
	0.78 kg protein in viscera		
	36.19 kg total mass		

Percent of sampled body by component equals:

Water - 64.6%
Fat - 13.7%
Protein - 10.8%
Bone - 10.7%

Reconstruction of body as a check on calculations: live mass = 42.7 kg. Subtracting the mass of 36.19 kg leaves 6.51 kg, and subtracting the mass of rumen/reticulum contents of 5.68 kg leaves 0.83 kg. This mass, minus gut contents of 0.75 kg, leaves 0.08 kg error, or an error of 0.2%.

RESULTS AND DISCUSSION

Range Resources

Botanical Composition of Diets:

The null hypothesis, that sheep from the different areas sampled in this study eat the same plants, was rejected. The study groups had different winter diets (Tables 1, 2). It appears that even within the high-quality study area, plant selection may be quite season- and location-specific (Appendix A). The differing frequency of *Oxytropis* sp. base parts in high-quality sheep rumens from different collections within the high-quality study area (ranging from a high mean of 21% at Tushtena Pass in November 1976 to a low mean of 3% from Clearwater Creek in November 1978) indicates caution should be used in extrapolating plant selection by sheep from area to area. The virtual absence of *Oxytropis* sp. from rumens collected in the low-quality study area demonstrates the hazards of characterizing "Dall sheep diets," even within a single mountain range. Sheep select different plants on different ranges.

Table 1. Composition of November diets (from washed rumen contents) of high- and low-quality Dall sheep populations in the Alaska Range.

Plant group	High-quality % (N = 14)	Low-quality % (N = 9)	Significant difference (P = 0.05)
Grass and sedge leaves and stems	56	74	yes
Oxytrope base parts	15	"trace"[a]	yes[a]
Woody stems and green leaves	19	15	no
Willow and dryas leaves	10	4	yes

[a] Only 2 low-quality sheep had measurable amounts (1% and 3%) of this plant. Since it accounted for 15% of rumen fill in high-quality sheep rumens and was quantitatively absent in low-quality rumens, it is presumed to be significantly more frequent in rumens of high-quality sheep.

Table 2. Composition of April/early May diets (from washed rumen contents) of high- and low-quality Dall sheep populations in the Alaska Range.

Plant group	High-quality % (N = 17)	Low-quality % (N = 11)	Significant difference (P = 0.05)
Grass and sedge leaves and stems	50	61	no
Oxytrope base parts	24	trace[a]	yes[a]
Woody stems and green leaves	5	26	yes
Willow and dryas leaves	9	6	yes

[a] Only 2 low-quality sheep had measurable amounts (5% and 8%) of this plant. Since it accounted for 24% of rumen fill in high-quality sheep rumens and was quantitatively absent in low-quality rumens, it is presumed to be significantly more frequant in rumens of high-quality sheep.

Sheep from the high-quality group not only had more base parts from *Oxytropis* sp. in their rumens, but significantly greater amounts of moss and lichen ($P = 0.05$). Probably as a result of selecting these low-growing plant forms, sheep also had a significantly greater incidence of *Dryas* sp. and low-growing willow species, *Salix arctica* and *Salix reticulata*.

The other significant difference between the high- and low-quality diets is apparent in comparisons of the role played by woody stems and green leaves associated with them, usually *Vaccinium* spp. or *Ledum palustre*. There was no significant difference in use of this plant group in high- or low-quality diets in early winter. However, in spring, the high-quality individuals appear to shift their diet toward *Oxytropis* sp. base parts and away from woody stems and leaves (Tables 1, 2). Ewes of the low-quality group appeared to shift dietary preference from grass and sedge leaves and stems to woody stems and their green leaves. Cranberry, *Vaccinium vitis-idaea*, was the most common woody plant selected in spring; berries as well as leaves and stems were eaten.

It is not known if a caloric advantage results from these shifts in food selection. Analysis of forage plants should reveal the nutrient quality for both summer ranges, and the nutrient quality of rumen contents should reveal any effects in changing diets.

Nutritive Quality of Summer Food Plants:

Whitten (1975) and Winters (1980) gathered data on nutrient values for summer plants from low- and high-quality sheep ranges. Both investigators emphasized crude protein as an index to forage quality, stating this characteristic was important because ruminants can normally use all forage nitrogen for protein synthesis. They also reported values for calcium, phosphorus, and magnesium. Plants from both areas showed typical changes with advancing maturity. Crude protein and phosphorus decreased with advancing maturity, and calcium increased.

Winters (1980) used these findings to compare Whitten's data from the low-quality area with his data from the high-quality area (data gathered during summers 1974, 1977, and 1978, respectively). The date of shrub leaf emergence in each study site was identified by Winters as the beginning of the growing season. He also applied the correction factor of 1 day/25 m for altitudinal differences suggested by the observations of Hopkins (1920) and Costello and Price (1939).

Once the nutrient values from the high-quality area in 1977 and 1978 were standardized with those of the low-quality area in 1974, Winters ran statistical comparisons using the Mann-Whitney U-test (Conover 1971). He found no significant differences ($P = 0.05$) between the 2 areas using 4 nutrients and 12 plant species which were important for, and common to, both sheep groups. Winters (1980) concluded there were no significant differences in the nutrient quality of forage plants supporting high- and low-quality populations during summer.

Protein and Fiber Content of Washed Rumen Contents:

In addition to the absence of significant differences in nutrient quality of summer forage plants, there was no significant difference in the protein or fiber content of washed rumen contents from both populations collected on winter ranges (Table 3).

