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COMPARATIVE DYNAMICS OF DISSIMILAR DALL SHEEP POPULATIONS

By

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SUMMARY

A long-term study of Dall sheep (*Ovis dalli dalli*) in the central Alaska Range of Interior Alaska provided data on population responses to variations in weather, predator density, and changes in human management which greatly altered the abundance of rams. Two populations with different management schemes were compared. One population was lightly hunted at the beginning of the study and then heavily hunted. During the period of heavy hunting, regulations were altered to increase legal ram horn size from 3/4 to 7/8 to full curl. The 2nd population was lightly hunted for only full-curl rams throughout the study. Results indicated ewes in the heavily hunted population with few mature rams began breeding at an earlier age and had a lower reproductive frequency than ewes in the lightly hunted population. Following a regulation change that increased legal horn size to 7/8 curl, the ram population increased and ewes began breeding at a later age, had greater reproductive frequency, and there was an increased lamb:ewe ratio. Changes in reproductive frequency and lamb:ewe ratio following the regulation change were statistically significant $\underline{P} \leq 0.05$), and the values approached those of the less dense and less heavily hunted population where a full-curl minimum horn size regulation had been in place for 12 years.

Weather and predator abundance also influenced population dynamics parameters, but not to the extent attributed to ram abundance. Range condition and body condition of the sheep was not correlated with changes in reproductive frequency or lamb:ewe ratios.

A theory explaining the influence of ram age structure and abundance on reproductive performance is presented. Also, ram survival increased with establishment of an older age structure among rams. However, concurrent reductions in predator abundance and favorable weather may have also contributed to the increased survival. Hunter harvest and success did not decline with establishment of the regulation which raised legal horn size from 3/4 to 7/8 and full curl.

Key words: Dall sheep, management, mortality, *Ovis dalli*, population dynamics, predation, reproduction, weather.

CONTENTS

BACKGROUND

Basic Ecological Theory of Mountain Sheep

Geist (1971), in his classic work on the behavior and evolution of mountain sheep, detailed a unified theory to account for differences in population characteristics of mountain sheep. This hypothesis, now known as "Geist's dispersal theory," details 2 syndromes or complexes of characteristics that define extremes of the "population quality" spectrum in mountain sheep. On 1 end are high-quality populations (composed predominantly of individuals with dispersal phenotypes) which are characterized by high lamb production, high yearling recruitment, rapid body and horn growth to large size, and vigorous social interaction. Populations of this type are thought to exist on expanding ranges and demonstrate rapid population turnover caused by young age at death. On the other end of the spectrum are populations of low quality (composed predominantly of individuals with a maintenance phenotype). These populations are characterized by relatively lower lamb production, lower yearling recruitment, less rapid body and horn growth to modest size, infrequent and generally nonvigorous social interactions, and relatively longer life expectancy. These populations are thought to inhabit fixed or constricting ranges and, according to the theory, tend toward population stability.

Previous Work on Alaskan Dall Sheep

Another tenet of Geist's dispersal theory (1971) holds that sheep population quality can be assessed by the rate of growth and ultimate size of horns produced by rams. This followed from the observation that horns are extremely important social organs among the mountain sheep (Geist 1971). Heimer and Smith (1975) characterized ram horn growth in 18 physiographic regions throughout Alaska's Dall sheep (*Ovis dalli dalli*) ranges and found significant differences ($P \leq 0.05$) in population quality as determined by ram horn growth rate and size.

Heimer and Smith (1975) also found a significant ($P \leq 0.01$) inverse relationship between population density and population quality as inferred from horn growth. Because Geist's original work (1971) was based on a postulated difference in range resources as a selective factor for either the dispersal (energetically extravagant) or maintenance (energetically conservative) phenotype, the next logical investigation centered on energetic comparison of a high-quality (dispersal phenotype) population with a low-quality (maintenance phenotype) one. This comparison was made between 1976 and 1980.

Two populations of Dall sheep in the Alaska Range east of Mt. McKinley were selected for comparison of range resource availability. The low-quality group was assessed by Heimer and Smith (1975) and found to have the 2nd lowest horn growth (i.e., 2nd lowest population quality) in Alaska. The high-quality population ranked 3rd for best horn production among rams in the areas sampled. These populations are at the ends of the horn growth spectrum (and hence, by inference, the population quality spectrum).

Energy accumulation in the sheep's body was used as an index of the balance between energy availability and energy utilization (Heimer 1983). Ewes were collected during the rut, the presumed time of maximum fatness, and at winter's end, the time of probable minimum fatness. To minimize the effects of short-term variations in range production which have been shown to affect Dall sheep populations (Hoefs and Brink 1978), ewes were shot over a 4-year period. All samples from each study area were then pooled for that population and analyzed as a group. This was done to characterize, generally, the resources for each range by damping weather-specific, short-term variations. Pooling was also necessary because of the small sample sizes involved. Age at collection, body mass, body composition (energy storage), and quality of food selected, as indicated by nutrient analysis of washed rumen contents, were compared. The sample of ewes taken from the low-quality population had a significantly greater ($P \leq 0.05$) mean age, averaging 2 years older than the high-quality group. No significant ($P \geq 0.05$) differences in body size, body composition, or quality of range resources were identified. The differences in mean age and the historic differences in population performance indicated that Geist's hypothesis (though not supported by the quantitative, nutritional aspects of this work) was nonetheless worth investigating further. Hence, we began a comparative study of dynamics of the 2 study populations.

Study Areas

Both study areas are located on the north side of the Alaska Range east of Mt. McKinley (Fig. 1). Characteristics of each study population are listed in Table 1.

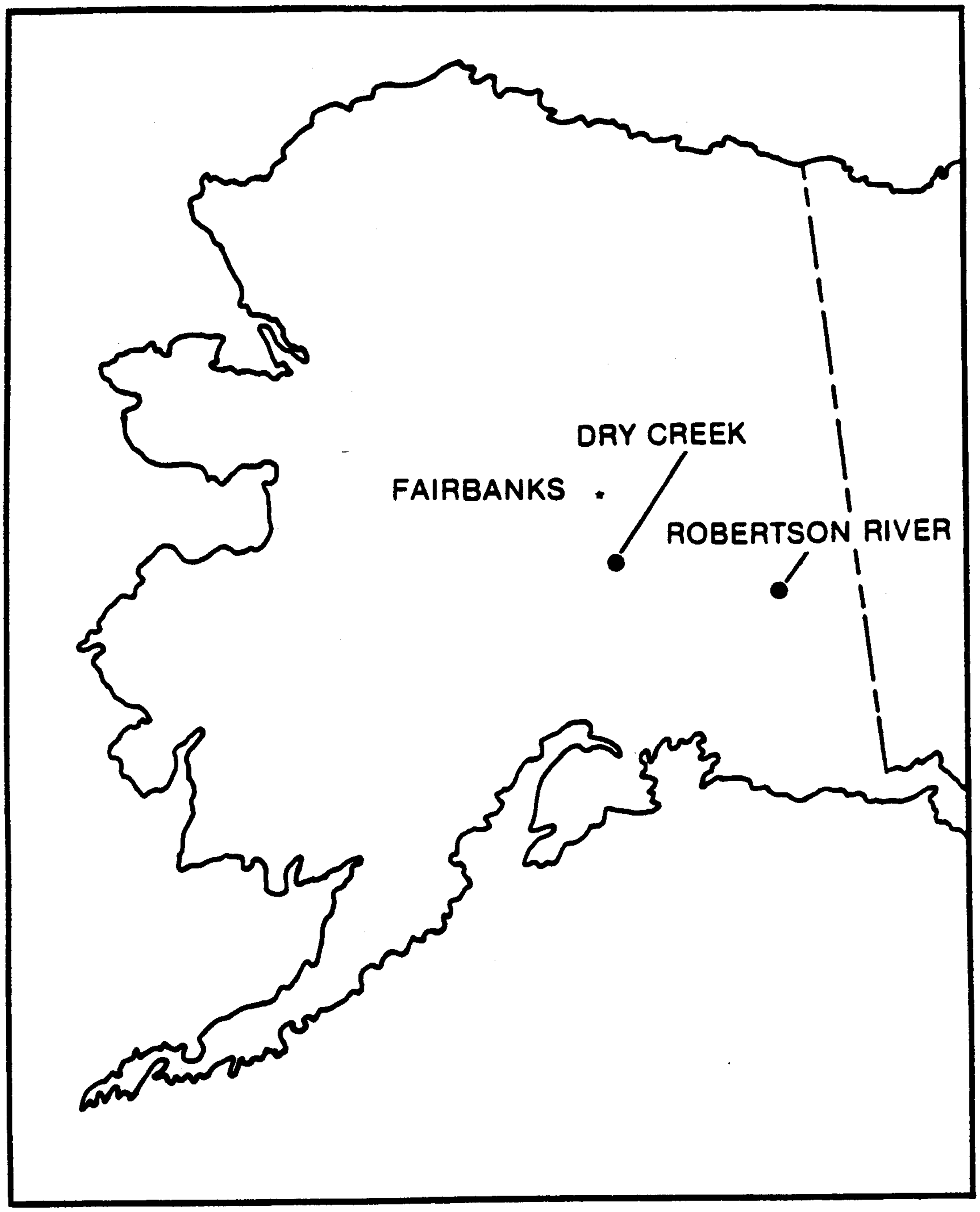

Fig. 1. Location of Dall sheep study areas within Alaska.

Table 1. Characteristics of Dall sheep populations from the Dry Creek and Robertson River study areas in Interior Alaska.

Dry Creek	Robertson River
Population ranges defined by movement study of marked Dall ewes.	Population ranges defined by movement study of marked Dall ewes.
Summer range size: 680 km^2 (260 mi^2)	Summer range size: 750 km^2 (290 mi^2)
Population size: 1,200-1,500 sheep	Population size: 1,000-1,200 sheep
Habitat character: gentle hills short drainages elevation relief 830 m glaciers absent	Habitat character: steep hills long drainages elevation relief 990 m glaciers present
Mean summer range density: 2-2.5 sheep/km^2 (5-6 sheep/mi^2)	Mean summer range density: 1-1.5 sheep/km^2 (3-4 sheep/mi^2)
Mean winter range density: 5 sheep/km^2 (14 sheep/mi^2)	Mean winter range density: 2 sheep/km^2 (5 sheep/mi^2)

Population Histories

The recent histories of the 2 populations are markedly different. Both have been essentially protected from human exploitation, except for the harvest of rams, since well before Alaska statehood in 1959. Between statehood and the beginning of sheep research in the Alaska Range in 1968, the legal size for rams at harvest was 3/4 curl (approximately 4-5 years of age), and ram harvests were small.

Dry Creek:

In the late 1960's the human population of Interior Alaska began to increase, and hunter pressure was high in the low-quality Dry Creek area because of its ready access from Fairbanks. Furthermore, publicity associated with the beginning of the sheep research effort raised hunter interest in the area.

Both study populations presumably benefited from the widespread predator control programs carried out before statehood in 1959, from the bounty on wolves (*Canis lupus*), and from the unrestricted shooting of wolves from aircraft. Other ungulates in Interior Alaska also benefited from low predator abundance and favorable weather conditions which resulted in generally high ungulate numbers in the mid-1960's. When the wolf was classified as a big game animal in 1963 and aerial wolf shooting was prohibited, wolf populations grew dramatically (Harbo and Dean 1981). By 1970, wolves were abundant in the low-quality Dry Creek area, and that sheep population was at a recorded maximum. Over the next 5 years, caribou (*Rangifer tarandus*) and moose (*Alces alces*) in the surrounding area declined rapidly. The sheep population also began a slow, steady decline of approximately 20% over the next 5 years.

In 1975, a wolf reduction program was undertaken to aid declining populations of caribou and moose in the area adjacent to Dry Creek. Many wolves were removed from the sheep ranges as well, and by spring 1977 wolves were scarce in the Dry Creek study area. With commencement of the wolf reduction program, the Dry Creek sheep population stopped declining and numbers remained about the same for the next 3-4 years (Heimer and Stephenson 1982).

Winter weather was also a factor in the overall sheep population changes. The greatest snowfall record for Fairbanks (approximately 70 miles north of the Dry Creek study area), occurred in 1970-71. The sheep population did not show decreased lamb production or yearling survival that year. In 1972, lamb production (15 lambs:100 ewes) was the lowest on record, and survival of the lambs produced in spring 1971 was very low. Travel on foot was extremely difficult that spring; we have never seen as much snow in the Dry Creek country as in April 1972. Between 1972 and 1982, all indications are that snowfall was above average only twice; 1975 and 1979 averaged 3.5 inches above average (Table 2). Snow accumulation during winter 1981-82 was followed by low lamb survival, large loss of old ewes, and increased observed mortality for marked ewes of the young and middle age classes. Since 1982, weather has been considered normal.

In 1979, the minimum age at ram harvest was raised about 2 years by changing the legal horn definition to 7/8 curl (Heimer 1980). In 1984, the ram age for legal harvest was raised again. This was done by establishing a full-curl legal horn size; this size horn is attained when a ram is approximately 8 years of age.

Robertson River:

In the high-quality Robertson River study area, population monitoring began in 1974. Up to this time, harvest had been light, but hunting pressure and harvest were increasing. In 1974, this area was established as a trophy management area. Since then, total harvest in this area has been limited to less than the recruitment to the full-curl class. This population did not experience the high level of wolf predation, the heavy exploitation by hunters, or the population fluctuations shown by the lower quality Dry Creek sheep. Consequently, we considered this a control population, and in 1974 we began to compare factors influencing population gain and loss in these 2 groups of sheep.

The Study Rationale

We gathered data in an experiment testing the null hypothesis that a change in the minimum ram harvest size/age from 3/4 to 7/8 curl would have no effect on lamb:100 ewe ratios, observable age at 1st reproductive activity for ewes, and observed frequency of reproductive success in consecutive years. The alternate hypothesis was that the change in minimum age/horn size from 3/4 to 7/8 curl would be accompanied by increased lamb:100 ewe ratios, decreased early-age reproductive activity, and increased observed frequency of reproductive success in consecutive years. A corollary to the alternate hypothesis was that these changes should approach or equal those in the control population where heavy hunting did not occur and the minimum age/size class at harvest was full curl.

By using the data collected to test this specific hypothesis as well as data gathered primarily for descriptive purposes, we shall generate other alternate hypotheses which can be

Table 2. Relative lamb production and ecological influences for the Dry Creek, Alaska study area, 1968-84.

Variables	Year	Rams: 100 "ewes"	Lambs: 100 ewes		
3/4-curl regulation	1968	--[a]	63		
Light harvest	1969	--	64	$\bar{x}$ = 58	
Human use increases	1970	32	55	SD = 7	
	1971	--	50		Difference significant $P \leq 0.014$
Unusually severe winter	1972	--	15		
Very heavy harvest	1973	--	38	$\bar{x}$ = 29	
from 1972 on	1974	--	28	SD = 7	
	1975	17	28		
Wolf control begins	1976	--	36		
	1977	--	58		Difference significant $P \leq 0.008$
	1978	--	41		
7/8-curl regulation	1979	--	65		
Wolf control ends	1980	32	67	$\bar{x}$ = 54	
	1981	--	60	SD = 12	
	1982	--	31		
	1983	--	57		
Full-curl regulation	1984	39	51		
		$\bar{x}$ = 49 SD = 15			

[a] Data not collected.

tested through further work. We propose to place these hypotheses in a working, conceptual frame which, we are hopeful, will provide a basis for further refining of future Dall sheep management.

"Population dynamics" may be defined as the relationship between population gain (through production and eventual recruitment or immigration) and population loss (through mortality or emigration). However, the very use of the term "population dynamics" seemingly evokes the expectation that virtually all aspects of population increase and decrease will be rigorously elucidated and expressed mathematically. If our use of this term leads readers to anticipate such a total exposition, we apologize. Difficulties in gathering complete data on wild populations subject to the vicissitudes of nature preclude an exhaustive investigation of all aspects of population change for Dall sheep at this time. We are forced to the simple view with the realization that our conclusions may be compromised by details which are as yet beyond our reach. We hope to acknowledge the deficiencies of our data as we discuss them.

Even simple treatment of data related to population dynamics requires that certain conditions exist. One basic condition is that emigration and immigration not be complicating factors. Many studies of mountain sheep in general (Geist 1971, Shackleton 1973, and Wishart 1978) and Dall sheep in particular (Heimer 1973, Horejsi 1976) have shown that emigration and immigration are unlikely for marked mountain sheep. Mountain sheep are loyal to their home ranges. Emigration and immigration were not assumed to play a role in this work.

Traditionally, differences in population performance have been attributed to differences in weather, nutrition, and predation. We chose to consider ram abundance, a consequence of human hunting, as a possible cause as well.

OBJECTIVES

In 1981, the following objectives were defined:

Study Objective: To determine total numbers, composition, lamb production, yearling recruitment, range ecology, and population dynamics of high- and low-quality populations.

Job Objective: To determine initial lamb production, yearling recruitment, survival, and reproductive frequency in the low-quality Dry Creek population and these same parameters in the high-quality Robertson River population.

Since that time, objectives have been written in less expansive and more specific language. Consistent with this trend, more discrete objectives were defined. These objectives included the attainable portions of the original study and job objectives, and clarified the direction of the work. They are listed below.

1. To test the hypothesis that establishing an older ram age structure by replacing the 3/4-curl regulation with a 7/8-curl harvest minimum would have no effects on lamb production, age at 1st observable reproduction, and consecutive-year reproductive success by ewes.

2. To examine factors which may influence lamb production: ovulation rate, age at beginning of reproductive activity among ewes, and frequency of reproductive success among ewes in 2 differing Dall sheep populations.

3. To determine lamb survival to yearling age, and to measure yearling recruitment in 2 differing Dall sheep populations.

4. To determine survival of rams beyond yearling age in 2 differing Dall sheep populations.

5. To determine survival of ewes beyond yearling age in 2 differing Dall sheep populations.

6. To integrate data gathered in achievement of the stated objectives and make recommendations for improving Dall sheep management in Alaska.

PROCEDURES

Objective 1: Testing the Hypothesis About 3/4- to 7/8-Curl Hunting Effects

Determining Lamb Production:

Countable lamb production is the most common indicator of population well-being in sheep management. It is usually represented as lambs:100 ewes or lambs:100 "ewes" when all sheep not clearly identifiable as rams (adult ewes, yearlings of both sexes, and young rams) are combined, as in data gathered during aerial surveys. Lamb:100 ewe ratios were calculated by dividing the number of lambs by the number of ewes classified in the last half of June, when sheep used the mineral lick in Dry Creek. All sheep entering the lick were classified with respect to sex and age. Classifications were done at 50-200 m with the aid of 15-60X spotting scopes.

Mineral licks were observed from 0400 to 1200 hours (Alaska Standard Time [AST]) in all years. During 1972 the lick was observed 24 hours per day. In 1973 the lick was observed for 18 hours per day beginning at 0400 hours AST.

Weather Effects During Gestation:

Conditions which are likely to be unfavorable for gestation, such as severe cold and/or deep snow which precludes feeding, may cause low observable lamb:100 ewe ratios. Snow depth along transects established by the Soil Conservation Service (USDA) to predict spring runoff were used as indices of winter severity effects on gestation. Lamb:100 ewe ratios were regressed against mean snow depth averaged across the north side of the Alaska Range for Tok, Ft. Greely, Big Delta, and Lake Minchumina snow transects.

Weather Effects at Parturition:

Weather conditions which promote heat loss from newborn lambs may lower observable lamb:100 ewe ratios. These conditions include low temperatures and persistent precipitation. To derive an index of weather conditions for the experimental (Dry Creek) population during the lambing period, we used temperature and precipitation data gathered at Big Delta, Alaska. Big Delta is 65 km (40 mi) northeast of the Dry Creek study area. The weather at Big Delta is more indicative of Dry Creek weather than any constantly maintained weather station along the Alaska Range. We averaged the daily minimum temperatures for the parturition period (26 May-7 June) for each year. Deviations from the mean (either plus or minus) were calculated. These deviations were then multiplied by 10 times the total precipitation (which was frequently less than 0.5 in) for the lambing period in each year. Indices were adjusted so the least favorable (coolest and dampest) year was equal to zero for purposes of statistical computation.

Weather Effects on Breeding Condition:

Hoefs (1984a) reported statistical correlations of presumably favorable growing conditions with good lamb production in Kluane, Yukon Territory. He found high rainfall (which generally accompanies cool weather in Alaska) was correlated with increased food production. Presumably, better plant production leads to better breeding condition and/or better winter nutrition. We evaluated this relationship in Dry Creek by taking Big Delta temperature and precipitation data from summaries published by the U.S. Weather Bureau for the months of June, July, and August. Mean low temperature for each month was averaged, and total precipitation recorded for the 3-month period. Then a weather index combining temperature and actual rainfall was calculated as described above for the lambing period.

Aggregate Weather Effects:

Once weather indices relating to breeding condition, gestation, and parturition period were derived, the overall mean and standard deviation for all years for each parameter were calculated. The deviation of each year's index from the mean was arbitrarily expressed as either positive or negative depending on which side (favorable or unfavorable) of the mean weather condition it fell. The distance from the mean in "half standard deviation" units was then calculated for each parameter each year. The algebraic sum of these deviation units was totaled for all weather components each year, thus producing an overall or aggregate weather index. The lamb:100 ewe ratio was regressed on this aggregate index of weather influence (Fig. 2).

