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DIFFERING REPRODUCTIVE PATTERNS IN DALL SHEEP:

POPULATION STRATEGY OR MANAGEMENT ARTIFACT?

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ABSTRACT

Observed lamb:ewe ratios, collection prgrams, and studies of marked Dall sheep (Ovis dalli dalli) indicate differing reproductive patterns between ewes of two populations in Interior Alaska. The Dry Creek (low-quality) population has a high incidence of lambing at age 2 and a subsequent alternate-year production of lambs. In the Sheep Creek (high-quality) population, ewes have their first lambs a year later, at age 3, and then produce lambs annually. Nutrition and body composition data reveal no differences between ewes in the two populations and suggest no differences in energy availability on the two ranges. The major difference between the two groups is age composition of the breeding rams. In the Dry Creek population, maximal harvest at 3/4 curl has been practiced for more than a decade; consequently, young rams are able to take part in the rut. The Sheep Creek group has an essentially undisturbed ram age-structure as it has been managed for trophy production since 1974. We suggest that behaviorial differences due to the removal of dominant males before the rut may result in the breeding of 18-month-old ewes in the Dry Creek group. Early breeding in these populations is not a direct result of density-mediated nutritional conditions.

INTRODUCTION

In 1978, Heimer reported on alternate year lambing by ewes of a low-quality, declining population of Dall sheep in Dry Creek. Irregular reproduction has also been documented in bison (Bison americanus) (Fuller 1955), caribou (Rangifer tarandus) (Dauphine 1976) and red deer (Cervus Elaphus) (Lowe 1969, Mitchell and Brown 1974, Hamilton and Blaxter 1980). Explanations for irregular reproduction are often based on nutrition. Mitchell and Brown (1974), Dauphine (1976), and Hamilton and Blaxter (1980) found a strong correlation between body weight and fertility for a particular year in mature females. The existence of barren mature females in a population appears to be a symptom of nutritional stress reflecting environmental or physiological conditions. Lactation is especially thought to create nutritional stress, reduce body weight, and lower the probability of annual breeding (Fuller 1955, Lowe 1969, Mitchell and Brown 1974). Heimer (1978) proposed similar explanations for the Dall sheep population.

The age of first estrus is also thought to be influenced by nutrition. Daniel (1963) found that red deer on high-quality forage came into estrus as fawns while those on poorer range did not breed until age 3. Wegge (1974) and Hamilton and Blaxter (1980) attributed early fertility to high-quality summer forage, high body weight, and, possibly, genetics, while Stains (1978) concluded low population density was a main contributor to early fertility.

The purpose of this paper is to report on observed differences in the reproductive onset and frequency between two Dall sheep populations. We also propose a model which may explain these differing patterns on the basis of behavior during rut and offer methods by which the prime hypothesis generated by the model can be tested.

METHODS

Two sheep populations fron the Alaska Range were the focus of this study. The Sheep Creek population is located 30 km. from Tok, Alaska, between the Robertson and Tok Rivers. The area is characterized by steep hills and long drainages with glaciers. Vegetation is relatively sparse. THe Dry Creek area is 200 km east of Sheep Creek and located between the Wood River and the West Fork of the Little Delta River. It is characterized by comparatively gentle hills and short drainages without glaciers. Vegetation is relatively abundant. In the Sheep Creek population, sheep were trapped at a mineral lick as described by Heimer et al. (1980). The ages of ewes captured were determined, and individuals were marked with numbered neckbands and large eartags. Data on reproductive status were gathered at capture and upon resightings at the mineral lick from 1977 through 1981. Ewes were classified as reproductively active on the basis of suckling a lamb. Sheep at the mineral lick were observed from 0400 through 2000 hours throughout June 1980 (except for 6 days) and June 1981.

In Dry Creek, methods for determining age at first parturition and subsequent reproductive performance were similar to those used in Sheep Creek and are described by Heimer (1978). Field studies were conducted from 1972-77 and 1981.

