ALTERNATE YEAR REPRODUCTION IN A LOW QUALITY, DECLINING DALL SHEEP POPULATION: MANAGEMENT CONSIDERATIONS

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INTRODUCTION

Alaska Department of Fish and Game research efforts in the Dry Creek area of the eastern Alaska Range (Heimer 1973) required marking individaul Dall sheep. These studies resulted in close monitoring of herd numbers, initial lamb production by individual ewes, and survival of lambs to yearling age. Reproductive frequency of marked individual ewes was also observable. This paper reports on the reproductive interval of ewes in the Dry Creek study area in the early 1970's while the population was in a slow but steady decline, and discusses some theoretical aspects of alternate year reproduction in Dall sheep.

MATERIALS AND METHODS

Dall sheep were trapped as reported by Erickson (1970) and marked with permanent collars (Heimer 1973). Subsequently, marked ewes were observed each year as they utilized the main mineral lick on Dry Creek. Observation schedules varied from year to year (Heimer 1976), and population estimates were based on the return frequency of collared sheep at mineral licks (Heimer 1973). Population size was also estimated in 1970 and 1975 from aerial censuses (Heimer 1976) once movements were known. During periods of mineral lick observation, all collared ewes were carefully observed to determine whether they were leading a lamb. The criterion for defining a ewe with a lamb was the observation of suckling. This criterion is admittedly strict, but was necessary because some observers were unable to accurately recognize a ewe-lamb pair on the basis of behavioral displays and contact patterns. In all years except 1975, the number of collared ewes with lambs determined, using this restrictive criterion, was in substantial agreement with that determined by traditional composition counts at the mineral lick. Data gathered since 1975 were valid only for ewes definitely confirmed to have a lamb in 1975. Also, the mean lamb:ewe ratio of 33 lambs:100 ewes among the marked ewes from 1972 through 1974 corresponds exactly to the mean lamb:ewe ratio observed for the total population for those years from Table 1. Hence, use of this strict criterion did not underestimate lamb production.

RESULTS

Lamb:ewe ratios, survival of lambs through the first winter, and total numbers of sheep using the Dry Creek mineral lick suggest that sheep populations in the Dry Creek study area were declining through 1975 (Table 1). The total population estimates of 1970 and 1975 are

Table 1. Productivity, survival and estimated number of Dall sheep influenced by the Dry Creek mineral lick from 1970 through 1975.

Year	Lambs per 100 ewes	Yearlings per 100 ewes	% of lambs surviving 1st winter	Estimated population
1968*	63	13	--	--
1969*	64	31	49	--
1970*	55	31	48	1500
1971*	50	51	93	--
1972	15	16	32	1473
1973	38	11	73	1315
1974	28	25	66	1270
1975	28	23	82	1150
1976	36	16	57	1240
1977	58	17	47	1400

*Data gathered at mineral lick using observation schedules not described in procedures (see Heimer 1975).

based on aerial censuses; data for 1972-1975 are based on mineral lick use. The magnitude of this decline has totaled about 20 per cent since 1970, although some populations within the study area have declined more than others.

All instances of successive annual sightings of individual ewes with known reproductive history, where the presence or absence of a lamb could be definitely determined, are summarized in Table 2. In only seven per cent of the paired observations were ewes seen to lead a lamb in two successive summers. In 53 per cent of the observations, ewes were seen to lead a lamb only in alternate summers, and in 40 per cent of the observations, ewes were observed not leading lambs in two successive years.

Throughout the period of population decline, predator densities were high in the study area. Wolf (Canis lupus) densities in the Game Management Unit 20A are known to have been high (1 wolf per 30 square miles) and prey densities were relatively low for Alaska (45 ungulates per wolf; at least half of these ungulates were sheep) (Stephenson 1978). Wolves were reduced by aerial shooting and trapping during 1976 and 1977 to a density of 1 wolf/100 mi^2 causing a relative prey density increase to 130 ungulates/wolf.

