Range Ecology of Bighorn Sheep in Relation to Self-Regulation Theories

A paper presented at the
Range Management Convention in Tucson, Arizona,
February 3-8, 1974

by

John G. Stelfox
(Research Scientist)
Canadian Wildlife Service

February 15, 1974

INTRODUCTION

The Rocky Mountain bighorn sheep (Ovis c. canadensis) occurs in Jasper, Banff, Waterton Lakes and Kootenay National Parks* in southwestern Alberta and southeastern British Columbia (Figure 1). These parks comprise 7,511 square miles and have existed at their present size since just prior to 1915. Since their establishment, bighorn 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 two-year period, with the majority dying within six months.

In two of these parks, namely Jasper and Kootenay, numbers increased following the die-offs to return to previous peak populations within 20 to 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.

The die-offs have been attributed to pneumonia-lungworm disease, deteriorated ranges, and inclement winter weather. Govenment officials and the general public have been concerned about the effects of these die-offs on the long-term welfare of bighorn sheep. Since 1940 there has also been concern over the effects which increasing numbers of elk and, forest encroachment on grassland sheep pastures,

* Hereafter referred to as Jasper, Banff, Waterton and Kootenay.

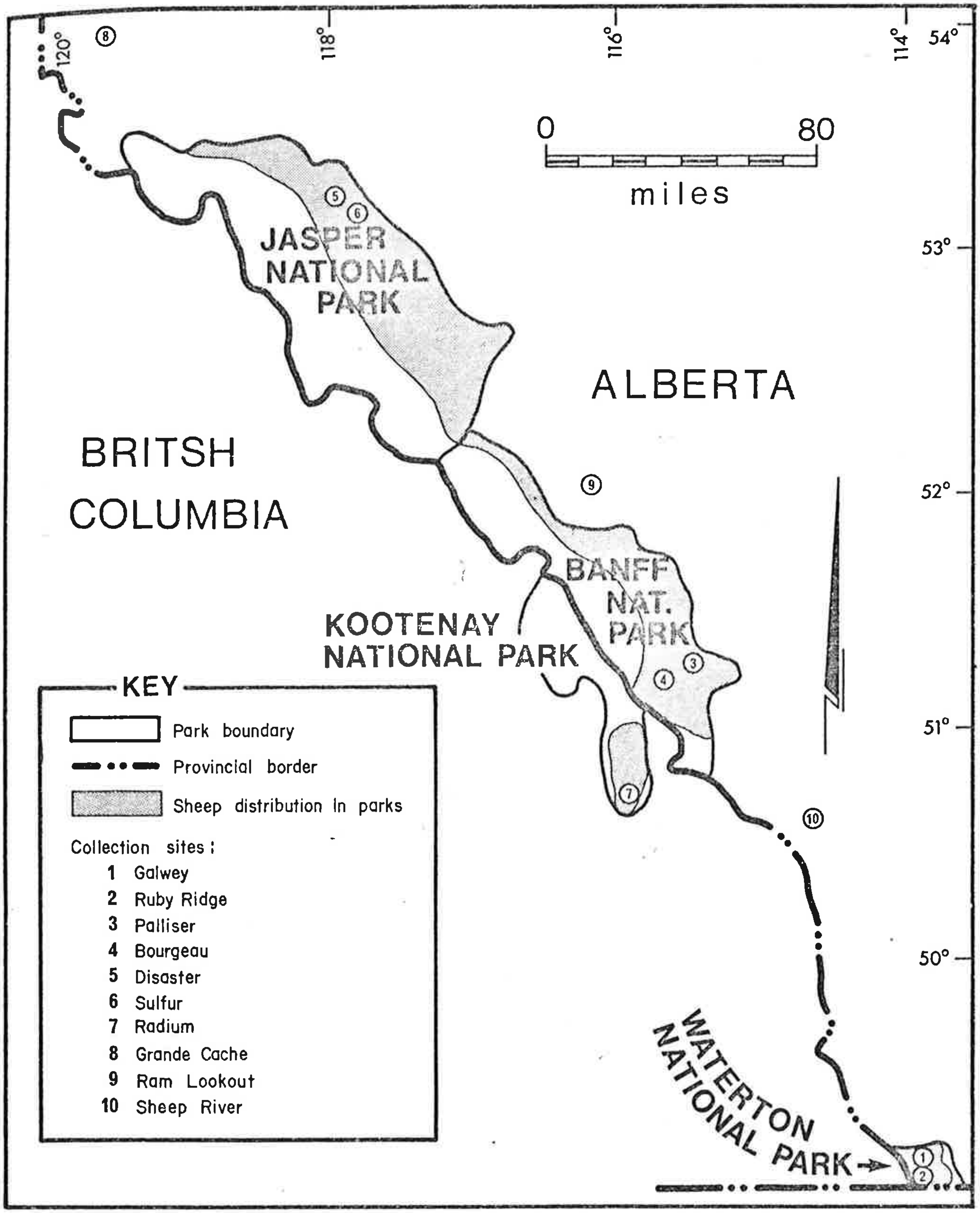

Figure I. Locations of Jasper, Banff, Waterton, and Kootenay National Parks, bighorn sheep distributions and locations where samples collected.

will have on future sheep populations.

Considerable factual evidence has been accumulated on native and domestic ungulate population trends, on range condition and trend, on ungulate diseases and parasites, and on climatic trends since about 1920, and to a limited extent as far back as 1800. However, the role and interrelationship of each factor has not been clearly understood.

In the fall of 1966, a major die-off began in the Kootenay sheep herd. The Canadian Wildlife Service began a study to determine the extent and cause of the die-off and of the prospects of similar declines in the other three parks. This study lasted seven years and involved myself, our Wildlife Pathology section, three other federal, provincial and university pathology-parasitology laboratories, and the Resource Conservation staff of the National Parks. Major emphasis was placed on range ecology, population dynamics, disease-parasitism, and interspecific competition.

OBJECTIVES

The objectives were three-fold, namely:

