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POPULATION DYNAMICS OF TWO TRANSPLANTED BIGHORN SHEEP HERDS IN SOUTHCENTRAL WYOMING

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Abstract: Success of transplanting Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) herds in Wyoming has been limited. A goal of this study was to identify reproductive and mortality patterns contributing to poor population performance in 2 transplanted herds in Wyoming. After release in the 1970s, both herds rapidly increased during the first 6-10 years, subsequently declined, and currently appear to be stable, but at levels potentially predisposing to long-term losses in genetic heterozygosity. During this study (1986-88), high mortality of lambs restricted population growth. Approximately 55% of lambs died each year, resulting in 22 lambs/100 adult ewes after winter. Most lamb mortality (75%) occurred during late summer and fall, with relatively little occurring during winter. Diseases were proximate causes for most lamb deaths. Mortality of adult ewes was low; only 2 of 18 radio-marked ewes died. Birth rates and lamb survival declined substantially after the initial phase of population growth in the 1970s, and these changes appear responsible for population declines and current herd stagnation. Population trends are consistent with classical density-dependent population regulation via limited food resources for ungulates that are released into largely unexploited and restricted habitats.

Transplanting frequently has been used to establish new herds of bighorn sheep in the central and northcentral Rocky Mountains. Sufficient time (15-30 years) has elapsed to assess many transplanting efforts, and results are not particularly encouraging (Bailey 1988, Smith and Butler 1988, Risenhoover et al. 1988). In Wyoming, most transplanted populations remain

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small and have poor reproductive success, potentially predisposing to reductions in genetic heterozygosity and inbreeding depression (Cook 1990).

We began studies in 1986 to identify factors that contributed to the poor population performance of 2 transplanted herds in southcentral Wyoming. Population history for each is typical of other herds introduced throughout the state. One herd is considered to be relatively successful, whereas the other suffered severe declines, requiring a supplemental release of 19 sheep in 1989. In this paper, we describe population dynamics of these 2 herds during 1986-88, and describe long-term population dynamics from herd establishment through 1988.

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DESCRIPTION OF STUDY AREAS

The 2 herds in this study were established by transplanting on ranges that historically supported bighorns (Haas 1979). Transplant stock for both releases came from the Whiskey Mountain herd near Dubois, Wyoming. Forty-one sheep were released in the North Platte River Canyon in 1971. This herd subsequently separated into 3 subherds, 1 at Bennett Peak (BP), a second near the A Bar A Ranch, and a third at Douglas Creek (DC). The second herd resulted from a release of 69 sheep in the Encampment River Canyon (ENC) in 1976 (Haas 1979, Cook 1990).

Sheep occurred on ranges that primarily supported big sagebrush/antelope bitterbrush (Artemisia tridentata/Purshia tridentata) communities. Important, but less common communities included juniper (Juniperus spp.) on xeric, rocky sites; aspen (Populus tremuloides), Douglas-fir (Pseudotsuga menziesii), or lodgepole pine (Pinus contorta) forests on more mesic sites; and grass-dominated communities on windblown ridges. Sheep occupied steep, V-shaped canyons along the North Platte and Encampment Rivers. Elevations ranged from 2230 m to 2800 m. Annual precipitation averaged about 30 cm at lower elevations but exceeded 40 cm at higher elevations. Temperatures ranged from over 26 C in summer to below -30 C in winter, with an average annual temperature of 3 C (Haas 1979, Cook 1990).

METHODS

Population dynamics were evaluated by repetitive sampling to estimate numbers of sheep in sex and age classes and to identify changes in sex/age composition through time. Sex/age composition was determined for all groups of sheep encountered while searching for 20 radio-marked adult sheep. During most of the study, we located each marked sheep at least 10 times monthly. This approach resulted in visual observations of 1/2 to 3/4 of the sheep within a subherd each sampling day, and approximated a complete census over a season.

Sheep were classified based on the following sex/age categories: (1) adult males and females, at least 2 years-old; (2) yearling males and females, ranging from 13-24 months; and (3) lambs, less than 13 months old. We classified adult rams based on horn size as described by Geist (1971). Because rams occupied ranges away from ewes in most seasons, we estimated numbers of rams and ram:adult ewe ratios from data collected in December only, when ram numbers peaked on ranges occupied by ewes.