DISCUSSION

Two possible causes for the observed decline may be insufficient production to compensate for "normal" mortality or unusually high mortality. The latter possibility might result from predator pressure. Murie (1944) concluded that wolves mainly utilized the old or weak (diseased or young) classes of Dall sheep in McKinley Park. This conclusion was based on the assumption that sheep with skulls having evidence of lump jaw were diseased and consequently weak. Murie's conclusion that wolf predation is concentrated on diseased sheep may be spurious. The frequency of lump jaw in Dry Creek sheep has been higher (N=35) in living sheep than in Murie's death assemblage (Nielsen and Neiland 1974) and survival of lambs through their first winter has been high (Table 1). Hence, a more correct interpretation of Murie's death assemblage data may be that the "diseased" and young sheep were represented as they occurred in the population. The influence of wolves as a factor in the decline of these sheep populations is probably directed at adults as well as lambs.

Predators were abundant in the area during the recent past, but removal of 40 wolves from the study area by trapping and aerial shooting left a minimum of 10 wolves in the area as of spring 1977 (Buchholtz, pers.comm.). Evidence of Dall sheep was seen in the stomach of only one wolf killed in the area. Primary prey species for these wolves are moose (Alces alces) and caribou (Rangifer tarandus).

Although predators have certainly contributed to the decline, evidence indicates that the decline is due primarily to lamb production below that necessary to compensate for "normal" adult mortality. During the population decline, 15 adult ewes were collected after the rut when a fetus would be visible (Heimer 1973). Of these 15 ewes, 7 were pregnant. Of the eight nonpregnant ewes, six were lactating strongly and two showed evidence of having resorbed a fetus. The low pregnancy rate in this admittedly small sample of ewes, frequent observations of 10-month-old lambs nursing in April, chronically low initial production, and observations of yearlings nursing at the mineral lick, indicate that the lowered rate of re-production and prolonged lactation may be adaptations favouring enhanced survival of lambs through their first winter.

The low percentage of ewes reproducing in successive years (7%), the low pregnancy rate (in our small collection), and the high incidence of extended lactation by nonpregnant ewes in this same sample, raise the possiblility that when a ewe leads lambs in two successive years, early summer mortality may have occurred during the first year. Certainly, annual production of lambs in Dry Creek is the exception rather than the rule, and the most common pattern is biennial reproduction. That is, a lamb is born in June, the ewe does not breed during the rut of the following December or she may breed and then resorb the fetus, the lamb is weaned at about one year of age, and the ewe regains her decreased energy reserves before breeding again in December. The mean reproductive interval in the paired observations (Table 2) calculates to be one lamb every 4 years (65 lambs per 260 ewe-years or 0.25 lambs per ewe year). If this were indeed the average reproductive rate, the maximum number of lambs would be 25 per 100 ewes. This figure is, of course, unreasonably low since the observed mean is about 30 lambs per 100 ewes. It is obvious, then, that some ewes do produce lambs annually. Any ewe which did not participate in extended lactation could probably produce a lamb each year.

Table 2. Successive annual resightings of 69 collared ewes with and without lambs in subsequent years at the Dry Creek mineral lick.

Total successive sightings	Total with-with	Total with-without	Total without-with	Total without-without
98	7 (7%)	28 (28%)	25 (26%)	39(40%)
		52(53%)		

98 total observation pairs
69 ewes

Some theoretical calculations may be based on this alternate year reproductive strategy. The average initial production, observed over the last 6 years in Dry Creek, has been about 30 lambs per 100 ewes. Hence, the percentage of ewes presumed capable of reproduction in December (those without a lamb in summer) was 70 per cent. If all of these animals breed and produce a lamb, and the observable production is 30 lambs: 100 ewes, mean mortality associated with parturition or shortly thereafter was 57 per cent. (100 minus 30% with observable lambs + 70% giving birth). This is the maximum possible parturition-associated mortality, since it assumes that all breeding ewes will carry their lambs to delivery. However, severe winters, as well as other factors, probably result in some in utero mortality.

In the small sample of collected ewes, fetal death occurred in 2 of 8, or in 25 per cent, of the ewes taken near term. If this figure is incorporated into the above calculation, 70 per cent of the ewes breed each year, minus 25 per cent of this number or 45 per cent of the ewes carry lambs to term. This calculates to a parturition-associated mortality of 33 per cent.