Funding after 1976 limited these analyses to protein and lignin determinations. Crude protein and lignin were selected because protein is an indicator of general forage quality (Deitz 1970). Lignin was selected because it is indigestible and was presumed to be an index of plant material ingested but of no use to the sheep.

Within each population, the protein and lignin content of forage plants selected by sheep was significantly different ($\underline{P}$ = 0.05) between early winter and spring. The low-quality sheep selected plants with more lignin as well as more protein in April. High-quality ewes also selected plants with more lignin in April ($\underline{P}$ = 0.05), but showed no difference in the percentage of protein in contents from November and April rumens (Table 3 and Appendix B).

Comparisons of April and November rumen contents between the high- and low-quality populations showed no differences ($\underline{P}$ = 0.05) in protein or lignin content. Thus, while there were differences in nutritive content of plants selected within each area, there was no significant difference between high- and low-quality diets during the same season. It appears that both groups of sheep consumed plants with higher lignin content, a presumed indicator of low food quality in spring. However, the higher lignin content could have resulted from ingesting woody stems along with their green leaves, presumably increasing food quality. These indicators suggest there is no nutritional advantage to living in the area which produces high-quality sheep. However, other nutrient components of forage must be evaluated before concluding there is no nutritional advantage in grazing the high-quality area between November and April.

The Van Soest (1963) analysis of foodstuffs provided another index to nutritional quality of forage. During this procedure, dried plant matter is first extracted with neutral detergent to remove soluble cell components. The remaining fiber is later analyzed for cellulose, hemicellulose, structural nitrogen, ash, and lignin. The soluble components (first extracted by neutral detergent) are 98% usable by the ruminant. Values for cell soluble fractions from washed rumen contents of high- and low-quality sheep at the beginning and end of winter are presented in Table 3. There are no significant differences ($\underline{P}$ = 0.05) among any of these values for soluble cell components. However, soluble cell components are rapidly removed from the rumen, so it may be specious to consider values for cell soluble materials from washed rumen contents. Still, the evidence suggests that no

Table 3. Chemical composition of rumen contents from high- and low-quality sheep populations. Samples collected in 1976-78 in Alaska Range.

Study area/ time	Lignin (%)	Cell solubles (%)	Crude protein (%)
Low-quality/Nov	15	21.5	6
High-quality/Nov	20	25.0	8
Low-quality/Apr	20	22.6	9
High-quality/Apr	23	22.0	10

nutritive difference exists between the 2 ranges. Any differences present were not detected by my approach. Plant species known to be important to sheep on both winter ranges should be clipped in November and April. Analyses of these plants for the same nutrient components measured in rumen contents should clarify this issue.

The overall consistency of these forage nutrient component values considered with the uniform nature of plant nutrient quality reported by Whitten (1975) and Winters (1980) lead me to conclude high-quality Dall sheep derive an insignificant nutritional advantage from their range compared with low-quality Dall sheep, even though botanical composition of their diets differ.

Body Composition

Ewe Body Condition:

Body condition of ewes was selected as another indicator of available energy on high- and low-quality ranges. Collection periods were designed to give maximal information on the contribution of summer as well as winter ranges. Individuals were collected in early winter just prior to rut to investigate the nutritional contribution of summer ranges to animal preparedness for winter. Weather during this time is generally stable enough to allow consistent collection dates from year to year, yet animals have not been subjected to a serious restriction of food intake by snow accumulation nor a great deal of winter stress. Hence, they should be at their peak physical condition with maximal quantities of stored energy.

Spring collections were made in early April, before segregation into lambing groups could bias possible pregnancy rate determinations. This time period also coincides with the low point in ewe body condition before animals benefit from emerging vegetation in early summer. In early April, snow begins to melt on the south-facing slopes, and sheep often forage along the edge of the alpine habitat where cranberries and other green vegetation are exposed. Lignified cranberry stems and their associated green leaves and berries become a more important dietary component at this time.

As sheep of both sexes are subjected to winter stress, there should be marked changes in relative body composition. Stored fat and protein should decrease and body water should increase proportionately as other stores diminish (Kleiber 1975). In the case of ewes, bone mass should also decrease if sufficient minerals are not present in the diet to support the demands of maintenance, lactation, and gestation. Consequently, the percentages of fat, protein, water, and bone in ewe carcasses were measured to assess general body condition and infer the relative amount of stored energy used and not replaced from winter ranges. If either range offered a nutritional, climatic, or physiographic advantage over winter, it should be reflected in decreased weight, fat, and protein losses as well as in smaller attendant increases in body water percentage. Fetuses from both groups were also analyzed to determine whether energy store differences could be related to fetus viability potential. Data gathered on body composition of ewes collected are presented in Appendix C.

Since this approach to the study of wild ungulate-range relationships has not been widely applied, its validity should be scrutinized carefully. For example, the technique should be capable of identifying animals having obviously different nutritional status with all other factors equal before attempting to quantify differences which may be more subtle. This question was answered by comparing spring-collected pregnant and nonpregnant ewes of the low-quality group. Fortunately, the low-quality populations exhibited alternate-year reproduction and extended lactation (Heimer 1978). These conditions provided approximately equal numbers of pregnant and nonpregnant ewes. Since all ewes of breeding age were pregnant in the high-quality population, this test was not conducted for those sheep.

Weight measurements showed that pregnant ewes have greater body weights than nonpregnant ewes ($\underline{P} = 0.05$), other things equal Table 4). The mean weight difference of 7.6 kg is not simply due to the presence of the fetus and its life support systems. The mean mass of uterus, membranes, fluids, and fetus is 3.6 kg less than the mean difference in body weight. There was no significant difference ($\underline{P} = 0.05$) in age, but the nonpregnant group averaged a year older than the pregnant ewes. Since sheep grow throughout their lives, this group should have been heavier than the pregnant ewes. It has been shown in domestic cattle that pregnancy alters energy metabolism significantly, particularly by shortening rumen turnover time which should lead to increased ability to process winter forage and enhance caloric extraction from poor winter food (Flatt et al. 1967).