We estimated the number of animals in each sex and age class based on single-day counts of sheep when confident that no groups of sheep were double-counted. The highest counts during a season provided the best estimate of total sheep in each sex/age category for the season. Summing these categories provided a minimum estimate of total population size. Estimates of annual juvenile mortality were calculated by dividing the number of lambs dying at the end of their first spring by number of lambs born. A conservative estimate of birth rates was derived from mid-June through mid-July lamb:adult ewe ratios. Birth, death, and lamb:adult ewe estimates were multiplied by 100 and presented as percentages.

Population data prior to this study were obtained from the Wyoming Game and Fish Department's (WGFD) annual job completion reports and from Haas (1979). Annual juvenile mortality was estimated by dividing post-season lamb:adult ewe ratios by pre-season lamb:adult ewe ratios. The WGFD generally collected pre-season data during summer and post-season data in early winter to early spring (B. Rudd, pers. commun.). Linear regression analyses were used to detect significant trends in population characteristics.

RESULTS

Pre-study Population Dynamics

The North Platte herd was established with 17 ewes, 3 rams, and 21 lambs in winter, 1970-71. WGFD estimated 200 sheep were present by 1976, suggesting an annual rate of increase of about 30%. However, Muchmore (1975) reported an annual rate of increase of 13% during the first 4 years after release. By 1979, WGFD indicated 300-350 sheep were present. But this estimate was reduced to 160 sheep with development of a ONEPOP simulation model in the early 1980s. Although these records are inconsistent, WGFD personnel who have monitored this herd since the late 1970s believe there were 50-100 more sheep present in 1979-1981 than today (J. Bohne, pers. commun.). Thus, the herd apparently increased from 41 to about 200 sheep in 1980 and declined to about 130-140 sheep by 1986. This suggests an increase of about 20% per year during the 1970s, and a decline of 5% per year between 1980 and 1986.

The Encampment herd was established with 30 ewes, 8 rams, and 31 lambs in 1976-77. This herd increased to 85 the first 2.5 years (Haas 1979) and apparently peaked at 120 in 1983 based on WGFD ONEPOP simulation modeling, an increase of 10-15% per year. The herd decreased to about 45 sheep by 1986. This suggests a rate of decline averaging 30% per year, but the decline may have been precipitous based on sketchy information.

Initiation of declines in both herds apparently coincided with severe winters. Moderate mortality was suspected during the severe winter of 1978-79 in the North Platte herd, with reduced recruitment of lambs since then. Possibly substantial mortality occurred in the Encampment herd during the severe winter of 1983-84, and lamb recruitment also was reduced in subsequent years (J. Bohne, pers. commun.).

Lamb:ewe ratios for both herds suggest substantial changes in birth and mortality rates since 1972 (Fig. 1). Percentages of ewes with lambs in early to mid-summer declined from about 80 to 46% in the North Platte herd, and declined from 70 to 42% in the Encampment herd. Lamb mortality increased from about 20% [including 1976 mortality estimates from Haas (1979)] to 53%. Mortality could not be estimated during the first 10 years of the North Platte herd, but estimates of mortality were high (50%) and roughly constant during the last 9 years (Fig. 1).

Current Population Characteristics

Numbers of adult ewes ranged between 20 and 30 in each subherd during most years of the study (Table 1). Numbers of yearlings ranged between 5 and 10 at DC and 2 to 9 in the other subherds. We estimated 8 adult rams each at DC and A Bar A, 5 at BP, and 7 at ENC, with data pooled among years. About 14, 48, 20, and 18% of adult rams were class I, II, III, and IV, respectively.

We estimated the average minimum population at about 105 yearling and adult sheep in the North Platte herd and 38 yearling and adult sheep in the Encampment herd during 1986-88. Although 3 years' population data may be insufficient to determine population trends, data suggest numbers of adult ewes declined at A Bar A and BP and increased at DC and ENC (Table 1). There was a net loss of about 5 adult ewes and a net gain of 2 adult ewes in the North Platte herd and Encampment herds, respectively. This evidence suggests the herds were either declining slightly or approximately stable.

Lamb production and mortality varied among years and subherds (Table 2). Birth rates averaged 50%, but ranged from 32% at A Bar A, about 47% at BP and ENC, to 75% at DC. Lamb mortality averaged 55% during 1986-88, ranging from 26% at DC to 80% at BP. Lamb:adult ewe ratios averaged nearly 50% just after lambing, but declined to 22% by the following spring.

