RANGE ECOLOGY OF BIGHORN SHEEP IN RELATION TO SELF-REGULATION THEORIES

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INTRODUCTION

In the Canadian National Parks, the Rocky Mountain bighorn sheep *(Ovis c. canadensis* Shaw) occurs in Jasper, Banff, Waterton Lakes and Kootenay in southwestern Alberta and southeastern British Columbia. These parks comprise 7,511 square miles and have existed at their present size since just prior to 1915. Since their establishment, sheep numbers have fluctuated between 1,000 and 5,000 and there have been five major "die-offs." Each die-off resulted in the loss of at least 75 percent of infected herds within a 2-year period, with the majority dying sithin 6 months. In Japser and Kootenay, numbers increased following the die-offs to return to previous peak populations within 20-25 years. A second die-off has not occurred in the parks except for Kootenay where die-offs occurred in 1941 and 1966. A second die-off appears imminent in Jasper. These die-offs have been attributed to "pneumonia-lungworm" or "verminous broncho-pneumonia" disease, inclement winter weather and deteriorated ranges.

The government and public alike are concerned about the long-term effects which these die-offs will have on future sheep populations. Since 1940 there has also been concern over the effects of increasing elk numbers, and encroaching forests onto grasslands, on the welfare of bighorn sheep.

STUDY

In the fall of 1966, a cooperative study between the Canadian Wildlife Service and the National Park Service began in these four parks and continued through 1973. Major emphasis was placed on range ecology, population dynamics, disease-parasitism, and interspecific competition. The basic objectives were three-fold, namely:

1. To determine the causes of population fluctuations, in particular, die-offs.
2. To determine the effect and interrelationship of various intrinsic and extrinsic factors in limiting sheep numbers. The intrinsic factors included animal condition, reproduction-recruitment rates, and disease-parasitism. Extrinsic factors included range condition and trend, weather, interspecific competition and predation.
3. To determine if any population-regulating mechanisms (intrinsic and/or extrinsic) exist which will prevent native ungulate populations from increasing to a level deleterious to the long-term welfare of both the sheep and their ranges. Of particular interest was the possible existence of self-regulating mechanisms which could limit native ungulate populations before densities surpassed range carrying capacities and before food supplies became depleted. A recent philosophy believes that there exists an effective density-dependent, self-regulating mechanism which functions to limit animal numbers before food supplies become depleted. If this mechanism exists,

then the need to consider "man-made" controls of high native ungulate populations within parks would be unnecessary and unjustified. The presence of short-term ungulate surpluses and range forage depletions, if they existed, could be viewed as unimportant to the long-term well-being of both the ungulates and their ranges.

SELF-REGULATION PHILOSOPHIES

Malthus in his 1824 essay stated that human populations tend to grow in a geometric progression at a rate that would double numbers every 25 years. Food supplies could increase in arithmetic progression. The superior power of population growth required that population growth must inevitably be checked, if not by preventive measures, then by starvation, disease, wars, etc. (Malthus 1960).

Darwin and Wallace modified the Malthusian Principle to include predation as a limiting factor (Eiseley 1961). The four limiting factors which they believed limited animal numbers were:

1. Amount of available food.
2. Predation.
3. Physical factors such as climate.
4. Disease.

From 1920 to the early 1940's, several ecologists such as Chapman (1928), Andrewartha and Birth (1954), and Darling (1937) presented views on animal rates of increase and population regulation. They explained that animal numbers were limited by the species "biotic potential" or "innate capacity for increase," within the limits imposed by food, weather, space and competition. By the early 1940's it became apparent that previous philosophies did not explain some of the observed declines in populations or cases of relatively static populations. It was suggested that factors intrinsic to the population were involved in its regulation (Leslie and Ransom 1940).

Since 1949, there have been many studies on density-dependent changes that occur within the animal when subjected to various combinations of food, competition, weather, predation, etc. (Chitty 1952, Davis 1953, Errington 1956, Christian 1963, Edwards 1956). In addition, the theories of Lack (1954) and Andrewartha and Birch (1954), which leaned heavily on food and weather to explain population control, remained popular.

