CAN POPULATION QUALITY BE RELATED TO POPULATION DENSITY THROUGH NUTRITION?

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Abstract: A comparative study of 2 sheep populations with vast difference in population quality determined by ram horn growth revealed no data supportive of the hypothesis that population quality is a function of nutrition. The low quality population was about 3 times more dense per unit area, but no differences were found in forage quality of plants on the range, forage quality of rumen contents, or gross body composition of ewes collected from each group. The relationship of the concept of population quality to carrying capacity is discussed.

INTRODUCTION

Since Geist (1971) scientifically formalized the common observation that not all populations of wild mountain sheep were the same in his "Quality Hypothesis" (now referred to as the Dispersal Theory, Geist 1979), students of wild sheep have made much of the differences observed and have speculated on their causes. Shackelton (1973) and Horejsi (1976) documented the phenomenon of population differences in bighorn sheep (Ovis canadensis), and Heimer and Smith (1975) published similar data showing differences in Dall sheep (Ovis dalli) populations. Many hypotheses have been proposed to explain these differences but nutritional considerations are common to virtually all of them. Simply stated, the common hypothesis is: "Some populations of wild mountain sheep are more vigorous than others because they eat better than others." This has been extended to the classic concept of population limitation through nutritional carrying capacity, and it is commonly hypothesized that low quality populations are at or above carrying capacity while those of higher quality are well below carrying capacity.

The purpose of this paper is to share information gained in a comparative study of 2 Alaskan Dall sheep populations on the extreme ends of the population quality spectrum. I hope to address the hypothesis that population density mediates population quality through a nutritional (caloric) mechanism.

MATERIALS AND METHODS

Study Populations

Both study populations inhabit the north side of the Alaska Range in interior Alaska. They are separated by a distance of about 200 km. Table 1 compares parameters commonly used to define population quality for both study populations.

Density

Summer range densities were determined by low level aerial surveys. Winter ranges were identified by locating collared sheep populations with known summer ranges during winter. Winter range area was determined by making low-level helicopter flights to determine areas available to sheep. Snow depth, hardness, feeding sites, tracks, and the presence of sheep were used as indicators.

Body Condition and Nutritional Profile

Dall ewes were collected in late winter (n=16) and early spring (n=18) from 1975-1977. It was assumed that collecting at these times would yield individuals in best and worst possible conditions following summer fattening and winter stress. Ewes were shot at random and transported by helicopter to the laboratory where standard body measurements were taken and the animals weighed. Animals were then necropsied and prepared for determination of gross body composition. Viscera were

Table 1. Comparison of commonly used quality parameters for the high and low quality Dall sheep populations studied.

Parameter	Low Quality	High Quality
Ram horn growth quality index (Heimer and Smith 1975)	14th of 18	4th of 18
Mean lamb production during study period (1974-79)	43 lambs/100 ewes	51 lambs/100 ewes
Mean yearling recruitment during study period (1974-79)	21 yearlings/100 ewes	27 yearlings/100 ewes
Percent survival of lambs to 1 year of age	49 percent	53 percent
Near-term fetal weight	2.95 kg	3.45 kg
Suckling duration	14 seconds	--
Mean age in collected ewes (n = 35)	7 years	5 years
Summer range density	3.3 sheep/km^2	1.3 sheep/km^2
Winter range density	5.3 sheep/km^2	1.8 sheep/km^2
Habitat character	gentle hills short drainages elevation relief = 830m glaciers absent abundant vegetation	steep hills long drainages elevation relief = 990m glaciers present sparse vegetation

removed, frozen, and stored, and each carcass divided by a median sagittal section. One half was frozen for subsequent fat, water, and protein determination, and the other half was boned to determine skeletal weight. Bones were cleaned, boiled, and dried before weighing (hooves and horns were not included). Carcass halves and viscera were then separately ground using an Autio 801 B grinder in cooperation with the reindeer research group at the University of Alaska.

Frozen carcass halves were divided into small chunks using a band saw. These pieces were then randomly mixed and fed through the grinder using a cutting head with openings of approximately 2 cm. The pieces were then mixed and run through the grinder 2 additional times. A high speed chopper was then used to complete homogenizaton. The homogenate was run through this machine twice with mixing in between using a cutting head with openings of about 0.7 cm. Samples were then randomly selected from the total homogenate to assemble a composite carcass sample. Visceral organs were homogenized in the high speed chopper only.