1. to determine the causes of population fluctuations, in particular die-offs in bighorn sheep.

2. to determine the effect and interrelationship of various intrinsic and extrinsic factors in limiting sheep numbers. The intrinsic factors included disease-parasitism, animal condition, reproduction and recruitment. Extrinsic factors included range condition and trend, weather (in particular winter weather), interspecific competition by native

ungulates (in particular elk) and by domestic ungulates (in particular horses), and predation.

3. to determine if any population-regulation 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 bighorn sheep populations 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. The Canadian National Park Act and Wildlife Managment Regulations promote the "laissez-faire" philosophy of leaving ecosystems alone so that natural checks and balances can maintain pristine or near-pristine conditions. Provisions for wildlife management do exist however, in the event that a species is altering a community so as to endanger the long-term well-being of important faunal or floral species. Herd control programs have been in effect since 1942 to reduce elk populations which were apparently overgrazing grasslands and overbrowsing poplar and willow ranges to an unacceptable level of deterioration and where populations of other ungulates, notably bighorn sheep, were adversely affected. As wildlife management in the form of population regulation is distasteful in Canadian National Parks, natural population regulation would be preferred.

A recent philosophy believes 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 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 ungulates and their ranges. Considering this new philosophy, it was decided to examine both short and long-term changes in grassland ungulate populations and their ranges as correlated with changes in weather, disease-parasitism, in interspecific competition, predation, and man-made influences. It was hoped that results would provide National Park administrators with basic ecological facts to serve as guidelines in the consideration of ungulate management objectives, and also to provide some sound biological facts concerning population regulation in native ungulate populations.

LITERATURE REVIEW

Malthus (1960) in his essay of 1824 said, after studying human population trends in England, that populations tend to grow in a geometric progression at a rate that would double the numbers every twenty-five 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, war etc.