Differences in body weight, then, should be reflected in greater stored energy reserves in pregnant than nonpregnant ewes. Comparisons of body condition parameters show that pregnant ewes have higher percentages of fat and protein as well as less total body water ($\underline{P} = 0.05$) (Table 4). This indicates pregnancy is not a stress, but an advantage in maintaining body condition over winter, given sufficient availability of winter forage to take advantage of increased efficiency in energy metabolism.

If the weight difference due to pregnancy is subtracted from the difference in mean weights, the total difference becomes nearly accountable as shown below.

Difference in mean weights	=	7.6 kg
Minus:		
Mean mass of uterus and contents	=	4.0 kg
Mean greater fat mass	=	1.6 kg
Mean greater protein mass	=	1.8 kg
		0.2 kg error

Table 4. Body composition of pregnant and nonpregnant ewes collected from the low-quality study group in spring at Dry Creek, Alaska Range.

Component	Pregnant	Nonpregnant	Significant difference (P = 0.05)
Age (months)	78	91	yes
Body weight (kg)	51.2	43.6	yes
% water	67.2	72.0	yes
% fat	9.3	6.2	yes
% protein	14.7	13.5	yes
% bone	8.8	8.4	no

This 200 gm error factor is only 2.6% of the difference or 0.4% of the mean pregnant body mass. Hence, it appears the body composition approach to range relationships has, in this case, a very low error and is able to discriminate reliably between pregnant and nonpregnant ewes taken from the same range on the same collection date.

This analytical technique also discriminates between nonpregnant ewes taken from the same population at the beginning of winter and in spring. This comparison was made with data from the low-quality group since no nonpregnant ewes were collected from the high-quality group in spring. These comparisons revealed no significant age difference between early winter and spring specimens ($\underline{P}$ = 0.05) (Table 5). Early winter weights were significantly ($\underline{P}$ = 0.05) greater than spring weights. Early winter fat and protein content were greater than in spring ($\underline{P}$ = 0.05), and early winter water content was lower ($\underline{P}$ = 0.05) than water content in spring. There was no significant difference in percentage bone weight. The fall mean was 8.9% and the spring, 7.8%.

Comparisons between the low- and high-quality sheep populations revealed no significant differences in body components (Table 6 and Appendix C). Percentage changes for high- and low-quality ewe groups over the course of winter are consistent for body weight, fat, and water. There are, however, noticeable differences in the percentage of protein and bone lost from the maternal carcass over winter. The only explanations which come to mind for this seeming aberration in an otherwise consistent pattern are analytical errors or greater maternal bone and protein transfer to the developing fetus in the high-quality population. Analysis of fetal size and composition may help to resolve this question.

Fetal Condition:

Analysis of fetal homogenates showed no significant difference in percentages of fat, protein, or water. However, fetal weights from the high-quality study group were significantly greater ($\underline{P}$ = 0.05) than for the low-quality study group (Table 7 and Appendix D).

Fetuses from the high-quality study group were heavier, but there was no significant difference in body weights of the ewes carrying fetuses (in fact, high-quality ewes had lower mean body weights). Apparently, high-quality ewes can devote more resources to fetal growth than low-quality individuals. Calculations from the data in Table 6 showed the mass of protein lost over winter in the low-quality group averaged 2 kg. Protein loss averaged 3.3 kg in the high-quality group. Similar calculations for bone show a difference of 1 kg between populations. Since fetal mass for the high-quality group is greater by an average of 0.6 kg/fetus, an efficiency of conversion from ewe to fetus of at least 30% by mass would totally account for the increased losses of protein and bone in high-quality ewes.

Table 5. Body composition of nonpregnant ewes collected from the low-quality study group in early winter and spring at Dry Creek, Alaska Range.

Component	Winter	Spring	Significant difference ($\underline{P}$ = 0.05)
Age (months)	95.1	91	no
Body weight (kg)	59.4	43.6	yes
% water	62.4	72.0	yes
% fat	14.3	6.2	yes
% protein	14.4	13.5	yes
% bone	9.1	8.4	no

Table 6. Mean age, body weight, and component composition of ewes from high- and low-quality Dall sheep populations in Alaska Range.

Component	Low-quality	% change	High-quality	% change	Significant difference (P = 0.05)
Age (months)					
early winter	83.5	-	63.3	-	no
spring	83.5		77.5		no
Body weight (kg)					
early winter	61.0	16(-)	57.9	17(-)	no
spring	51.3		48.3		no
% fat					
early winter	14.3	45(-)	14.3	43(-)	no
spring	7.9		8.1		no
% protein					
early winter	14.8	7(-)	15.0	21(-)	no
spring	13.7		11.9		no
% water					
early winter	62.1	12(+)	61.8	14(+)	no
spring	69.8		70.7		no
% bone					
early winter	9.1	4(-)	9.8	22(-)	no
spring	8.7		7.6		no

Table 7. Body weight and composition of fetuses[a] from high- and low-quality Dall sheep ewes in the Alaska Range.

Component	Low-quality	High-quality	Significant difference (P = 0.05)
Body weight (kg)	2.2 (N = 5)	2.8 (N = 7)	yes
% fat	8.3	10.4	no
% protein	17.0	17.2	no
% water	73.8	70.1	no

[a] Raw data are given in Appendix D.