Rumen samples were collected for analysis of forage and botanical composition. After washing identifiable plant fragments were separated by plant group and the volume of each group determined by water displacement.

Protein determinations were determined from Kjeldahl total nitrogen, lipids by ether extraction, and water by evaporation. Proximate analysis of washed rumen contents was determined by the method of Van Soest (1963). Body composition of component parts was calculated as illustrated below.

Basic Data

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

Total live mass - 42.7 kg

Rumen-Reticulum fill - 5.68 kg

Other gut contents - 0.75 kg

One-half carcass at analysis - 14.1 kg

One-half carcass fresh weight - 16.4 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, 22.59% protein

Carcass homogenate composition - 15.2% fat, 11.1% protein, 33.8% water

Calculations

14.1 kg carcass at analysis x 0.152	= 2.14 kg fat
14.1 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

Similarly:	3.46 kg viscera x 0.54	=	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:	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 sample 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 leaves 0.08 kg error, or an error of 0.02%.

RESULTS

Density

In 1975 a summer aerial survey of the low quality area (Heimer 1976) indicated a total estimated population of 350 sheep. Another survey during summer 1979 yielded an estimated total population of 410. There is little doubt that the post-lambing population actually increased from the 1975 level. Favorable conditions resulted in high initial lamb production during the 1976-1979 period.

In the high quality study area during 1974 (Heimer 1975) the summer population was estimated at 450 sheep. A casual early winter survey supported this estimate when 360 sheep were observed on winter ranges in the same area before snowfall in 1976.

Table 2 shows the calculated density of sheep on summer and winter ranges from 1975 through summer 1979 for both study areas. Estimates of summer density indicate sheep in the high quality area exist at 39 percent of the density in the low quality area. Expressed another way, the population in the poorer quality area is 2.5 times more dense than that where the population shows signs of high quality.

Winter range density averaged 5.3 sheep per km^2 in the low quality area, and the single measurement from the high quality area was 1.8 sheep per km^2. Thus, densities on winter range in the low quality population are almost 3 times greater than those for the high quality population.

Dall Ewe Body Composition

Data for gross body composition of Dall ewes collected from both study populations are summarized in Table 3. From the summary it can be

Table 2. Dall sheep density on summer and winter ranges for the high and low quality study areas.

Study Area	Year	Summer Population	Summer Range Area (km^2)	Summer Density Sheep/ (km^2)	Winter Population	Winter Range Area (km^2)	Winter Density Sheep/ (km^2)
Low Quality	1975	350	112	3.1	350	80*	4.4
	1976	350**	112	3.1	350	62*	6.0
	1977	370**	112	3.3	370	65***	5.7
	1978	390**	112	3.5	390	75***	5.2
	1979	410	112	3.7	410	--	--
				x = 3.3			x = 5.3
High Quality	1974	450	350	1.3	450	--	--
	1975	450	350	1.3	450	--	--
	1976	450	350	1.3	450	250***	1.8
				x = 1.3			

* Fixed-wing survey of winter range availability.

** The population increased between 1975 and 1979, but there was probably no increase in 1976 because of poor lambing that spring. The increase was arbitrarily calculated as linear from 1976 through 1979.

*** Helicopter survey of winter range availability.

Table 3. Summary of mean composition of adult ewes* collected in early winter.

Population Quality	Age (mo)	Weight (kg)	% Water	% Fat	% Protein	% Bone
Low quality	88	59.9	66.3	14.3	11.1	8.6 (n=7)
High quality	64	57.5	67.6	11.8	12.2	10.2 (n=7)

*At least 18 months of age.

noted that the low quality sheep averaged 2 years older than the high quality sheep, and their weights were about 2.5 kg greater. There was no great difference between the 2 populations. The low quality sheep were older, larger, slightly fatter, and slightly lower in protein and bone content than the high quality sheep at the end of summer.

Data for gross body composition of Dall sheep ewes collected from both study populations at winter's end are summarized in Table 4. From the summary it can be seen that little difference is apparent in body composition among the pregnant ewes.

Diet

Data on plant group selection by ewes in both study populations are presented in Table 5. This table shows sheep from the high quality population have a more varied diet consuming less grass and more willow leaves, moss, and lichen.