Four periods of rapid mortality were documented, with the majority of this mortality occurring from mid-July through November. In addition, most lambs born at ENC in 1986 died by the following spring, but no data were collected between August and the next spring, so timing of mortality was not determined. During the 3 years of study, 61 of 141 lambs born died before their first winter (43% pre-winter mortality). Significant lamb mortality also occurred during several winters, particularly at A Bar A and BP. Of 80 lambs alive before winter, approximately 16 died during winter (11% of all lambs born).

Mortality of adult ewes was low. Two of 18 radio-collared adult ewes died. Radio-marked ewes were monitored an average of 2.1 years, suggesting that about 5% of adult ewes, or 5 ewes in both herds combined, died each year. However, there were 10-12 yearling ewes produced each year (Table 1).

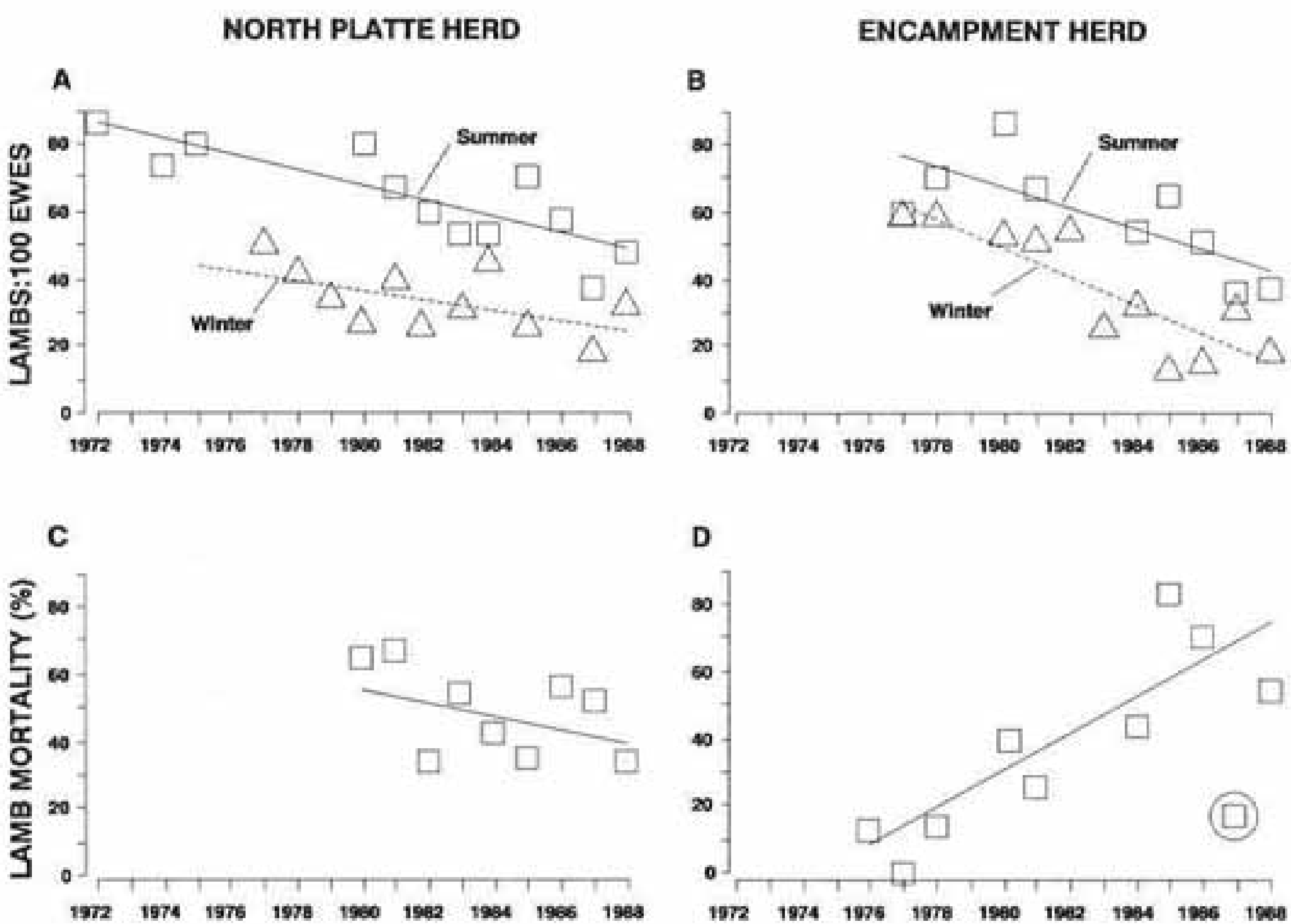

Figure 1. Summer and winter lamb:ewe ratios for the North Platte (A) and Encampment herds (B), and lamb mortality rates (winter lamb ratios/summer lamb ratios x 100) for the North Platte (C) and Encampment herds (D). Summer and winter lamb:ewe ratios in both herds were significantly ($P < 0.05$), inversely correlated to year. Lamb mortality rates were significantly correlated to year at Encampment (with or without the circled outlier), but were uncorrelated ($P > 0.05$) to year in the North Platte herd.

Table 1. Minimum, non-repetitive estimates of sheep in each sex and age class (except adult rams) at Douglas Creek, A Bar A, Bennett Peak, and Encampment, 1986-88.

Year	Adult ewes	Yearling ewes	Yearling rams	Summer lambs	Spring[a] lambs
			Douglas Creek		
1986	19	6	2	12	11
1987	23	6	4	19	6
1988	21	4	1	13	12
			A Bar A		
1986	25	2	4	15	4
1987	28	0	1	2	1
1988	23	1	1	8	5
			Bennett Peak		
1986	27	2	6[b]	15	1
1987	26	1	1	10	5
1988	22	2	0	12	2
			Encampment		
1986	26	0	2	13	4
1987	26	2	1	10	9
1988	28	5	4	11	5

[a] Spring lambs are those that survived their first winter.

[b] These 6 yearling rams were probably not born at Bennett Peak. This group of 6 was observed together in late winter 1986-87 at Bennett Peak and most were observed several weeks later at A Bar A.

Table 2. Minimum, non-repetitive estimates of lamb numbers just after lambing (post-lambing), pre-winter, and post-winter (April), 1986-88.

Year	Season	Douglas Creek	A Bar A	Bennett Peak	Encampment