Darwin and Wallace modified the Malthusian principle to include predation as a limiting factor (Eiseley 1961). Darwin stated that four limiting factors prevented animals from increasing at their biological capacity. These factors were:

1. the amount of available food, which must give the extreme limit to which the species can increase.
2. the effects of predation by other animals.
3. the effects of physical factors such as climate.
4. the inroads of disease.

From 1920 to the early 1940's several ecologists such as Chapman (1928), Andrewartha and Birch (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). However, some ecologists expressed disagreement with this recent philosophy (Elton 1942, Clarke 1949). 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. Many theories have been advanced explaining population growth and decline in terms of biological mechanisms intrinsic in the populations in addition to the action of external factors (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.

In the mid 1950's although most wildlife ecologists agreed that food, climate, and disease could cause population change, they also realized that populations could be coincident with social disturbances rather than with environmental changes. An effort was made to integrate social actions and habitat factors into a scheme to explain population changes. A theory originated which states that, within broad limits set by the environment, density-dependent mechanisms have evolved within the animals themselves to regulate population growth and curtail it short of the point of destruction of the environment (Nicholson 1958, Wynne-Edwards 1956, Chitty 1960, Milne 1962, Christian 1963). Working within this broad concept, several ecologists ascribed much of population regulation to a "feed-back" control, working through the endocrine system, which functions as a behavioral-physiological mechanism (Christian and Davis 1964). As population density increased, reproductive function was inhibited by stimulation of the pituitary-adrenocortical activity. This increased activity increased mortality indirectly by lowering resistence to disease, parasitism, environmental stress, or more directly through "shock disease". Christian and Davis (1964) in an article entitled "Endocrines, Behavior and Population" summarized this philosophy by stating (pp 10 and 11): "......there are mechanisms for the regulation of mammals within the limits imposed by the environment; including food ...... density dependent mechanisms which have evolved in many forms, and probably in most mammals. Thus mammals avoid the hazard of destroying their environment, and thus the hazard of their own extinction. We believe that the evidence, as summarized here, supports the existence of endocrine feedback mechanisms which can regulate and limit population growth in response to increases in overall "social pressure" and which in turn are a function of increased numbers and aggressive behavior. Neither increased numbers nor increased aggressiveness can operate wholly independently. Furthermore, we believe that environmental factors in most instances probably act through these mechanisms by increasing competition... increased strife, with increased movement, will also increase losses through predation, another way of increasing mortality of subordinate animals."

Ardrey (1961, 1966) described the various social-behavioral characteristics of primates and showed that they do regulate their numbers, through self-regulating mechanisms, without damaging their food supply from a long-term standpoint.

Several workers have shown that large North American carnivores such as wolves and cougars have self-regulating density-dependent mechanisms which limit their numbers before they deplete their food supply (Cowan 1947, Mech 1970, Hornocker 1970).

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 has been reported that an elk (Cervus canadensis) population of about 1,000 animals in the Madison, Firehole, and Gibbon areas of Yellowstone Park were self regulated by density-influenced mortality from intraspecific competition for food, and by compensating natality (Cole 1969). The principal mortality factors were rigorous winters and limitations to food supplies, with a complimentary action of predators, parasites and disease. Similarly, moose (Alces alces) in Grand Teton National Park, bison (Bison bison) along the Pelican Valley of Yellowstone Park, and elk and mule deer (Odocoileus hemionus) in the Middle Fork of the Flathead River drainage in Glacier National Park have shown population stability resulting primarily from heavy winter mortality and low recruitment rates plus immigration of subadults (Houston 1968, 1971, Martinka 1969). The conclusions drawn from these cases of ungulate population stability in Yellowstone, Grand Teton and Glacier National Parks are that: "Realized annual recruitment to the population is low. Range conditions fluctuate, and some areas appear to be periodically "overgrazed", in terms of the usual criteria. 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." Klein (1970) summarized the case of self-regulation in North American "deer" as follows: "In the case of ungulates there appears to be a relationship between the self-regulatory ability of their populations and the stability of the environments within which they have evolved. North American deer that are of a transitory nature, appear not to have well developed self-regulatory mechanisms and are normally characterized by wide population fluctuations."