Throughout the last six years, harsh weather conditions were recorded during the lambing seasons of 1972, 1973, 1974 and 1975. Here harsh weather is defined as a 24 to 36-hour period of snow, freezing rain, rain accompanied by wind, or subfreezing temperatures. The effects of this weather on parturition mortality are unknown for Dall sheep, but are highly significant in domestic sheep neonate death (Watson et al., 1968). In winters of 1975-76 and 1976-77, snow was minimal, temperatures were generally mild, and no adverse weather was measured during the lambing seasons. Still, the production was well below the theoretical maximum of 72 lambs per 100 ewes in 1976 (100%-28% lambs in 1975) and 64 lambs per 100 ewes for 1977. One case of fetal resorption was documented from five ewes collected in late May, 1976. If fetal death in winter of 1975-76 is assumed to have been 38 per cent (given 28% with countable lambs in 1975 or 72% of the ewes capable of breeding; 20% fetal death; 36% of the ewes seen with lambs in 1976). Using the same assumptions for 1977, the calculation is: 64 per cent capable of breeding (100 - 1976 production) minus 13 per cent (.20 x 64) for fetal death, or 51 per cent giving birth. Production in 1977 was 58 lambs per 100 ewes, so fetal death must have been reduced, parturition-associated mortality nil,or there was consecutive year breeding by a significant proportion of ewes. Observations in 1977 indicated no increase in reproductive frequency. Hoefs (1975) observed mortalities of 15 and 20 per cent in 1971 and 1972 under favorable conditions in Kluane Park, Yukon. Pitzman (1970) documented no early neonate mortality in births observed on Alaska's Kenai Peninsula.

Consequently, lambing mortality, associated with parturition when unfavorable weather conditons occur, may range between 40 or 60 per cent. Under favorable weather conditons, it may range from 0 per cent to 40 per cent.

In summary, data indicate that rates of initial lamb production in the Dry Creek populations may be sacrificed as an adaptation favoring enhanced survival of lambs. This is accomplished by extended lactation which leads to reproduction in alternate years. Weather probably influences initial production by affecting in utero and neonate mortality.

The decline in numbers of sheep in Dry Creek is thought to be due to relatively low reproductive rates, rather than high yearling and adult mortality. Parasitic fauna and burdens have been described (Neilsen and Neiland 1974), but their actual effects on condition and reproduction of Dall sheep are unknown.

Reasons for low, alternate year reproduction and the decline of Dry Creek sheep populations are unclear. One suspected cause is lack of sufficient energy availability in winter. Comparative studies of rumen fermentation (unpubl. data), high sheep population densities, slow horn growth rates for rams, small body size of ewes, and subjective determinations of range utilization made in numerous field trips, suggest that range conditions are relatively poor. Further work will be needed to test this hypothesis.

Recognition of alternate year breeding in these low-quality populations, resulting from a seeming energy insufficiency, immediately suggests that a profitable management strategy may be herd reduction. To evaluate the possible benefits of herd reduction on initial lamb production, a review of the responses of Dall sheep populations, which have been reduced, is in order. Nichols (1976) has seen an increase in initial production (lambs:100 ewes) following population reductions by ewe hunting on Crescent Mountain, Kenai peninsula, Alaska. Data relating subsequent initial production (lambs:100 ewes) to population reductions are also available from natural population fluctuations on Cooper Landing and Surprise Mountain (Nichols 1976), Kluane Park, Yukon (Hoefs 1975), and Dry Creek, Alaska (Table 1). These data are presented in Table 3. The population trends in Table 3 represent year-to-year changes in competing adults (ewes and yearlings) on the winter range during gestation. For purposes of this analysis, rams were excluded from the calculation as suggested by Geist and Petocz (1977). The maximum observed population of ewes and yearlings was taken as 100 per cent, and reductions were expressed as a per cent of this maximum figure. A winter-severity index was derived by multiplying snow depth by hardness from Nichols (1976) for the Kenai and using recorded snowfall in Fairbanks as an index of severity in Dry Creek. Winters having severity indices greater than the mean for the years sampled were arbitrarily classed as "harsh". Winters when the severity index was less than the mean were termed "mild".

Analysis of data in Table 3 shows that two trends are evident. First, when winters are harsh, populations of competing adults on winter range are reduced, and this is followed by low initial production the following spring. Second, when winters are mild, the number of competing adults is increased, and this is followed by increased initial production the following spring. These two situations account for 14 of the 21 data years available. The mean increase in competing adults, following mild winters, has been 10 per cent, and the mean decrease in competing adults, due to harsh winters, has been 16 per cent.

In the remaining seven data years, for which winter sevrity can be assigned, the winters were classified as mild.