From the mid-1950's, there has been an effort to integrate social actions and habitat factors into a scheme to explain population changes. A theory originated which states that within the broad limits set by the environment, density-dependent mechanisms have evolved within the animals themselves to regulate population growth and curtail it short of environmental destruction (Nicholson 1958, Wynne-Edwards 1956, Chitty 1960, Milne 1962, Christian 1963). Many believed this mechanism functioned through a "feed-back" control via the endocrine system, operating as a behavioral-physiological mechanism. As population density increased, reproduction was inhibited by stimulation of pituitary-adrenocortical activity. This increased activity resulted in greater mortality indirectly from lowered resistance to disease, parasitism, environmental stress, or more directly through "shock diseases" (Christian and Davis 1964).

Ardrey (1961, 1966) illustrated this mechanism in primates, while Hornocker (1970), Mech (1970), Cowan (1947) and others showed that large North American carnivores such as wolves and cougars self-regulated their numbers before their food supply became depleted.

Concerning the large native ungulates, densities of the Uganda kob and the roe deer in natural unfenced and unhunted areas were shown to be limited by territorial behavior which prevented overcrowding and which served to expel surplus animals into inferior habitat where they were controlled by increased mortality (Buechner 1963, Anderson 1961, Kurt 1968). In North America, it was reported that an elk population in part of Yellowstone National Park was self-regulated by density-influenced mortality from intraspecific competition for food, and by compensating natality (Cole 1969). Similarly, moose in Grand Teton National Park, bison along the Pelican Valley of Yellowstone National Park, and elk and mule deer along the Middle Fork of the Flathead River drainage in Glacier National Park were reported to show population stability primarily due to heavy winter mortality and low recruitment rates plus emigration of sub-adults (Houston 1968, 1971, Martinka 1969).

The general conclusions from Yellowstone, Grand Teton and Glacier National Parks appears to be that "Realized annual recruitment is low; range conditions fluctuate, and some areas appear periodically 'overgrazed.' Ungulates participate in plant successional processes and may be capable of reducing or eliminating remnant vegetation types that are no longer a number-limiting food source. Large predators represent only one of a complex of regulatory factors on ungulates and may have been overrated as a major control in harsh environments." (Houston 1971).

Geist (1971) has suggested that native ungulates associated with climax vegetation associations, such as wild sheep and goats may be self-regulated. In opposition to the above views on self-regulation in wild ungulates, there are numerous reports suggesting that nonterritorial ungulates normally "outstrip" their predators in population growth and denude their food supply before their numbers are finally limited by the quantitative and qualitative limits of their food supply (Klein 1970, Cowan 1950, Flook 1964, Riney 1964, Rasmussen 1941, Pengelly 1963, Cauley 1970, Eddleman and McLean 1969, Morris 1956, Moss and Watson 1970, Lowdermilk 1953, Cottam 1961).

RESULTS

1. <u>Historical</u>. Bighorn sheep numbers in the region which is now the Canadian National Parks described above, had been reduced to low levels in the late 1800's and the early 1900's by excessive, indiscriminate hunting plus the effects of a few catastrophic winters (1886-88, 1906-07). When these lands became National Parks just prior to 1915, sheep numbers increased from 1500 up to 4500 by 1936. In the late 1930's and early 1940's, winter range conditions in all four parks were reported in a poor, overgrazed condition (Clarke 1941, Green 1949, Cowan 1950, Pfeiffer 1948, Flook 1964). A series of die-offs in all four parks, and adjacent provincial lands, reduced park numbers from 4500 to 1000. Die-offs resulted from poor range conditions due to overgrazing by bighorn sheep, elk, deer and to some extent from livestock. The terminal factor was a "pneumonia-lungworm" disease. For example, in Waterton Lakes National Park (204 square miles), park files indicate an estimated 1000 bighorn sheep, 1500 mule deer plus elk, and 2211 livestock, or 5000 ungulates grazed the park in 1936. As only about 50 square miles of this park are suitable winter range,