The idea that larger lambs are produced by mobilization of body components among high-quality sheep seems to argue that energy contribution by their ranges is at least somewhat greater than that of low-quality populations. Since the body composition data are generally consistent and the washed rumen contents show no nutritive differences, it is probable that any caloric advantage comes from summer range. Certainly, the data on summer nutritive quality of plants selected are the weakest I have used in this approach to the problem, since they were gathered some 4 years and 70 km apart from the sample areas.

Still, the argument that range is inherently better because fetuses are somewhat larger may be specious. Density of the low-quality populations is 1.65 times that of the high-quality groups. Yet individual fetal mass for the high-quality groups is only 30% greater than low-quality fetuses. Consequently, it seems unlikely that the high-quality area will produce a significantly greater biomass of lambs in equally severe or benign seasons than the low-quality group. Further support for this argument comes from countable lamb numbers reported for each population. Spring 1981 was one of unusually high lamb production for both groups. The low-quality group produced 422 lambs and the high-quality group, 346. Clearly, more individuals (76) were produced by the low-quality group, a fact of great importance to wildlife managers. If lamb mass on the high-quality population were greater for each lamb by the same fraction that in utero fetuses were heavier in the high-quality population, the greater biomass produced in the high-quality population would come to about 4%.

CONCLUSIONS

No differences were found in the nutrient quality of summer food plants consumed by high- and low-quality study groups (Whitten 1975, Winters 1980). Proximate analysis of washed rumen contents indicated there is no nutritional advantage available to ewes wintering on the high-quality ranges. These findings lead to failure to reject the null hypothesis: there is no difference in range resources. This conclusion is supported by data on ewe body condition. Body composition techniques applied here were able to show differences between low-quality sheep from winter to summer and declines in general body condition manifested by depletion of stored energy. Differentiation between pregnant and nonpregnant ewes from the same study group was also accomplished. Yet, these same techniques failed to demonstrate any differences in body composition between high- and low-quality sheep during either early winter or spring. On the basis of these results, I conclude that differences in quality detailed in Table 8 are not results of nutritional advantages enjoyed by the high-quality study group.

Failure to identify differences in stored reserves at the end of summer is interpreted as evidence there is no significant difference in net energy stored by sheep on summer ranges. In

Table 8. Indicators of quality of high- and low-quality Dall sheep populations in the Alaska Range.

Parameter	Low-quality	High-quality
Ram horn growth quality index[a]	14th of 18	4th of 18
Mean lamb production[b]	55 lambs/100 ewes	65 lambs/100 ewes
% lamb survival to yearling age[b]	51%	54%
Mean yearling recruitment[b]	26 yearlings/100 ewes	32 yearlings/100 ewes
Near-term fetal weight	2.2 kg ($\underline{N}$ = 7)	2.8 kg ($\underline{N}$ = 8)
Mean suckling duration	15 sec ($\underline{N}$ = 139)	14 sec ($\underline{N}$ = 60)
Mean age in collected sheep	91 months ($\underline{N}$ = 24)	66 months ($\underline{N}$ = 17)
Summer range density	3.5 sheep/km^2	1.5 sheep/km^2
Winter range density[c]	5.3 sheep/km^2	2.0 sheep/km^2
Habitat character[d]	gentle hills short drainages elevation relief = 830 m glaciers absent abundant vegetation	steep hills long drainages relief = 990 m glaciers present sparse vegetation

[a] Horn quality index is calculated by system of Heimer and Smith (1975).
[b] See Appendix E.
[c] See Appendix F.
[d] See Heimer (1975).

addition, failure to identify significant differences at the end of winter indicates the net balance between winter range energy contribution and habitat energy requirements for both groups are equivalent.

These conclusions raise the question of whether the definition of population quality is sufficient. Certainly, genetics could play a role which we fail to appreciate, and other techniques may be applied which might correlate observed quality differences with more subtle nutritional differences. Nevertheless, examination of the concepts of population quality and carrying capacity is worthwhile. Many wildlife managers have inferred that low-population quality is indicative of a population at or above carrying capacity. Conversely, high-quality populations are usually considered to be well below carrying capacity and exhibit a complex of characteristics which indicate to the wildlife manager that all is well between the resource base and the sheep population. These include high productivity, high survival rates, and physical characteristics generally related to nutrition in other species.

In this study only half of the characteristics which classically define populations well below carrying capacity correctly predict the quality status of sheep populations (Table 9). These inconsistencies not only force reexamination (and perhaps rejection) of the hypothesis that quality is determined by resource abundance. They also demand careful application of population quality determinations to population management. Is quality a true population syndrome or simply a complex of population characteristics which may not necessarily be related?

MANAGEMENT RECOMMENDATIONS

Wildlife managers frequently express concern that sheep populations which exist at high density may be damaging their range and should be reduced in number, so winter forage available per individual will be increased and population declines averted. However, information on the relationship between carrying capacity and population dynamics should be collected before such manipulation is attempted. The relationship between population dynamics and carrying capacity has been demonstrated for some species. Still, it can be seen from these data that a misjudgment would be made by assuming this low-quality population shows signs of "overgrazed" range and hence is in need of reduction to forestall a major nutrition-related catastrophe.

These results suggest a reevaluation of some basic tenets of wildlife management as they apply to Dall sheep in intact ecosystems. It has been axiomatic for at least 2 decades that ungulate populations are limited by availability of winter range. This axiom was generated by sound research work done in fragmented ecosystems of temperate regions where weather and predators had less significant effects on ungulate abundance than in Alaska. Logically extended to Dall sheep, these results predict

Table 9. Comparison of population quality status with characteristics usually indicative of resource abundance (populations well below carrying capacity.