Table 3. Trends and percent reduction of competing "adults" (ewes and yearlings) on winter ranges during gestation and initial relative production of lambs the following spring.

	Ewe and yearling population trend (%)	Production trend (%)	Winter severity
Kluane			
1970-71	(+6%)	(+27%)	
1971-72	(+1%)	(-11%)	
1972-73	(-2%)	(-28%)	
Cooper			
1970-71	(+5%)	(+39%)	
1971-72	(-10%)	(+18%)	harsh
1972-73	(+15%)	(+11%)	mild
1973-74	(+8%)	(-46%)	mild
1974-75	(-3%)	(-15%)	harsh
1975-76	(-5%)	(+48%)	mild
1976-77	(-7%)	(-65%)	harsh
Crescent			
1970-71	(-29%)	(-35%)	
1971-72	(-4%)	(+70%)	mild
1972-73	(+16%)	(+29%)	mild
1973-74	(-8%)	(+7%)	mild
1974-75	(-27%)	(-19%)	harsh
1975-76	(-9%)	(+46%)	mild
1976-77	(-15%)	(-57%)	harsh
Surprise			
1970-71	(-12%)	(+29%)	
1971-72	(+2%)	(+111%)	mild
1972-73	(+8%)	(+3%)	mild
1973-74	(-7%)	(-31%)	harsh
1974-75	(-14%)	(-37%)	harsh
1975-76	(-15%)	(+171%)	mild
1976-77	(-26%)	(-100%)	harsh
Dry Creek			
1973-74	(-3%)	(-26%)	mild
1974-75	(-8%)	(0%)	harsh
1975-76	(+12%)	(+29%)	mild
1976-77	(+5%)	(+61%)	mild

In six of these years, populations of competing adults declined by a mean of 8.5 per cent. One of these declines was attributable to hunting, and had a magnitude of 8 per cent. The remaining 5 years range in population reduction from 4 per cent to 15 per cent. It is possible that changes in this range, from one aerial survey to the next, are inherent error in the technique, particularly when no general trend is evident. It should also be noted that these declines also coincide with generally increased wolf abundance on the Kenai.

Whatever the causes, the apparent beneficial effects of ewe hunting on initial production of lambs the following spring can be plausibly rationalized in terms of the effects of weather; i.e., following the ewe hunt, a mild winter occurred which was subsequently followed by increased initial production (lambs:100 ewes). This predictably results in an increased lamb production because of decreases in fetal and adult death; hence, the observed result is explainable as a phenomenon of weather rather than hunting-stimulated reproduction.

If weather effects are neglected, it is possible, through the use of statistical correlation coefficient, to test the relationship predicted by the hypotheses that reduction of animals on the range stimulates initial production. The hypotheses predicts that a plot of initial production, as a function of the per cent of maximum observed competing adults, should give a line having negative slope and a high value for the correlation coefficeint. Figure 1 shows this plot. It can be seen that there is no significant correlation between the two variables, and the sign of the coefficent is opposite to that predicted by the hypotheses. Consequently, ignoring the possible effects of weather appears to force the conclusion that many population reductions, of the magnitude practiced on Dall sheep by man and nature in Alaska, have not resulted in increased initial production. Hence, population reductions, even in populations judged to be near carrying capacity, have had no beneficial effects on relative initial production (increased lamb ; ewe ratios), when the reductions have been as high as 25-30 per cent.

As the magnitude of population reduction, necessary to evoke an increase in relative production (improved lamb : ewe ratio), approaches 50 per cent in populations where alternate year reproduction occurs, the possibility of beneficial effects of this management tool diminish. It may be impossible to evoke a doubling in reproductive frequency, with a 50 per cent reduction in the number of ewes. If so, the levels of absolute production will never be as great as they were before the herd control was begun, even through increases in relative production (lamb : ewe ratio)might occur.

