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TIME AND AREA SPECIFIC VARIATIONS IN DALL SHEEP LAMB PRODUCTION: AN EXPLANATORY HYPOTHESES

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Abstract: Lamb production as indicated by lamb:100 ewe ratios was studied in two differing Dall sheep (*Ovis dalli dalli*) populations. One population was affected by changes in hunting and predator management; the other population was subjected to little change in management. Lamb production was more variable in the population with variable management history. Lamb production correlated significantly ($P < 0.01$) with an aggregate weather index which included weather influencing breeding condition of ewes, weather during gestation, and weather during lambing. However, weather did not seem to be an important factor in other determinants of lamb production: ovarian activity, age at 1st reproductive success, and frequency of reproductive success. Decreased ram abundance and the concomitant skewing of ram age structure toward young rams were associated with maximum 3/4-curl harvest and maladaptive changes in lamb production. Reproductive frequency and age at first breeding appear to have been reestablished at levels found in unhunted populations following establishment of the 7/8-curl regulation in the heavily hunted Dall sheep population.

A long-term comparative study of two Dall sheep (*Ovis dalli dalli*) populations in the eastern Alaska Range revealed notable variations in lamb production data between the populations. One population, Dry Creek, was considered the experimental situation. Over the last 16 years, during which lamb:100 ewe ratios were collected, changes in hunting pressure, predator abundance, weather conditions, and changes in ram harvest regulations from 3/4 curl to 7/8 curl affected this population. A control population, Robertson River, was similarly monitored for 11 years. Throughout this study period, weather conditions were the main influence on this study population. Hunting pressure in the Robertson River was held below that required to harvest estimated annual recruitment to the full-curl ram class by lottery permit to meet a trophy management goal. The number and age distribution of rams was, thus, influenced little by hunter harvest.

METHODS

Study Area

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.

Study Components

Lamb production is influenced by many components. We investigated ovulation rate, age at onset of reproductive activity, frequency of observed reproductive success, and general weather conditions. The methods for each component are detailed below.

Lamb Production: Lamb production was determined by classifying sheep from both populations as they used important mineral licks during the last half of June. Heimer (1974) detailed the reasons for this sampling period. Sheep were classified as lambs, yearlings, ewes, and rams according to degree of horn development. Observations were made with the aid of 15-60X spotting scopes and binoculars at distances up to 200 m. Results of these classification counts were used to calculate lamb production ratios for the sample period and expressed as lambs:100 ewes excluding yearlings.

Ovulation Rate: Ovaries were collected from ewes in each population from 1972 through 1979. Ewes were shot at random, and ovaries were preserved in 10% formalin as soon as possible after death. Ovaries not preserved within 48 hours were discarded. Fixed ovaries were trimmed of connective tissue, measured, weighed, and the volume estimated by water displacement. They were then sliced in 1 mm sections along the longitudinal axis and examined. Pigmented areas were counted in each ovary as described by Kirkpatrick (1980). Faces of individual slices were sketched 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 hematoxylin and eosin. When pigmented bodies could not be classified using this procedure, Masson's stain for connective tissue was used. Sectioning and staining were necessary because some of the pigmented areas discernible upon gross examination are not the result of ovarian cycling. 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. Mean ovulation rates were determined for each population, and Student's t-test of ratio estimators was used to establish the probability that observed differences were due to sample variance (Cochran 1977).

Age at First Successful Lamb Production: Successful reproduction was documented by observing marked ewes suckling or mothering lambs between