Population characteristics	Fits model	Fails to fit model	Comments
Low density	X		
Varied diet	X		
Larger fetuses	X		
Higher lamb production	X		
Better lamb survival		X	
Younger age structure	X		
Higher quality forage		X	
Early sexual maturity		X	High-quality ewes lamb at 3 years; low-quality ewes at <3 years [a]
Better body condition		X	
Greater body size		X	

[a] See Heimer (1982).

that reducing sheep numbers in populations at or near carrying capacity will increase lamb production and survival to yearling age. Some managers have even predicted reductions through ewe cropping will increase the quality of Dall sheep populations involved. Clearly, the results of this study show that confusion of low-population quality with severely range-limited populations is a real possibility which should be carefully avoided. All aspects of population vigor should be evaluated before concluding that high density and low quality equate with overpopulation.

Implicit in the management pattern of presumably benefiting populations and maximizing harvestable biomass by reducing herd numbers is the assumption that something can be done about the presumed winter bottleneck. Winter range is limiting, at least to a degree, for sheep populations. However, data gathered here suggest that reducing the number of competing adults will have little nutritional benefit for the remaining individuals. That is, providing sheep with a greater quantity of low-quality forage will probably have no beneficial results for the remaining animals. Whether the numbers of sheep surviving a winter catastrophy will be enhanced or reduced if population numbers are high at the beginning of a severe winter is not known. In the Alaskan Interior, very severe cases are quite infrequent and should not play a major role in management planning. Sheep ranges which are subject to stronger maritime influences may require a different approach to management. Still, caution should be exercised in determining whether populations are simply of low quality or actually range-limited in a traditional sense.

If a population-limiting range relationship exists for Dall sheep in Interior Alaska, it may well be on summer ranges because of the role they play in supporting lactation. Further attention should be focused on the physiological and behavioral aspects of production and their interrelationships with all seasonal ranges rather than the traditional heavy emphasis on winter range as a limiting factor.

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PREPARED BY:

Wayne E. Heimer
Game Biologist III

APPROVED BY:

Robert A. Hinman / JB
Acting Director, Division of Game

Steven R. Peterson / JB
Research Chief, Division of Game

SUBMITTED BY:

Wayne L. Regelin
Regional Research Coordinator

APPENDIX A

Species Composition of Dall Sheep Diets
from Washed Rumen Contents

APPENDIX A, Table 1. Composition of rumen contents from low-quality sheep collected on No-Name Ridge during early winter, Alaska Range.

Acc. no.	Sex	Age (months)	Collection date	% grass and sedge leaves and stems	% woody stems and green leaves	% willow and dryas leaves	% moss and lichen
4565	F	18	10/29/76	68	26	4	2
4566	F	162	10/29/76	78	17	3	2
4567	F	78	10/29/76	52	21	5	22
4568	F	78	10/29/76	60	30	4	6
5009[a]	F	101	11/18/79	76	11	4	8
5010	F	89	11/18/79	83	8	3	6
5011	F	113	11/18/79	73	8	7	12
5012	F	125	11/18/79	86	10	3	1
5013	M	18	11/18/79	89	3	4	3
Means		85.6		74	15	4	7

[a] Contained measurable amounts of oxytrope base parts (No. 5009 = 1% and No. 5013 = 3%).

APPENDIX A, Table 2. Composition of rumen contents from low-quality sheep collected during spring near Dry Creek, Alaska Range.

Acc. no.	Sex	Age (months)	Collection date	% grass and sedge leaves and stems	% woody stems and green leaves	% willow and dryas leaves	% moss and lichen
4384	F	71	5/5/76	73	18	9	trace
4385	F	119	(Art Mtn.)	99	0	trace	trace
4386	F	59		93	0	4	3
4387	F	59		85	8	7	trace
4388	F	83		93	7	trace	trace
4741	F	11	4/18/77	69	29	3	trace
4742	F	11	(No-Name Ridge)	51	44	1	4
4743[a]	F	71		36	48	8	4
4744[a]	F	71		62	15	15	trace
4745	F	131		78	14	8	trace
4746	F	71		79	10	5	6
5034	F	106	4/17/79	68	25	3	3
5035	F	82	(No-Name Ridge)	61	31	4	3
5036	F	94		46	30	10	14
5037	F	58		47	47	2	3
5038	F	94		77	8	10	5
Means		67.5		69.8	20.9	5.6	3.0

[a] Contained measurable amounts of oxytrope base parts (No. 4743 = 5% and No. 4744 = 8%).

APPENDIX A, Table 3. Composition of rumen contents from high-quality sheep collected during early winter near Robertson River, Alaska Range.

Acc. no.	Sex	Age (months)	Collection date (place)	% grass and sedge leaves and stems	% oxytrope base parts	% woody stems and green leaves	% willow and dryas leaves	% moss and lichen
4593[a]	M	6	11/19/76	48	24	8	6	13
4594	F	30	(Tushtena Pass)	58	25	8	3	5
4595[a]	F	6		57	trace	2	29	12
4596	F	66		44	38	3	4	11
4597	F	90		50	27	13	1	9
4598	F	54		74	12	3	3	8
4599	F	90		63	16	3	6	13
4600	F	30		50	22	10	3	15
4601	F	90		56	21	18	4	2
4992[a]	F	6	11/8/78	68	4	11	7	11
4993	F	65	(Clearwater Creek)	48	2	6	12	32
4994	F	53		53	9	23	8	7
4995	F	65		65	3	16	8	8
4996	F	53		45	1	36	9	9
4997[a]	M	65		81	1	15	3	1
Means		62		56	15	19	10	11

[a] Excluded from analyses of mature ewes only.