In opposition to the views that self-regulation plays a vital role in regulating ungulates, there is an abundance of literature illustrating that non-territorial 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. The consequences of food shortage are - increased mortality and decreased natality due to inadequate nutrition and high population stress. Examples illustrating the lack of self-regulating mechanisms are:

1. Klein (1970), concerning North American deer.
2. Cowan (1950) and Flook (1964), concerning elk, moose, deer and bighorn sheep in the Canadian National Parks.
3. Riney (1964), concerning the introduction of large

herbivores on tropical environments.

4. Rasmussen (1941), concerning deer on the Kaibab Plateau.
5. Pengelly (1963), concerning elk throughout western United States.
6. Cauley (1970), concerning the Himalayan thar in New Zealand.
7. Eddleman and McLean (1969), concerning livestock and wild ungulates in Montana and British Columbia.
8. Morris (1956), concerning elk and livestock.
9. Moss and Watson (1970), concerning domestic sheep in the British Isles.
10. Lowdermilk (1953), concerning the effects of livestock grazing throughout Asia.
11. Cottam (1961), concerning the devastation of native ranges by cattle and domestic sheep in Utah.

METHODS

Helicopter and ground census techniques were used to obtain information on:

1. Population densities, park populations, seasonal distributions and conditions, plus interspecific competition.
2. Reproductive and recruitment rates, and
3. Seasonal Habitat preferences.

Range condition and trend data were obtained from six winter grassland ranges, two in each of three parks. These winter ranges consisted of three low-elevation grasslands of the "steppe formation" class located at the 3,100 to 4,500 foot elevation, and three high-elevation ranges of the "shrub" or "short grass savanna" formations at the 5,500 to 6,500 foot elevation (Fosberg 1967). On each range, ten 100-foot linear transects provided 2,000 vegetative points for plant composition, frequency and forage preference information. They also served as the center of a belt-transect 99 ft. x 6.6 ft., used to count ungulate fecal groups to obtain range-use results. Forage production and utilization information was obtained from twenty pairs of exclosure cones (9.6 sq. ft.) for each of three years. Range site potential and forage production relative to potential was obtained from 9.6 sq. ft. clip plots and linear transects within and adjacent to a 45 ft. x 45 ft. exclosure fence.

The effects of summer climate on forage production was obtained from soil and ambient temperature and moisture measurements at 20 sites on each range for a three-year period.

The effects of winter climate (snow, temperature, wind and barometric pressure) on ungulate range use was obtained from one weather station and 20 snow stations on each range for three winters.

Ungulate use and interspecific competition on each range on a monthly basis was obtained from aerial and ground observations.

Disease-parasite information on bighorn sheep was obtained from 73 complete or partial cadavers and 139 fecal samples.

A literature search was conducted of published and unpublished reports, journals and stories to obtain information on historic trends in the abundance and distribution of bighorn sheep and other competitive species.

RESULTS

A. Population Trends in Bighorn Sheep 1800 to 1973

1. 1800 to 1966--

During pristine times, bighorn sheep populations fluctuated sporadically due to severe winters, disease, and changes in the condition of their ranges resulting from weather, fire, and interspecific competition. Between 1860 and 1910, their numbers were depleted to one-fourth of their former level by year-long hunting from an influx of miners, loggers, traders, railroad workers, settlers and resident Indians (Stelfox 1971).

Between 1910 and 1915, 7,511 square miles of sheep country were established as National Parks. This action in addition to increased acreages of grasslands resulting from extensive wildfires during the late 1800's and early 1900's, plus improved range conditions due to low sheep and elk numbers, resulted in a tripling of sheep numbers by 1936.

Between 1936 and 1950, a series of die-offs in all four parks, and adjacent provincial lands, reduced park numbers from 4,500 to 1,000. The die-offs resulted from poor range conditions as a result of overstocking by bighorns and elk during the late 1930's and early 1940's (Clarke 1941, Green 1949, Cowan 1950).