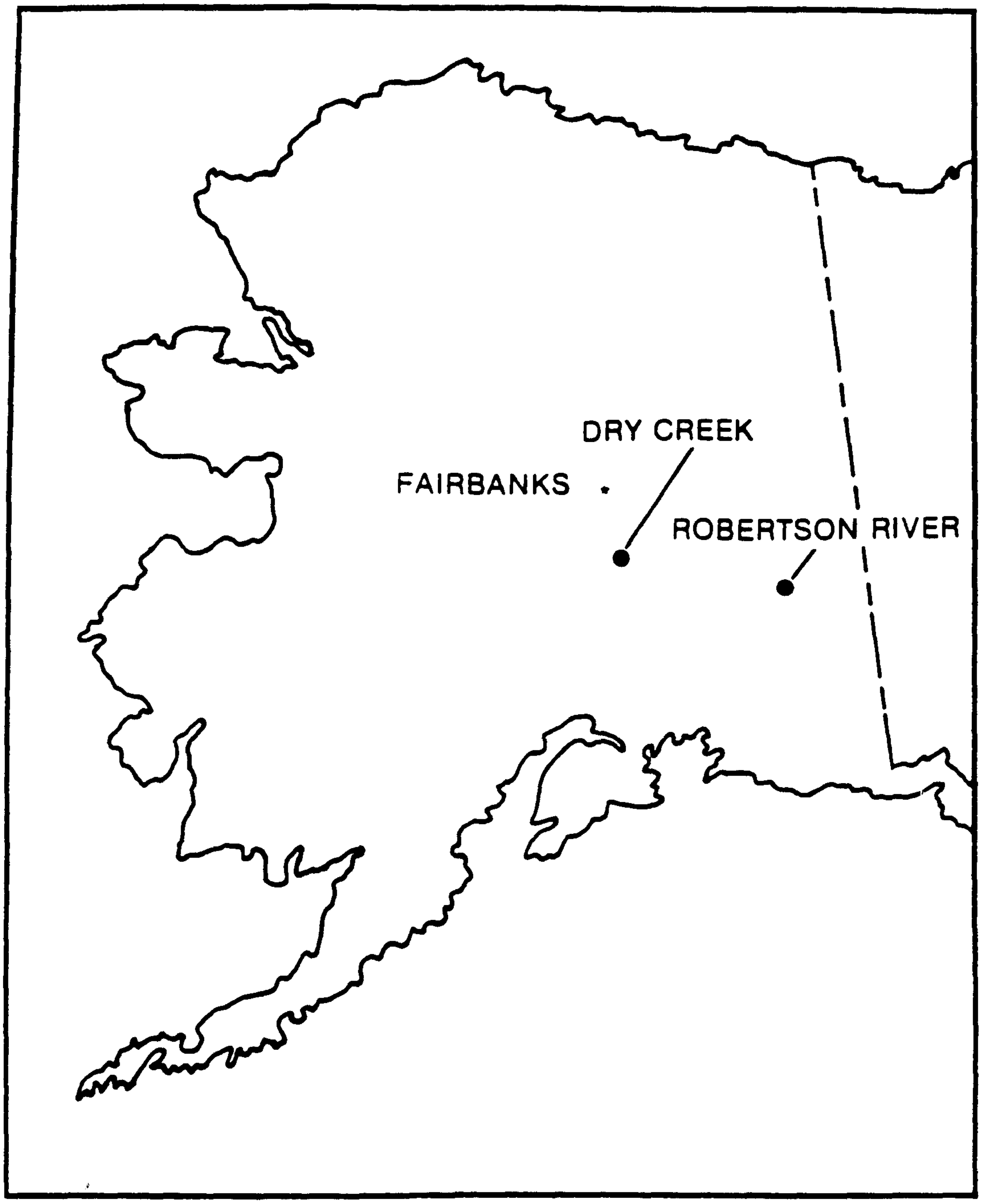

Fig. 1. Location of Dall sheep study areas within Alaska.

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)

1 June and 31 June. The earliest age at which ewes successfully reproduced was determined by three methods. The reproductive status of each ewe trapped and marked in June (Heimer et al. 1980) was determined by examination of external genitalia and mammary development. Also, yearling ewes were marked in both study populations. Careful observations of reproductive activity were made when these ewes were annually resighted at mineral licks. Limited numbers of ewes age 18 and 30 months were collected from both populations in April. Reproductive activity in these ewes was determined by autopsy.

Frequency of Observed Reproductive Success: Once marked ewes became reproductively active, they were observed each June as they came to the mineral lick. If they were observed mothering or suckling lambs, or if they had distended, depilated mammaries, they were classified as reproductively active that year.