APPENDIX A, Table 4. Composition of rumen contents from high-quality sheep collected during spring near Robertson River, Alaska Range.

Acc. no.	Sex	Age (months)	Collection date (place)	% grass and sedge leaves and stems	% oxytrope base parts	% woody stems and green leaves	% willow and dryas leaves	% moss and lichen
4762[a]	F	11	4/21/77	65	18	7	7	3
4763	F	95	(Tushtena Pass)	24	52	3	10	10
4764	F	35		39	27	2	16	16
4765	F	23		37	37	8	10	8
4766	F	95		36	36	7	7	9
4767	F	95		47	23	9	11	9
4768	F	71		23	50	6	9	12
5039[a]	M	22	4/9/79	63	18	5	5	9
5040[a]	M	22	(Clearwater Creek)	55	27	2	9	7
5041[a]	M	22		62	25	2	7	4
5042	F	106		79	2	2	9	9
5043	F	46		67	22	3	6	2
Means		71		50	24	5	9	9

[a] Excluded from analysis of mature ewes only.

APPENDIX B

Proximate Analysis of Washed Rumen Contents

APPENDIX B, Table 1. Nutritive analysis of washed rumen contents from low-quality Dall sheep ewes collected in early winter 1976 and 1978 in Dry Creek, Alaska Range.

Acc. no.	Year	% neutral detergent Fiber	% neutral detergent Ash	% acid detergent Fiber	% acid detergent Lignin	% protein
4565	1976	77	2.5	39	9	9
4566	1976	78	1.5	44	10	4
4567	1976	76	3.0	39	19	13
4568	1976	83	2.5	45	10	8
5009[a]	1978	--	--	--	18	6
5010[a]	1978	--	--	--	23	5
5011[a]	1978	--	--	--	15	3
5012[a]	1978	--	--	--	16	4
5013[a]	1978	--	--	--	14	6
Means		79	2.4	42	14.9	6.3

[a] Only protein and lignin tests completed.

APPENDIX B, Table 2. Nutritive analysis of washed rumen contents from low-quality Dall Sheep ewes collected in spring 1976, 1977, and 1979 in Dry Creek, Alaska Range.

Acc. no.	Year	% neutral detergent		% acid detergent		% protein
		Fiber	Ash	Fiber	Lignin	
4384	1976	77	2.0	45	15	7
4385	1976	77	2.5	45	14	6
4386	1976	75	3.0	44	14	6
4387	1976	77	3.0	44	14	8
4388	1976	76	2.0	46	13	5
4741	1977	75	3.0	54	26	15
4742	1977	79	3.5	53	25	13
4743	1977	81	2.5	53	25	12
4744	1977	77	3.0	50	26	13
4746	1977	80	3.0	51	24	10
5035[a]	1979	--	--	--	17	8
5037[a]	1979	--	--	--	18	8
5038[a]	1979	--	--	--	24	8
Means		77.4	2.8	48.5	19.6	9.2

[a] Only protein and lignin tests completed.

APPENDIX B, Table 3. Nutritive analysis of washed rumen contents from high-quality Dall Sheep collected in early winter 1976 and 1978 near Robertson River, Alaska Range.

Acc. no.	Year	% neutral detergent Fiber	% neutral detergent Ash	% acid detergent Fiber	% acid detergent Lignin	% protein
5493	1976	75	2.5	46	23	9
5494	1976	82	3.0	46	19	7
5495	1976	69	1.5	41	18	10
4596	1976	76	2.0	46	23	11
4597	1976	71	2.0	44	21	8
4598	1976	75	2.5	51	22	12
4599	1976	74	3.0	48	22	10
4600	1976	77	3.5	49	24	8
4601	1976	76	2.0	52	25	9
4992[a]	1978	--	--	--	12	4
4993[a]	1978	--	--	--	16	7
4994[a]	1978	--	--	--	20	7
4995[a]	1978	--	--	--	15	7
4996[a]	1978	--	--	--	23	7
4997[b]	1978	--	--	--	14	6
Means		75	2.4	47	19.8	8.1

[a] Only protein and lignin tests conducted.
[b] 5-year-old ram.

APPENDIX B, Table 4. Nutritive analyses of washed rumen contents from high-quality Dall Sheep collected in spring 1977 and 1979 near Robertson River, Alaska Range.

Acc. no.	Year	% neutral detergent Fiber	% neutral detergent Ash	% acid detergent Fiber	% acid detergent Lignin	% protein
4762	1977	79	3.0	46	21	11
4763	1977	75	2.0	42	23	8
4764	1977	79	2.5	44	20	13
4765	1977	78	3.0	43	24	12
4766	1977	77	2.5	46	27	9
4767	1977	81	2.5	46	26	13
4768	1977	77	2.0	47	25	10
5039[a]	1979	--	--	--	20	6
5040[a]	1979	--	--	--	24	9
5041[a]	1979	--	--	--	22	9
5042[b]	1979	--	--	--	20	8
5043[b]	1979	--	--	--	23	7
Means		78	2.5	45	22.9	9.6

[a] Only protein and lignin test conducted.
[b] 2-year-old rams.

APPENDIX C

Body Composition of High- and Low-quality Dall Sheep

APPENDIX C, Table 1. Body composition of Dall sheep ewes collected from the low-quality study group in early winter in Dry Creek, Alaska Range.