Determining Age at 1st Successful Reproduction:

The age at which ewes became reproductively active was determined by 3 methods. The reproductive status of each ewe trapped in June (Heimer et al. 1980) was determined by external palpation, examination of external genitalia, and mammary development. Also, yearling ewes were marked. Careful observations were made when these ewes were resighted at mineral licks the following years. Ewes were said to have reproduced if they suckled a lamb, showed bloody discharge from the vulva, had dried blood on their tail or legs, or had fully developed udders. Small numbers of young ewes aged 18 and 30 months were also collected in April. Reproductive activity in these ewes was determined by autopsy.

Determining Frequency of Reproductive Success:

All marked ewes were carefully observed each June as they used the mineral lick. If ewes were observed mothering or suckling a lamb, they were classified as having succeeded reproductively that year.

Objective 2: Factors Which Affect Lamb Production

Ovulation Rate:

Ovaries were collected from ewes in each study population from 1972 through 1979. Ewes sampled were shot at random for use in other studies. Ovaries were preserved in 10% formalin as soon as possible after death; ovaries not preserved within 48 hours were discarded. Collected ovaries were sent to Dr. Beth Williams of the University of Wyoming. Fixed ovaries were trimmed of connective tissue, measured, weighed, and the volume estimated by water displacement. Ovaries were then sliced in 1 mm sections along the longitudinal axis and

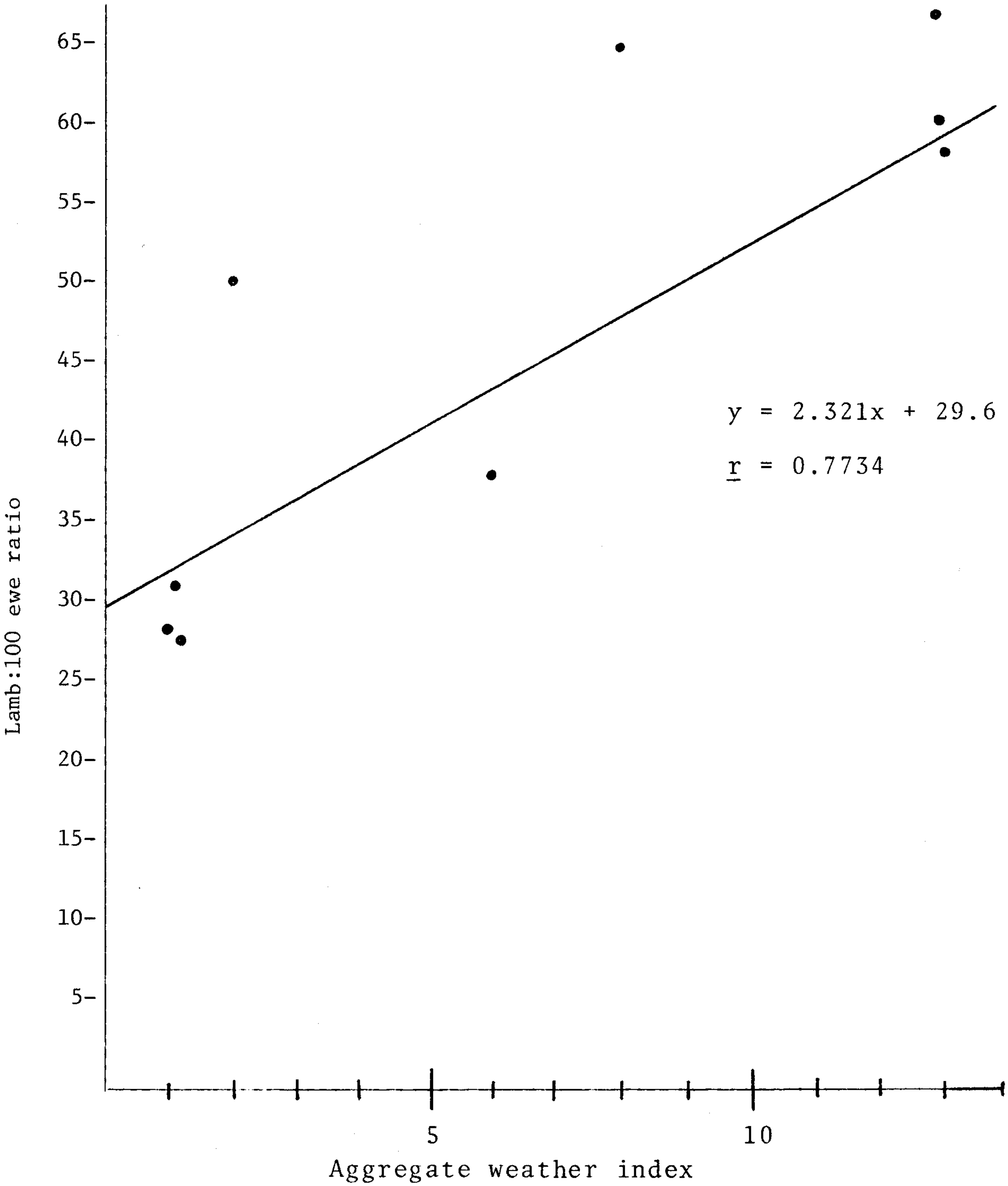

Fig. 2. Lamb:100 ewe ratio as a function of aggregate weather index for Dry Creek, Alaska Range, 1971-82.

examined grossly. Pigmented areas were counted in each ovary according to standard techniques (Kirkpatrick 1980). Faces of individual slices were drawn and labeled so gross structures could be correlated with structures observed microscopically. Individual slices were then embedded in paraffin, sectioned at 6-7 microns, and stained by hematolxylin and eosin. Cases in which pigmented bodies could not be identified were also examined using Masson's stain for connective tissue. Dr. Williams stained and sectioned the ovaries because significant ovarian events leave "tracks" or pigmented areas in ovarian tissue. These pigmented areas are discernible upon gross examination of the ovaries. However, some pigmented areas are not the result of ovarian cycling, and confirmation of the exact nature of each pigmented body requires sectioning, staining, and microscopic examination.

The number of significant ovarian events was considered equal to the sum of corpus luteum bodies (produced by ovulation) plus the number of corpora albicantia (produced by degenerating corpora lutea). The number of active breeding seasons possible in the life of each ewe was computed from her age, after establishing that 1st ovulation occurs at 18 months. Ovulation rates were then expressed as the quotient of possible active years divided into the events recorded in ovaries from each ewe. Means were determined for each population, and a Student's _t_ test of ratio estimators was used to establish the probability that differences were due to sample variance (Cochran 1977).

Age at 1st Successful Lamb Production:

See Objective 1.

Reproductive Frequency:

See Objective 1.

Objective 3: Lamb Survival and Yearling Recruitment

Yearling recruitment is a more meaningful indicator of population gain than lamb production. Mortality patterns for Dall sheep (Murie 1944, Bradley and Baker 1967, Hoefs and Cowan 1979) indicate a high probability of survival and reproductive contribution to the population once a Dall sheep reaches 1 year of age. Yearling recruitment is most frequently expressed as yearlings:100 ewes or "ewes" as discussed above. Because the number of ewes was determined in each study population from aerial censuses and mineral lick composition counts, the actual number of yearlings in the population was calculated as well as the ratio of yearlings:100 ewes.

Survival from lamb to yearling age in both populations was calculated from lamb and yearling:100 ewe ratios and from the absolute numbers of lambs and yearlings in each population. These survival percentages were then compared with those derived using ratios to see if a change from the standard usage of ratios for calculating survival was warranted.

Objective 4: Ram Survival Beyond Yearling Age

Survival of rams was estimated by the observed persistence of marked individuals in each population and by reports of hunters who harvested marked, legal rams. Methods and schedules used to determine ram mortality in the low-quality, Dry Creek population are detailed in Appendix A.

Ram survival to 3/4-curl legal horn size was also calculated from yearling recruitment, assuming that half of the yearlings recruited into the Dry Creek population each year were rams (Nichols 1978, Hoefs and Cowan 1979). Mortality was estimated from observations at the Dry Creek lick. Comparative survival data were taken from Murie (1944).

Objective 5: Ewe Survival Beyond Yearling Age

Mortality during the 1st year of life usually has greater impact on population dynamics than mortality beyond yearling age (Bradley and Baker 1967). Still, environmental resistance which operates on sheep once they have been recruited to the population is of intense interest to the wildlife manager. The survival of ewes in both populations was determined by resighting marked animals. Ewes, if alive, have been shown to return to their mineral lick at a rate which closely approaches 100% (Heimer 1974). Ewes whose status was in doubt because of our failure to see them at the mineral licks were not presumed dead until they had not been seen for 2 successive summers. When this occurred, unsighted ewes were presumed to have died during the winter following the last resighting. Observation methods and schedules are in Appendix B, Heimer (1978), and Heimer and Watson (1982).

Objective 6: Estimation of Population Size

Population size was initially estimated by aerial census. Subsequently, the presence of marked individuals allowed refinement of these figures by allowing computation of a "sightability" factor. Summer ranges, as defined by presence of marked sheep (Heimer 1973), were flown after mineral lick observations had established the total number of marked ewes present. Our efficiency or "sightability factor" was then determined by dividing the number of marked sheep sighted on census flights by the number known to be present in each study population. It was assumed that the sightability of ewes was equal to that of rams. After the 1st segment of our work, rams were marked with ear tags only, and their sightability from aircraft could not be determined.

Aerial censuses were not conducted each year. In years when aerial censuses were not conducted, population size was estimated by modeling the Robertson River population and from the intensity of mineral lick use in a standardized sample period in the Dry Creek population. Details of this method are presented in Heimer and Stephenson (1982).

RESULTS AND DISCUSSION

Objective 1. Testing the Hypothesis About 3/4- to 7/8-Curl Hunting Effects

Lamb Production:

Lamb production, expressed as lambs:100 ewes, was more variable in the Dry Creek population than in the Robertson River population. In Dry Creek (Table 2), the values for lamb production ranged from 15 to 67 lambs:100 ewes with a mean of 49 lambs:100 ewes (SD = 15). The standard deviation for Dry Creek was 31% of the mean. Also in Dry Creek, good lamb production and poor lamb production occurred in groups of consecutive years which appeared to be separated by identifiable changes in environmental variables (Table 2). Lamb production was significantly lower during the 1972-76 period than for years before ($P \leq 0.014$) or since ($P \leq 0.008$) when tested using the Mann-Whitney U-test.

In the Robertson River populations, the lamb:100 ewe ratio also averaged 49 lambs:100 ewes, but the standard deviation (12 lambs:100 ewes) was only 24% of the mean (Table 3). The poorest production period for this population was 1982-85 ($\bar{x}$ = 44 lambs:100 ewes; SD = 11). Production was highest for the years 1977-81; lamb production averaged 59 lambs:100 ewes (SD = 7). There was no significant difference between mean lamb:100 ewe ratios for these periods ($P \geq 0.05$) using the same statistical test.

Relative lamb production in Dry Creek varied more than at Robertson River, suggesting greater variation in environmental conditions at Dry Creek. These variations could be due to weather, nutrition, predation, and/or ram abundance.

Weather:

In Dry Creek, the best relationship was between summer weather (which might influence lamb production through ewe breeding condition and/or nutrition during pregnancy) and the lamb:100

Table 3. Relative lamb production in the lightly hunted Robertson River, Alaska Dall sheep population 1974-85. Full-curl, restricted permit hunts in effect since 1974.

Year	Lambs:100 ewes		
1974	56		
1975	43	$\bar{x} = 45$	
1976	35		
1977	52		
1978	57		
1979	63	$\bar{x} = 59$	
1980	69		
1981	52		Difference not significant ($P \geq 0.05$)
1982	29		
1983	43	$\bar{x} = 44$	
1984	45		
1985	57		
	$\bar{x} = 49$		

ewe ratio the following spring. Warmer and drier weather during the June-August plant growing season was positively correlated (*P* ≥ 0.05) with increased lamb production the following spring. This finding was contrary to that found by Hoefs (1984*a*) who found a positive correlation between increased precipitation and increased lamb production. This difference may be explained by the more xeric nature of the Kluane Lake sheep ranges compared with Interior Alaska (Hoefs and Brink 1978). The equation generated by linear regression of the lamb:100 ewe ratio as a function of this composite weather index was $y = 0.824x + 28.7$ (Table 4). The correlation coefficient ($r = 0.64$) indicated the probability of this relationship being invalid because sample variance was less than 0.02.

Neither of the other indices, weather during gestation and weather at lambing, showed a significant statistical correlation ($P \geq 0.05$) with lamb:100 ewe ratios in Dry Creek. Weather effects during gestation were described by the regression equation, $y = -1.07x + 65.0$; $r = 0.36$ (Table 5). This relationship has a probability of being invalid due to sample variance of 0.10.

Lambing weather index as a determinant of lamb:ewe ratio (Table 6) produced the equation, $y = 0.25x + 27.5$. The correlation coefficient for this regression, $r = 0.46$, indicated the probability that this relationship is invalid because sample variance was 0.12. Generally, it appears that lambing weather had the least influence on lamb production of the 3 weather components we identified.

We hypothesized that the effects of weather were additive, so we developed and tested an aggregate weather index. This index correlated strongly with lamb production ($r = 0.77$, $P \leq 0.01$) (Fig. 2 and Table 7).

The strong correlation of the lamb:100 ewe ratio with our aggregate weather index seems to provide support for the common observation that "good" weather frequently occurs with high lamb production. Still, it is worth noting that the correlation of lamb production with the aggregate weather index is much stronger than for any of the individual indices. In the past, the study of weather as an influence on lamb production has centered on winter severity as it influences foraging ability during gestation. A broader approach to the effects of weather may be more productive.

Nutrition:

The data we have on nutritional condition of ewes do not bear directly on the hypothesis under examination here. We have no nutritional data from either the Dry Creek or Robertson River

Table 4. Composite weather index from temperature and precipitation for June, July, and August 1970-85, and regression equation of composite weather index on next June lamb:ewe ratios at the Dry Creek mineral lick, 1970-85.

Year	Mean low temp. (F)	Deviation from overall mean low (F)	Total precipitation (in)	Index[a]	Standardized index[b]	Next June's lamb: 100 ewe ratio
1970	47	-1.3	3.84	-4.95	12	50
1971	47	-1.3	5.46	-7.10	15	15
1972	49	+0.7	5.88	+4.12	21	38
1973	46	-2.3	7.36	-16.93	0	28
1974	47	-1.3	6.96	-9.15	8	28
1975	48	-0.3	8.29	-2.49	14	36
1976	50	+1.7	7.40	+12.58	30	58
1977	51	+2.7	7.59	+20.49	37	41
1978	50	+1.7	5.51	+9.37	26	65
1979	51	+2.7	8.60	+23.22	40	67
1980	49	+0.7	5.74	+4.02	21	60
1981	48	-0.3	5.99	-1.79	15	31
1982	47	-1.3	7.15	-9.30	8	57
1983	48	-0.3	8.06	-2.42	15	51
1984	47	-1.3	12.47	-16.32	1	

$y = 0.824x + 28.7$ (Note: y = lamb:100 ewe ratio
Average index = 18 ± 6.65 (95% CI) x = Standardized Index)
$\underline{r} = 0.639$
$\underline{P} \leq 0.02$

[a] Index equals deviation from mean temperature (+ or -) times total precipitation.

[b] Index standardized by setting most negative values to zero (add 16.93 to each value).

Table 5. Mean snow depth on the north face of the Alaska Range in April and lambs:100 ewes in June and regression equation relating snow depth to lambs:100 ewes, 1968-82.

Year	Mean snow depth (in)	Lambs:100 ewes
1968	18.0	63
1969	18.0	64
1970	5.5	55
1971	26.3	50
1972	24.3	15
1973	12.8	38
1974	17.3	28
1975	20.3	28
1976	17.5	36
1977	13.7	58
1978	15.8	41
1979	20.7	65
1980	17.0	67
1981	8.8	60
1982	22.5	31

$y = -1.07x + 65$ (Note: y = lamb:100 ewes, $x = \bar{x}$ = snow depth)

Average depth = 17 inches ± 3.3 (95% CI)

$r = 0.3556$

$P \leq 0.10$

Table 6. Composite weather index for weather during peak lambing period and regression equation for composite weather index on lamb:ewe ratios in June, Dry Creek study area, Alaska, 1970-85.

Lamb: 100 ewe ratio	Year	Mean minimum temperature 26 May-7 Jun (F)	Deviation from overall mean (F)	10X total precipitation (in)	Index[a]	Standardized index[b]
55	1970	44	-0.2	3.90	-7.8	76
50	1971	43	-1.2	0.01	-0.1	84
15	1972	43	-1.2	9.10	-10.9	73
38	1973	40	-4.2	6.50	-27.3	57
28	1974	42	-2.2	8.40	-18.5	66
28	1975	47	-2.8	7.80	-21.8	62
36	1976	40	-4.2	20.00	-84.0	0
58	1977	48	+3.8	5.00	+19.0	103
41	1978	43	-1.2	7.60	-9.1	75
65	1979	47	+2.8	1.60	+4.5	89
67	1980	49	+4.8	0.20	+9.6	94
60	1981	46	+1.8	12.30	+22.1	106
31	1982	--[c]	--	--	--	--
57	1983	45	+0.8	10.00	+8.0	92
51	1984	40	-4.2	11.50	-48.3	36
--	1985	46	+1.8	11.70	+11.7	96

$y = 0.25x + 27.5$
Average index = 74 ± 15.5 (95% CI)
$\underline{r} = 0.4570$
$\underline{P} \leq 0.12$

(Note: y = lamb:100 ewe ratio
x = Standardized Index)

[a] Index equals deviation from mean temperature times 10X total precipitation.

[b] Index standardized by setting most negative values to zero (add 84.0 to each value).

[c] Data not available.

Table 7. Aggregate weather index of potential influences on lamb production and regression equation of aggregate weather index to lamb:ewe ratio, Dry Creek, Alaska, 1970-81,

Lamb: 100 ewe ratio	Year	Effect on breeding condition	Lambing weather	Gestation weather effect[a]	Index[b]	Standardized index[c]
50	1971	-1	+3	-3	-2	+2
15	1972	-2	+1	-3	-4	0
38	1973	+1	-1	+2	+2	+6
28	1974	-3	+1	-1	-3	+1
28	1975	-2	+1	-2	-3	+1
36	1976	+1	-4	-1	-4	0
58	1977	+2	+5	+2	+9	+13
41	1978	+4	+3	+1	+8	+12
65	1979	+2	+4	-2	+4	+8
67	1980	+4	+4	0	+8	+12
60	1981	+1	+5	+3	+9	+13
31	1982	-1	0	-2	-3	+1

$y = 2.231x + 29.6$ (Note: y = lamb:100 ewe ratio
$\underline{r} = 0.7734$ x = Standardized Index)

[a] Units (+ or -) = 0.05 standard deviations from mean for available data, 1970-82.

[b] Index equals algebraic sum of component deviation units from mean for each parameter.

[c] Index standardized by setting most negative values to zero (add 4 to each value).

population after the change to 7/8-curl ram hunting. However, the lack of difference between Dry Creek and Robertson River populations before the change to 7/8-curl hunting (Heimer 1983) suggests it is unlikely nutritional changes, apart from those which may be weather mediated, could account for changes in lamb:ewe ratio. We doubt there could have been sufficient deterioration in Dry Creek range resources from the early (1968-71) period of high lamb production, to cause the low lamb production of the middle period (1972-76), followed by sufficient range recovery to produce and maintain the high lamb productions of the years from 1977 to the present.

Predation:

Heimer and Stephenson (1982) discussed wolf predation on the Dry Creek sheep population, and Gasaway et al. (1983) detailed the dynamics of wolf populations which inhabit the Dry Creek study area. These authors agree that wolves were a major influence on resident ungulate populations as early as the late 1960's, and following the unusually difficult winters of the early 1970's (Table 2), wolves depressed ungulate populations in the Tanana Flats and the vicinity of Dry Creek. Reduction of wolves by aerial shooting began in spring 1976. One hundred forty-five wolves were killed in the Tanana Flats in 1976, 53 wolves in 1977, 43 in 1978, and 30 in 1979. Table 2 shows that lamb:100 ewe ratios increased markedly from a low period (1972-76) when the average production was 29 lambs:100 ewes to an average of 54 lambs:100 ewes for the 1977-84 period. This difference is statistically significant at $\underline{P} \leq 0.008$ using the Mann-Whitney U-test. It is not certain whether the wolf population should be implicated in this change. The uncorrected aggregate weather indices for the period of low lamb production averaged -2.4 (Table 7). During the period of high lamb productions since 1977, the same index of weather influences averaged +6. It is impossible to separate the influences of weather from those of wolf reduction using this approach.

However, survival of lambs to yearling age in the years when wolves were most abundant, from 1970 through 1975, averaged 66%. This was the highest average survival for any period in Dry Creek. We think this means wolves were not preferentially taking lambs after the month of June. It is generally held that wolves are not serious mortality factors during lambing because mountain sheep select lambing areas among cliffs, in what is classically considered escape terrain. If this is true, wolves would have had to exert their major impact on lamb survival between the time lambs and their ewes left the lambing cliffs and the time we counted them at the mineral licks. We think it unlikely that wolves would prey on lambs at this time and not during the rest of the year. Consequently, we think wolf predation changes were not a primary influence on changes in lamb:100 ewe ratios.

Ram Abundance:

The occurrence of good lamb production beginning in 1977 correlates not only with good weather conditions, but also with increasing ram abundance. The period before the difficult winter of 1972 was one of relatively high lamb production averaging 58 lambs:100 ewes. This coincided with a ratio of 32 total rams:100 "ewes" and a Class III and IV ram:100 ewe ratio of 12:100 "ewes." (Aerial classification of ewes is imperfect because yearlings and rams less than 2 years of age cannot be consistently identified from aircraft.) It was also a period of high wolf abundance. There is little reason to suspect the population composition observed during the 1970 survey was not typical.