Weather Conditions

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

Weather Effects at Parturition: Weather conditions which promote heat loss from newborn lambs should lower observable lamb:100 ewe ratios. These conditions include low temperatures and 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 the total precipitation for the lambing period in each year. Indices were arbitrarily adjusted so the least favorable (coolest and dampest) year was equal to zero for purposes of statistical computation.

Weather Effects on Breeding Condition: Hoefs (1984) reported statistical correlations of presumably favorable growing conditions with good lamb production the next year in Kluane, Yukon Territory. He found high rainfall (which accompanies cool weather in Alaska) was correlated with increased food production. Presumably better plant production lead to better breeding condition. 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 rainfall was calculated as described above for the lambing period. Similar weather data from the Robertson River study area were not available.

Aggregate Weather Index: 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 then totalled for each year, thus producing an overall or aggregate weather index. Lamb:100 ewe ratio was regressed on this aggregate index of weather influence.

RESULTS

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 ($P < 0.014$) or since ($P < 0.008$) when tested using the Mann-Whitney U-test (Cochran 1977).

In the Robertson River population, 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 ($P > 0.05$) using the same statistical test.

Relative lamb production varied more at Dry Creek than in the Robertson River population. This may suggest greater variations in environmental components in Dry Creek.

Ovulation Rate

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 4 and 5).

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
Unusually severe winter	1972	--	15		$P \leq 0.014$
Very heavy harvest	1973	--	38	$\bar{x}$ = 29	
from 1972 on	1974	--	28	SD = 7	
	1975	17	28		
Wolf control begins	1976	--	36		
					Difference
	1977	--	58		significant
	1978	--	41		$P \leq 0.008$
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.

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		

Table 4. 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 5. 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.

The lower ovulation frequency among Dry Creek ewes coincided with low lamb:100 ewe ratios, low pregnancy rate, and extended lactation. This low ovarian activity also accompanied low population numbers, and, because most collections occurred right after the wolf reduction program, presumably low predator densities.

Age at First Successful Lamb Production

The age at first successful lamb production appeared to be different between the 1972-77 and 1981-84 periods in Dry Creek, but the change was not statistically significant ($P > 0.05$). During the 1972-77 period, 7 of 30 2-year-old ewes (23%) successfully produced lambs. In the latter period (1981-84), only 2 of 22 2-year-olds (9%) produced lambs ($X^2 = 1.94$, $P > 0.05$). 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 ($X^2 = 4.448$, $P < 0.05$) (Table 6).

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.

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 7). The difference in the early and later Dry Creek consecutive-year success frequencies is statistically significant ($P < 0.05$). The chance of mistakenly concluding that the differences are real with respect to the variability is less than 0.005.

Weather Conditions

Weather Effects on Breeding Condition: Warmer and drier weather during the June-August growing season was positively correlated with increased lamb production the following spring. The equation generated by linear regression of lambs:100 ewes as a function of this composite weather index was $y = 0.824X + 28.7$ ($r = 0.639$; $P < 0.02$) (Table 8).

Weather Effects During Gestation: The relationship between mean snow depth on the north face of the Alaska Range and lamb production the following spring was not strong. Linear regression of lambs:100 ewes on mean snow depth on 1 April produced an equation, $y = 0.25X + 27.5$; $r = 0.457$; $P < 0.01$ (Table 9).

Weather Effects at Parturition: The relationship of weather during the period of parturition to lamb:100 ewe ratio was not strong. There was a tendency to observe higher ratios when weather during parturition had been warmer and drier. Linear regression of lambs:100 ewes on this composite weather index was $y = -1.073X + 65$ ($r = 0.3557$; $P < 0.15$) (Table 10).

Table 6. 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%)	

Table 7. 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		Robertson River	
	1972-77 (n = 88) (%)	1981-84 (n = 73) (%)	1979-81 (n = 74) (%)	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

Table 8. 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	

$y = 0.824x + 28.7$
Average index = 18 ± 6.65 (95% CI)
$r = 0.639$
$\underline{P} \leq 0.02$

[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 9. 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

$y = -1.07x + 65$

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

$r = 0.3556$

$\underline{P} \leq 0.10$

Table 10. 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	45	+1.8	11.70	+11.7	96

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

[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 11. 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

$y = 2.231x + 29.6$
$r = 0.7734$

[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).