Acc. no.	Age (months)	Weight (kg)	% water	% fat	% protein	% bone
4331	114	62.3	69.3	11.7	11.9	8.0
4332	78	55.9	65.9	13.9	11.6	8.6
4333	90	67.5	65.0	14.1	11.8	9.1
4565	18	42.7	64.6	13.9	10.8	10.7
4566	162	66.3	70.9	13.6	9.5	5.9
4567	78	55.7	63.5	16.9	10.7	8.9
4568	78	68.6	64.0	15.7	11.7	8.7
5009	101	56.7	58.1	15.3	18.0	8.8
5010	89	58.5	57.1	16.6	17.6	8.7
5011	113	57.6	57.3	8.5	22.6	11.6
5012	125	61.2	50.2	16.6	22.3	10.9
Means	95.1	59.4	62.4	14.3	14.4	9.1

APPENDIX C, Table 2. Body composition of Dall sheep ewes collected from the low-quality study group in spring in Dry Creek, Alaska Range.

Acc. no.	Age (months)	Weight (kg)	% water	% fat	% protein	% bone	Pregnant
4384	71	51.4	75.5	5.4	10.8	8.3	yes
4385	119	42.3	78.7	3.2	11.4	6.8	no[a]
4386	59	42.3	73.5	5.6	12.9	8.0	no[a]
4387	59	42.7	77.3	5.6	11.1	5.9	no
4388	83	41.4	79.8	2.5	8.9	8.8	no[a]
4741[b]	11	30.4	70.4	11.5	10.7	7.4	no
4742[b]	11	32.3	71.9	7.7	11.7	8.8	no
4743	71	51.8	69.9	9.0	10.8	10.3	yes
4744	71	49.9	72.1	8.4	11.4	8.1	yes
4745	131	48.1	72.1	6.4	11.8	9.7	no
4746	71	53.2	72.7	7.0	12.5	7.8	yes
5034	106	49.9	48.9	19.6	21.7	9.8	yes
5035	82	49.9	69.1	7.4	14.9	8.6	yes
5036	94	52.6	62.8	9.4	18.4	9.5	yes
5037	58	51.3	66.9	8.4	16.8	8.0	yes
5038	94	44.9	50.4	13.8	24.7	11.2	no
Means	74.4	45.9	69.5	8.2	13.8	8.6	

[a] Lactating when collected.
[b] Not included in statistical analyses because of young age.

APPENDIX C, Table 3. Body composition of Dall sheep ewes collected from the high-quality study group in early winter near Robertson River, Alaska Range.

Acc. no.	Age (months)	Weight (kg)	% water	% fat	% protein	% bone
4593[a]	6	27.7	74.1	8.3	9.0	8.4
4594	30	54.5	65.4	14.1	21.9	15.4
4595[a]	6	30.9	68.7	12.5	10.8	8.0
4596	66	53.6	67.4	9.9	13.1	9.6
4597	90	63.6	74.8	6.8	6.2	12.2
4598	54	56.8	68.1	12.4	9.5	9.0
4599	90	65.5	68.3	12.2	11.5	8.0
4600	30	54.6	62.3	15.4	10.8	8.5
4601	90	53.7	67.0	11.9	12.4	8.7
4992[a]	5	30.4	52.7	19.7	19.3	16.4
4993	65	63.5	52.2	15.8	20.3	12.5
4994	53	53.1	49.2	19.0	19.2	12.6
4995	65	60.0	51.6	21.8	19.4	7.3
4996	--	59.0	53.5	18.5	21.4	6.6
Means	50	51.9	62.5	14.1	14.6	9.8

[a] Not included in statistical analyses because of young age.

APPENDIX C, Table 4. Body composition of Dall sheep ewes collected from the high-quality study group in spring near Robertson River, Alaska Range.

Acc. no.	Age (months)	Weight (kg)	% water	% fat	% protein	% bone	Pregnant
4762[a]	11	20.5	77.2	5.0	11.8	6.0	no
4763	95	49.5	71.4	7.6	11.3	8.4	yes
4764	35	51.4	71.9	10.2	9.3	8.5	yes
4765	23	45.0	71.4	7.3	11.7	10.1	yes
4766	95	53.6	75.5	6.1	10.5	7.9	yes
4767	95	50.0	70.8	8.4	11.7	9.1	yes
4768	71	44.1	72.8	6.6	11.0	9.6	yes
5042	106	49.9	51.2	20.6	20.1	8.2	yes
5043	46	44.2	62.5	10.4	17.6	9.5	yes
Means	63.3	43.4	69.4	9.1	12.8	8.6	

[a] Not included in statistical analyses because of young age.

APPENDIX C, Table 5. Body composition of pregnant Dall sheep ewes collected in spring from both high- and low-quality groups in the Alaska Range.

Acc. no.	Quality group	Weight (kg)	% water	% fat	% protein	% bone
4743	low	51.8	69.9	9.0	10.8	10.3
4744	low	49.1	72.1	8.4	11.4	8.1
4746	low	53.2	72.7	7.0	12.5	7.8
4384	low	51.4	75.5	5.4	10.8	8.3
5034[a]	low	49.9	48.9	19.6	21.7	9.8
5035	low	49.9	69.1	7.4	14.9	8.6
5036	low	52.6	62.8	9.4	18.4	9.5
5037	low	51.3	66.9	8.4	16.8	8.0
Means		51.3	69.8	7.9	13.7	8.7
4763	high	49.5	71.4	7.6	11.3	8.4
4764	high	51.4	71.9	10.2	9.3	8.5
4765	high	45.0	71.4	7.3	11.7	10.1
4766	high	53.6	75.5	6.1	10.5	7.9
4767	high	50.0	70.8	8.4	11.7	9.1
4768	high	44.1	72.8	6.6	11.0	9.6
5042[a]	high	49.9	51.2	20.6	20.1	8.2
5043	high	44.2	62.5	10.4	17.6	9.5
Means		48.3	70.4	8.1	11.9	7.6

[a] Values for water, fat, and protein not included in statistical analyses since they fall more than 3 standard deviations away from the mean of the other values.