Forage Quality

Table 6 contains data from proximate nutrient analysis of rumen contents. Note that the table indicates minimal differences in percent protein and gross available nutrients between the 2 populations (100% minus % neutral detergent fiber = soluble carbohydrate content which is 100% digestible).

Table 4. Summary of mean composition of adult ewes* collected in spring.

Population Quality	Age (mo)	Weight (kg)	% Water	% Fat	% Protein	% Bone
Low quality	70	51.4	72.3	7.5	11.4	8.6 (n=4)
High quality	88	48.9	72.3	7.7	10.9	8.9 (n=6)

*Pregnant adults greater than 18 months of age.

Table 5. Plant group selection identified from rumen samples.

	Grass and Sedge Leaves and Stems	Base parts of *Festuca*	Woody stems (incl. leaves)	Willow and *Dryas* leaves	Lich and M
Early Winter					
Low quality (n=9)	83%	0%	11%	2%	4%
High quality (n=9)	53%	21%	8%	7%	10%
Late Winter					
Low quality (n=23)	78%	1%	14%	6%	2%
High quality (n=7)	39%	35%	6%	10%	11%

Table 6. Mean values for forage quality from ewe rumens.

Collection Period	Acid Detergent Fiber	Acid Detergent Lignin	Neutral Detergent Fiber	Neutral Detergent Ash	Percent Protein
Early Winter					
Low quality	42	12	79	2.4	8 (n=4)
High quality	47	22	75	2.4	8 (n=9)
Late Winter					
Low quality	49	20	77	2.8	11 (n=10)
High quality	45	24	78	2.5	10 (n=7)

The only notable difference is the lower lignin value for early winter forage of the low quality population.

DISCUSSION

It was assumed that the collection periods at the end of the summer fattening period and after the stresses of winter are past would allow comparisons of energy availability on summer and winter ranges. That is, differences in energy availability on these seasonal ranges would be reflected in the amounts of energy stored in the body at the end of summer and remaining unused at the end of winter.

Failure to identify any differences in stored reserves at the end of summer is interpreted as evidence that there is no significant difference in energy availability on summer ranges. There is probably energy available in excess of each individual's need regardless of his quality status. Also, failure to identify noticeable differences in stored energy at the end of winter indicates that during the years sampled there was no great difference in winter range energy contribution and energetic requirements even though diets and habitats were different.

These conclusions are reinforced by the data relevant to the nutritional quality of forage ingested. The only parameter which is possibly indicative of differences is the lignin content in early winter rumens from the low quality population. This lower lignin would indicate greater digestibility for this forage and indicate better forage for the low quality population.

This study did not directly address the nutritional quality of plants on the ranges. However, Winters (1980) gathered data from plants in the area of the high quality population and compared their nutrient quality with the collections of Whitten (1975) from a low quality area adjacent to the low quality population. Winters reported no differences in plant nutrient quality between the high and low quality population areas once values had been adjusted to equivalent phenological stage through compensations for altitude.

Based on the data gathered so far, there is no obvious quantitative nutritional advantage for the high quality sheep population. Sample sizes are small, to date, and further collections have provided an equal amount of material which is still being analyzed. Still, the failure of these analyses to demonstrate differences in gross body composition, nutritive quality of rumen contents, and lack of difference in quality of forage plants indicates that food resource quality is not the sole and perhaps not a major contributing factor to the differences interpreted as indicators of population quality.

This raises the question of whether the definition of population quality is sufficient. Certainly, genetics could play a role which we fail to appreciate, and other mechanisms may be discovered which can relate quality differences to more subtle nutritional differences. Still, it is worthwhile to examine the concepts of population quality and carrying capacity. Many have inferred that low population quality is indicative of a population at or above carrying capacity. Generally, populations considered to be well below carrying capacity are expected to exhibit a complex of characteristics which indicate to the wildlife manager that all is well between resources and the population. Several

Table 7. Comparison of population quality status with traits usually indicative of resource abundance (populations well below carrying capacity).

Population Characteristic	Fits Model	Fails to Fit Model	Comments
Low density	X		
Varied diet	X		
Higher lamb production	X		
Better lamb survival		X	no significant difference in lamb survival
Early sexual maturity		X	high quality population ewes lamb at 3 years, low quality at 2 years
Better body condition		X	
Greater body size		X	no detectable difference
Larger fetuses	X		
Younger age structure	X		
Higher quality forage		X	

of these are listed in Table 7 in the context of what is considered favorable, or beneficial, to a population which is below classical carrying capacity with respect to nutrition.