the stocking rate must have been close to 100 ungulates per square mile. In the spring of 1937 a major die-off occurred in the bighorn sheep herds. The die-off was attributed to "verminous broncho-pneumonia," but undoubtedly depleted winter forage supplies was a major factor. The unfavorable range/ungulate situation in the parks in the 1940's was aptly described by Cowan (1950) who remarked, "...National Parks of Canada between 1943 and 1946 supported over-capacity populations of big game in which moose, elk, mule deer and bighorn were in competition for a declining food supply on the winter ranges."

By 1966, sheep populations climbed to 4400 prior to the fifth die-off which occurred in Kootenay in 1966-67. This die-off was again attributed to "pneumonia-lungworm" disease precipitated by constricted and overgrazed winter ranges (Stelfox 1971). In 1969, sheep populations in Jasper were similar to those in 1946 just prior to an 85 percent die-off. Although a second die-off has not occurred in Jasper, high ungulate densities on the winter ranges and high endoparasite loads indicate that another die-off is imminent.

Historically, die-offs occurred concurrently on both park lands and on adjacent provincial lands subjected to hunting. This indicates that past hunting pressures on Alberta and British Columbia bighorn sheep herds were not effective in preventing major population fluctuations similar to those occurring in the national parks.

2. Range Ecology. Tables 1 and 2 compare forage production and utilization, range stocking rates, endoparasite burdens and overwinter sheep weight losses in Jasper, Banff and Waterton. On the overgrazed Jasper ranges, forage production was only 36 percent as great as that on the productive and moderately-grazed Waterton ranges. Forage utilization was 64 percent in Jasper, 46 percent in Banff and 34 percent in Waterton. There was a strong correlation between forage:ungulate ratios and overwinter weight losses. The Waterton ranges supported 38.6 wild ungulate days-use/acre and the adult ewes only lost 13.2 percent of their fall weight during the winter. Conversely, the Jasper ranges supported 138.1 wild ungulate days-use/acre and the adult ewes lost 20.1 percent of their fall weight overwinter. Corresponding lungworm burdens were 594 larvae/gm. feces in Waterton compared to 2375 larvae/gm. feces in Jasper. On the heavily grazed Jasper ranges, forage production was 168 percent and 104 percent higher within the exclosures, 2 and 5 years after protection from grazing than on adjacent grazed ranges that were only protected from grazing during the preceding growing season. On the moderately grazed Waterton ranges, forage production was only 80 percent and 6 percent higher within the exclosures 2 and 5 years after protection compared to adjacent grazed ranges. Thus the Jasper winter ranges were significantly affected by the heavy grazing pressure.

Reproductive rates were not significantly lower in sheep herds on heavily grazed ranges (Jasper) than in herds on moderately grazed ranges (Waterton) as revealed in Table 1. However, recruitment rates (yearlings:100 ewes) were significantly different with the lower recruitment rates occurring in herds on overgrazed ranges. The sheep evidently continued to reproduce at, or close to, their innate capacity regardless of range conditions, overwinter weight losses, or endoparasite loads. Those lambs produced on overgrazed ranges were apparently weaker neonates at birth or else, because of poorer post-natal nutrition, were unable to make satisfactory growth rates to prevent heavy winter mortality.