In Waterton's 204 square mile area there were approximately 1,000 bighorn sheep, 1,500 mule deer and elk, plus 2,211 livestock, or almost 5,000 ungulates wintering on some 50 square miles of winter range (100 per square mile) during the winter of 1936-37. In the spring of 1937, a major die-off occurred in sheep herds both within this park and in the neighboring Glacier Park of Montana. The die-off was due to a verminous broncho-pneumonia caused by the lungworm (Protostrongylus stilesi) and undoubtedly from depleted forage reserves.

In Banff (2,564 square miles), sheep numbers declined from 2,000 to less than 500 between 1941 and 1950. In 1943, when the elk population in Banff was estimated at 3,500 to 4,000, Green (1949:33) stated: "The elk pressure on all ranges, especially those of limited extent, has had the effect of confining sheep to range edges where forage is inferior, or driving them to less favorable localities nearby where elk do not occur." The unfavorable range - ungulate situation in the parks in the 1940's was aptly described by Cowan (1950:587) 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 from a declining food supply on the winter ranges." Cowan (1947a), Pfeiffer (1948), and Flook (1964) all reported that along the

Athabasca Valley in Jasper, ranges were in an acutely overbrowsed and/or overgrazed condition, with elk in serious competition with both sheep and mule deer. Elk numbers peaked in the early 1940's in Banff and Jasper at which time they adversely affected bighorn sheep by depleting south-facing grassy slopes that were critical bighorn ranges.

When the Jasper sheep population declined 85 percent from 1946 to 1950, winter ranges were in poor condition. Three successively severe winters also contributed to the decline of sheep, elk, deer and moose. Wolves which were abundant in the 1940's were ineffective in controlling the excessive ungulate populations. The winter ranges contained one wolf per 10 square miles compared to 30 to 40 wild ungulates per square mile, or 300-400 ungulates per wolf (Cowan 1947b). Sheep populations suffered the heaviest losses from 1946 to 1950 presumably because of their vulnerability to the pneumonia-lungworm disease which was evidently present during the die-off. Although elk losses were significant, their decline was less evident and 697 were slaughtered from 1946 to 1949 in an attempt to reduce grazing pressure and competition with bighorn sheep. Pneumonia-lungworm disease and severe winter weather were therefore responsible for the four major die-offs in the parks from 1936 to 1950. The proximate factor however, was undoubtedly malnutrition resulting from depleted winter ranges caused by excessive ungulate populations. Physiological stress caused from malnutrition would make the sheep vulnerable to the effects of disease-parasitism and inclement weather.

From 1950 to 1966, sheep numbers in the parks increased from 1,000 to 4,425. This increase was attributed to improved range conditions due to light stocking rates of bighorns, elk and livestock following the previous die-offs, to annual elk reduction programs, to predator-control programs in the 1950's, and to near-normal winters (Stelfox 1971).

2. 1966 to 1973--

From September 1966 to the spring of 1968 in Kootenay, the sheep population declined 75 percent due to deteriorated winter range conditions, excessive ungulate populations, a pneumonia-lungworm disease, and possibly the after-effects of the severe winter of 1964-65, which presumably initiated the disease (Demarchi 1967, Bandy 1968, Stelfox 1971). In the spring of 1967, during the die-off, the weight of adult ewes was 19 percent below the average for the other three parks and 21 percent below the average ewe weight in Kootenay five years later. By 1970 animal condition had improved from poor - fair up to good.

In the other parks, populations continued to increase slightly from 1966 to 1973. The increase was slow with some evidence of stability due to two severe winters of 1968-69 and 1970-71. The 1973 sheep population was approximately 4,300, comprised of 2,500 in Jasper, 1,300 in Banff, 425 in Waterton and 75 in Kootenay. Animal condition from 1966 to 1973 varied from fair in Jasper to good in Banff and Waterton.