1986	Post-winter	10	7	5	-
1986	Post-lambing	13	15	15	13
1986	Pre-winter	11	7	3	7
1987	Post-winter	11	4	1	4
1987	Post-lambing	19	2	10	10
1987	Pre-winter	7	1	9	9
1988	Post-winter	6	1	5	9
1988	Post-lambing	13	8	12	11
1988	Pre-winter	13	7	2	5
1989	Post-winter	12	5	2	5[a]

[a] One of these 5 lambs died in April due to a broken leg.

This suggests actual adult ewe mortality averaged about 10% per year, assuming high survival of yearling ewes and a stable population.

DISCUSSION

The Encampment and North Platte herds have been typical of populations that were introduced into largely unexploited habitats (Caughley 1970, 1976). After a single eruptive oscillation, both herds stabilized at levels apparently in equilibrium with forage resources. The North Platte herd increased about 5-fold and the Encampment herd increased about 2-fold before declining.

Marginal production and high mortality of lambs are the most important proximate mechanisms currently restricting both herds. Lamb mortality averaging 55% resulted in 22 lambs per 100 adult ewes after winter. Thorne et al. (1979) indicated 8-36 lambs per 100 ewes may result in declining populations. Festa-Bianchet (1987) reported an Alberta population increased when lamb survival to weaning varied from 51-87% and October-May lamb survival averaged between 80-100%. Geist (1971) identified lamb mortality of 55% in a declining population in Alberta. Moreover, our estimates of lamb:ewe ratios are low compared to other herds in Wyoming (Oldemeyer et al. 1971, Thorne et al. 1979, Hurley 1985, Smith 1988), Colorado (Streeter 1969, Baumann 1978), and Montana (Erickson 1972, Brown 1974, Pallister 1974); their winter/spring estimates of lamb:ewe ratios ranged from 34 to 77%.

Declines in birth rates and lamb survival (Fig. 1) after introduction are consistent with classical density-dependent population theory (Caughley 1979, Caughley and Krebs 1983). As herbivore density increases, intraspecific competition would reduce forage availability per sheep. Density-dependent theory of Caughley (1976, 1979) also predicts that relatively intense use of preferred forages at high herbivore density would reduce carrying capacity of ranges, by reducing abundance and productivity of selected forages. Thus, sheep populations would be less productive after declines then before declines, even though sheep densities before and after declines might be roughly equal (Cook 1990).