Following the severe winter of 1972, through 1976, a period of poor lamb production occurred in which lamb:100 ewe ratios averaged 29. This low production accompanied low total ram and >3/4-curl ram ratios of 17 and 8:100 "ewes," respectively, gathered from the 1975 aerial survey. Following the change to 7/8-curl ram hunting, lamb production increased to the levels of the years before low ram:ewe ratios. An aerial survey in 1980 indicated a total ram:100 "ewe" ratio of 37; another survey in 1984 gave a total ram:100 "ewe" ratio of 39 and a >3/4-curl ram:100 ewe ratio of 16:100 "ewes." The increase in ram numbers was probably a combined result of the 7/8-curl regulation and the reduction in wolf numbers beginning in 1976. If wolves take the most vulnerable prey animals, it seems reasonable that they were specializing in rams from 1972 through 1976. Ram numbers declined during this period; the total number of rams seen on replicate surveys dropped from 173 seen in 1970 to 78 seen in 1975.

In terms of vulnerability to wolves, this meant that ram bands had fewer individuals to watch for predators, a social anti-predator strategy cited by Geist (1971). Also, experienced rams, which presumably were successful at predator avoidance, were rare. Furthermore, the surviving young rams may also have been in poor condition due to their participation in rut in the absence of dominants. Geist (1971) postulated that in circumstances such as these, young rams would be in unusually poor physical condition. The work of Hogg (1984) and Jenni et al. (1986) confirms greater activity during rut by young rams in this circumstance. All these factors may have predisposed these young rams to early mortality due to wolf predation.

Following wolf control, if young ram survival increased, the number of rams should have increased. This increase was amplified when, in 1979, the legal harvest definition was raised from 3/4 curl to 7/8 curl. This certainly would have led to more rams in the population (even disregarding possible survival benefits) (Appendix A) because 2 more ram cohorts were present. Age at 7/8 curl is roughly 2 years greater than age at 3/4 curl. This change (or perhaps these changes) coupled with large cohorts recruited prior to 1972 resulted in higher ram:100 ewe ratios as early as 1977. These higher ram:100 ewe ratios correlate with a mean lamb:100 ewe ratio of 54 for this period. We think these data suggest that ram abundance may also influence lamb production.

This is neither a new nor a revolutionary idea. Allison (1977), working with domestic sheep, related decreasing ram:ewe ratios to a lower probability of ewes becoming pregnant. More importantly, Nichols (1978) also reported a significant correlation (r = 0.62, df = 16, $P \leq 0.01$) between the ratio of Dall rams:100 ewes and the ratio of lambs produced per 100 ewes when all years and all data from his 3 Kenai Peninsula study areas were combined. He wrote (Nichols 1978:578) "Correlation could not be discerned within herds, however, probably due in part to the smaller sample sizes involved. The critical ratio of rams to ewes, below which lambing success suffered, was not determined. I suspect it may depend upon age distribution of rams as well as upon numbers present." We point to another reason correlation could not be discerned within herds. No changes in ram abundance should have occurred in 2 of the 3 herds. One of these was totally cropped during the study; the other was unhunted.

Age at 1st Successful Lamb Production

The age at 1st successful lamb production appeared to be different between the 1972-77 and 1981-85 periods in Dry Creek, but the change was not statistically significant ($P \geq 0.05$). During the 1972-77 period, 7 of 30 2-year-old ewes (23%) successfully produced lambs. In the latter period (1981-85), only 2 of 22 2-year-olds (9%) produced lambs (X^2 = 1.94, $P \geq 0.05$). In contrast, 2 of 40 (5%) 2-year-old ewes from the Robertson River population successfully produced lambs between 1978 and 1985. This was significantly less than in Dry Creek (X^2 = 4.448, $P \leq 0.05$) (Table 8).

After the regulatory change to 7/8 curl in Dry Creek, the measured frequency of successfully reproducing 2-year-old ewes decreased from 23% to 9%. This decrease occurred during a period of generally favorable weather as determined by the aggregate weather index, larger population size, and higher lamb:100 ewe ratios, indicating the drop in successfully reproducing 2-year-old ewes was probably not due to weather or range influences. The conspicuous increase in ram abundance suggests this drop may have been the cause and is

Table 8. Number of reproductively successful 2-year-old ewes determined by 3 methods from Dry Creek (1972-77 and 1981-85) and Robertson River (1978-85), Alaska Range, Alaska.

Method	Reproductively active ewes	Reproductively inactive ewes
	Dry Creek 1972-1977	
Genital inspection	5	18
Collection/Autopsy	1	0
Observations of marked yearlings	1	4
Total	7	22
Frequency	7 of 29 (24%)	
	Dry Creek 1981-1985	
Genital inspection	2	9
Observations of marked yearlings	0	11
Total	2	20
Frequency	2 of 22 (9%)	
	Robertson River 1978-1985	
Genital inspection	0	18
Collection/Autopsy	1	0
Observations of marked yearlings	1	17
Total	2	35
Frequency	2 of 39 (5%)	

consistent with differences in hunting management between Dry Creek and the Robertson River. The abundance of rams has been relatively high and constant in the Robertson River population (48 total rams:100 "ewes" and 19 Class IV [full-curl] rams:100 "ewes" from the 1980 survey where $\underline{n}$ = 1,128), and the incidence of reproductively successful 2-year-old ewes has been reliably low (at 5%) since 1978.

In the Robertson River population, 25 marked ewes were monitored between 1978 and 1985. Only 1 ewe (4%) successfully reproduced at age 2, at least 19 (77%) brought lambs to the lick at age 3 years, and 5 (25%) were first observed to lead lambs at 4 years of age.

It may be notable that 1st reported delivery of lambs on a ewe's 3rd birthday is associated with high ram numbers and/or the presence of old rams in Dall sheep populations. Hoefs and Cowan (1979) reported ewes in unhunted Kluane Park usually did not deliver lambs until their 3rd birthday. Similarly, 2-year-old ewes in the unhunted sheep populations of Denali National Park have not been observed leading lambs in 3 searches of the Savage River summer ranges. Murie (1944) concluded ewes in McKinley Park bred at age 2.5 years and delivered 1st lambs at age 3. Palmer (unpubl. data) concluded ewes in the vicinity of the then virtually unhunted Dry Creek population were characterized by breeding at 30 months and lambing on their 3rd birthdays.

Lambing at age 2 years is associated with low ram abundance and scarcity of old rams. Nichols (1978) reported that 3 of 4 ewes collected before their 2nd birthdays were pregnant. These ewes were taken from a Dall sheep population where 3/4-curl hunting removed every legal ram on the mountain each year. Two-year-old ewes do not routinely deliver lambs in unhunted populations. The observed decrease in reproductive activity among 2-year-old ewes as the number of Class III and IV rams increased in Dry Creek is consistent with this finding.

Other evidence that ewes deliver lambs at 24 months in the absence of old rams comes from captive animals. Four Dall ewes held in captivity in Fairbanks, Alaska, delivered lambs at 24 months of age. These ewes were bred by 18-month-old rams. Hoefs and Cowan (1979) reported that captive 18-month-old Dall ewes from populations which regularly produce lambs on their 3rd birthdays in the wild, produced them on their 2nd birthdays in captivity. Their sires were 18 months to 4 years old. The ram age structures in other captive herds where Dall ewes bred early are not known to us.

Data from the Dall sheep breeding program at the Milwaukee County Zoo (1971-79) indicate 12 of 15 ewes delivered lambs on their 2nd birthday. These lambs were sired by young rams, the oldest being a 4-year-old ram which bred 1 ewe. Three lambs were sired by 2.5-year-old rams, and the remaining 8 were sired by rams aged 1.5 years. In a breeding pen where all rams had access to all ewes, the 1 mature ram, aged 9.5 years, did not mate with ewes below the age of 3.5 years (Bullerman, pers. commun.).

In an earlier paper, we proposed a behavioral mechanism, operative in the absence of mature rams, that leads to early breeding of 18-month-old ewes (Heimer and Watson 1982). We suggested juvenile rams harassed fertile 18-month-old ewes into copulation even though the ewes were not behaviorally mature. This explanation must center on preferential courtship of these young ewes. Given the differences in body size between young rams and mature ewes, this appears plausible when one reads Geist's (1971) accounts of the difficulty bighorn (*Ovis canadensis*) yearling rams experience in attempting to dominate their dams. Relative body size is important in these interactions and may function in aspects related to courtship as well as to ram hierarchy during the rut.

We do not view early breeding by 18-month-old Dall ewes as an advantageous, compensatory population response to disturbance. Breeding domestic sheep at 1st estrus commonly results in offspring of low survivability and compromised reproductive fitness in the dam. Rattray (1977) showed early breeding in domestic ewes resulted in a reproductive advantage only if heavy supplemental feeding followed during both gestation and lactation. A similar requirement has been shown for domestic cattle (Minsh and Fox 1979). In the wild, small ewes have lesser status and must subsist on forage not selected by more dominant sheep (Geist 1971). Therefore, we think early breeding among wild Dall ewes is maladaptive.

Frequency of Observed Reproductive Success:

Documented reproductive frequency in the Dry Creek study population varied markedly between the 1972-76 period and the 1981-84 period. During the former period, the frequency of observed consecutive-year reproduction was 6%. In the latter period, the frequency of observed consecutive-year reproduction in the Dry Creek population increased to 40%. This same statistic was never lower than 44% in the less disturbed Robertson River population (Table 9). The difference in the early and later Dry Creek consecutive-year success frequencies is statistically significant ($P \leq 0.05$). The chance of mistakenly concluding that the differences were real with respect to the variability is less than 0.005.

The aggregate weather index in Dry Creek suggested weather during the latter period was more favorable for lamb production than during the earlier period. Weather may influence

Table 9. Reproductive frequency patterns observed in the heavily hunted Dry Creek and lightly hunted Robertson River Dall sheep populations in the Alaska Range, 1972-84.

Consecutive-year reproductive performance	Dry Creek 1972-77 (n = 88) (%)	Dry Creek 1981-84 (n = 73) (%)	Robertson River 1979-81 (n = 74) (%)	Robertson River 1981-84 (n = 137) (%)
With/with lamb	6	40	66	44
With/without lamb	26	24	13	28
Without/with lamb	24	21	17	17
Without/without lamb	44	15	4	15

observed consecutive-year reproductive success. For us to document consecutive-year reproductive success, ewes must ovulate, breed, carry the fetus to term, deliver a living lamb, and bring it to the lick. At the mineral lick, we must verify the pair-bond. Then, the next year, the sequence must be repeated. If a marked ewe delivered a lamb, and the lamb died before we could verify the pair-bond or observe lactating udders at the mineral lick, the ewe would be recorded as reproductively inactive. This probably happened, but the frequency of its occurrence is unknown. When weather is unfavorable for lamb production, this frequency probably increases because more lambs are likely to die than when conditions are good. Thus, it is probable that we will always underestimate the frequency of consecutive-year reproductive activity. Furthermore, we may be more likely to underestimate it in years of unfavorable weather than when weather favors lamb production. Hence, the question of the magnitude of weather influence on our ability to accurately detect changes in frequency of consecutive-year reproductive success merits discussion.

We can gain some insight about the magnitude of weather influence on this reproductive parameter by considering the mean lamb:ewe ratios for the 2 differing periods in Dry Creek. During the 1972-76 period, when consecutively observed reproductive success was 6%, the mean lamb:100 ewe ratio was 29. For the 2nd period, 1981-84, when consecutively observed success was 40%, the mean lamb:100 ewe ratio was 54. This is an increase of 1.9 times. If our ability to document consecutive-year production were directly proportional to changes in lamb:100 ewe ratio, we should have seen a consecutive-year frequency increase of 1.9 times. The documented increase was 6.7 times. This increased frequency was 3.5 times greater than expected from the increased lamb:100 ewe ratio. Something besides weather appears to be influencing changes in frequency of consecutively observed reproductive success. Pregnancy rate in ewes collected during this period was only 36% of 11 ewes collected in springs of 1972, 1973, 1975, 1976, and 1977. We think this probably confirms the significantly ($P \leq 0.05$) lower incidence of consecutive-year reproductive success during the mid-1970's was real, and suggests that it resulted from a failure to ovulate and/or breed.

We have already discussed the possible influences on lamb production and found range resources to be a difficult cause to rationalize. Also, in an earlier section, we discussed the mechanisms by which predation might have influenced lamb:100 ewe ratios as well as the probable effects of ram abundance and age structure. The Robertson River population also presumably responded to the influences of weather, range resources, and predators. Still, it has maintained a consistently high consecutive-year reproductive frequency equal to or greater than that of Dry Creek since the 7/8-curl hunting regulation and predator control raised the ram:100 ewe ratios in Dry Creek (Table 3). Hence, we think the consistent occurrence of higher consecutive-year reproductive success with high ram:100 ewe ratios is the most logical explanation of these changes seen in the Dry Creek population.

Our early a priori assumptions that the dense Dry Creek population must be nutritionally limited led us to suggest (Heimer 1980, Heimer and Watson 1982) that low consecutive-year reproductive success and early breeding were linked. We hypothesized that extended lactation (Heimer 1980, 1983) was a sufficient energy demand that early-breeding ewes on crowded ranges did not regain sufficient body condition by the rutting season, so they failed to ovulate and did not produce lambs. We speculated further that this alternate-year pattern of reproduction might be an adaptation to limited range resources. We think this hypothesis has now been shown to be false for the following reasons.

First, Thorne et al. (1984) reviewed evidence which showed that a lactation-induced anestrus occurs in domestic sheep that are not nutritionally stressed. If this physiologic mechanism also exists in Dall sheep, which is a good possibility given the phylogenetic relationshp between the two, extended lactation would inhibit ovulation in Dall sheep. Second, Heimer (1980, 1983) showed there were no different ($P \leq 0.05$) nutritional differences between the Dry Ceek and Robertson River drainages even though the reproductive frequencies and ages at 1st breeding were significantly different ($P \leq 0.05$). Finally, lactation was prolonged in Dry Creek, but not in the Robertson River. Heimer (1983) collected 12 ewes during rutting seasons from 1977 through 1979, and none were lactating. Also, none of 8 Robertson River ewes were lactating when collected in April. Among ewes collected in Dry Creek during April, the lactation rate matched the yearling:100 ewe ratio from 1972 through 1979.

This does not explain why ewes in the Robertson River weaned lambs before the rut and ewes in Dry Creek did not. If the reasons are not nutritional, it is possible they may be related to ram abundance. We hypothesize that increased ram abundance in Dry Creek, following wolf control and changes in harvest management which increased ram abundance, was not only associated with increased consecutive-year reproductive success as described, but also with lowered frequency of extended lactation. We have no data to test the prediction about extended lactation.

If the time of weaning is influenced by the abundance or age structure of rams arriving on rutting ranges for prerut (Geist 1971), ram abundance could provide a reasonable hypothesis explaining these changes. However, such a hypothesis rests, at the present time, completely on interpretations of perceived benefits of a stable social structure. Still, it may be worth considering since we can offer no other reasonable explanation at this time.

In summary, the data gathered in this study indicate that lamb:100 ewe ratios were higher following the establishment of the 7/8-curl regulation than when maximal harvest was practiced under the 3/4-curl limit ($P < 0.05$). The data also indicate a significant difference ($P < 0.05$) in age at 1st successful reproductive activity when Dry Creek (under 3/4-curl management) is compared with the full-curl managed Robertson River population. Furthermore, the data indicate the frequency of consecutive-year reproductive success increased significantly after establishment of the 7/8-curl regulation ($P < 0.05$). The change in frequency of reproductively active 2-year-old ewes, from 24% with the 3/4-curl regulation to 9% under 7/8-curl management, was not significant ($P \geq 0.05$).

On the basis of these findings, we rejected the null hypothesis outlined in Objective 1: that establishment of an older ram age structure by replacing the 3/4-curl regulation with a 7/8-curl harvest minimum would have no effects on lamb production, age at 1st observable reproduction, and consecutive-year reproductive success by ewes. The fact that the changes documented above were observed on either side of 1979, when horn curl restrictions were changed from 3/4 to 7/8 curl, does implicate the change, but does not establish it as the sole cause. We found that the increased lamb:100 ewe ratio was correlated with more favorable weather conditions. The same statement may be made about the change in frequency of consecutive-year reproduction, though there were other factors which influenced that parameter more than the favorable weather. Changes in ram abundance and age structure were associated with all reproductive changes studied. However, changes in ram:100 ewe ratios resulted from wolf population reduction as well as changes in hunting regulations.

The data do indicate that ram abundance and age structure are major (if not dominant) influences on Dall sheep population performance. We think social organization as it influences production and survival of sheep should be an important consideration when interpreting the responses of Dall sheep populations. These conclusions are consistent with those proposed by Geist (1971). Additional work is required to further define the effects of ram age structure on population dynamics of Dall sheep.

Objective 2: Factors Which Affect Lamb Production

Dall ewes from the Robertson River study area ($n = 13$) had significantly ($P < 0.05$) higher ovulation rates than ewes from Dry Creek ($n = 19$). The chance of mistakenly concluding the observed differences in ovulation rate are not due to sample variance is only 0.01 as indicated by Student's t test for ratio estimators (Cochran 1977). Histological examination of corpora lutea and corpora albicantia indicated ovarian function occurred at a rate of 0.70 ovulations per ewe-year in the Dry Creek ewes and 0.99 ovulations per ewe-year in the Robertson River populations (Tables 10 and 11).

The lower ovulation frequency among Dry Creek ewes coincided with low lamb:100 ewe ratios, low pregnancy rate, and extended lactation (see Objective 1). This low ovarian activity also accompanied low population numbers, and, presumably, because most collections occurred right after the wolf reduction program, low predator densities. Factors that may influence the ovulation rate include ewe nutritional status, ewe age structure, and ram abundance.

Nutrition:

Ovulation in wild ungulates should most logically be influenced by body condition at rut (Clutton-Brock et al. 1982, Dauphine 1976), and body condition at rut is dependent on nutrient intake between green-up and rut. Hence, we examined nutrient quality and body condition for the study populations.

Ewes were collected from both populations immediately before rutting time in winters 1976 and 1978. These ewes, as well as those taken 2 months before lambing, provided the data on ovarian activity. Proximate analysis of washed rumen contents provided a mean estimate of food quality on the day the ewes were collected. Rumen contents in ewes from the low-quality Dry Creek population averaged 14.9% lignin and 6.3% protein ($n = 9$). The high-quality Robertson River ewes averaged 19.8% lignin and 8.1% protein ($n = 15$). Heimer (1983) reported differences in these mean nutrient values were not statistically significant ($P > 0.05$). Hence, differences in forage quality just before the rut do not account for differing ovarian activities between the 2 populations.

Food quality on sheep summer range was not statistically different ($P > 0.05$) between Denali National Park and the Robertson River (Winters 1980). Whitten (1975) has gathered nutrient data from Denali Park. We suspect the nutritional values from Denali are representative of those in Dry Creek because the vegetation on the 2 ranges is similar. Winters (1980) compared his data with those of Whitten (1975) (data

Table 10. Ovarian activity of Dall sheep ewes collected in Dry Creek, Alaska Range, 1973-79.

Accession number	Possible seasons of ovarian avtivity (total ruts experienced minus 1)	Ovarian events recorded as CL or CA[a]
3559	3	3
3580	5	4
3624	10	8
3696	10	2
3888	9	7
3889	10	6
3890	10	8
3891	7	6
3892	9	5
3894	1	1
3895	6	4
3896	7	3
3897	4	1
4385	9	6
4741	0	0
4743	5	5
4745	10	9
5009	7	3
5012	10	7
5036	7	5
Total	139	93

[a] CL = corpora lutea; CA = corpora albicantia.

Table 11. Ovarian activity of Dall sheep ewes collected in the Robertson River, Alaska Range, 1976-79.

Accession number	Possible seasons of ovarian activity (total rut experienced minus 1)	Ovarian events recorded as CL or CA[a]
4569	0	0
4594	2	2
4596	5	4
4598	4	6
4599	4	8
4601	7	6
4762	0	0
4763	7	8
4765	1	1
4767	7	5
4768	5	4
4992	0	0
4994	4	2
4995	5	2
5042	8	7
5043	3	4
Total	62	59

[a] CL = corpora lutea; CA = corpora albicantia.

gathered in summers 1977 and 1978 at Robertson River and summer 1974 from Denali) and found no statistically significant differences ($P > 0.05$) among 4 nutrients in the 2 areas. See Heimer (1983) for further details. We think this indicates differences in summer range quality were probably insufficient to account for observed differences in ovarian activity between Dry Creek and Robertson River ewes.

This conclusion is supported by body condition data from both the Dry Creek and Robertson River populations. Body composition was determined for the ewes which provided the data on ovarian activity. Dry Creek ewes shot just before rut averaged 62.4% water, 14.3% fat, 14.4% protein, and 9.1% bone. In the high-quality Robertson River population, the ewes averaged 62.5% water, 14.1% fat, 14.6% protein, and 9.8% bone. There were no differences in body composition ($P \leq 0.05$).

We conclude differences in ovulation rate are not explained by factors which determine body condition. There was no statistically significant difference in the nutritive values for washed rumen contents, no reasonable expectation of significant differences between the nutritive values for summer range plants, and no difference in breeding body condition between the 2 study populations.

Age Structure:

Age structure of the population could influence ovulation rate if ovarian activity declines with increasing age. Heimer (1983) found a significant ($P \leq 0.05$) difference in the mean ages of ewes collected; the Dry Creek ewes were, on average, 2 years older than the Robertson River ewes.