It can be seen from Table 7 that only half of the characteristics which classically define populations well below carrying capacity with respect to food correctly predict the quality status of the sheep populations studied here. This failure rate is sufficient that it forces re-examination of the hypothesis that quality is determined by resource abundance. It also forces a careful application of population quality determinations to population management with respect to carrying capacity and forces a re-examination of the "Quality concept." Are the definers of quality a true population syndrome or simply a complex of population characteristics which may not necessarily be related at all?

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QUESTIONS - RESPONSES

Jim Peek: Is there a difference in the utilization levels on those ranges?

Wayne Heimer: I think there is. I think the low quality population utilizes the range considerably to a greater extent. I don't have data in hand, but its difficult to find a blade of grass in winter that hasn't been eaten in the low quality population. With all the talk of conditioning and one thing or another, I might suggest you people around here may want to consider doing it like we do with mountain sheep instead of putting cows on there to do it for you. We condition our ranges by letting the sheep do it.

Jim Peek: I think that's an important issue here because even if the sheep don't show any differences; you know in their nutritional status from one population to the next, there could still be more effort expended to get the forage where the use is heaviest. So you got a density relatedness problem; density dependent problem. It may be competition on that range; intraspecific competition density related on the range that may be tied into these things. It seems to me like if you went in through the Alaska Game Department: they would just love to have you kill off about half of the whole productive population, and see what happened. You would probably get your high quality herd out of it again wouldn't you?

Wayne Heimer: I don't think we would and the reason I don't think we would, is because we're in an alternate year reproduction situation anyhow. If we kill half of them maybe quality will go up. I don't think it will.

Jim Peek: We surely know that if productive; you know these kinds of things are subject to change. What you're considering phenotypic response implies that these things can change without a genetic relatedness. I'm not agruing that there isn't some genetics in it. I'm just saying it seems to me that it gets back to just an old range problem and a density problem.

Wayne Heimer: I think when you walk around in the two study areas; you talk about extra effort being exerted in the low quality population to obtain an equivalent amount of forage, again I'm even a worse range man than I am bunch of other stuff, but the terrain is so different and is so steep, I can walk all over Dry Creek without getting too tired. But, when I go down to the high quality population the effort just in getting around in that population, in that terrain, if it indeed costs you more to walk uphill and more to go up a steeper hill I think probably the effort involved is going to be: I don't know, it's difficult for me to relate to the idea of having to work hard to bite more grass.

Jim Peek: These are highly social animals. And there's no reason at all then for me not to believe that sociality doesn't have some impact on them physically and phenotypically. That's the density relatedness. One of the problems of these things is just what you just said. We look at half of the issue. I don't know what you classify yourself as, maybe a population ecologist of some sort, but it seems to like if there was a team tied in, a good range ecologist, population person, these are kind of things that seem to me to require some joint work by different people that have expertise in different disciplines; inter-disciplinary type work.

Anonymous: I think you need to be pretty careful in talking about interpreting your diet quality data. I think it for this reason, as you know most of the readily available nutrients are in cell solubles. If an animal has a diet which is higher quality than say another animal then the rate of digestion of that material is going to be greater on the higher quality diet and the rate of disappearance of cell solubles will consequently be higher. Now the Van Soest analysis procedure depends very heavily on that first step where you divide out cell solubles and cell wall and if cell solubles are disappearing more rapidly from the rumins of your higher quality population animals then that is going to inject strong bias in all the subsequent steps in the Van Soest analysis. So your body composition data are extremely interesting and lend alot of support to your conclusions. I wouldn't if I were you, rely very heavily on those diet quality data because I don't think they are anywhere near conclusive.