APPENDIX C, Table 6. Body composition of nonpregnant Dall sheep ewes collected in spring from low-quality groups in Dry Creek, Alaska Range.

Acc. no.	Weight (kg)	% water	% fat	% protein	% bone	Lactating
4745	48.1	72.1	6.4	11.8	9.7	no
4385	42.3	78.7	3.2	11.4	6.8	yes
4386	42.3	73.5	5.6	12.9	8.0	yes
4387	42.7	77.3	5.6	11.1	5.9	no
4388	41.4	79.8	2.5	8.9	8.8	yes
5038[a]	44.9	50.4	13.8	24.7	11.2	yes
Means	43.6	76.3	4.7	11.2	7.8	

[a] Values for water, fat, and protein not included in statistical analyses since they fall more than 3 standard deviations away from the mean of the other values.

APPENDIX D, Table 1. Body composition of Dall sheep fetuses carried by low-quality ewes in Dry Creek, Alaska Range.

Acc. no.	Weight (kg)	% water	% fat	% protein
4743	3.11			
4744	2.24	71.0	6.0	19.0
4746	2.35			
5034	1.30	70.0	13.1	16.9
5035	2.19	76.3	8.2	15.5
5036	1.94	75.3	7.2	17.5
5037	1.94	76.8	7.2	15.9
Means	2.15	73.9	8.3	17.0

APPENDIX D, Table 2. Body composition of Dall sheep fetuses carried by high-quality ewes near Robertson River, Alaska Range.

Acc. no.	Weight (kg)	% water	% fat	% protein
4763	3.20	70.0	9.0	17.0
4764	2.59	72.0	7.0	16.0
4765	2.76	78.0	4.0	15.5
4766	3.61	73.0	6.0	19.0
4767	2.73	76.0	6.0	15.5
4768	3.50			
5042	2.23	64.6	18.8	16.6
5043	2.13	57.3	22.1	20.7
Means	2.84	70.1	10.4	17.2

APPENDIX E

Relative Lamb Production and Yearling Recruitment for the High- and Low-quality Populations of Dall Sheep in the Alaska Range

APPENDIX E, Table 1. Mean lamb:ewe ratios observed in high- and low-quality study areas, 1976-81 in Alaska Range.

Year	Low-quality lamb:ewe ratio		High-quality lamb:ewe ratio	
1976	36		35*-39	
1977	58		52*-64	
1978	41	$\bar{x}$ = 55	57*-67	$\bar{x}$ = 65
1979	65	SD = 12.91	66** (N = 44)	SD = 14.95
1980	67		71** (N = 41)	
1981	60		85** (N = 63)	

Note: In the low-quality area, ewes breed at 18 months, so the observed lamb:ewe ratio reflects initial production (because all classified ewes are breeding females). However, in the high-quality populations, ewes breed 1 year later, so observed lamb:ewe ratios are not valid as an indicator of relative lamb production. Those observed values marked with (*) indicate observed values; corrected values, following the dash, were derived by the following procedure: One half of the yearling:100 ewe ratio observed 2 years earlier was subtracted from the "hundred ewes" (in lambs/100 ewes). The observed lamb:ewe ratio was then divided by this difference to give the estimated initial relative production.

Those values indicated by (**) are observed lamb:ewe ratios among collared ewes of breeding age. The estimated technique described for (*) values applied to overall observed values for years 1979-1981 gave a mean initial production of 73 lambs/100 ewes. The observed mean among collared ewes for the same period was 74 lambs/100 ewes. I think this shows, at least for those years, the estimation technique was not seriously compromised by mortality among yearling and 2-year-old ewes.

Differences between means for high- and low-quality populations were not statistically significant (P = 0.05).

APPENDIX E, Table 2. Yearling:ewe ratios in high- and low-quality study areas, 1976-81 in the Alaska Range.

Year	Low-quality yearling:ewe ratio		High-quality yearling:ewe ratio	
1976	16		26-29	
1977	17		18-22	
1978	25	$\bar{x} = 26$	35-41	$\bar{x} = 32$
1979	19	SD = 11.13	25-28	SD = 7.03
1980	36		29-36	
1981	43		32-37	

Note: Adjustments to yearling:ewe ratios for the high-quality populations were made as above. Yearling ratios necessary for the 1976 and 1977 adjustments were taken from Heimer (1980) Table 5. Differences between high- and low-quality population means are not statistically significant ($P = 0.05$).

APPENDIX E, Table 3. Survival rates of lambs to yearling age in high- and low-quality study areas in the Alaska Range.

Year	Low-quality population % survival		High-quality population % survival	
1977	47		56	
1978	43		64	
1979	46	$\bar{x}$ = 51	41	$\bar{x}$ = 54
1980	55	SD = 8.51	55	SD = 8.32
1981	64		52	

Note: Differences in population means are not statistically significant (P = 0.05).

APPENDIX F. Densities of sheep on high- and low-quality study areas in the Alaska Range.

Study group	Season	Area (km^2)	Number of sheep	Density
Low-quality	summer	112	400[a]	3.5 sheep/km^2
Low-quality	winter	76	400[a]	5.3 sheep/km^2
High-quality	summer	714	1,050[b]	1.5 sheep/km^2
High-quality	winter	507	1,050[b]	2.0 sheep/km^2

[a] The average population size from 1975-80 (Heimer 1979, 1980).

[b] Determined by aerial survey (Heimer 1980).