If ovarian function declines with age, a shift to a younger age structure should be reflected in increased ovarian activity.

Our data on age-specific reproduction collected from both Dry Creek and the Robertson River sheep populations are in agreement with those published by Bunnell and Olsen (1981). They observed marked Dall ewes in their delivery of lambs; our data were gathered as marked ewes and their lambs were observed at mineral licks from birth to 30 days after parturition. Our data were accumulated from 1972 through 1985. In addition, 142 ewes were classified as reproductively active or inactive when captured at the Dry Creek mineral lick from 1968 through 1971 (Table 12).

The percentage of reproductively active ewes aged 4 through 8 equals 64%, while ages 5 through 13 averaged 63%. This difference is not statistically significant. Hence, an older

Table 12. Age-specific reproductive activity for Dall ewes in lightly or unhunted populations, Dry Creek and Robertson River study areas, Alaska, and Kluane Park, Yukon Territory, 1968-84.

Age	Fraction determined to be reproductively active by area						
	Dry Creek 1968-71[a]	Dry Creek 1981-84[b]	Robertson River 1977-84[b]	Kluane Park 1971-72[c]	Total	Percent active	
1	--	--	--	--	0	0	
2	5/32	2/16	1/29	--	8/77	10	
3	12/23	6/28	25/40	0/12	43/103	42	
4	3/9	15/30	28/48	2/4	48/91	53	
5	5/8	17/33	39/57	9/11	70/109	64	$\bar{x}$ of
6	16/27	17/23	40/60	9/10	82/120	68	4-8 yr
7	11/14	12/20	35/52	4/6	62/92	67	= 64%
8	4/8	5/12	25/35	10/11	44/66	67	
9	10/13	3/4	14/28	4/4	31/49	63	
10	3/3	1/2	11/22	3/3	18/30	60	$\bar{x}$ of
11	1/3	2/2	6/10	--	9/15	60	9-13 yr
12	0/2	1/4	5/6	1/2	7/14	50	= 63%
13	--	2/2	2/3	--	4/5	80	
Overall:	70/142	83/176	231/390	38/63	426/771		
Mean %:	49	47	59	60	55		

[a] Determined at capture.

[b] Observed with lambs at lick. Lambs aged 0-30 days.

[c] Observed delivering lambs (Bunnell and Olsen 1981).

age structure in the Dry Creek population could not have caused the significantly lower ovarian activity. We emphasize that this data set contains only information on reproductive performance from ewes in populations with relatively high ram abundance.

If age structure were to have any effect on lamb production, the results should have been reversed from what was observed in this study. Productivity should have been higher in the older Dry Creek population; it was not. A population of ewes with its age structure skewed heavily toward very young ewes should be less productive than one with an age structure skewed toward old ewes. This is because ewes at ages 2 and 3 are less productive than any other reproductively active age grouping of ewes. In Dall ewes, the reproductive system seems to be at least as robust as other life support systems. Ewes are likely to die before they lose reproductive capacity.

We also compared the reproductively active fraction of marked ewes for each age class from the 1972-76 period ($\bar{x}$ lamb:100 ewe ratio = 29) with that from 1981-84 ($\bar{x}$ lamb:100 ewes = 50). These data (Table 13) show, as did those from lightly hunted or unhunted sheep populations (Table 12), that effects of increasing age on reproductive activity are negligible after age 3 years. However, the reproductively active fractions during the period of low lamb production were about half those from the period of high lamb production. Not only was the frequency of consecutive-year reproductive success low during the early 1970's, overall production among all marked ewes, regardless of their previous reproductive activity, was also reduced. We believe this further demonstrates that consecutive-year reproductive success functions as an adequate index of reproductive frequency in spite of the uncertainty which exists about the fate of lambs between parturition and the time they are seen at mineral licks.

<u>Low Ram Abundance</u>

Low ram abundance, which usually includes low Class III and IV ram abundance, may be the most likely cause of lowered ovarian activity. When ovarian activity was low in Dry Creek (1972-79), the total ram:100 ewe ratio was 17, and the Class III and IV ram:100 ewe ratio was 8. In contrast, when ovarian activity was determined for the Robertson River population, there were 40 total rams:100 ewes and 15 Class IV rams:100 ewes. Lower ovarian activity appears to attend low ram:ewe ratios in the 2 examples given above. Similarly, the data on consecutive-year reproductive success in Dry Creek since 1981 (which increased significantly [$P \leq 0.05$] with ram abundance) may reflect increased ovarian activity there. We have

Table 13. Age-specific reproductive performance in marked Dry Creek ewes, Alaska Range, 1968-77.

Age	Reproductively active 1968-71[a] (%)	Reproductively active 1972-77[b] (%)	Reproductively active 1981-84[c] (%)
1	--	--	--
2	16	25	13
3	53	0	21
4	33	23	50
5	63	20	52
6	59	36	74
7	79	29	60
8	50	25	42
9	77	27	75
10	100	8	50
11	33	36	100
12	0	33	25

[a] Determined in hand.

[b] With low ram:100 "ewe" ratios.

[c] Observed at lick.

gathered no data on ovarian activity in Dry Creek since the ram:100 ewe ratios were restored to pre-1972 levels (see earlier section on ram abundance).

One possible mechanism which would produce this effect relates to the extended lactation observed in Dry Creek. Lactation inhibits ovulation in domestic sheep (Thorne et al. 1984), and if the presence of many, or a sufficient number, of mature rams facilitates weaning, increased ram abundance should be followed by increased ovarian activity. We hypothesize that the presence of many rams (or a required number of mature rams) using ewe ranges prior to the rut induces ewes to terminate suckling, or regiments all sheep sufficiently that ewes are better able to wean lambs than when social order is less well defined.

Breeding during a 2nd estrus (Bunnell 1982) may also be linked to high ram abundance. When we compared the number of ovulations for each individual with the number of possible reproductive seasons, we found about 1 in 3 (29%) of the Robertson River ewes ovulated more than once per season sometime in their life. None of the Dry Creek ewes showed this pattern (Tables 10 and 11). Similarly, presence of many adult rams may facilitate or induce later estrous cycles in Dall ewes as it does in domestic sheep (Redford and Watson 1957, Watson and Redford 1960). A young Dall ram apparently induced estrus in a Dall ewe during April at the Denver Zoo. The ewe stood for the ram after extended courtship and a lamb was born in October (P. Smith, pers. commun.).

The hypothesis that low ram abundance causes low lamb production appears to be supported by data from the Kenai Peninsula. Nichols (1976, 1978) reported that a population subjected to maximum cropping for 3/4-curl rams averaged 26 lambs/100 ewes from 1970 through 1975. An unhunted population in close proximity was considered a control in Nichols' experiment. Even though the unhunted population averaged 34 lambs:100 ewes (a relative difference of +31%) during the same period, Nichols (1976) found no statistically significant difference ($\underline{P} \geq 0.05$) in relative lamb production between these populations. We think this difference is biologically significant even though it was not statistically significant due to inherently high variability in lamb:ewe ratios and the small ($\underline{n}$ = 5 yr) sample size.

There may be some concern regarding the methods chosen to determine ovarian activity. However, the origin of corpora albicantia in ovaries is well understood, and histological ovarian examination as a means of determining past activity has been proven reliable (Hadek 1958).

Likewise, some criticism may reasonably result from our aging techniques. Aging ewes by counting horn annuli is difficult, and age determination is variable among observers (Hoefs 1984b). Geist (1966) states only a minimum estimate of age is attainable. In this study, errors should be consistent for both populations because 1 individual aged all sheep. Also, when the ewes 9 years and older from the Dry Creek data set are considered separately, the ovulation frequency changes little (from 70% to 68%). We conclude possible errors in age determination did not materially affect the results in this comparison.

Objective 3: Lamb Survival and Yearling Recruitment

Table 14 summarizes the production of lambs, percentage of lamb survival, and yearling recruitment data for both study populations. Survival to yearling age was quite variable and did not correlate well with winter severity. When lamb survival to yearling age was regressed on mean snow accumulation across the north slope of the Alaska Range, the regression coefficient was only 0.099. Intuitively, it seems that greater snow accumulation should lower lamb survival to yearling age, but these data indicate this was not true. Variability in survival of lambs to yearling age may be a result of other complex influences such as predation by wolves and size of the lamb crop.

Survival to yearling age from 1972 through 1976, when wolf numbers were high, averaged 62%. During the 5 years (1977-81) immediately following wolf population reduction, the mean survival to yearling age was 53%. Clearly wolf population reduction did not produce an important increase in survival. It is also unlikely the poorer survival following wolf population reductions can be attributed to winter severity. Mean snow depth for the pre- wolf reduction period was 18.4 inches per year. For the post- wolf population reduction period snow depth averaged 15.2 inches per year (Table 2).

To test the hypothesis that poor survival was associated with increased lamb production, we regressed percentage survival on size of lamb crop. This correlation (r = 0.1) was not significant.

Survival of lambs to yearling age did not correlate well with any of the variables we could test. Most mortality must occur after we have assessed lamb production in June. Something causes mortality of about 40% to 80% of the lamb crop from July to the next June. The only possibility we can offer is that eagles may be taking significant numbers of lambs. We have documented 4 golden eagle (*Aquilia chrysaetos*) strikes in the past 2 years. Similarly, investigators in the Yukon

Table 14. Dall lamb production, survival, and yearling recruitment in the Alaska Range study areas, Dry Creek, Alaska 1968-83 and Robertson River, Alaska, 1974-83.

	Dry Creek			Robertson River		
Year	Lamb: ewe ratio	Yearling: ewe ratio	Percent survival	Lamb: ewe ratio	Yearling: ewe ratio	Percent survival
1968	63	13				
1969	64	31	49			
1970	55	31	48			
1971	50	51	93			
1972	15	16	32			
1973	38	11	73			
1974	28	25	66	56	21	
1975	28	23	82	43	37	66
1976	36	16	57	35	26	60
1977	58	17	47	52	18	51
1978	41	25	43	57	35	67
1979	65	19	46	63	25	44
1980	67	36	67	69	29	46
1981	60	43	64	52	32	46
1982	31	25	41	29	36	69
1983	57	7	22	43	13	45

Territory (Nette et al. 1984) have recently reported observing eagles killing Dall lambs during summer. The actual number of incidents is small, but considering that we had seen no such interactions in the 12 years before 1984, the increase may be meaningful. We know little about the causes of lamb mortality during the 1st year of life and this subject needs further investigation.

Use of lamb:100 ewe ratios did not introduce significant errors in our analysis. For some years, we had actual estimates of the numbers of lambs and yearlings produced (Tables 15 and 16). When percentage survival was calculated using these figures, there was little difference between the percentage survival calculated by the 2 differing methods. Hence, ratios of lambs and yearlings:100 ewes give an acceptable estimate of survival to yearling age.

Objective 4: Ram Survival Beyond Yearling Age

Age-specific survival of rams beyond age 1 has been measured for several unhunted populations (Murie 1944, Deevey 1947, Bradley and Baker 1967, Geist 1971, Murphy and Whitten 1976). Mortality during the 1st year ranges from 40% to 60%. The 1st year is followed by 2 periods characterized by radically different mortality rates. As Geist (1971:295) said: "It can be seen that there are 2 general phases in the survivalship curve.... There is a phase of low mortality between the ages of 2 and 8 years and a phase of accelerated mortality in the higher age categories." Data taken from Murie (1944) are given in Appendix A, Table 2, and the plot of unhunted ram survival over time is displayed in Fig. 3. Mean mortality for the low mortality phase averaged about 2.3% per year over the time period when the skulls Murie collected were deposited.

For purposes of analysis and simplicity of comparison, we fitted the least squares straight line to both phases of the survival curve. The equation for the accelerated mortality phase was found to be $y = -92x + 1,228$. This represents a 7.7-fold increase in mean mortality rate beginning at age 8 in Dall sheep (Fig. 3). These mortality rates and the ratios between them are typical for mountain sheep populations (Bradley and Baker 1967).

Geist (1971:295-296) predicted increased mortality in a population where younger rams actively participate in breeding. Based on energetic considerations, he said:

> "The ages of low mortality in rams coincide with their dominance status and near exclusion from breeding by larger horned, older rams. Conversely, when rams reach near ultimate body and horn size and become dominant breeding rams during the rut, their mortality

Table 15. Production, survival, and recruitment for Dall sheep populations in Dry Creek, Alaska Range, 1968-84.

Year	Lambs: 100 ewes[a]	Yearlings: 100 ewes[a]	Percent survival[a]	Ewes[b]	Lambs[b]	Yrlg[b]
1968	63	13		--[c]	--	--
1969	64	31	49	--	--	--
1970	55	31	48	734	404	228
1971	50	51	93	--	--	--
1972	15	16	32	--	--	--
1973	38	11	73	--	--	--
1974	28	25	66	--	--	--
1975	28	23	82	685	181	141
1976	36	16	57	--	--	--
1977	58	17	47	--	--	--
1978	41	25	43	--	--	--
1979	65	19	46	--	--	--
1980	67	36	55	707	474	255
1981	60	43	64	810	486	348
1982	31	25	41	787	244	197
1983	57	7	22	743	424	52
1984	51	25	39	783	399	196

[a] From mineral lick data.

[b] From corrected aerial survey.

[c] Data not collected.

Table 16. Production, survival, recruitment, composition, and population size for the lightly hunted Robertson River Dall sheep population in the Alaska Range, 1974-84. Harvest limited to full-curl rams by lottery permit.

Year	Lambs: 100 ewes[a]	Yearlings: 100 ewes[a]	Percent survival[a]	Ewes[b]	Lambs[b]	Yrlg[b]	Pop. size[c]
1974	56	21		520	291	109	1,250
1975	43	37	66	--[d]	--	--	--
1976	35	26	60	--	--	--	--
1977	52	18	51	--	--	--	--
1978	57	35	67	--	--	--	--
1979	63	25	44	--	--	--	--
1980	69	29	46	456	314	132	1,244
1981	52	32	46	522	272	167	--
1982	29	36	69	513	149	185	--
1983	43	13	45	595	256	77	--
1984	45	27	62	550	248	149	1,251

[a] From mineral lick data.

[b] Modeled from aerial survey with known mortality from collars present (see Survival of Ewes Beyond Yearling Age in text).

[c] From aerial survey.

[d] Data not collected.

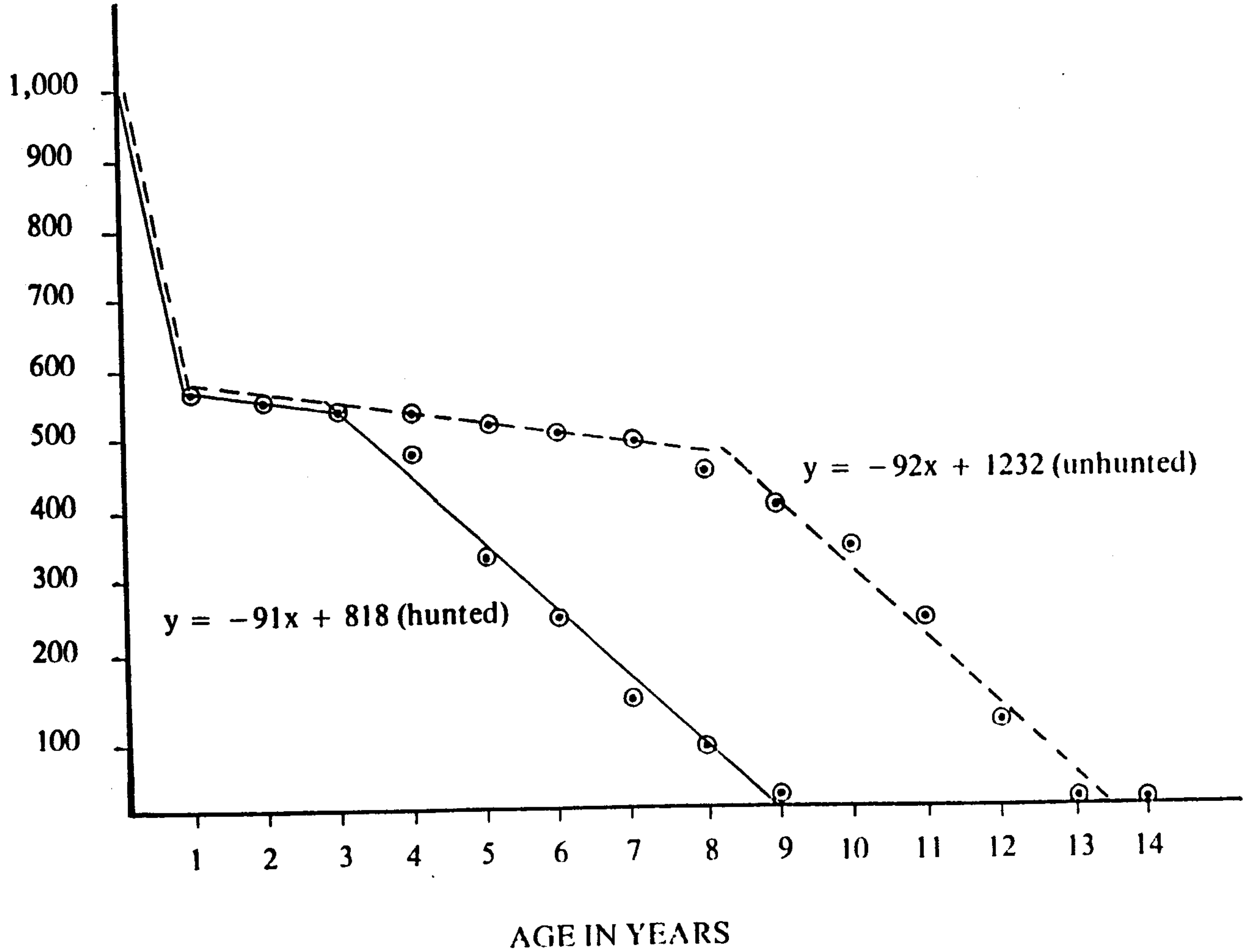

Fig. 3. Survival of Dall rams in the heavily hunted (Dry Creek) and unhunted (Mt. McKinley Park) sheep populations.

increases. This relationship between dominance and high mortality appears to be causal for the following reasons: large, dominant rams which breed most ewes virtually do not feed while guarding ewes and they fight extensively and do much running and chasing when following the estrous ewe and discouraging competitors. Unlike small rams, the large breeding males often return exhausted from the rut. They have probably lost most of their fat deposits whereas subordinate rams probably retain theirs. In the severe winter months following the rut, the rams that have lost their energy reserves probably succumb (see Heptner et al. [1961] for other ruminants). Two predictions, as yet unverified, are that large rams should lose more weight during the rut than small-horned rams and that YOUNG RAMS WILL DIE OFF MORE RAPIDLY IF, DUE TO CIRCUMSTANCES, THEY ARE ALLOWED TO PARTICIPATE IN BREEDING AT THE SAME LEVEL AS OLDER RAMS" [emphasis ours].

If the cause of accelerated mortality is the same for both younger and older rams, we think Geist is predicting the mortality rate for rams involved in rut should be similar regardless of age. That is, it represents the cost of dominance.

When maximum harvest of 3/4-curl rams is permitted, younger rams probably participate in breeding at the level older rams would if they were present. The work of Hogg (1984) shows ram rutting strategies in bighorn sheep vary with social status. Jenni et al. (1986) reported that disruption of the same bighorn population by transplanting all mature (Class III and IV) rams from the group altered the predominant strategies employed. The result was more chasing and less tending. More energy was probably expended by the younger rams.

The data from Dry Creek indicated the least squares line describing accelerated mortality was the same between marked rams subjected to 3/4-curl hunting and rams 8+ years old from the unhunted population in Denali Park (Fig. 3).