Attempts to define the role of nutrition in both study groups were made by assessing nutrient quality of food plants on the range (Winters 1980), the nutritive content of plants selected (rumen contents), as well as body condition (Heimer 1982). The latter was determined by homogenizing ewe carcasses and analyzing for percent bone, fat, protein, and water.

RESULTS

In ewes from the Sheep Creek population, evidence indicates the age of first parturition is 3 years. Only 1 of 24 marked ewes aged 2 years and under was found to lead a lamb. Ten 3-year-old ewes were trapped; eight of them were lactating or had lambs. Eighty-three percent of the 24, 2-year-old ewes had lambs at age 3. These data show the dominant pattern is first lambing at 3 years of age.

Once a ewe from the Sheep Creek population has become reproductively active, it appears highly probable that she will produce a lamb annually. Of the 74 consecutive-year observations made where the earlier year's reproductive status was known, 49, or 66 percent, had lambs in consecutive years. Only 23 ewes, or 30 percent, of the marked individuals have missed reproducing each year. There have shown two consecutive failures to lamb.

In the Dry Creek population, ewes were found to breed at 18 months and give birth to lambs at 2 years as reported in Heimer (1978). Of the 88 consecutive-year observations where the earlier year's reproductive status was known, 5, or 6 percent, had lambs in consecutive years, while 44 ewes, or 50 percent, were without lambs one of the years. Thirty-nine ewes have shown two consecutive failures to lamb. Table 1 summarizes data on reproductive frequency for both populations.

Three 2-year-old ewes of the Dry Creek population were trapped on 9-11 June 1981. None of these were lactating when captured, but all three had swollen vulvae and enlarged, but unpigmented, udders. One died of internal hemorrhage resulting from capture. When necropsied in the field, she was found to be pregnant. The fetus was still covered with darkly pigmented hair, and its hooves were yellow and cartilaginous in texture. We believe the fetus was at least 4 weeks from term. One of the surviving 2-year-old ewes was seen at the end of June with a small lamb. The third ewe was not resighted. During the same trapping period, three 3-year-old ewes were captured. One was lactating and had a lamb, the other two were not lactating. Thirteen older ewes were caught, and eight were lactating. The total frequency of lactation in ewes, including the 2-year-olds which could have borne lambs in spring 1981, was 11 of 18. This small sample size indicated 61 percent of the marked females were reproductively active. The observed lamb:ewe ratio was 60 lambs/-100 ewes in the entire population. Table 1 summarizes data on reproductive frequency for both populations.

Winters (1980) and Whitten (1975) found no significant difference in the nutritive quality in the food plants on the two ranges. There was also no difference in nutritive quality of rumen contents analyzed for soluble cell components, protein, lignin, and other fiber. Neither was there any detectable difference in amount of fat, protein, or water in ewe carcasses from either group (Heimer 1982).

DISCUSSION

There is little doubt the reproductive patterns of these populations are strikingly different. Table 2 (from Heimer 1982) shows other contrasts in the two populations. These data, along with the finding that no detectable differences could be identified in nutritional and body condition components, suggest the difference in onset of reproduction is not range-related. Indeed, the earlier onset of reproductive activity for the Dry Creek (low-quality) population suggests range resources are better for that population group.

We think another mechanism may be responsible for the age differences at the onset of breeding in these two groups. The Dry Creek group, those with early breeding followed by alternate-year lambing, was managed as an open hunting area for rams with a 3/4-curl legal minimum horn size until 1979. After 1979, the legal definition for ram horns was raised to 7/8 curl. Ram harvest in this area has been heavy and equals recruitment to the legal age class. In a 1980 preharvest census, only 4.9 percent of the population (n = 1,417) were legal (7/8 curl) or older rams. This represents 27 percent of the ram population (69 rams) at or above 6 years of age. In contrast, the Sheep Creek population has been managed for trophy production since 1974. Hunting pressure there has been held at a low level by permit regulations, and ram harvest is limited to a number less than the full-curl recruitment. A 1980 preharvest census of this group showed 7.1 percent of the total population (n = 892) legal at or above full curl. This is 31 percent of the ram population (63 rams) at or above 8 years of age.