Figure 2 shows the increases in realtive production, which would be required to meet an absolute production of 30 lambs by a population of 100 ewes initially having a relative production of 30 lambs : 100 ewes, if the population were reduced. This example demonstrates that a reduction of 50 per cent would have to elicit a relative production of 60 lambs per 100 ewes to meet the initial level of absolute production. Individual lamb productions of this magnitude have been observed in

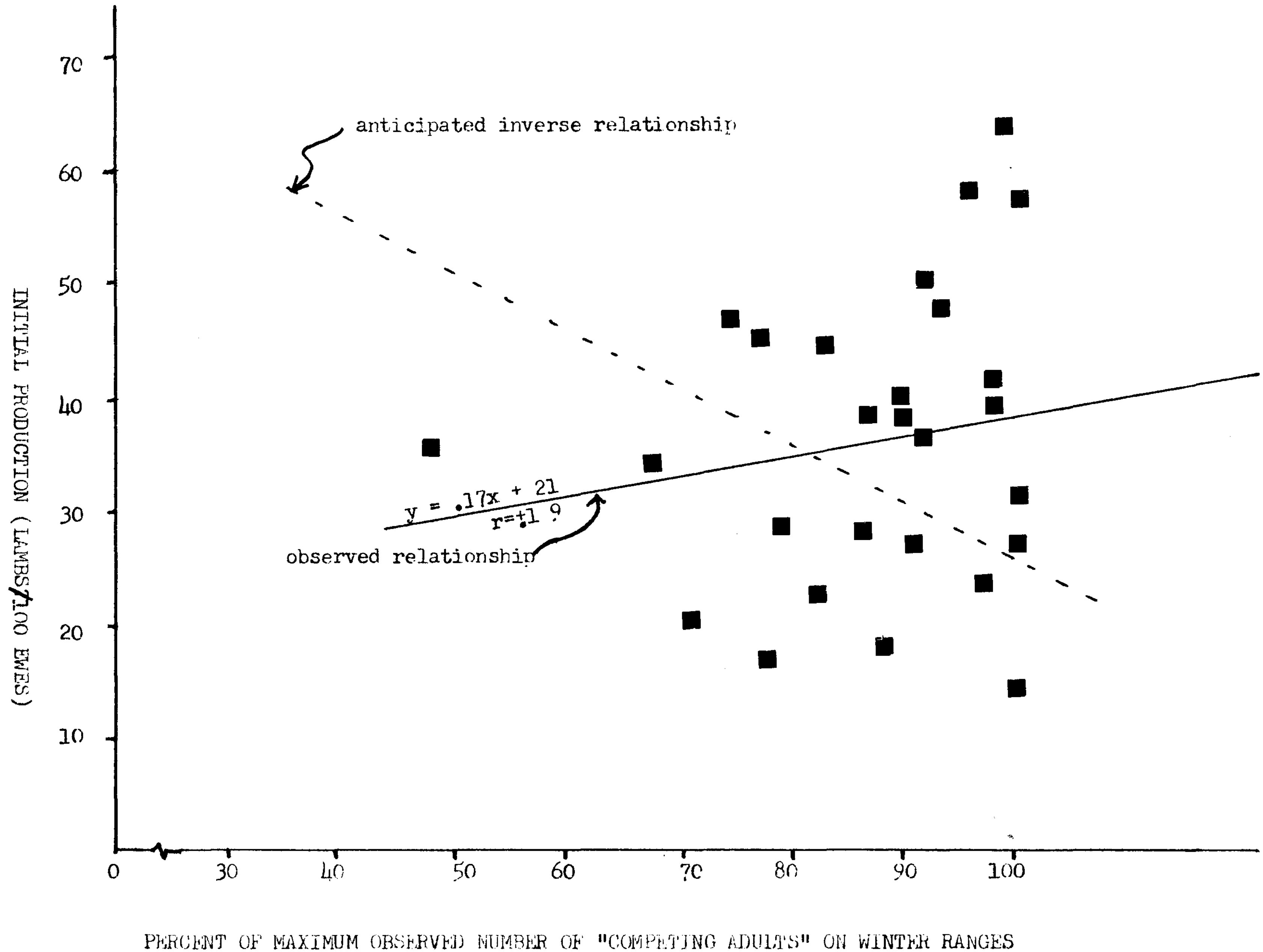

Figure 1. Relationship of percent of "competing adult" reduction and relative initial production of lambs in the following spring.for Dall sheep.