If our findings, which support Geist's hypothesis about early death, are generally applicable, it becomes possible to predict the number of rams available to hunters under various ram harvest schemes at maximum harvest levels. Fig. 4 is used to make these predictions. In this figure, a survivorship curve for Dall sheep (adapted from Murie 1944, to fit survival and recruitment levels at Dry Creek) was plotted, and the slope of the accelerated mortality phase for dominant rams determined. The ram age/status classes (Geist 1971) have been superimposed on the abcissa at their corresponding ages for

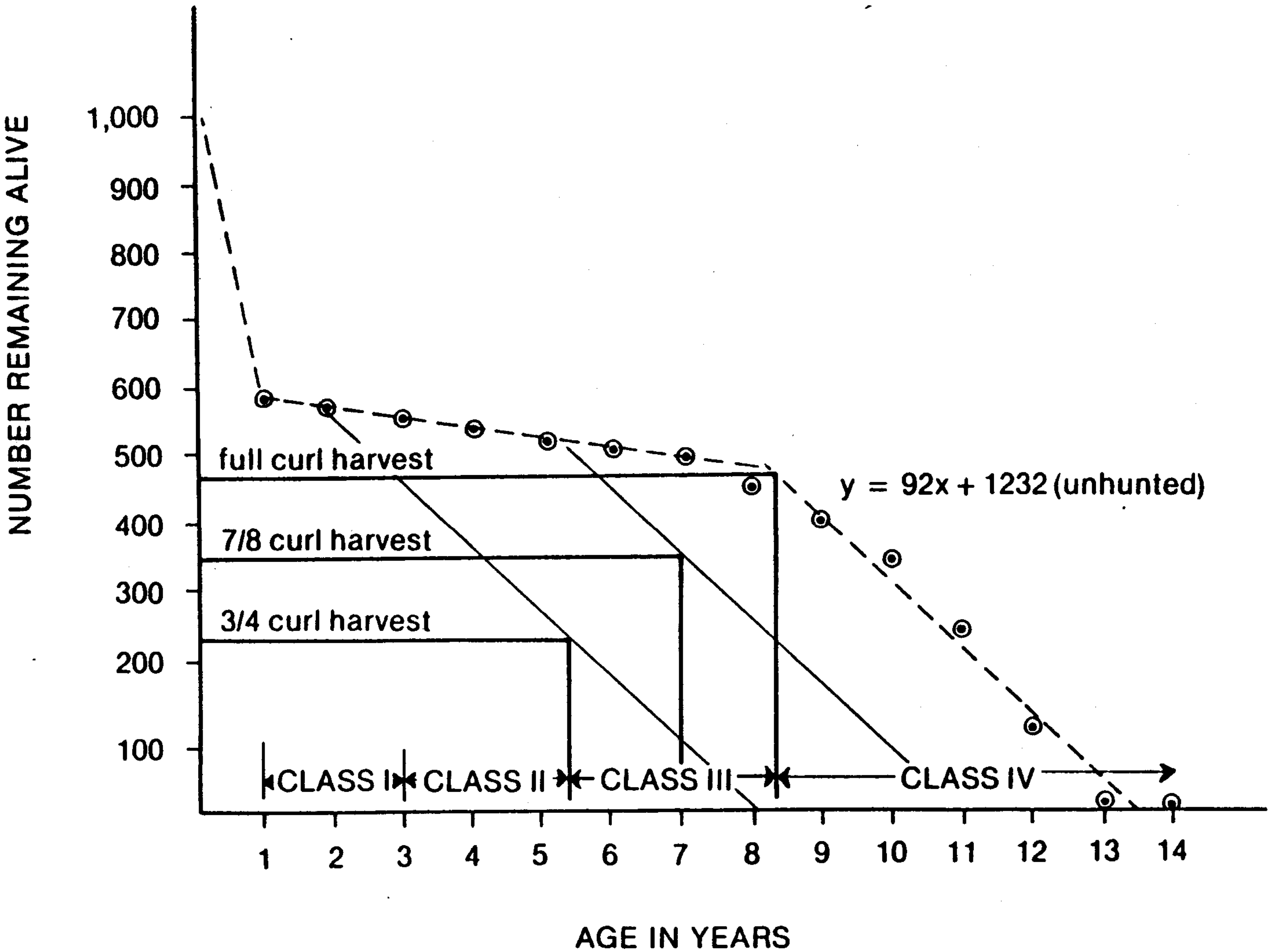

Fig. 4. Ram survival in an unhunted population (dashed line) and survival of sublegal rams under different hunting regulations assuming maximum harvest of legal rams.

Dall sheep in Alaska. Predictions of sustainable harvest with more permissive legal ram definitions are derived by shifting the best straight line for the accelerated mortality phase of the curve toward the left. If removal of dominants has a constant effect on the opportunity of young rams to participate in the rut, and if rutting increases probability of death, the extent of the leftward shift will predict the number of rams of any given cohort which would be expected to survive. Of course, the function is not continuous because rutting is limited to the winter rutting period, and some care must be exercised in placement of the line describing the anticipated accelerated mortality effect.

As a 1st approximation, we could place the accelerated mortality phase line so it intersects the survivorship curve at the 1st possible active rut in a ram's life. This is the 2nd rut when a ram is aged 18 months. If rams in this age/status class had the same opportunity to rut as all other rams in the population, and suffered the consequent mortality increase, the predicted harvest would be about 200 of the 570 rams recruited as yearlings. However, Nichols (1972) gathered data on rutting behavior from a population heavily cropped at 3/4 curl. These data suggested the 1/4-curl rams (Class I) did not participate in the rut as much as rams which are another age/status class higher (Class II). These data suggest the line describing the accelerated mortality phase should be placed so it intersects the survival curve at the rut before the beginning of age/status Class II, the 1/2 curl rams. When this is done, the prediction comes to about 275 rams. Marked rams began to disappear at the increased mortality rate at age 3 in Dry Creek (Fig. 3). This seems to support the argument that under these circumstances, Dall sheep begin actively participating in rut before age 3.

It is important to note that this prediction (a maximum sustainable harvest of 275 rams) slightly exceeds the sustainable ram harvest empirically determined by maximal harvest at 3/4 curl in Alaska. Heimer (1980) reported the observed maximal harvest from steady-state non-lamb cohorts in Alaska was about 2.5% from 4 different areas throughout Alaska over a cumulative period of 14 years.

For Fig. 4, the sustainable harvest <u>rate</u> was estimated by calculating the number of sheep (excluding lambs) required to produce a "cohort" of 1,000 lambs. The sex ratio of mountain sheep is about 50-50 at birth (Hoefs and Cowan 1979), so the production of 1,000 ram lambs required the birth of 2,000 lambs. Based on the mean production rate required for stability in the Dry Creek population since 1970, 42 lambs:100 ewes, the number of ewes required to produce 2,000 lambs would be 4,671. Population composition in Dry Creek averaged 54%

ewes during the aerial surveys of 1970, 1975, and 1980. When this mean figure is applied to the data, it yields a calculated population of 8,817 sheep (excluding lambs) required to produce 1,000 ram lambs. When the predicted sustainable harvest (275 rams) is divided by the non-lamb population, the result is a harvest rate of 3.0%. This prediction exceeds by 20% the sustainable cropping rate empirically determined in Alaska. Other factors may cause the theoretical rate to be greater than the observed rate. In any case, it appears that greater survival of recruited ram yearlings to shootable age when old rams are present should provide significantly more rams for maximum harvest than are available for maximum harvest at 3/4-curl age/size.

Also, the 1980 survey of the full-curl area showed a Class IV (full-curl) ram:100 "ewe" ratio of 19. This value (in the presence of a 3.5% harvest of full curls (Heimer 1980) is greater than any 3/4-curl:100 "ewe" ratio ever observed in Dry Creek. This suggests greater ram survival under these conditions.

Further supportive evidence comes from marked rams in the Robertson River study area. In Appendix A, we showed that in the heavily hunted 3/4-curl Dry Creek population, hunters returned only 16% of the tags placed on sublegal rams. Tag returns were monitored over the 12-year life span anticipated for these rams. In contrast, 27% (9 of 33) of the rams marked in a similar manner at the Robertson River lick survived, not only to 3/4 curl, but to full curl. As of September 1985, 6 of these rams had been killed by hunters, and 3 others were observed alive at the mineral lick. This immediate hunter return from the less hunted population (18%) is comparable to the long-term return from the heavily hunted Dry Creek population. We anticipate even higher returns as more marked rams attain full-curl horns. We think these 3 data sets strongly support Geist's 1971 hypothesis that social dominance leads to death.

The above data have important management implications. If the management goal is to maximize ram harvest, then higher harvest levels are likely to be sustained by taking rams from only the upper age/status classes (Class IV). Certainly, some rams will be lost to natural mortality between 3/4 and full curl, but the potential harvest should increase noticeably if only full-curl size/age rams were harvested (Fig. 4). If the limit is set at 7/8 curl, as in most of Alaska at the present time, the model predicts an increase in harvest of approximately 30% over that at 3/4 curl in areas of maximal harvest. This predicted increase in sustainable harvest should result not only from greater recruitment (see earlier sections) but also from decreased mortality among young rams which have not yet assumed the taxing energetic demands of social dominance.

It is possible that the anticipated Class IV harvest may not be fully realized. Based on computer simulations of horn growth, Nichols (1984) suggested that in some Dall sheep populations up to 15% of the rams may never reach full-curl horn development. Should this prediction be correct, the efficacy of setting a legal age minimum as well as a degree of horn development (such as in British Columbia) when maximum harvest is desired becomes apparent. However, even a maximally restrictive full-curl rule could still be expected to increase sustainable Dall sheep harvest, even though the increase would theoretically be less. There is little reason to suspect harvest would decrease under a simple full-curl regulation. In the eastern Alaska Range, hunter success in the 2nd year of full-curl ram hunting equaled that for a comparable heavily hunted 7/8-curl area (GMU 11).

Further evidence of poor young ram survival in a population heavily skewed toward young rams comes from the Dry Creek mineral lick. In 1972, the mineral lick was observed 24 hours per day for 6 weeks. These data, plus records of the number of visits by collared rams in 1973, showed that marked rams aged 5+ years visited the lick 2.25 times during the observation period. The number of rams, aged 5+ years, using the lick was estimated by dividing the total number of lick visits by rams in this age class by 2.25. An expansion factor used to estimate the total ram population in this age class was derived by dividing the number of collared rams known to be in the population (as determined by all resighting data from 1972 and 1973) by the number which visited the lick. The number of rams in the 5+ years (3/4 curl and larger) category was then divided by the number of yearling rams recruited from 4 years earlier so a percentage survival could be calculated (Table 17).

Recruitment to the 3/4-curl class for the years 1976 through 1979 averaged 31% of the yearlings recruited 4 years earlier. Changes in ram fidelity to the mineral lick were not considered. However, unless fidelity increased dramatically from 1972 through 1979, there should have been no effect on ram survival to 3/4-curl size at age 5. Survival of rams from yearling to this age is 98% in an unhunted population (Appendix A). Because of the change to 7/8-curl ram hunting, survival of rams from 1 year to legal age was not comparable after 1979.

The ram survival of 31% calculated above is not in close agreement with that reported in Heimer et al. (Appendix A). However, the data for survival of young Dry Creek rams presented in Appendix A were corrected for the severe winter of 1971-72 by deleting yearling and 2-year-old rams that disappeared during that difficult winter. Consequently, they

Table 17. Survival of Dall sheep rams from age 1 through 5 years in Dry Creek study area, Alaska Range, 1972-79.

Cohort	1972-76	1973-77	1974-78	1975-79
Number recruited to age 1	61	45	94	82
Number surviving to age 5	25	9	18	34
Survival	41%	20%	19%	42%

should not be expected to match the 31% survival rate. If all raw data for young marked ram survival from Dry Creek (Table 18) are plotted (Fig. 5), it can be seen that the survivorship curve has a greatly different shape (from that of Fig. 3). In this case, the survival from yearling age through age 5 is 172 of 571 yearlings entering the hypothetical cohort. This is a survival of 30%, nearly an exact match of the survival estimated using marked ram survival. We think the close agreement speaks for the validity of the figures. This agreement shows that total ram mortality was not greatly different than that observed in the marked sample. Hence, the marked sample reasonably represented the population.

We may be criticized for deleting the missing yearling and 2-year-old rams from the sample used to construct the survivorship curve in Appendix A. Our purpose in deleting the 16 young rams in question was to limit the influences of atypical weather. The same conclusions would have been reached had we started the life table at age 3 instead of age 1, an accepted actuarial procedure (F. Dean, pers. commun.).

Similarly, some readers may be skeptical of using Murie's skull collection as dx-type data (mortality determined from sheep which died naturally at the end of a normal life span to construct a partial life table. Because of the emphasis Murie (1944) placed on the die-off associated with the heavy snow and icing conditions in winter 1931-32, many have made the *a priori* assumption that Murie's data are lx type (mortality which samples uniformly across all living age classes). We think this is highly unlikely. The population of Dall sheep in the Park had been static for several years prior to the bad winter (Murie 1944:65). During this period, skulls were presumably deposited at the end of normal life spans for sheep, so they can be used as dx-type data. We think it extremely unlikely that the deep snows and icing inflicted uniform mortality across all age classes of sheep. If the data reported by Murie (1944) are to be considered lx-type data, this had to be the dominant mechanism of skull deposition. Our experience with a 25% die-off due to weather reported in Appendix B, and the observations that severe weather affects primarily young and old animals more than prime-aged animals, lead us to doubt that Murie's skull collection was a sample of the living. Likewise, other skull collections where unusual weather was not a factor have given survivorship patterns for bighorn rams similar to those generated using Murie's data (Bradley and Baker 1967). As pointed out by Murphy and Whitten (1976), we should expect variability in cohort size and survival. Still, we think that because the skulls Murie found were probably deposited over a sufficiently long period, they are most likely a sample of the dying. Furthermore, we believe this sample represents,

Table 18. Survival of all marked rams from the Dry Creek, Alaska Range captures of 1968-71.

Age	Number survivors from previous year	÷	Number possible	=	Percent survival	Number alive of 1,000 born
0	--		--		0.571[a]	1,000
1	22		31		0.710	571
2	41		50		0.820	405
3	44		53		0.830	332
4	30		48		0.625	276
5	20		32		0.667	172
6	14		20		0.700	121
7	10		14		0.714	85
8	2		10		0.200	60
9	0		2		0.000	0

[a] Long-term calculated survival for Dry Creek.

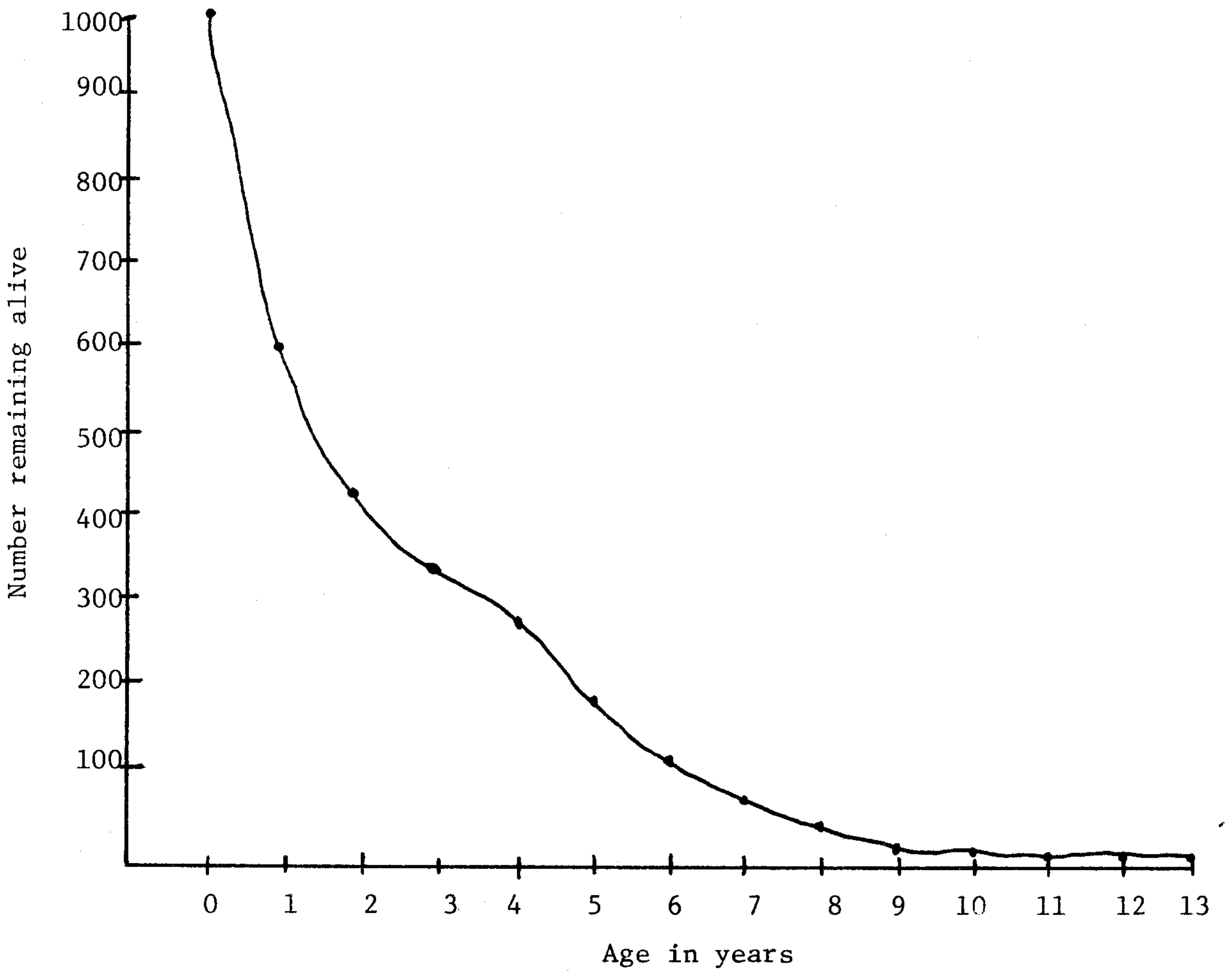

Fig. 5. Hypothetical survival of rams living in Dry Creek, 1971-83. Curve based on 77 marked rams not killed by hunters (see Appendix A).

generally, the survivorship pattern one may expect in an unhunted sheep population subject to relatively high predation and some severe weather influences, situations which were documented in Dry Creek.

We should also note that other investigators have found a survivorship curve similar to that presented in Fig. 5. Festa-Bianchet (1986) and Jorgensen and Wishart (1986) reported that survivorship of young bighorn rams in heavily hunted populations closely matches that of the Dall rams in our heavily hunted population.

In practice, a numerical increase in sustainable harvest rate has yet to be demonstrated when only 7/8- or full-curl rams are taken. Areas where population sizes are known with sufficient certainty to measure harvest rate and where harvest is maximal have been either placed on restrictive permit systems or have suffered population fluctuations which limit interpretation of present harvest levels. Harvest in Dry Creek since 1979 has shown that harvest levels at 7/8 curl have at least equalled those sustained under the 3/4-curl rule. In GMU 20, an average of 530 hunters had a harvest success of 36% for 3/4-curl rams from 1974 through 1978. From 1979 through 1983, an average of 480 hunters had a success rate of 41% for 7/8-curl rams. Since 1984, an average of 522 hunters have had an average success rate of 36% for full-curl rams. Two years are required to grow from 7/8 to full curl, and harvest of full curls should continue to increase over the next several years according to our model. Percentage hunter success did not change in the Dry Creek area even though legal horn size was increased in 1979 and 1984. Similarly, British Columbia has implemented a series of progressively more "restrictive" horn development regulations (Demarchi 1978). Their current full-curl regulations have been in effect since 1978 and no decline in harvest has been observed (Demarchi, pers. commun.).

Modeling Sublegal Ram Populations:

From the foregoing discussion, we hypothesize that the presence of more mature rams should increase survival of sublegal rams. This hypothesis predicts sublegal ram survival in Dry Creek should have increased after the regulation change from 3/4 to 7/8 curl. It was tested by modeling the sublegal (<7/8-curl) component of the Dry Creek ram population from 1980 through 1984. The modeling approach allowed comparison of survival rates necessary to match observed gain or loss to the sublegal ram population, in addition to testing this hypothesis by comparing predicted and observed population sizes.

First, we assumed no mortality beyond yearling age. The final population size predicted by this exercise was, of course, greater than the number of sublegal rams estimated from the 1984 survey. The difference between predicted and observed sublegal population sizes resulted from mortality in the sublegal ram component. This mortality was compared with that empirically determined for rams of the same ages in unhunted Denali Park and in Dry Creek during the maximum harvest at 3/4 curl (Appendix A).

Size of the sublegal ram component (ages 3-6 years) is determined by the balance between rams gained from the "ewe" group (as classified on aerial surveys) and those "lost" to the legal ram category because of continuing horn growth and death. Consequently, the model required knowledge of the number of sublegal rams (less than 7/8 curl) present in 1980. These data were obtained from the aerial survey of 1980 when 200 sublegal rams were counted. This was an accurate survey with excellent flight conditions, a high survey intensity of 1.6 min/km^2 (4.3 min/mi^2), and an experienced survey team. Unfortunately, the population contained no marked sheep in 1980. Extrapolation of sightability (on the basis of differential survey effort) from a survey with less intensity but a known efficiency produced a calculated efficiency of 0.850. Hence, the initial size of the sublegal ram population was estimated at 235. Sublegal ram population size was then calculated for each successive year.

The calculations required estimates of actual yearling numbers for some years when only relative yearling:100 ewe ratios were available because aerial surveys were not done. These yearling ram numbers were estimated by plotting the known number of yearling rams recruited in years of complete data as a function of half the yearling:100 ewe ratio for the same year. We assumed half the yearlings were rams. This plot (Fig. 6) predicts the number of yearling rams recruited for the normal range of observed yearling:100 ewe ratios.

The sublegal ram population size for each year (assuming no mortality) was derived from Table 19 by adding the year column over age classes 3, 4, 5, and 6. When this was completed, the model predicted a sublegal ram population (with no mortality) of 465 in 1984. The survey of 1984 produced an estimate of 396 sublegal rams. The difference is due to mortality factors that were not included in the model. This difference of 69 rams indicates a mortality of 15% over the 3 mortality periods between ages 3 and 6.