Aggregate Weather Index: The aggregate weather effects index was significantly correlated with lamb production ($r = 0.773$; $P < 0.01$) (Table 11).

DISCUSSION

Variations in lamb production in the Dry Creek population correlated significantly with the aggregate weather index. This seems to provide justification for the common, empirical observation that good weather leads to high lamb production. Still, it is worth noting that the correlation of lamb production with the aggregate index is much better than for any of the individual indices. This may indicate there are more weather influences on lamb production than winter severity as it influences foraging ability during gestation. Weather is probably not closely related to ovarian activity or age at first breeding.

However, weather may influence the frequency of consecutively observed reproductive success. For us to document consecutive-year reproductive success, a ewe must ovulate, breed, carry the fetus to term, deliver a living lamb, and bring it to the lick. At the 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 and the frequency of its occurrence is unknown. When unfavorable weather occurs at lambing, this frequency probably increases because more lambs are likely to die than when conditions are good. Thus, we are always likely to underestimate the actual frequency of consecutive-year reproductive activity. The technique is more likely to underestimate it in years of unfavorable lambing weather than in favorable years.

During the years (1972-77) when observed consecutive-year reproduction was only 6% in Dry Creek (Heimer 1978), the lambing aggregate weather index had a value of -3. For the second period (1981-84), the aggregate index had a value of +12 (Table 11). The real meaning of this difference is unknown, but it probably indicates weather-influencing components of lamb production were more favorable.

We may gain some insight into the magnitude of the influence weather had on this reproductive parameter by considering mean lamb:ewe ratios for the two differing periods. During the period 1972-77, when consecutively observed reproductive success was 6%, the mean lamb:100 ewe ratio was 29. For the second period, 1981-84, when consecutively observed success was 44%, the mean lamb:100 ewe ratio was 50. This is an increase of 1.7 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 increase in frequency of 1.7 times. The documented increase was 7.3 times. This increased frequency is 4.3 times greater than should be expected on the basis of increased lamb:100 ewe ratio. Something besides weather appears to be influencing changes in frequency of consecutively observed reproductive success.

We do not think changes in range resources could account for this change. We doubt there could have been sufficient deterioration in range resources from the early (1968-71) period of high lamb production, to cause the low lamb production of the middle period (1972-77), followed by sufficient range recovery to produce and maintain the high lamb productions of the latter (1981-84) period.

These are two likely possibilities (Table 2): wolf control, and changes in ram harvest level and age. Reduction in wolf populations began in 1975, and was followed by stabilization of the declining Dry Creek sheep population (Heimer and Stephenson 1982). Then, in 1979, hunting regulations were changed from 3/4 curl to 7/8 curl for legal rams (Heimer 1980). We suspect these actions may have worked in concert to effect a change in ram abundance and age structure. Survival of lambs to yearling age in the years when wolves were most abundant, from 1970-75, averaged 66%. This is the highest average survival for any period of years in Dry Creek. This indicates wolves were not preferentially taking lambs after the month of June. Heimer and Stephenson (1982) suggested wolves take sheep in an opportunistic manner. Murie (1944) observed that wolves took sheep that were easiest to catch. We think young rams in Dry Creek may have been the sheep most readily available to wolves during this period. We propose the following explanation:

Ram abundance was relatively high before 1972. An aerial survey of the Dry Creek study area in 1970 showed a total of 32 rams per 100 "ewes." (Aerial classification of ewes is imperfect because yearlings and rams less than 2 years of age cannot be consistently identified from aircraft.) There were 12, 3/4-curl and larger rams for each 100 "ewes" classified. Following winter 1972, the most severe recorded for sheep in the Dry Creek area, few old-age animals would have survived (Heimer and Watson 1984). Compounding this natural lowering of old ram numbers was an increase in hunter pressure on the Dry Creek populations. The net result was that legal, 3/4-curl rams were very scarce, and ram populations were generally depleted. Another survey of the area in 1975 indicated the ratio of total rams per 100 "ewes" had dropped from 32 to 17. The 3/4 curl and up ratio was found to be 8:100 "ewes." The total number of rams seen on the equivalent surveys dropped from 173 seen in 1970 to 78 seen in 1975.