We hypothesize that the absence of behaviorally and sexually mature rams in the heavily hunted, Dry Creek population leads to active participation in the rut by young, inexperienced rams which would be virtually excluded from participation by the presence of mature (Class IV) rams in a population with a less distorted age distribution (Geist 1971, Nichols 1971). Data presented by Geist (1971) and Nichols (1971) indicate the younger rams participate more in chasing behavior, less in guarding, and more frequently in courtship of anestrous ewes. The cue given by an estrous ewe is running after being approached and front-kicked by a ram (Geist 1971). Anestrous ewes are thought to signal their condition and lack of receptiveness to breeding by urination. We hypothesize that young rams, in the absence of mature dominants, eventually pester the 18-month-old ewes into flight which results in breeding. We also suggest these ewes are physiologically capable of breeding, but behaviorally immature. Suche ewes would not be bred if breeding were restricted to mature rams that rut in accord with accepted social constraints. Courtship-induced estrus in 18-month-old ewes resulting from attention by immature rams could also explain early breeding.

We are unsure of the specific relationship between nutrition and biennial lamb production; however, this behavioral model more adequately explains the earlier onset of reproduction in the Dry Creek population. Our hypothesis predicts that an alternate-year lamb production pattern will change to annual lamb production once a ram age structure exists in which the very young rams do not actively participate in the rut. The mangement benefits of annual production are easily demonstrated. In a given life-span of 10 years, the number of lambs produced by an individual ewe beginning at age 2 and continuing with alternate-year lambing would be five lambs. For a ewe lambing the first time at 3 years of age, the lifetime production would be eight lambs. The increase in initial lamb production is 60 percent.

The hypothesis is testable by one of the following three methods. First, if young ewes from the Dry Creek population could be marked and prevented from breeding during their frst estrus at 18 months and their reproductive pattern followed, the hypothesis predicts futher annual production. Second, cultivation and establishment of a normal ram age structure by closure of ram hunting in the area of alternate-year lambing and continued studies of reproductive frequency should show whether the hypothesis predicts correctly. Finally, monitoring reproductive pattern and frequency in an unhunted population similar to the Dry Creek population should show a delayed breeding age and greater reprodutive frequency. Such a potential study exists in Denali National Park, about 70 km to the west of the low-quality group. We favor the third option in order to test the hypothesis and intend to pursue it as funding becomes available.

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Table 1. Annual resightings of collared ewes with or without lambs at the Dry Creek and Sheep Creek study sites.

	Dry Creek (n = 88)		Sheep Creek (n = 74)	
With/with	6%		66%	
With/without biennial	26%	= 50%	13%	= 30%
Without/with production	24%		17%	
Without/without	44%		4%	

Table 2. Dall sheep population characteristics at the Dry Creek and Sheep Creek, Alaska Range study sites.

Characteristic	Dry Creek (low-quality)	Sheep Creek (high-quality)
Ram horn growth quality index (Heimer and Smith 1975)	14th of 18	4th of 18
Mean lamb production	55 lambs/100 ewes	65 lambs/100 ewes
Percent lamb survival to yearling age	51 percent	54 percent
Mean yearling recruitment	26 yearlings/100 ewes	32 yearlings/100 ewes
Near-term fetal weight	2.2 kg (n = 7)	2.8 kg (n = 8)
Mean suckling duration	15 seconds (n = 139)	14 seconds (n = 60)
Mean age in collected sheep	91 months (n = 24)	66 months (n = 17)
Summer range density	3.5 sheep/km2	1.5 sheep/km2
Winter range density	5.3 sheep/km2	2.0 sheep/km2
Habitat character	gentle hills short drainages elevation relief = 830 m glaciers absent abundant vegetation	steep hills long drainages relief = 990 m glaciers present sparse vegetation

CONFERENCE DISCUSSION

Q. I think you are suggesting you could produce more sheep for harvest in the low quality population by having more mature rams present there. That is, going to harvest of older males such as you do in the Tok study area is the cure for alternate year breeding. Would you discuss the impact this has on hunter opportunity within these populations? Are you going to increase the sheep populations, but offer reduced hunting opportunity.