As reported in Appendix A, 548 3-year-old rams existed in the hypothetical cohort followed through the life table for Dry Creek rams under maximum harvest at 3/4 curl. Rams contributing these data were not killed by hunters but were presumed

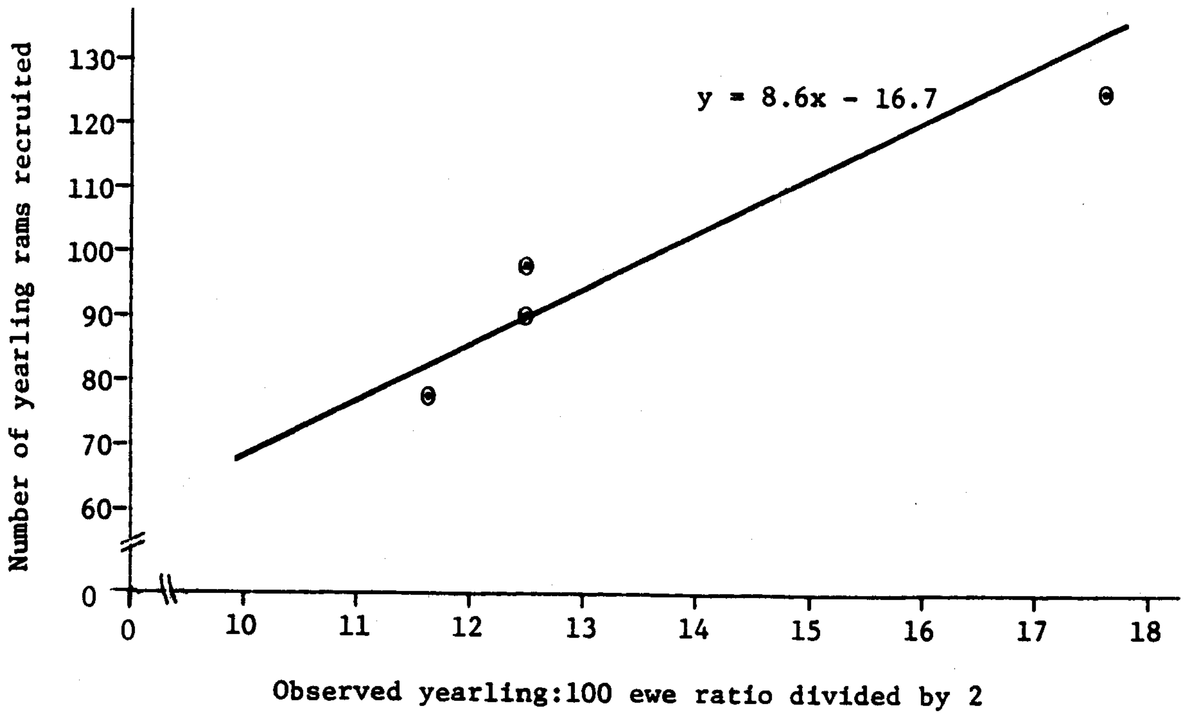

Fig. 6. Number of yearling Dall sheep rams recruited in relation to the yearling:100 ewe ratio in Dry Creek, Alaska.

Table 19. Number of Dall sheep rams in each age class (1-6) from 1975 through 1984, assuming no mortality occurred past yearling age. Data primarily from mineral lick population composition counts of yearlings, Dry Creek, Alaska.

Year	1975	1976	1977	1978	1979	1980[a]	1981	1982	1983	1984[a]
Age 1	80	54	58	90	64	128	174	99	26	98
Age 2		80	54	58	90	64	128	174	99	26
Age 3			80	54	58	90	64	128	174	99
Age 4				80	54	58	90	64	128	174
Age 5					80	54	58	90	64	128
Age 6						80	54	58	90	64
Sublegal ram population size						282	266	340	456	465

[a] Aerial survey.

dead when no longer observed. By the end of year 6, this number had declined to 266. This decrease (or mortality) of 282 rams was 51% over the 3 mortality periods. Hence, mortality of rams from ages 3 to 6 years was 15% under heavy 7/8-curl cropping but 51% under heavy 3/4-curl cropping, a decrease of 71%. This represents a change in survival from 49% (owing to the ecological variables associated with the 1972-79 3/4-curl harvest period) to an 85% survival after the 7/8-curl regulation. In the unhunted Denali Park sheep herd, rams aged 3-6 years had a mortality over these age classes of only 7% (Appendix A). These data support the hypothesis that survival of young rams increases when older rams are present. Specifically, our calculations indicate mortality decreased from 51% over ages 3-6 years to 15% over the same ages after establishment of the 7/8-curl regulation. If this change is due to more and older rams being present, it is possible that mortality could be further reduced by establishing a full-curl minimum horn size for hunting purposes (Fig. 4).

Of course, factors besides the change in harvest management could have contributed to the increased survival. Chief among these was wolf predation. Wolves were presumably abundant when the 51% mortality from age 3 to 6 was observed in Dry Creek. Wolves were also present in Denali National Park during the years Murie gathered data there. Wolves were sufficiently abundant that Murie documented 17 interactions between sheep and wolves between 1939 and 1941. Ten of these resulted in death of sheep. Murie (1944) concluded wolves controlled the sheep population. This appears to be similar to the Dry Creek situation (Heimer and Stephenson 1982). Still, Murie's data suggest a low 3-period cumulative mortality of 7%. Similarly, the latter-time data set for Dry Creek survival was gathered from 2 to 6 years after aerial wolf shooting had been terminated. The extent of predation by wolves as a cause of the observed changes in young ram survival remains speculative, but we think lowered ram abundance due to hunting and weather events had synergistic actions which amplified this influence.

Also, weather could have been a contributing factor to the increased survival of sublegal rams because the mean snow depth across the north face of the Alaska Range was greater in the late 1970's and early 1980's than in the early 1970's. Still, reference to the table on snow depths (Table 5) reveals only 1 notably heavy snow deposit could have affected the 1st data set (1975 had a mean snow depth across the north slope of the Alaska Range of 20.3 inches). Winter 1979, which would not have influenced survival of rams in the 1st data set, and winter 1982, were both winters of greater than average snowfall (21 and 23 inches, respectively). These would have compromised survival of rams contributing to the 2nd data set, where survival was much greater. This leads us to think snow depth was not the major influence on the observed change in ram survival rate. Because weather mediates nutrition, we think food availability and quality were relatively minor mortality factors.

Also, the high mortality rates observed in both Dry Creek data sets (15% and 51%) appear to be specific to rams. Heimer (1973) estimated ewe mortality between ages 2 and 9 (from 1968 through 1973) at 9% based on return of marked ewes to the Dry Creek lick. This mortality rate for Dry Creek ewes was greater than that from Denali Park ewes (Bradley and Baker 1967) or from the Robertson River (Appendix A). It was also greater than ewe mortality in Dry Creek after 1981 (see next section). Either wolves were preying preferentially on young rams, or weather and nutrition were selecting against young rams more than young ewes. Both scenarios are consistent with the mechanism of fasting during rut that Geist (1971) suggested for increased young ram mortality.

When we recalculated the sublegal ram population sizes for years since the 7/8-curl regulation was established, we produced the data array in Table 20. The modeled sublegal population predicted for 1980 was 211 sublegal rams. The estimated number from the 1980 survey was 235. The model predicted low by a difference of -9%. This prediction is of uncertain validity because rams aged 6 in 1980 would have lived 5 years under the 3/4-curl cropping regime. They would also have benefited from wolf population reduction from age 2 onward.

The model predicted the sublegal ram population size in 1984 would be 435. The population estimated from the aerial survey in 1984 was 396. In this case, the model predicted high by a difference of 39 rams or about +9%. This could have been due to at least 2 possible causes. The severe winter of 1982-83 could have caused higher mortality, or the high mortality from the 3/4-curl period could have persisted longer than we allowed in the model.

In these 2 tests, the model predicted within plus or minus 9% of the estimated ram population. Considering the changes in influential variables, the uncertainties of sheep population estimates, and the reliance on extrapolation required for our applications here, we think the method shows promise. It is unlikely to be less accurate than present methods of estimating ram populations which are even more subjective and depend upon untested assumptions. We think it can be developed for use by managers in setting maximum harvest quotas for restrictively managed areas. At present, such quotas are conservatively set to safely meet management objectives. Use of this or a similar technique could justify providing more hunting opportunity in restricted opportunity management situations.

Table 20. Number of Dall sheep rams in each age class (1-6) from 1980 through 1984 if the following mortality rates are applied. For 1975-80, 2% per year for ages 1-3 and 17% for ages 3-6; for 1980-84, 2% per year for ages 1-5 and 5% for age 6, Dry Creek, Alaska.

Year	1975	1976	1977	1978	1979	1980[a]	1981	1982	1983	1984[a]
Age 1	80	54	58	90	64	128	174	99	26	98
Age 2		78	53	57	88	63	125	171	97	25
Age 3			76	52	56	86	62	122	168	95
Age 4				63	43	46	84	61	120	165
Age 5					52	36	45	82	60	118
Age 6						43	34	43	78	57
Sublegal ram population size						211	225	308	426	435

[a] Aerial survey.

Objective 5: Ewe Survival Beyond Yearling Age

Ewe survival, particularly in the more lightly hunted Robertson River population, is better known than ram survival. By continuous trapping, we kept approximately 10% of this ewe population marked throughout the study. This allowed determination of mortality across age classes each year (Appendix B). Ewe mortality beyond yearling age has, like ram mortality, 2 distinct phases (Bradley and Baker 1967). The low mortality phase, from age 1 through age 8 years, had a nearly constant mortality of 6%; mortality beyond age 8 years averaged about 18% per year.

Modeling Ewe Populations:

A model similar to the one used to predict ram mortality was developed using the following formula:

$$E_t = [E_{t-1} \times S_{(t-1)\ \mathrm{to}\ t}] + [F_{t-1}]$$

where:

- t = year
- E = total ewes in population age 2 years and older
- F = number of yearling ewes recruited in June
- S = survival rate (number of collars seen ÷ number possible)

This formula requires aerial survey data, mortality estimates, and ground-based composition data to estimate population size and composition. Our data are summarized in Table 21.

The model for the Robertson River population began with data from the aerial survey of 1980. During this survey, flight time for the 750 km^2 (290 mi^2) study area was 16.1 hours, resulting in a survey intensity of 1.3 min/km^2 (3.3 min/mi^2). Sightability was established at 76.2%, based on observation of 48 of a possible 63 collars. The ewe/"ewe" factor was determined at the mineral lick where a sample of 585 sheep which would have been classified as "ewes" from the air was accurately classified. This sample contained 434 "true ewes," 127 yearlings, and 24 1/4-curl rams. On the survey, 468 "ewes" were seen. For the 1980 data, we multiplied 468 "ewes" times the classification correction factor 0.742 ewe/"ewe" to obtain 347 "true ewes." This figure, divided by a sightability correction factor of 0.762, estimated 456 ewes in the population. To establish the number of yearling ewes essential for calculation of the next year's ewe population, we multiplied the ewe population by the yearling:100 ewes ratio obtained at the mineral lick (29 yearlings:100 ewes). The result is 132 yearlings of both sexes. We assumed half of these yearlings were females, so 66 yearling ewes were present.

Winter 1980-81 was mild with no mortality among the 63 marked ewes. Consequently, before June 1981 the number of ewes had increased to 456 plus 66 yearlings produced the previous year, or 522 ewes. The yearling:100 ewe ratio was 32. Multiplying 32 by 5.22 hundred ewes results in 167 yearlings of both sexes, or 84 yearling ewes.

Observed mortality during winter 1981-82 was high (Appendix B); 14 of the 63 marked ewes died, so the number of ewes decreased to 552X (49/63) or 429 ewes. These ewes, plus the 84 yearlings recruited from the previous year, gave a population of 513 ewes in June 1982. The yearling:100 ewe ratio for 1982 was 36. Multiplying this by 5.13 hundred ewes gave 185 yearlings of both sexes, or 92 female yearlings.

Winter 1982-83 was apparently mild, and 48 of the 49 marked ewes survived. The number of ewes surviving was calculated by multiplying 513 ewes times 48/49, or 502 ewes. This number was increased by the number of yearlings produced in the previous year (92), for a total of 595 ewes in June 1983. Yearling:100 ewe ratio was 13 that June. Consequently, multiplication of 5.95 hundred ewes resulted in 77 yearlings of both sexes, or 39 yearling ewes.

Winter 1983-84 resulted in the survival of 40 of 48 marked ewes. Multiplication of this survival rate (40/48) by the number of ewes present the previous summer (595) totaled 496 ewes. Adding the 39 recruited female yearlings resulted in a prediction of 534 ewes present in June 1984.

The aerial survey of 1984 (intensity of 0.9 min/km^2 [2.44 min/mi^2], sightability of 0.8, and ewe/"ewe" factor of 0.8) revealed an estimated 550 ewes. In this case, the model predicted 16 fewer ewes than the survey estimate, a difference of 2.9%.

The mean number of ewes in the population during the study period was 524. Variations ranged from +14% to -13% on either side of this mean. Between-year variations ranged from an increase of 16% to a decrease of 10%. This population, if sampled only in 1980 and 1984, would have appeared to be increasing by 17%. Clearly, this conclusion would have been misleading. The population size appeared to fluctuate around a mean of 524 ewes over the course of this study. Consequently, intermittent point-in-time samples, which are used for survey and inventory purposes, are unreliable indicators of trend. To be meaningful, management inventories should be made annually unless the presence of marked individuals can establish survey efficiencies and overall ewe mortality. These data can be used in conjunction with accurate ground composition counts to interpolate between surveys at 3- to 5-year intervals. This is not to imply that survey and inventory assessments are not useful because they do provide minimum estimates of population size, give biologists a feeling for what is occurring if done frequently, and may detect major disasters or unusually vigorous population growth. Still, quantitative projections based on management inventories are likely to be questionable, particularly if infrequently conducted and not supported by ground composition count data.

These data support the conclusions of Murphy and Whitten (1976) that variations in cohort size greatly influence observable population size at any given time. We believe this approach to modeling demonstrates that practical low-cost application of their findings is possible in Alaska. Realistic, data-based harvest quotas may now be established on the basis of population recruitment size and year-to-year composition.

Age-specific mortality of ewes from the Robertson River and Dry Creek populations since 1981 are presented in Tables 21 and 22. By using these tables, we can generate survival curves for ewes in both populations under differing conditions of environmental resistance. The data we present on this aspect of ewe mortality are preliminary, and data gathering should continue. All age classes of ewes were represented in the marked sample (Appendices C and D).

Integration of Findings

Findings resulting from our involvement in Dry Creek since 1968 and in the Robertson River since 1974 can be divided into 3 basic categories. These include overall population size, impacts of disrupting ram age structure, and factors affecting lamb production.

Population Size:

We found that Dall ewe populations can fluctuate up to 17% between successive years without materially affecting the long-term productive segment of the population. This occurs when favorable weather allows survival of older age ewe cohorts beyond their normally expected life span. If surveyed before, during, or after such a transient high ewe population, the population may be interpreted as expanding or declining when it is, in reality, not greatly affected with respect to its long-term productive potential. Consequently, intermittent point-in-time aerial surveys are a poor method of monitoring population trend. Effective population monitoring requires knowledge of recruitment, survival, and overall population size for ewes. This can be accomplished by marking individual ewes, defining a population trend, and determining

Table 21. Cohort sample sizes and percentage mortality by year and age class among collared Dall sheep ewes in the Robertson River study area, Alaska Range, 1977-84.

Year	Age in years													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1977	0	0	0	4	0	0	0	0	0	0	0	0	0	0
1978	6	0	4	0	6	1	3	0	1	1	0	0	0	0
1979	7	19	2	10	6	11	5	4	1	4	1	0	1	0
1980	0	6	17	2	9	5	11	5	3	1	4	1	0	0
1981	0	0	6	17	2	8	5	10	5	3	1	4	1	0
1982	0	0	0	6	16	2	6	5	10	2	2	1	0	0
1983	1	1	3	2	8	18	4	7	3	9	2	1	1	0
1984[a]	0	2	5	6	9	10	17	6	6	3	7	1	1	1
Total	14	28	37	47	56	55	47	37	29	23	17	8	4	1
Total mortality	1	2	0	4	5	3	1	4	4	3	2	4	2	0
Percent mortality	7	7	0	9	9	6	2	11	14	13	12	50	50	
Percent survival	93	93	100	91	91	94	98	89	86	87	88	50	50	

[a] Mortality assumed with 1 year's absence.

Table 22. Cohort sample sizes and percentage mortality by year and age class among collared Dall sheep ewes in the Dry Creek study area, Alaska Range, 1981-84.

Year	Age in years													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1981	7	2	4	6	4	1	2	0	0	0	0	0	0	0
1982	0	2	6	2	5	2	1	2	1	1	1	0	0	0
1983	3	6	4	3	3	2	3	0	1	0	0	1	0	0
1984	6	0	3	3	1	0	1	1	0	0	0	1	0	0
Total	16	10	17	14	13	5	7	3	2	1	1	2	0	0
Total mortality	2	1	1	2	3	0	2	2	2	0	0	0	Unk	Unk
Percent mortality	13	10	6	14	23	0	29	67	100	0	0	0	Unk	Unk
Percent survival	87	90	94	86	77	100	73	33	0	100	100	100	Unk	Unk

annual yearling recruitment and marked ewe mortality. Aerial surveys to verify population size may then be flown intermittently. Such a program might require more money, but would entail less risk and provide better information than aerial surveys as presently used. This ineffective technique is expensive, dangerous, and provides data which are, at best, subjectively interpreted.

Impacts of Disrupting Ram Age Structure:

Disruption of ram age structure by removal of most Class III and Class IV rams reduces survival of the young rams which remain in the population. This has been demonstrated for Dall sheep in Dry Creek and for 2 populations of bighorn sheep in Alberta. Also, heavily hunted populations with 3/4-curl regulations yielded low sustainable harvest rates. The mechanism apparently involves increased physical activity for young rams which achieve dominance rank before reaching full physical maturity. Increased activity depletes energy stores and lower body condition early in winter. These rams have poor survival rates, leading to lower population size and attendant increased susceptibility to predation. Data on age-specific mortality patterns for unhunted Dall sheep, accepted behavioral theory, and evidence gathered from populations subjected to heavy exploitation by hunters, as well as natural predation, are all consistent with this hypothesis.

Weather, predator abundance, and sport hunting as practiced in Alaska and the western United States all lower ram population numbers and frequently select against survival of larger rams. If management goals call for maximum harvest by people, production of legal rams should be maximized. Conditions favoring ram production are: (1) maximum ewe population sizes, (2) favorable weather, (3) low predator abundance, and (4) a relatively undisturbed ram age structure. Managers cannot influence weather, and only occasionally can they influence predator abundance. Managers routinely have considerable influence on ewe population size and ram age structure. If maximal production of legal rams is desired, managers should strive to achieve both of these conditions.

Factors Affecting Lamb Production:

Lamb production is affected by many ecological variables. These include weather (which may influence breeding condition through ovulation rate), ram abundance (through insemination rate), food quality and availability throughout gestation (through winter severity, i.e., range restriction by accumulated snow), and neonate survival (through weather at lambing and abundance of predators which can kill newborn lambs). Because the entire sequence begins with ovulation, it is certain that ewes which fail to ovulate will not produce lambs. The Dry Creek population in the mid-1970's had a lower ovulation rate than did the Robertson River population. We found no suggestion of nutritional inadequacy accompanied this phenomenon. Because weather must mediate nutrition, we concluded weather was not a satisfactory explanation for the decreased ovulation rate. Furthermore, we could not account for the difference due to predation, and studies of reproductive activity by age class showed changes in age structure were not a viable explanation. We think extended lactation was the most likely cause of decreased ovarian activity. The differences in ram abundance, given that other factors presented unsatisfactory explanations, were hypothesized as the cause. We suggest that low ram abundance may lead to prolonged lactation, failure to ovulate, and lowered lamb production. This hypothesis is consistent with the data suggesting a more frequent reproductive interval in situations with high or relatively high ram abundance. Consequently, we suggest that low ram abundance affects not only a compromised survival among rams which remain, but lowers lamb production as well.

Given that sufficient sheep habitat exists, managers should first maximize ewe numbers at levels supportable by the habitat. Second, managers should provide for a minimally disrupted ram age structure, which, if rams are managed simply by general regulation, should assure increased ram abundance. Third, managers should seek to reduce predator abundance. Finally, when considering the effects of weather on Dall sheep production, managers and researchers should broaden their perspective to include all aspects of weather influence instead of concentrating on weather limitations to foraging during gestation.

MANAGEMENT RECOMMENDATIONS

This study presents information that is in conflict with the current thinking of many sheep managers and the assumptions under which sheep have been traditionally managed. The hypothesis that high ram harvests affect population well-being appears reasonable and leads us to the management recommendations listed below relating to Dall sheep hunting. Specifically, we recommend:

1. Managers examine the assumptions under which they work and consider population age and sex structure in their analysis.

2. Managers should not return to 3/4-curl regulations where Dall sheep are subjected to heavy hunting. All Class III (3/4-curl) rams should be protected as well as some Class IV (full-curl) rams. This can be accomplished by a full-curl regulation for hunting.

3. Full-curl regulations should be accompanied by a minimum limit on ram age and provision for taking broomed rams if maximum harvest is desired.

4. Managers should inform the public about the importance of maintaining an undisturbed ram social structure.

5. Managers desiring maximal production from sheep populations should maintain and increase ewe numbers consistent with the capacity of habitat to support them.

6. Managers should discontinue intermittent aerial surveys for the purpose of determining population health and trend.

7. Annual aerial surveys should be supplemented by ground classification counts to measure lamb survival and recruitment.

8. Managers with programs involving restrictive permitting procedures should determine population size and production with reasonable confidence limits.

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A long-term project of this type requires a great deal of effort on the part of many. In our case, this was particularly important, for funding was minimal. Because of this, we have solicited, and benefited from working with, many volunteers who are not professionally trained in wildlife management. We will probably make omissions because we did not keep careful records of the contributions made by others along the way. Still, the contributions made by the following persons come to mind.

The decision to study Dall sheep in Dry Creek was made in 1967. Those who played major roles in that decision are in large measure responsible for all that has been learned there. They include Robert Rausch and Frank Jones initially, and, later, James Erickson and Lyman Nichols. James Erickson did the early trapping and marking work until his untimely death while on a sheep survey. Tony Smith, Wayne Heimer's 1st partner and mentor, carried on the trapping and marking which were the basis of all that has transpired since. It is impossible to sufficiently credit these individuals. Of course, they received administrative support from Robert Hinman and James Harper.