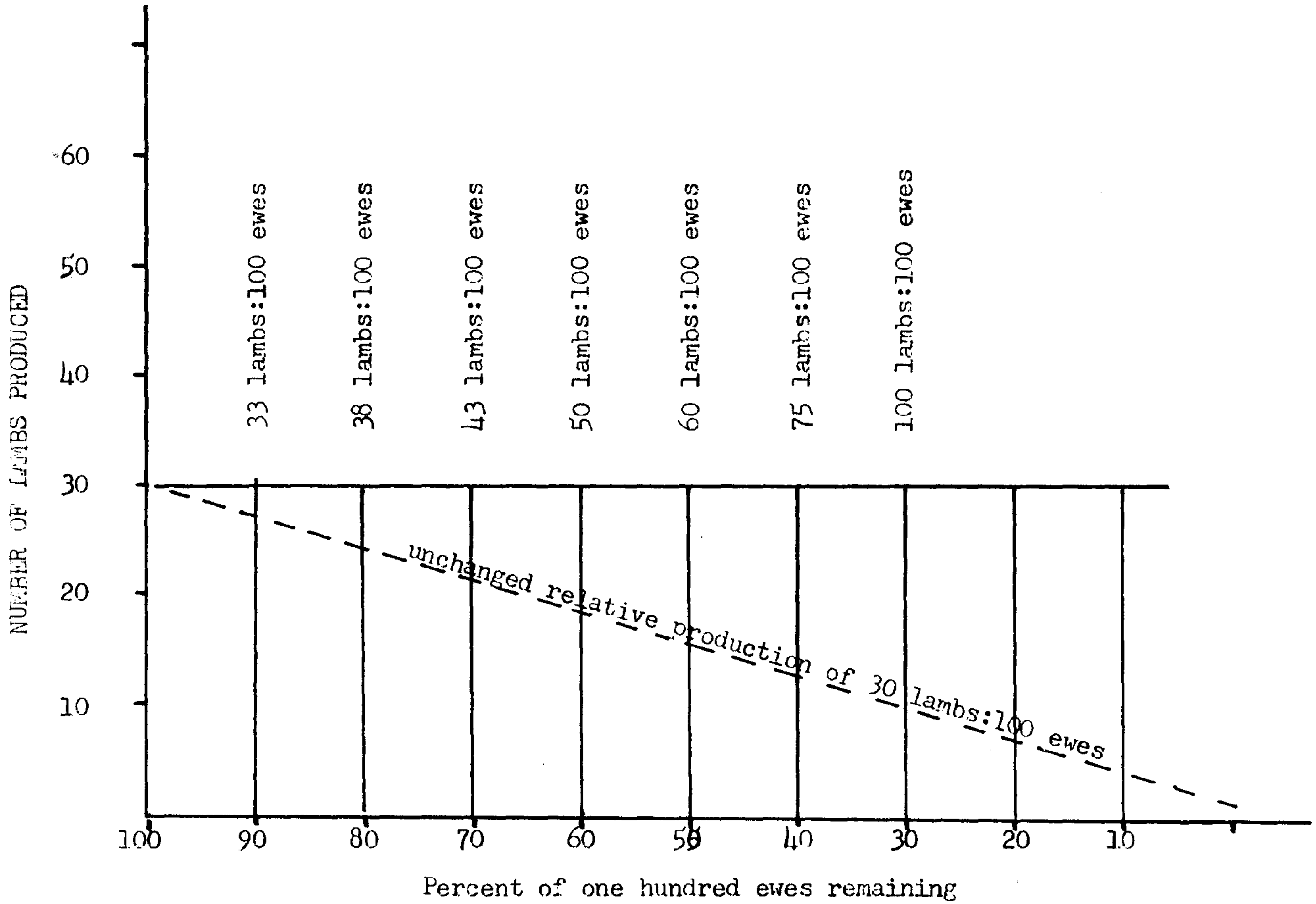

Figure 2. Necessary adjustments in relative production required to maintain initial lamb production of 30 lambs in a hypothetical population of 100 ewes, and the decrease in absolute production of lambs if relative production is unchanged when the number of breeding ewes is reduced.

Alaska, but the maximum attainable mean appears to be in the low 40's of lambs per 100 ewes. The dashed line on Figure 2 demonstrates the decreased absolute production of lambs resulting from herd reduction, if there is no stimulatory effect on initial production.

If there is a demand for trophy rams which equals or exceeds the supply, or if trophy management is the primary management goal, it should be understood that herd reduction will, in all likelihood, decrease the absolute supply of trophy rams and compromise the primary management goal. In herds where alternate year reproduction is not the case, there is even less possibility of benefit, and either sex sheep hunting should be clearly understood to result in reduced availability of trophy rams for harvest with no assurance that compensatory reproduction will result.

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