In our study, nutrient quality of food during summer, rather than forage abundance, was correlated to lamb survival (Cook 1990). Alpine ranges were unavailable, precluding access to high quality forage during summer (Hebert 1973, Thilenius 1975), when nutrient requirements for lactation and lamb development are high (National Research Council 1985). This indicates the amount of food meeting nutritional requirements for reproduction, rather than standing crop of all forages, most influenced population dynamics. In addition, the limiting effects of food were exacerbated by poor habitat conditions (Risenhoover and Bailey 1985, Wakelyn 1987). Gentle slopes (< 25%), sparse escape terrain, and dense forests around occupied ranges restricted sheep to small portions of total potential range (Arnett 1990, Cook 1990).

However, the sensitivity of bighorns to disease confounds simplistic food-limitation mechanisms. Frequent, and often spectacular declines in populations due to disease (Spraker 1979, Goodson 1982, Hibler et al. 1982, Coggins 1988, Festa-Bianchet 1988) suggest parasites and pathogens may limit populations below forage-determined carrying capacities. Nearly all lamb mortalities documented in our study (13) resulted from disease. We also observed sick lambs that were never recovered for necropsy. Most mortality occurred during brief die-offs in summer and early fall, a mortality pattern not likely stemming from predation.

Disease offers an alternative hypothesis of population regulation. As sheep populations increase, densities of parasites (Hibler et al. 1982) and pathogens in hosts and habitats may increase, thereby increasing infection and transmission rates in sheep. However, 3 lines of evidence in our study refute this hypothesis: (1) lungworm (Protostrongylus spp.) and gastro-intestinal parasite levels were low in these herds (as low as any reported in the bighorn literature, in the case of lungworms) (Arnett et al. 1989, Cook 1990); (2) declining birth rates, which generally should be unaffected by the diseases that affected lambs (Cook 1990), accounted for much of the declines in lamb recruitment; and (3) one subherd (DC) in the North Platte herd maintained high birth and survival rates, even though this subherd occupied its range as long as the other subherds.

Our data suggest disease in lambs was a proximate mechanism through which food limited survival and thus regulated population size. Festa-Bianchet (1987) believed susceptibility of bighorns to disease precluded the occurrence of visibly emaciated animals, but forage conditions nevertheless ultimately determined population size by influencing susceptibility to disease. The relationship between summer nutrition and summer lamb survival has long been recognized (Streeter 1969, Horesji 1972, Douglas and Leslie

1987, Festa-Bianchet 1987), and the relationships among nutrition, disease, and survival of sheep are receiving greater recognition (Schwantje 1986, Festa-Bianchet 1987, Cook 1990).

MANAGEMENT IMPLICATIONS

This study and the mediocre or poor success of transplanting bighorns in the central Rocky Mountains indicate: (1) managers should adopt transplanting techniques to compensate for the poor dispersal and colonizing tendencies of bighorns (Geist 1983); and (2) intensive management will be required to produce populations of adequate size to preclude inbreeding depression over the long-term.

Transplanting in Wyoming has usually been conducted in winter, restricting opportunities (due to accumulation of snow) to spread sheep throughout all portions of suitable ranges. After 20 years, sheep in southcentral Wyoming have failed to colonize suitable or superior areas that are close (< 7 km) to occupied ranges. Potential exists to double or triple population sizes by releasing sheep into these unoccupied areas. Use of helicopters to place groups of sheep throughout potential range would have increased initial release costs, but may have resulted in larger populations with a higher probability of long-term persistence.

Habitat management that would permit expansion of occupied ranges or facilitate establishment of migratory routes between seasonal ranges should be beneficial. Treatments that would improve the quality of habitats (Wakelyn 1987, Risenhoover et al. 1988) or quality/quantity of forage in occupied ranges may increase the probability of long-term success with transplanting. Prescribed fire is useful for improving forage conditions for bighorns during all seasons in southcentral Wyoming (Cook et al. 1989, Arnett et al. 1989, Cook et al. 1990). In conclusion, we concur with Bailey (1986, 1988) and Risenhoover et al. (1988) that management problems with bighorns present particularly difficult challenges; expecting long-term success after transplanting without subsequent management has proven to be unrealistic in most cases in the central Rocky Mountains.

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