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We apologize to anyone we have overlooked. This report has, because of its scope and the unexpected implication it produced for sheep management, been difficult to write, comprehend, and edit. We are grateful to our critics, who are our friends, for their suggestions. We are grateful to those friends, who are not our critics, for their encouragement and support.

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Appendix A.

EXCESS RAM MORTALITY IN A HEAVILY HUNTED DALL SHEEP POPULATION

Presented at the Biennial Symposium of the Northern Wild Sheep and Goat Council, April 30-May 3, 1984
Whitehorse, Yukon Territory, Canada

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ABSTRACT

The basic assumption underlying management of Dall sheep (Ovis dalli dalli) for maximum hunting opportunity and maximum sustainable ram harvest is that heavy harvest of legal (3/4 or 7/8 curl) rams has no effect on the survival of sublegal rams. This assumption was tested by studying Dall ram mortality in a heavily hunted population in interior Alaska. Between 1969 and 1971, 23 legal (at 3/4 curl) and 93 sublegal rams ranging in age from 1 through 5 years were trapped and marked. The population was then monitored through 1983 by aerial survey, hunter reports, ground survey, and mineral lick observation. When marked individuals were no longer observed, they were presumed dead. The age at last observation was recorded as the age at death. A life table for rams which were not killed by hunters was constructed and their survival was compared with that of unhunted rams in McKinley Park, 64 km (40 miles) to the east. Slope of survivorship curves for unhunted rams was nearly identical to that of the heavily hunted population. However, the age at which increased mortality became evident shifted downward from about 8 years in the unhunted group to about 3 years in the heavily hunted population. This finding indicates the assumptions underlying most ram management are not correct and suggests reevaluation of management philosophy. A behavioral mechanism and a more productive management approach are suggested.

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INTRODUCTION

Regulation of mountain sheep hunting throughout North America usually limits harvest to rams in the upper age classes. This practice has been widely applied by wildlife managers because it is presumed to offer maximum opportunity to harvest mountain sheep while providing a horn size acceptable to most hunters. The underlying assumption of this management scheme is that heavy or even total cropping of rams at 3/4 curl provides the maximum harvest of acceptable trophies. After all, common sense tells us the number of rams in a cohort is highest at birth, after which natural mortality begins to reduce numbers in each cohort. Hence, the highest possible harvest would be immediately following birth, and harvests at later dates would be progressively lower because some individuals had succumbed to environmental resistance along the way. This is correct only if the basic assumption is valid.

Stated in greater detail, the major assumption predicts heavy harvest of legal rams (traditionally 3/4 curl) has little or no effect on the survival of sublegal rams. This assumption has come under increasing scrutiny as more has been learned about mountain sheep behavior. Still, it survives without experimental demonstration. In this paper we report on a test of this basic assumption and its relevance to traditional management of wild sheep in Alaska.

MATERIALS AND METHODS

Twenty-three legal (3/4 curl or greater) and 93 sublegal rams (about 35-40% of the ram population) were trapped and marked in the Dry Creek area of the eastern Alaska Range in 1969, 1970, and 1971. Dry Creek was heavily hunted, and legal, 3/4-curl-or-greater rams composed only 3% of the population. Rams were captured at a mineral lick during early summer with a drop net (Erickson 1970) as part of a larger study of Dall sheep movements, mineral lick use, and ewe mortality in the Alaska Range (Heimer 1974). Forty-seven rams were marked with metal eartags in both ears and large canvas neckbands. Thirty-eight rams were marked with rope and pendant collars and plastic and metal eartags. Thirty-three rams were marked with plastic and metal eartags, but no collar.

Marked rams were repeatedly sighted from aircraft. Frequent flights were made to search for these sheep, and to assess their home ranges (Heimer 1974). Marked rams were also repeatedly sighted by investigators on 5 foot trips throughout the area each year. These trips were made during all seasons of the year to enhance resolution of data gathered from aircraft. Marked rams of legal size were available to hunters, and hunters and guides were made aware of the necessity of reporting sightings. Hunters taking legal, marked rams were also required to report their kills to the Alaska Department of Fish and Game. Mineral licks were monitored each year and marked sheep were observed as they returned to the mineral lick each year. The observed return rate for rams (80%) was found to be lower than that for ewes (98%). Heimer (1974) interpreted this as a genuine lack of fidelity to home ranges by rams.

However, results of this study suggest it may have been an artifact of mortality. Other mineral licks in the area were also monitored in the course of foot searches for collared rams. Records were kept of all resightings and hunter kills through 1983, the year in which the youngest rams marked would have been 12 years of age.

Mortality of marked rams was determined from harvest reports and failure to resight rams for an entire year. Rams were presumed dead if not sighted for 2 years, and age at death was listed as their age at the last observation. Sixteen 1- and 2-year-old rams marked in 1970 and never resighted were deleted from the sample because winter 1970-71 was very severe, and many rams of these age classes probably died during that severe winter. A life table was then constructed for the remaining 100 rams and compared with a similarly constructed life table for rams in an unhunted population. Unhunted population data used were those reported by Murie (1944) from Mt. McKinley National Park 68 km (40 mi) to the east. Once life tables were constructed, the survivorship curve (lx) for each population was plotted. Equations describing the increased mortality phase of each curve (Geist 1971:295) were established by linear least squares fit.

RESULTS

Hunters killed 10 of the 23 rams that were legal when marked: 5 were killed in the first hunting season after they were marked, and 5 during the next hunting season. Of the other 13 legal rams, 1 was found dead of natural causes 2 months after capture; the rest were never seen again. These 12 rams were not reported killed by hunters. They were never found in broad aerial searches of adjacent habitat. They are presumed to have suffered early, natural mortality. Their mean age at capture was 6 years and their mean age when last sighted--at presumed death--was 7.5 years. The known harvest rate of legal rams in the population was 43% (10 of 23 in the marked sample).

Hunters reported killing an additional 12 marked rams which grew from sublegal to legal size during the study. When harvested, these rams had survived a mean of 5.3 years since being marked. The realized harvest was 16% of the sublegal marked sample. The ages and rate at which the 77 rams not killed by hunters disappeared (or died) are shown in Table 1.

DISCUSSION

The life tables for the Dry Creek (Table 1) and McKinley Park (Table 2) populations were compared to test the hypothesis that removal of most 3/4-curl and larger rams has no effect on survival of the remaining sublegal rams. The survivorship curves generated from these life tables show that accelerated mortality of McKinley Park rams begins at about age 8. It is described by the equation, $y = -92X + 1232$. The comparable equation for estimated mortality in Dry Creek rams is $y = -91X + 818$, with the rapid mortality phase beginning at about 3 years of age. This is 5 years earlier than for the unhunted population. The only difference in the survivorship curves for the 2 groups of rams is the age at which increased mortality begins. Young rams in the heavily hunted population exhibit a mortality pattern characteristic of older rams in the unhunted group.

Since data for lamb production and survival are not available from Murie's collections we applied the mean lamb survival (57%) observed between 1972 and 1982 in the Dry Creek study populations to the McKinley National Park data to make the plots comparable. Comparative observations of production and recruitment ratios for the last 10 years indicate these 2 populations are comparable (Heimer, unpubl. data).

The mortality among young Dry Creek rams is about 5 times greater than for ewes of the same ages. Heimer (1973) reported a mean mortality rate of marked ewes younger than 9 years of 7%; once ewes reached age 9 this increased to 50%. The mean mortality rate for marked rams 3 to 9 years of age averaged 37%. In light of these findings an earlier suggestion that ram fidelity to mineral licks is less than that of ewes (Heimer 1974) should be reexamined.

We think the observed differences in mortality patterns result from changes in behavior due to lack of large rams in the Dry Creek population. When socially dominant rams are removed from the population by hunters, younger rams assume the roles of dominant rams and exhibit adult behavior patterns (Geist 1971, Nichols 1971). This places additional energetic stress on young rams before they are physically and behaviorally mature. Geist (1971:349) concluded, "One effect of neoteny is a postpuberal maturation period of 5 to 6 years for rams in which they increase in body and horn size and mature in social behavior." "Promotion" of young rams (which are just entering this period of postpuberal development) by removal of their inhibitory social dominants leads to behavior which apparently increases mortality in young rams just as it does in older rams. We think evidence indicates the presence of a mortality cost associated with social dominance that is independent of age.

These findings show the underlying assumption implicit in mountain sheep management is incorrect. The alternate hypothesis, that social disruption caused by heavy ram hunting significantly reduces survival of the remaining sublegal rams, is consistent with behavioral analysis (Geist 1971) and our data. Managers seeking to provide maximum hunting opportunity through maximum harvest levels should consider the potential advantages afforded by setting legal definitions to select for older rams. This may decrease mortality among young rams and provide for increased ram harvest without adverse effects. Heimer (in prep.) details arguments that show such apparently "conservative" management approaches should increase harvest levels. This has already occurred in southern British Columbia where establishment of a full-curl or 8-year-old legal definition in 1976 was followed by increased harvests (DeMarchi, pers. commun.).

We have suggested a major departure from established sheep harvest management. We believe the data are sufficiently compelling that experiments with changes in harvest regime are in order. Still, we realize that much of what we have offered may be equivocal. Most criticism should be directed at our use of "presumptive death" when we could no longer locate marked rams. Cessation of resightings does not necessarily demonstrate a given ram is dead. He could have moved, or perhaps we were simply unable to locate him. It is most unlikely that marked individuals moved. All rams located were loyal to established ranges. Furthermore, hunting pressure was very high throughout the entire eastern Alaska Range during the study. Legal rams composed only 3% of a much larger population than that residing in the Dry Creek study area. Virtually all legal rams were being taken from areas up to 40 km on either side of this study area. Still, no marked rams were reported taken by hunters from areas outside of the defined home ranges.

Hunters reported killing only 22 of the 100 potentially available rams. This is less than half of the expected harvest given the observed harvest rate for legal rams in the marked sample. If this light level of harvest really occurred, horn size should have risen dramatically. It didn't. Old rams continued to be scarce in the population through the end of the study period. The remaining explanation is that hunters killed collared rams and did not report them. We find it inconceivable that only half of the successful hunters taking marked rams reported. All hunters who reported were very interested in the study. Some were negative about having shot a marked ram, but no one was disinterested. It is unlikely that marked rams were killed in large numbers and not reported.

We think these alternate explanations are so unlikely that "premature death" is a much more reasonable conclusion. At the very least, these data are sufficient to warrant further investigation of the effects of heavy hunting on survival of postpuberal rams. At most, they indicate that management philosophy should change and that legal definitions relevant to management of rams for maximum harvest and hunting opportunity should be realigned.

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Table 1. Life table for rams disappearing from the observable Dry Creek populations from 1969 to 1982.

Age at death (presumed)	Frequency in sample	Cumulative frequency	% survival of 1,000	% mortality of 1,000	No. alive of 1,000
0	--	135	--	--	1,000
1	2	77	0.570a	0.430	570
2	1	75	0.974	0.026	555
3	9	74	0.987	0.013	548
4	18	65	0.878	0.122	481
5	11	47	0.723	0.277	348
6	14	36	0.766	0.234	266
7	10	22	0.611	0.389	162
8	9	12	0.546	0.454	88
9	3	3	0.250	0.750	22

[a] 57% was the mean survival from lamb to yearling age in Dry Creek during the study.

Table 2. Life table for Dall rams from McKinley Park from Murie 1944.

Age	Frequency in sample (No. skulls)	Cumulative frequency	% survival of 1,000	% mortality of 1,000	No. alive of 1,000
0	--	547[a]	--	--	1,000
1	--	312[b]	0.570	0.430	570
2	5	305	0.978	0.022	557
3	6	300	0.984	0.016	549
4	7	294	0.980	0.020	538
5	8	287	0.976	0.024	524
6	8	279	0.972	0.028	510
7	17	271	0.971	0.029	495
8	26	254	0.937	0.063	464
9	37	228	0.898	0.102	417
10	52	191	0.838	0.162	349
11	75	139	0.727	0.273	253
12	60	64	0.460	0.540	117
13	1	4	0.063	0.937	7
14	3	3	0.750	0.250	5

[a] Calculated from mean survival in Dry Creek from 1972-82.

[b] From findings of Bradley and Baker (1967), Hoefs (1979), and Geist (1971) which show mean survival between years 1 and 2 equals that between ages 2 and 7 years.

Appendix B.

AN AGE-SPECIFIC WINTER DIE-OFF IN DALL SHEEP IN ALASKA

Presented at the Biennial Symposium of the Northern Wild Sheep and Goat Council, April 30-May 3, 1984 Whitehorse, Yukon Territory, Canada

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ABSTRACT

Dall sheep (Ovis dalli dalli) population estimates made in summer 1982 indicated a loss of 21% among collared ewes in the eastern Alaska Range. Reports of similar overwinter losses came from adjacent mountain ranges. Severe winter weather was presumed to be the cause of this heavy mortality. Analysis of age data for ewes missing from the marked sample population showed that 77% of the missing (presumed dead) ewes were 9 years of age or older. Mortality in age classes younger than 9 years was 6%. The high percentage population loss was probably due to unusually high survival of 12-year-old ewes during the previous winter (1980-81) which was quite mild. This cohort, then aged 13 years, died along with other old-age ewes in 1981-82. Age distribution and mortality data of collared ewes are presented. Caution should be exercised in generating mortality curves for ewes.

INTRODUCTION

It is the purpose of this paper to report on ewe mortality data which have been collected as part of a long-term study of Dall sheep ecology in the eastern Alaska Range (Heimer and Watson 1982). It is prompted by a die-off of marked ewes after winter 1981-82.

In June 1982, observations at the Sheep Creek mineral lick revealed a large proportion (21%) of the marked ewes (which constitute about 10% of the ewe population) did not return to the mineral lick. As ewes are virtually certain to appear at the lick if they are alive (Heimer 1973), missing ewes were presumed dead. A loss of this magnitude is highly unusual in the eastern Alaska Range, and was cause for concern. When reports of similar losses were received from local residents in the northern Wrangell Mountains, the Tanana/Yukon Uplands, and Sheep Mountain, Kluane Park, Yukon, corrective management actions were taken. In the study area near Tok, Alaska, the ewe hunt was closed by emergency order. This closure may, in retrospect, appear more cosmetic or philosophical than necessary.

METHODS

Ewes were marked with visual collars at the Sheep Creek mineral lick in the eastern Alaska Range during June 1977-1979. Trapping and marking techniques used were described by Heimer et al. (1980). In subsequent years, the mineral lick was monitored for collared ewes during June, the month in which lick use is most likely to occur (Heimer 1973). In 1977, 1978, and 1979, the lick was observed incidental to trapping operations from 0400 hrs to 2000 hrs daily from the second week in June through the first week in July. In 1980, the mineral lick was observed from 12-14 June and 19-28 June. Observations were made from 0400 through 2000 hrs on those dates. In 1981, 1982, and 1983, the lick was observed continuously from 28 May through 30 June. Observations were conducted from 0300 to 2000 hrs.

Collared ewes not returning to the lick were presumed dead in the year they first failed to return (Heimer 1973). Each year's "deaths" were checked by noting if the missing individual was seen in the following year. They were then either "confirmed as dead" or re-entered as still living in the population. Some deaths were confirmed through hunter kills and the discovery of dead ewes.

The list of "confirmed" dead collared ewes for each year was divided into 2 age groups: those less than 9 years of age at death and those with ages greater than or equal to 9 years at death. Hunter-killed ewes were deleted from both groups. Annual percent natural mortality in each age group was derived by dividing the number dead by the total number living at the end of mineral lick observations.

RESULTS

In June 1982, 14 of a possible 62 marked ewes failed to return to the mineral lick. One of these ewes was seen in 1983 so the confirmed overall mortality was 13/62 (21%) of the marked population. Of the 62 total collars in the population, 13 were 9 years of age or older. Ten of these 13 ewes died. These 10 ewes were 77% of the total year's mortality of 13 ewes. This compares with an annual 5% mortality averaged over the previous 3 years for ewes 9 years old or older. Mortality during the difficult winter was 15.4 times greater than earlier years for ewes of this age group.

Among ewes less than 9 years of age, mortality documented for winter 1981-82 was 3/49 or 6% (Table 1). This is identical to the average for the preceding 3 years. Sample sizes among each cohort of marked ewes and the mortality percentages by age class are given in Table 2.

DISCUSSION

The notable result of comparisons in mortality between the 2 age groups is the magnitude of percent mortality among ewes 9 years old or older during the 1981-82 winter. We realize that sample sizes are small, but we suspect the 15.4-fold increase in mortality recorded among older ewes that winter was caused by decreased ability to survive unusually severe weather.

Weather data from stations on either side of the study area (Northway 100 km east and Delta Junction about 100 km west) show winter 1981-82 was one with greater than average snowfall, and lower than average temperatures during February and March (National Oceanic and Atmospheric Administration [1982]). These data indicate those months were more severe than normal.

The low average mortality for ewes in the age classes above 9 years before 1981-82 is probably indicative of unusually mild conditions during the years from 1979 to the difficult winter of 1981-82. During these years, mortality among all age classes of ewes was low, and the population increased. This increase was due to good production and recruitment (Heimer and Watson 1982), a function of mild winters as well as very limited mortality in older ewe cohorts. Hence, the difficult winter of 1981-82 resulted in a percentage loss that was most impressive among the marked ewes, but which had minimal actual impact on the population. Ewes which were lost were, for the most part, near the end of natural life expectancy.

We support the conservative management actions taken in this case, and always recommend conservativism when there are questions about correct procedures. Still, our experience shows the possible consequences of applying population mortality figures across age classes when they are, in fact, specific to a given, identifiable cohort or group of cohorts.

The age-specific mortality rates in Table 2 appear to indicate an increase in ewe mortality at about age 8. This survivorship pattern (Fig. 1) is similar to that reported for bighorn ewes by Bradley and Baker (1967), and similar to that found in Dall rams in the Alaska Range by Murie (1944). It is more difficult to rationalize a sudden increase in ewe mortality than in ram mortality since ewe behavior shows no documented changes at this age. Of course, ram behavior changes markedly with attainment of Class IV status at 8 years of age (Geist 1971). Still, the apparent increase in ewe mortality represents only a doubling of the mortality rate compared with ewes of the young age group. Further data will be required to clarify the overall picture.

The high mortality between ages 1 and 2 is also worthy of note. It is clearly different from the other measured mortalities for ewes less than 7 years old, and we attribute it to the very small sample size for that cohort (n = 7).

We also note the observed mortality pattern would be greatly different if winter 1981-82 were not included in the data set. Had we omitted this difficult winter from the data set, calculations would have indicated very little effect of advancing age on ewe survival until incredibly old ages were reached. Simmons et al. (1984) reported a mortality pattern different from the one which appears to be developing here, and those cited above. The methods applied in Simmons et al. (1984) were quite different from those used in this study. We believe our work highlights the dynamic nature of Dall ewe mortality. When attempting to characterize a general phenomenon rather than reporting on a time-specific event, it is desirable to work over the longest practical time span.

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Table 1. Collared ewe mortality due to natural causes and hunter kill by age group.

Year of observation	Total collars possible			Mortality by hunters			Mortality overall natural mortality			Mortality % overall mortality		
	Total	<9yrs	≥9yrs	Total	<9yrs	≥9yrs	Total	<9yrs	≥9yrs	Total	<9yrs	≥9yrs
1979	24	22	2	0	0	0	2	2	0	8	9	0
1980	72	65	7	1	1	0	?*	?*	?*	5*	4.5	8*
1981	71	64	11	1	1	0	9	8	1	5	4.5*	8*
1982	62	49	13	0	0	0	13	3	10	21	6	77
1983	49	35	9	0	0	0	11**	8	3	22**	23	34

* Mortality averaged over 1979-80 and 1980-81; mineral lick observations not continuous in 1980.

** Mortality for each year is affirmed the following year. These mortalities to be reaffirmed in 1984.

Table 2. Cohort sample sizes and percent mortality by age class among collared ewes by year.