Ans. At the outset it appears hunting opportunity would be lessened under a system where harvest is limited to the take of rams above the age of 8 years. However, since we are dealing in hypothetical terms, here let's go just a bit further. A look at the survivorship curves published for unhunted mountain sheep populations suggests that mortality is greatly increased as rams mature socially and take a major role in the rut. If we apply the rate of mortality which is presumably rut-associated to the very young rams it appears we may be able to harvest more rams at full curl (maximally) than at younger ages. This presumably occurs because rut-associated mortality is transferred to younger rams which are not adapted to survive it. If this is true, we could harvest more rams by cropping maximally at full-curl age than by cropping maximally at 3/4 curl. Let me emphasize that we are working with a hypothesis here. This has yet to be tested, but we do have some data which indicate we can harvest as many or more sheep at full curl as we used to at 3/4 curl.

Q. Wayne, what you are saying is contrary to lots of traditional management theory, that the most productive herds have a young age structure. I believe you are saying that reestablishment of an older-age male segment in the population will make the herd "young" and productive again. This reminds me of the situation in our National Parks in Alberta where we see nice lamb crops with these "old" herds until winter and the followng spring. Then it seems that winter losses bring that survival way down. Do you have survival rates on lambs in your "old" herd, the high quality one, vs. your low quality herd, the one where rutting is run by younger rams?

Ans. Yes, survival in the low quality herd averages 51% and in the high quality herd it averages 54%. Of course, survival varies with winter severity which is not uniform for the 2 study areas. I don't believe there is any statistically significant difference in survival between the herds. We've seen an interesting relationship that we don't understand, or even have a hypothesis for; mortality seems higher (percentage-wise), the higher the lamb crop. Still, recruitment to yearling age is easily greater following a high initial lamb production (even with the increased percentage of mortality). Higher initial lamb production seems to result in greater yearling recruitment.

Q. In which herd?

Ans. Either one, or both. Even if there is a greater (percentage) mortality which seems associated with higher lamb producton, yearling recruitment doesn't seem to be low because of the higher mortality. We always come out ahead following years with great lamb production.

Q. Just a couple of points, Wayne, on the Kenai Peninsula study areas we've come through some difficult winters which caused significant adult mortality. The herd which had been heavily harvested, where there wasn't a ram older than 3/4 curl, produced the highest relative number of lambs last year, that is, had the greatest lamb:ewe ratio of all 3 populations studied. This includes a population where no hunting is practiced. This is just the opposite of what your hypothesis predicts. A question I have is: Have you made any comparisons of range conditions between your so-called high and low quality herds? Do you know that your low quality herd, for example, is actually a more dense population in terms of forage available per individual? You mentioned in one of your reports that vegetation was rather abundant in your low quality area and relatively sparse in the high quality area.

Ans. Concerning your first comment, I should stress that the hypothesis predicts generally, and I am not surprised nor alarmed that exceptions exist. This is particularly true for the Kenai study areas where you showed weather influences on the 3 sheep groups were quite variable among ranges. If we could be assured that weather influences were consistent among your 3 populations I'd be more prone to re-examine the hypothesis. The answer to your question is, no. We haven't done any classical range work, but we have looked at the quality of food plants between the 2 areas in summer. We have also looked at the quality of food plants during winter as reflected by the quality of washed rumen contents. This means we have examined the plants selected by sheep on winter range and compared them at the beginning and end of winter. There is no differnce in food quality of washed rumen contents. I think this suggests uniformly poor quality winter range is available to both populations to the extent that it isn't limiting in a classical, live or starve, sense. We suspect that it doesn't matter how much low quality food is available beyond what is necessary to keep the rumen full. As long as sheep can fill their rumens they will do as well as possible. Of course, winters of such severity that keeping the rumen full and active is not possible do occur. These winters result in death of unusually large numbers or percentages of adults. In the Interior of Alaska winters like this are rare, and a severe winter is usually indicated by low lamb production the following spring more than by death of large numbers of adults. Ewes apparently utilize the energy stored in the fetus before they expire.

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