Daryll Hebert: Wayne, I've looked at a part of your data anyway, over the last 4 or 5 years, I assume that I haven't seen it all, but you mentioned that you were considering quality times quantity. If you look at my nutritional data there are individuals, when you combine the quality and quantity that are nutritionally superior. There are individuals that at the same weight, same age and same quality diet, by taking in slightly more; depending on what that range of quality is, you can't go down too low or it doesn't work, but at least within that moderate range they can take in more feed which gives them more protein and more energy which improves their digestibility, improves their nitrogen balance and probably improves their metabolizable energy as well. If you look at those specific individuals they are nutritionally better able to handle the same type of material and it does show up in body weight and reduced body weight losses over winter. Now I don't know what that means in terms of population quality. I don't know whether those individuals are dispersed amongst both your high and low quality populations or whether they are segregated out individual so that there is a higher number of those nutritionally superior individuals in the high quality and a lower number in your low quality. If you start with an individual basis, and I again point out what the last fellow said about diet quality, I'm still not convinced that the range diet quality measurements that you are making are telling you the right answer to what that animal is doing, either nutritionally superior or not. To go from there to the population quality is again another big jump. I really don't know what that means.

Wayne Heimer: I don't either.

Frank DeShon: You mentioned that those ewes were only having a lamb every other year; that they are only ovulating every other year?

Wayne Heimer: No. It seems that they are breeding, well: see they are lactating throughout the winter and many times those that are attended by a lamb are not pregnant in the spring when we sample. Some are, there is a fair indication that many of them breed and resorb the fetus. Not many of them; I don't know that, but the percentage of fetal resorbtions that we've seen in our small collections; either we're very good at catching these or there are a lot of them there.

Nike Goodson: You did find lower fetal weights between the two different populations the low quality population had lower fetal weights?

Wayne Heimer: That's right.

Nike Goodson: And also lower lamb crop; lambs per ewe.

Wayne Heimer: That's right.

Nike Goodson: I think what may be going on to some extent, is conservation of body weight and condition in the mature animals and may be taking up some slack in the young. The difference may show up in reproduction of the young rather than the condition of the ewe. That may just be their strategy so that the ewes maintain their weight even if they don't produce a lamb that year. That doesn't answer the question as far as why the forage quality would be different, but it might answer why the body weights aren't different.

Lanny Wilson: I want to bring up a couple of things. You've touched on a problem that we've all seen and I don't care if you look at desert sheep or Dall sheep or what have you. First of all, it may be a genetic thing. That's something that we absolutely don't know anything about in wild sheep of any kind. The second thing is, you'll see this high quality, low quality thing, if you really know your population, within a population; what I call subpopulations. What I'm getting at, you may be having a behavioral thing that's causing internal stress and I don't know how you get at some of that. I don't think we're down the road far enough to figure all that out. But, I'll give you an example, I could show you a couple of populations that I'm familar with and you'll see the very, these are desert sheep, their a canyon apart. One's a high quality and one's a low quality.They're not 2 air miles apart. They never mix. You could throw sheep from the same populations or areas sometimes in a paddock. They won't even associate with each other as much as 4 to 5 months because their individual little behavior characteristics is so much different they really don't understand; it's like putting two people with foreign languages together, they really don't understand each other that well. I think these are the fine subtleties that we haven't really got at in some of these management problems. Did you observe any outward more aggression of fighting, this type of thing in your low quality compared to your high quality? Are they creating; I think Jim touched on it, they're creating internal stress and pressures because of their behavior norms that aren't over in your high quality. I just wondered if you've noticed that; anybody looked at that aspect?

Wayne Heimer: We have been interested in aggressive behavior by ewes, just because people thought for awhile it didn't happen. We found it does happen in low quality population and it does happen in the high quality population, I've no quantitative data on it. Ewes fight all the time both places.

Jim Bailey: Just a comment, another thing behaviorally that you might look at, or maybe you have, is group size and spacing of individuals within groups like Lanny is talking about. It could be measured.

PROCEEDINGS OF THE
BIENNIAL SYMPOSIUM OF THE
NORTHERN WILD SHEEP AND GOAT COUNCIL

Salmon, Idaho
April 23-25, 1980

CHAIRMAN: W. O. Hickey

HOSTED BY: IDAHO DEPARTMENT OF
FISH AND GAME

ASSISTED BY: SALMON NATIONAL FOREST,
Supervisor Office

Special thanks of gratitude are extended to Mrs. Norma Barr and Miss Sheryll Yarnell for retyping of manuscripts, the Goat Bibliography and editorial assistance.

Cover Art: Wendy Hass, Encampment, Wyoming, graciously contributed the drawing for the cover.