	WATERTON			BANFF			JASPER		AVERAGES
	Galwey		Ruby	Palliser		Bourgeau	Sulfur		Disaster	
Forage Production (lbs/Acre Dry Wt.)									
756	551	345	551	422	294	244	200	155	391
Percent Forage Utilization									
43.6	34.2	24.9	39.7	46.0	52.4	66.6	64.0	61.4	48.1
Ungulate Use As Sheep Days Per Acre									
295	216	138	426	400	375	941	774	606	464
Lungworms Per Gram of Feces									
	594			626			2375		1198
- % Winter Weight Loss of Adult Ewes									
	13			11			20		14
Production of Lambs (Fall) Per 100 Ewes									
	32.8			44.1			35.7		37.5
Recruitment of Yearlings (Fall) Per 100 Ewes									
	21.0			21.5			16.8		19.8

Table 2. Coefficient of determination r^2, and correlation coefficient r (Pearson's) between percent forage utilization (independent variable) and forage production, lungworm burdens, winter weight loss of ewes, sheep production (lambs:100 ewes), and recruitment rates (yearlings:100 ewes).

Correlation Symbol	Correlations of Forage Utilization (x) with Five Dependent Variables				
	Forage Production	Lungworms/ Gram Feces	% Winter Wt. Loss (Ewes)	Lambs:100 Ewes	Yearlings 100 Ewes
r^2	0.23	0.86	0.66	0.02	0.77
r	-0.48	+0.93	+0.81	+0.13	-0.88

However, the decreased recruitment rate in Jasper was insufficient to prevent sheep populations from exceeding range carrying capacities.

CONCLUSIONS

Bighorn sheep in the Canadian National Parks did not exhibit any density-dependent self-regulating mechanism to control their numbers when range conditions declined and disease-endoparasite loads climbed. Reproduction (6-8 month old lambs:100 ewes) remained normal, but lamb mortality increased in proportion to range deterioration as revealed in the ratio of yearlings (18-20 month old yearlings):100 ewes. This increased lamb mortality on overgrazed ranges was ineffective in reducing sheep numbers to within range carrying-capacity limits.

The major extrinsic factors operating to limit sheep numbers after range forage utilization exceeded 50 percent were:

1. Endoparasites - in particular lungworms and gastrointestinal helminths which stressed the animal and increased lamb mortality.
2. Pneumonia-Lungworm Disease - which culminated the physiological stress initiated by malnutrition and which caused a 75 percent plus decline in sheep numbers.
3. Range Condition and Trend - the primary extrinsic factor. It takes about one decade of overgrazing 50 percent plus) to weaken the animals to a level of advanced malnutriiton (high endoparasite loads, high winter weight loss, high lamb mortality), and to seriously deplete the forage resource. At this stage, pneumonia-lungworm lesions become prevalent in the lungs and the stage is set for a major die-off, once these conditions are combined with abnormally severe winter weather conditions. Such a combination produces the lethal "pneumonia-lungworm" disease.
4. Winter Weather - which combines with poor range and malnutrition to produce the "pneumonia-lungworm" disease which causes the major die-off. Occasionally catastrophic winters such as 1886-88, 1906-07 and 1947-49 act in a density independent manner causing major die-offs regardless of range conditions.

The major extrinsic factors limiting numbers of elk and mule deer were:

1. Range Condition and Trend - which acted in a density-dependent manner to increase juvenile mortality thus reducing population growth. However, range did not provide a sufficient influence on elk and deer numbers to prevent them from exceeding range carrying capacities and inducing a downward trend in the range.
2. Weather - elk and mule deer appear less hardy than bighorn sheep. Severe winters depress populations giving short-term relief to overgrazed ranges with greater mortality evident on overgrazed than on healthy ranges. Occasional catastrophic winters occurred about once every 50 years and temporarily annihilated elk and deer from extensive areas.

The national park ungulates, in particular elk, deer and bighorn sheep, are evidently not self-regulated. They increase in number until severe range deterioration occurs which induces a lethal pneumonia-lungworm disease in bighorn sheep but not in elk or deer. For this reason, elk and deer have the ability to maintain high numbers in the face of deteriorating range conditions at the expense of bighorn sheep. The only natural limiting factor which may occasionally cause greater mortalities in elk and deer than in bighorn sheep is severe winter weather. Because severe winters occur more or less randomly, they cannot be counted on to suppress elk and deer numbers before both the winter ranges and the sheep populations have been seriously depleted.

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