In terms of vulnerability to wolves, this could have meant that ram bands had less than half the number of individuals to watch for predators, a social adaptation cited by Geist (1971). It also meant that older rams which presumably had more experience with predator avoidance were absent. Furthermore, the surviving young rams should also have been compromised by their unscheduled participation in rut because of the absence of dominants. Geist (1971) postulated that in circumstances such as these, young rams would be in unusually poor physical condition. All these factors may have predisposed these young rams to early mortality.

Whatever the cause, the early mortality apparently took place. Heimer et al. (1984) reported greatly increased mortality among young rams in the Dry Creek populations during this period. They speculated that the energetic and behavioral causes listed above were operative, but failed to factor the likelihood of increased wolf predation into their explanation.

We note that the occurrence of good lamb production correlates not only with good weather conditions but also with high ram abundance. The period before the difficult winter of 1972 was one of high lamb production averaging 58 lambs:100 ewes. This coincides with the high ram:100 "ewe" ratio and the high 3/4-curl ram:100 "ewe" ratio given above. There is little reason to suspect the population composition from the 1970 survey was not typical of that period. Following the severe winter of 1972, a period of poor lamb production occurred in which lamb:100 ewe ratios averaged 29. This went with the low total ram and 3/4 and larger rams ratios (17 and 8, respectively) reported for the 1975 survey. Following wolf control, if young ram survival increased, the number of rams should have increased. This possible 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) (Heimer et al. 1984) because there were two more cohorts of rams on the mountain, and age at 3/4 curl is roughly 2 years less than age at 7/8 curl. This change (or perhaps these changes) coupled with good recruitment in lamb productions before 1972 could have resulted in higher ram:100 ewe ratios. In 1984 another aerial survey was flown. It showed the total ram:100 "ewe" ratio had risen to 39 and the 3/4-curl-and-larger ram:100 "ewe" ratio was 16 rams per 100 "ewes." The mean lamb production for this period was 54 lambs:100 ewes. We think these data suggest that ram abundance and possibly age structure 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 ($r = 0.616$, $df = 16$, $\underline{P} < 0.01$) 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 three 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."

The hypothesis that ram abundance or perhaps ram age structure influences lamb production serves well in rationalizing the data presented here on ovarian activity and age at first successful reproduction.

How might the proportion of old-age rams relate to a higher frequency of estrus in populations with high ram:ewe ratios? If rutting groups of ewes are small and widely dispersed, it is possible that estrous ewes could be "missed" by breeding rams. In such a situation, induction of subsequent estrous periods by ram presence or courtship would be quite important. In domestic sheep, the presence of rams affects beginning and synchronization of estrus (Redford and Watson 1957, Watson and Redford 1960, Fraser 1968). If Dall rams somehow facilitate or induce the 1st or subsequent estrous periods, and if more socially and physically mature rams (such as would be present at much higher frequency after years of limited full-curl hunting) are more likely to induce estrus, it follows that lowering the total number of rams present, and greatly reducing the number of mature rams, as in Dry Creek, should result in decreased ovarian activity. Bunnell (1980, 1982) reported that Dall ewes in the unhunted Kluane Park population of the

Canadian Yukon were frequently bred during later estrous cycles. Survival of lambs conceived during 2nd estrus has not been determined.

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 ovarian examination as a means of determining past activity has been proven reliable (Hadek 1958).

Likewise, some criticism may reasonably be a result of our aging techniques. Aging ewes by counting horn annuli is difficult, and age determination is variable among observers (Hoefs 1984a). 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 71.8% to 73.1%). We conclude possible errors in age determination did not materially affect the results in this comparison.