	Age in years													
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1977	0	0	6	0	0	0	0	0	0	0	0	0	0	0
1978	0	6	3	9	1	0	3	0	0	2	0	0	0	0
1979	7	13	8	9	15	7	4	4	1	3	2	0	1	0
1980	0	7	13	8	9	15	7	4	4	1	3	2	0	1
1981	0	0	7	13	8	9	15	7	4	4	1	3	2	0
1982	0	0	0	7	13	8	9	15	7	4	4	1	3	2
1983	0	0	0	0	7	13	8	9	15	7	4	4	1	3
Total	7	26	37	46	58	52	46	39	31	21	14	10	7	6
Total mortality	1	3	1	1	3	2	3	5	5	1	2	1	3	--
Percent mortality	14	8	3	2	5	4	7	13	16	5	14	10	43	--
Percent survival	86	92	97	98	95	96	93	87	84	95	86	90	57	--

Appendix C. Resightings of collared ewes at Robertson River mineral lick, 1977-84. C = capture date, (n) = age at capture, X = resighting, L = lamb, * = radio-collared.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
6	Yellow	Black	0	--	--	C(1)	X	X	X	X	X	81, 84	--
6	Yellow	Black	1	--	--	C(1)	X	X	X	X	X	81, 84	--
6	Yellow	Black	2	--	--	C(1)	X	X	X	X	X	81	--
6	Yellow	Black	3	--	--	C(1)	X	X	X	X	X	81, 83, 84	--
7	Yellow	Black	4	--	--	C(2)	--	X	X	X	X	81, 82, 83, 84	--
6	Yellow	Black	5	--	--	C(1)	X	X	X	X	X	81, 83, 84	--
6	Yellow	Black	6	--	--	C(1)	X	X	X	X	X	80, 81, 82, 83, 84	--
-	Yellow	Black	7	--	--	C(1)	--	--	--	--	--	--	Assumed dead: 79
7	Yellow	Black	1-	--	--	--	--	--	--	C(6)	X	83, 84	--
4	Yellow	Black	10	--	--	--	--	--	--	C(3)	X	--	--
6	Yellow	Black	1X	--	--	--	--	--	--	C(5)	X	83	--
9	Yellow	Black	00	--	--	--	--	--	--	C(8)	X	83	May be older
-	Yellow	Black	L07	--	C(L)	--	--	--	--	--	--	--	Assumed dead: 78
L	Yellow	Black	L-1	--	--	--	--	--	--	--	C(4)	--	--
L	Yellow	Black	L-3	--	--	--	--	--	--	--	C(L)	--	--
2	Black	Yellow	⊠0*	--	--	--	--	--	--	--	C(2)	--	--
4	Black	Yellow	⊠1*	--	--	--	--	--	--	--	C(4)	84	--
5	Black	Yellow	⊠2*	--	--	--	--	--	--	--	C(5)	84	--
3	Black	Yellow	⊠3*	--	--	--	--	--	--	--	C(3)	--	--
5	Black	Yellow	⊠4*	--	--	--	--	--	--	--	C(5)	84	--
6	Black	Yellow	⊠6*	--	--	--	--	--	--	--	C(6)	84	--
4	Black	Yellow	⊠7*	--	--	--	--	--	--	--	C(4)	84	--
5	Black	Yellow	⊠U*	--	--	--	--	--	--	--	C(5)	--	--

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
6	Black	Yellow	[redacted]V*	--	--	--	--	--	--	--	C(6)	84	--
3	Black	Yellow	[redacted]*	--	--	--	--	--	--	--	C(3)	84	--
--	Red	Yellow	0	--	C(1)	--	X	X	X	--	--	81, 82	Assumed dead: 82
7	Red	Yellow	1	--	C(1)	--	--	X	X	X	X	81, 83, 84	--
7	Red	Yellow	2	--	C(1)	X	--	X	X	X	X	81	--
7	Red	Yellow	3	--	C(1)	X	X	X	X	X	X	80, 82, 83, 84	--
7	Red	Yellow	4	--	C(1)	X	X	X	X	X	X	80, 81, 82	Quite small left horn: 78
7	Red	Yellow	5	--	--	C(2)	X	X	X	X	X	81, 82, 83, 84	--
7	Red	Yellow	6	--	--	C(2)	X	X	X	X	X	80, 81, 82	--
--	Red	Yellow	7	--	--	C(2)	X	X	--	--	--	80	Assumed dead: 81
7	Red	Yellow	X	--	C(1)	X	X	X	X	X	X	80, 81, 83	--
7	Red	Yellow	-	--	--	C(2)	--	X	X	X	X	80, 81, 83, 84	--
--	Red	Yellow	00	--	--	C(2)	--	--	--	--	--	--	Assumed dead: 79
--	Red	Yellow	01	--	--	C(2)	--	--	--	--	--	--	Assumed dead: 79
7	Red	Yellow	02	--	--	C(2)	--	X	X	X	X	81, 82, 83, 84	Right horn broken: 79
7	Red	Yellow	03	--	--	C(2)	X	X	X	X	X	81, 83, 84	--
7	Red	Yellow	04	--	--	C(2)	X	X	X	X	X	80, 81, 82	Right horn broken: 79

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
7	Red	Yellow	05	--	--	C(2)	--	X	X	X	X	82	--
7	Red	Yellow	06	--	--	C(2)	X	X	X	X	X	80, 81, 82, 84	--
7	Red	Yellow	07	--	--	C(2)	--	X	X	X	X	81, 82, 84	--
1	Red	White	L57	--	--	--	--	--	--	C(L)	X	--	Eartag only
1	Red	White	L67	--	--	--	--	--	--	C(L)	X	--	Eartag only
1	Red	White	L77	--	--	--	--	--	--	C(L)	X	--	Eartag only
10	Blue	Yellow	0	C(3)	X	X	X	X	X	X	X	77, 78, 79, 80, 81, 82, 84	--
9	Blue	Yellow	1	--	C(3)	X	--	X	X	X	X	78, 79, 82, 83	--
9	Blue	Yellow	2	--	C(3)	X	X	X	X	X	X	78, 79, 81	--
4	Blue	Yellow	3	--	--	--	--	--	--	C(3)	X	84	--
9	Blue	Yellow	4	--	C(3)	X	X	X	X	X	X	80	--
--	Blue	Yellow	5	--	C(3)	X	X	--	--	--	--	78, 80	Hunter kill: 80
8	Blue	Yellow	6	--	--	C(3)	X	X	X	X	X	80, 81, 82, 83, 84	--
--	Blue	Yellow	7	C(3)	--	--	--	--	--	--	--	77	Hunter kill: 77
--	Blue	Yellow	-	C(3)	X	X	--	--	--	--	--	77, 78, 79	Assumed dead: 79
10	Blue	Yellow	X	C(3)	X	X	X	X	X	X	X	77, 78, 79, 81, 82, 84	--

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
2	Blue	Yellow	11	--	--	--	--	--	--	C(1)	X	--	Trophy-sized horns: 83
3	Blue	Yellow	12	--	--	--	--	--	--	C(2)	X	84	--
8	Blue	Yellow	13	--	--	--	--	--	--	C(7)	X	83	Collar reads "E1," may be older
4	Blue	Yellow	14	--	--	--	--	--	--	C(3)	X	--	Right mandible large abcessed lesion, lump jaw: 83
7	Blue	Yellow	15	--	--	--	--	--	--	C(6)	--	83	--
6	Blue	Yellow	16	--	--	--	--	--	--	C(5)	--	83	--
6	Blue	Yellow	17	--	--	--	--	--	--	C(5)	X	83, 84	--
9	Blue	Yellow	1-	--	--	--	--	--	--	C(8)	--	83	--
7	Blue	Yellow	1X	--	--	--	--	--	--	C(6)	X	84	--
5	Blue	Yellow	XX	--	--	--	--	--	--	C(4)	--	83	--
8	Blue	Yellow	20	--	--	C(3)	--	X	X	X	X	81, 82, 83, 84	--
--	Green	Yellow	0	--	--	C(4)	--	--	--	--	--	--	Hunter kill: 79
9	Green	Yellow	1	--	--	C(4)	--	X	X	X	X	81	--
9	Green	Yellow	2	--	--	C(4)	X	X	X	X	X	81, 84	Contagious ecthyma lesions: 79
--	Green	Yellow	3	--	--	C(4)	X	X	--	--	--	79, 81	Assumed dead: 81
--	Green	Yellow	4	--	--	C(6)	--	X	X	--	--	79, 81	Assumed dead: 82
--	Green	Yellow	5	--	--	C(4)	X	X	--	--	--	--	Assumed dead: 81
9	Green	Yellow	6	--	--	C(4)	X	X	X	X	X	80, 83, 84	Lump jaw left mandible: 79
10	Green	Yellow	-	--	C(4)	--	X	X	X	X	X	78, 80, 81, 83	--

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
--	Green	Yellow	00	--	C(4)	X	X	X	X	--	--	78, 79, 80, 81 81, 84	Assumed dead: 82
--	Green	Yellow	01	--	C(4)	X	X	X	X	X	X	80, 81, 82, 83	--
--	Green	Yellow	02	--	--	C(6)	X	--	--	--	--	79	Assumed dead: 80
11	Green	Yellow	03	--	--	C(6)	X	X	X	X	--	79, 80, 81	--
--	Green	Yellow	05	--	--	C(6)	X	X	X	X	X	79, 81	Hunter kill: 84
11	Green	Yellow	06	--	--	C(6)	X	X	X	X	--	79, 80, 81	--
11	Green	Yellow	07	--	--	C(6)	--	X	X	X	--	79, 80, 81	--
--	Red	Black	0	--	C(5)	--	--	--	--	--	--	78	Lump jaw: 78, assumed dead: 78
10	Red	Black	1	--	--	C(5)	X	X	X	--	X	79, 80, 81, 82	--
--	Red	Black	2	--	--	C(5)	X	X	X	--	--	--	Assumed dead: 82
10	Red	Black	3	--	C(4)	X	X	X	--	X	X	79, 81, 83	--
10	Red	Black	4	--	--	C(5)	X	X	X	--	X	79, 81, 82, 84	--
10	Red	Black	5	--	--	C(5)	X	X	X	X	X	79, 81, 83, 84	--
10	Red	Black	6	--	--	C(5)	X	X	X	X	X	79, 81, 83, 84	Small udder with discolored milk, lamb died?: 79
--	Red	Black	00	--	C(7)	X	--	--	--	--	--	78, 79	Assumed dead: 79

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
--	Red	Black	01	--	C(7)	X	--	X	--	--	--	81	Assumed dead: 81
--	Red	Black	02	--	C(7)	X	X	X	X	--	--	78, 79, 80, 81, 82	Assumed dead: 82
--	Red	Black	03	--	--	C(7)	--	X	--	--	--	79, 81	Assumed dead: 81
--	Red	Black	04	--	--	C(7)	--	X	--	--	--	79, 81	Assumed dead: 81
13	Red	Black	05	--	--	C(7)	X	X	--	X	X	79, 80, 81, 83 84	--
--	Red	Black	07	--	--	C(7)	X	X	--	--	--	79, 81	Assumed dead: 81
8	Red	Black	0X	--	--	--	--	--	--	C(7)	X	83, 84	--
5	Red	Black	1X	--	--	--	--	--	--	--	C(5)	84	--
5	Red	Black	20	--	--	--	--	--	--	--	C(5)	84	--
5	Red	Black	21	--	--	--	--	--	--	--	C(5)	84	--
6	Red	Black	22	--	--	--	--	--	--	--	C(6)	84?	--
8	Red	Black	23	--	--	--	--	--	--	--	C(8)	--	--
8	Red	Black	24	--	--	--	--	--	--	--	C(8)	--	--
5	Red	Black	25	--	--	--	--	--	--	--	C(5)	--	--
13	Red	Black	30	--	--	C(8)	X	X	X	X	X	79, 80, 81, 84	--
3	Red	Black	31*	--	--	--	--	--	--	--	C(3)	84	--
5	Red	Black	32*	--	--	--	--	--	--	--	C(5)	84	--
3	Red	Black	34*	--	--	--	--	--	--	--	C(3)	84	--
5	Red	Black	35	--	--	--	--	--	--	C(4)	X	83, 84	
6	Red	Black	36	--	--	--	--	--	--	C(5)	X	83	
6	Red	Black	37	--	--	--	--	--	--	C(5)	X	83, 84	
7	Red	Black	3X	--	--	--	--	--	--	C(6)	X	83, 84	
3	Red	Black	3-	--	--	--	--	--	--	C(2)	X	84	
--	Red	Black	40	--	C(10)	X	--	X	--	--	--	78, 79, 81	Assumed dead: 81

Appendix C. Continued.

Age in 1984	Collar color	Number color	Number	Year 1977	1978	1979	1980	1981	1982	1983	1984	Years with lamb	Comments
--	Red	Black	41	--	C(9)	X	X	X	--	--	--	78, 79, 80, 81	Assumed dead: 81
--	Red	Black	42	--	--	C(10)	X	X	--	--	--	79, 80, 81	Confirmed dead: 81
--	Red	Black	43	--	--	C(9)	--	X	--	--	--	--	Assumed dead: 81
--	Red	Black	44	--	--	C(13)	--	--	--	--	--	--	Lump jaw left mandible: 79, assumed dead: 79
--	Red	Black	45	--	--	C(10)	X	X	--	--	--	80, 81	Assumed dead: 81
--	Red	Black	4-	--	--	C(10)	--	X	--	--	--	81	Assumed dead: 81

Appendix D. Resightings and reproductive status of marked ewes at Dry Creek mineral lick, 1981-84. (Eartag numbers are the same as collar numbers, except where indicated. C = capture, (n) = age at capture, * = radio-collared.)

Age in 1984	Collar color	Number color	Number	Eartag L	Eartag R	1981	1982	1983	1984	Years with lamb	Comments
2	Red	Yellow	04	Yellow	Green	--	--	C(1)	--	--	--
10	Red	Yellow	0-	Blue	Red	C(7)	--	X	X	83	With yearling Orange/Yellow X0:84
-	Red	Yellow	0X	Blue	Red	C(4)	--	--	--	--	Assumed dead: 82
-	Red	Yellow	11	Red	Blue	C(4)	--	--	--	81	Confirmed dead: 81, necropsy pregnant
6	Red	Yellow	12	Red	Red	--	C(4)	X	X	82, 83, 84	--
8	Red	Yellow	13	Red	Red	--	C(6)	X	X	82, 83	--
7	Red	Yellow	14	Red	Red	--	C(5)	X	X	82	--
6	Red	Yellow	15	Red	Red	--	C(4)	X	--	83	--
4	Red	Yellow	16	Yellow	Yellow	C(1)	X	--	X	--	--
-	Red	Yellow	17	Red	Red	--	C(2)	--	--	--	Assumed dead: 83
-	Red	Yellow	-1	Yellow	Yellow	C(1)	--	--	--	--	Assumed dead: 82
8	Red	Yellow	1X	Red	Red	--	C(6)	--	X	--	--
8	Red	Yellow	20	Red	Green	C(5)	X	X	X	81, 82, 84	--
7	Red	Yellow	21	Green	Red	C(4)	X	X	X	81, 82, 83, 84	--
4	Red	Yellow	22	Green	Red	C(1)	X	X	X	83, 84	--
6	Red	Yellow	23	Red	Green	C(3)	X	X	X	81, 82, 83, 84	--
7	Red	Yellow	24	Green	Red	C(4)	X	--	X	--	--
6	Red	Yellow	25	Green	Red	C(3)	--	X	X	81, 83, 84	--
-	Red	Yellow	26	Red	Green	C(7)	--	--	--	--	Assumed dead: 82

Appendix D. Continued.

Age in 1984	Collar color	Number color	Number	Eartag L	Eartag R	1981	1982	1983	1984	Years with lamb	Comments
8	Red	Yellow	27	Green	--	C(5)	X	X	X	81, 82	--
9	Red	Yellow	2X	Green	Red	C(6)	X	--	--	81, 82	Seen: 85
5	Red	Yellow	XX	Red	Blue	C(2)	X	--	X	81, 84	--
4	Green	Yellow	7	Green	Green	C(1)	X	--	X	--	--
4	Green	Yellow	X	Green	Green	C(1)	X	X	X	--	--
5	Green	Yellow	0-	--	--	--	C(3)	X	X	83, 84?	--
7	Green	Yellow	0X	Green	Green	--	C(5)	X	X	82, 83, 84	--
4	Green	Yellow	11	Green	Green	C(1)	--	X	--	--	--
-	Green	Yellow	14	Green	Green	C(1)	--	--	--	--	Dead, collar found: 84
-	Green	Yellow	16	Red	Red	--	C(8)	--	--	82	Assumed dead: 83
12	Green	Yellow	17	Red	Red	--	C(10)	X	X	82, 83	--
-	Green	Yellow	1-	Red	Red	--	C(9)	--	--	--	Assumed dead: 82
5	Green	Yellow	1X	--	--	--	C(3)	--	X	--	--
13	Green	Yellow	20	Green	Green	--	C(11)	X	X	82, 83, 84	--
5	Green	Yellow	21	Green	Green	--	C(3)	X	X	83, 84?	--
1	--	--	--	Green XO	--	--	--	--	C(1)	--	--
3	Blue	Yellow	00	Red	Red	--	--	C(2)	X	--	--
3	Blue	Yellow	01	Blue L7	Red	--	--	C(2)	X	--	Re-marked from lamb in 81
4	Blue	Yellow	02	Red	Red	--	--	C(3)	--	--	--
4	Blue	Yellow	03	Red	Red	--	--	C(3)	X	83? 84?	Seemed inactive when captured
7	Blue	Yellow	04	Red	Red	--	C(5)	X	X	82, 83	--
7	Blue	Yellow	05	Red	Red	--	--	C(6)	--	83?	--
8	Blue	Yellow	06	Red	Red	--	--	C(7)	--	83, 84	--
4	Blue	Yellow	07	Blue	Red	--	--	C(3)	X	--	--
4	Blue	Yellow	0-	Blue	Red	--	--	C(4)	--	--	--

Appendix D. Continued.

Age in 1984	Collar color	Number color	Number	Eartag L	Eartag R	1981	1982	1983	1984	Years with lamb	Comments
old	Blue	Yellow	0X	Blue	Blue	--	--	C(old)	X	84?	--
4	Blue	Yellow	21	Blue	Yellow	--	--	--	C(4)	--	--
8	Blue	Yellow	22	Yellow	Blue	--	--	--	C(8)	84	Lamb=Y/B2X male
3	Blue	Yellow	23	Yellow	Blue	--	--	--	C(3)	--	Heavy case lump jaw right mandible: 84
3	Blue	Yellow	25	Yellow	Blue	--	--	C(2)	X	84	Collar reads 2525
6	Blue	Yellow	26	Yellow	Yellow	--	--	C(5)	X	--	--
7	Blue	Yellow	27	Yellow	Yellow	--	--	C(6)	--	83?	Lost lamb: 83? teeth out
12	Blue	Yellow	2-	Blue	Yellow	--	--	--	C(12)	--	May be older
5	Red	Black	7	Red	Yellow	--	--	C(4)	X	83	--
6	Red	Black	-	Red	Yellow	--	--	C(5)	X	83, 84	No lamb seen: 83
2	Red	Black	X	Red	Yellow	--	--	C(1)	X	--	--
8	Red	Black	0-	Green	Red	--	--	C(7)	X	83, 84?	Lost lamb?: 84
8	Red	Black	0X	Red	Red	--	--	C(7)	X	83	--
9	Yellow	Black	02	Yellow	Green	--	C(7)	X	X	83? 84	--
5	Yellow	Black	03	--	Green	--	C(3)	X	X	82, 83, 84	--
5	Yellow	Black	04	Yellow	Green	--	C(3)	X	X	--	--
4	Yellow	Black	05	Green	Yellow	--	C(2)	X	X	84	--
7	Yellow	Black	06	Yellow	Green	--	C(5)	X	X	83, 84	--
5	Yellow	Black	07	--	--	--	C(3)	X	X	82, 84	--
8	Yellow	Black	0-	Green	Yellow	--	C(5)	--	--	--	Seen: 85
7	Yellow	Black	11	--	--	--	--	--	C(7)	84	Severe lump jaw, right mandible, lost lambs?: 84
5	Yellow	Black	12	Yellow	Yellow	--	--	C(4)	X	--	Odd serum, worst case of lump jaw: 83

Appendix D. Continued.

Age in 1984	Collar color	Number color	Number	Eartag L	Eartag R	1981	1982	1983	1984	Years with lamb	Comments
3	Yellow	Black	13	Yellow	Yellow	--	--	C(2)	X	--	--
3	Yellow	Black	14	Yellow	Yellow	--	--	C(2)	X	--	--
4	Yellow	Black	15	Yellow	Yellow	--	--	C(3)	X	84	--
3	Yellow	Black	16	Yellow	Yellow	--	--	C(2)	X	--	--
2	Yellow	Black	17	Yellow	Yellow	--	--	C(1)	X	84?	Duct-taped collar: 83
7	Yellow	Black	20	Yellow	Yellow	C(4)	X	X	X	81, 83, 84	--
7	Yellow	Black	21	Yellow	Yellow	C(4)	X	X	X	81, 83, 84	--
-	Yellow	Black	22	Yellow	Yellow	--	C(8)	--	--	--	Assumed dead: 83
-	Yellow	Black	23	Yellow	Yellow	C(5)	--	--	--	81	Assumed dead: 82
5	Yellow	Black	24	Yellow	Yellow	C(2)	--	X	X	81, 83	--
6	Yellow	Black	25	Yellow	Yellow	--	--	C(5)	X	83, 84	Bad lump jaw: 83
10	Yellow	Black	26	Yellow	Yellow	--	--	C(9)	--	83	Reproductively active, still pregnant?: 83
6	Yellow	Black	27	Yellow	Yellow	C(3)	X	X	X	82	--
6	Yellow	Black	2-	Yellow	Yellow	C(3)	--	--	X	84	--
8	Yellow	Black	2X	Yellow	Yellow	C(5)	X	X	X	81, 82, 83	--
-	Yellow	Black	--	Yellow	Green	--	C(5)	--	--	--	Assumed dead: 83
4	Orange	Yellow	⊠1*	Red	Red	--	--	--	C(4)	--	--
3	Orange	Yellow	⊠2	Red	Red	--	--	--	C(3)	--	Regressed lump jaw, left mandible: 84
1	Orange	Yellow	⊠3*	Red	Red	--	--	--	C(1)	--	--
3	Orange	Yellow	⊠4*	Red	Red	--	--	--	C(3)	--	--
4	Orange	Yellow	⊠6*	Red	Red	--	--	--	C(4)	84?	--
1	Orange	Yellow	⊠7*	Red	Red	--	--	--	C(1)	--	--

Appendix D. Continued.

Age in 1984	Collar color	Number color	Number	Eartag L	Eartag R	1981	1982	1983	1984	Years with lamb	Comments
5	Orange	Yellow	⊠U*	Red	Red	--	--	--	C(5)	--	Regressed lump jaw both mandibles: 84
1	Orange	Yellow	⊠V*	Green OX	Red	--	--	--	C(1)	--	Eartagged as lamb: 83
1	Orange	Yellow	⊠O*	Red	Red	--	--	--	C(1)	--	--
1	Orange	Yellow	⊠⊠*	Red	Red	--	--	--	C(1)	--	--