The observation that age at first breeding was different in the Robertson River and Dry Creek populations is also consistent with the hypothesis that ram abundance is a determinant of lamb production. Delivery of lambs on their second birthday seems to be associated with low ram numbers or the absence of old rams in Dall sheep populations. Hoefs and Cowan (1979) reported lambs in unhunted Kluane Park usually did not deliver lambs until their third birthday. Similarly, 2-year-old ewes in the unhunted sheep populations of Denali National Park have not been observed leading lambs in three searches, on foot, of the the Savage River summer ranges. Palmer (1941) concluded ewes in the vicinity of the then virtually unhunted Dry Creek population were characterized by breeding at 30 months and lambing on their third birthdays. In contrast, Nichols (1978) reported that 3 of 4 ewes collected before their second 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. We are aware of no reports of 2-year-old ewes routinely delivering lambs in relatively undisturbed populations. We have observed and handled a total of 17 2-year-old ewes since the changes which followed wolf control and the 7/8-curl regulation occurred in Dry Creek. Only one of them has had a lamb.

Other evidence that ewes are capable of delivering lambs at 24 months of age 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. Similarly, Hoefs and Cowan (1979) reported that captive 18-month-old Dall ewes from populations which regularly produce lambs on their third birthday in the wild, produced them on their second birthday in captivity. The ram age structures in captive herds where Dall ewes bred early is not known to us. We do know that Dall ewes kept in the Milwaukee County Zoo deliver lambs at 2 years of age, when immature rams are present.

Data from the Dall sheep breeding program at the Milwaukee County Zoo (1971-79) indicate 12 of 15 ewes delivered lambs on their second birthday. These lambs were sired by young rams, the oldest being a 4-year-old ram which bred one ewe. Three lambs were sired by 2.5-year-old rams, and the remaining eight were sired by rams aged 1.5 years. In a breeding pen where all rams had access to all ewes, the one 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 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 yearling rams experience in attempting to dominate their dams. Two-year-old Dall rams are typically subordinate to mature ewes in Dry Creek. 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 conclude early breeding by ewes in the Dry Creek population was most likely a consequence of ram scarcity or the young age structure among breeding rams. Scarcity of rams above the age at 3/4-curl horn size (approximately 5.5 years) probably resulted in rutting participation by young rams. The consequences of this circumstance included not only a lowered ovarian activity, but an earlier breeding age. We do not view this as an advantageous, compensatory population response. Breeding domestic sheep at first 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). Supplemental feeding of early-breeding Dall ewes in the wild is clearly impractical in Alaska at this time. In the wild, small ewes have lesser status and must get by on forage not selected by more dominant sheep (Geist 1971). Therefore, we think early breeding among wild Dall ewes is maladaptive.

We think these findings indicate that Dall sheep reproductive ecology is much more complicated than current management models seem to indicate. Weather appears to have a definable effect on lamb production, and there appears to be sufficient reason to investigate in greater detail the hypothesis that ram abundance or age structure is also a determinant of lamb production level.

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QUESTIONS AND ANSWERS

Jim Bailey, Colorado: There's a rule around that "sperm is cheap," "sperm are cheap," I guess it is. Why would an old ram with the opportunity to breed young ewes refuse that opportunity if he's an animal that has evolved to increase his relative fitness. Can you rationalize that problem?

Wayne Heimer, Alaska: First, I would stress that I am reporting an observation. Our ability to rationalize the observation within the concept of fitness as we interpret it today should not challenge the observation. Second, it may not increase a ram's relative fitness to mate with a ewe before she is physically mature. An 18-month-old ewe is not physically mature; they're small. If they are similar to domestic ewes, the young first-heat ewe will produce a less than optimally fit offspring. Unless you can provide supplemental feeding for earl-breeding domestic ewes during both gestation and lactation, the future reproductive fitness of both the ewe and the lamb will be compromised. Evolutionary selection has probably favored ewes that are behaviorally as well as physically mature.

Bailey: Yes, but sperm is cheap. Why save your sperm for the older ewe when you can distribute it loosely; and if you save the ewe, you perhaps don't save her for yourself. There's no selection for that kind of a ram.

Heimer: In a situation where there is an abundance of mature rams, young ewes apparently do not breed. An ideal situation would seem to call for ignoring young ewes until they are both physically and behaviorally mature. This would increase fitness for everyone.

Bailey: Yes, I can't rationalize how evolution can produce rams, or possibly Canadians as you suggested, who avoid young, estrous females.

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