Overwinter weight losses of ewes averaged 20% in Jasper, 11% in Banff, and 13% in Waterton. Native ungulate densities were very high in Jasper where range conditions were the poorest. Along the Athabasca Valley in Jasper there were an estimated 820 bighorns, 600 elk and 200 mule deer wintering on 20 square miles (81 per square mile). In Waterton there were 350 bighorns, 264 elk, 235 mule deer and 14 mountain goats observed wintering on 23 square miles (37.5 per square mile) during an aerial survey in February 1967. The actual density must have been considerably higher because many animals in forested and semi-forested areas were undoubtedly missed (Stelfox 1971).

B. Range Condition and Trend (1966 to 1973)

Table 1 and Figure 2 compare forage production and utilization, with range stocking rates, endoparasite burdens, bighorn sheep spring weights and overwinter weight losses among the parks of Jasper, Banff and Waterton. Table 1 shows that for each animal days-use/acre there were 10.1 and 4.1 times as much forage available in Waterton and Banff respectively as there was in Jasper. The relatively unfavorable forage: ungulate ratio in Jasper is further demonstrated by forage utilization values of 64% in Jasper compared to 46% in Banff and 34% in Waterton. A strong correlation between forage: ungulate ratios and overwinter weight losses of sheep is revealed in Table 1 and Figure 2. There is also a strong correlation between forage production - utilization, and endoparasite burdens. Thus a low ratio of forage production: forage utilization is directly correlated with a high overwinter weight loss in sheep, a high endoparasite load, and a reduced recruitment rate (yearlings: 100 ewes). There was no significant correlation between a low forage production: forage utilization ratio and animal productivity (lambs: 100 ewes), indicating that sheep do not respond to decreasing range conditions by limiting their numbers through reduced lamb crops.

The poor range conditions in Jasper compared to Banff and Waterton is also shown in the higher percent of bare soil, the lower amount of both vegetative and litter cover and the higher percentage of shrubs in Jasper vegetation. Jasper ranges averaged 21.3% bare soil, 36.6% basal and 39.1% foliage vegetative coverage, 13% litter cover and 43.2% of the vegetation were shrubs. Comparable values for the Waterton ranges were 7.0% bare soil, 43.8% basal and 140.3% foliage vegetative coverage, 45.3% litter cover and 24.6% shrubs. There was also a strong positive correlation between the degree of forage utilization and the percent of shrubby cinquefoil as shown in Figures 3 and 4. It appears from Figure 2 and Table 1 that 50% forage utilization is a good "cut-off" level in determining whether the range is overgrazed. The two ranges in Jasper plus Bourgeau in Banff received utilization in excess of 50 percent. They had the lowest forage production and the highest endoparasite loads and incidence of disease of the six ranges. Similarly, the

Table 1. A comparison of forage production and utilization, range stocking rates, endoparasite burdens and overwinter sheep weight losses (1967-71).

Subject		WATERTON Galwey	Ruby	Average	BANFF Palliser	Bourgeau	Average	JASPER Sulfur	Disaster	Average
Forage Production (lbs./Acre Dry Wt.)		756	345	550	551	294	422	244	155	200
Forage Utilization (%)		43.6	24.9	34.5	29.7	52.4	46.0	66.6	61.4	64.0
Ungulate Days-Use Per Acre	Sheep	23.6	20.3	21.9	48.7	58.1	53.4	167.9	101.9	134.9
	Total	52.6	24.7	38.6	76.0	67.0	71.5	168.1	108.2	138.1
Forage Production ÷ Days-Use (1968-71)		14.4	14.0	14.2	7.2	4.4	5.8	1.5	1.4	1.4
Ewe Weights (lbs.) in Spring		--	--	144	--	--	141	--	--	135
Winter Weight Loss (%)		--	--	13.2	--	--	10.8	--	--	20.1
G.I. Endoparasite Burdens (excluding lambs)		--	--	1214	--	--	1241	--	--	1391
Lungworms/Gm. of Feces 1967-69		--	--	594	--	--	626	--	--	2375

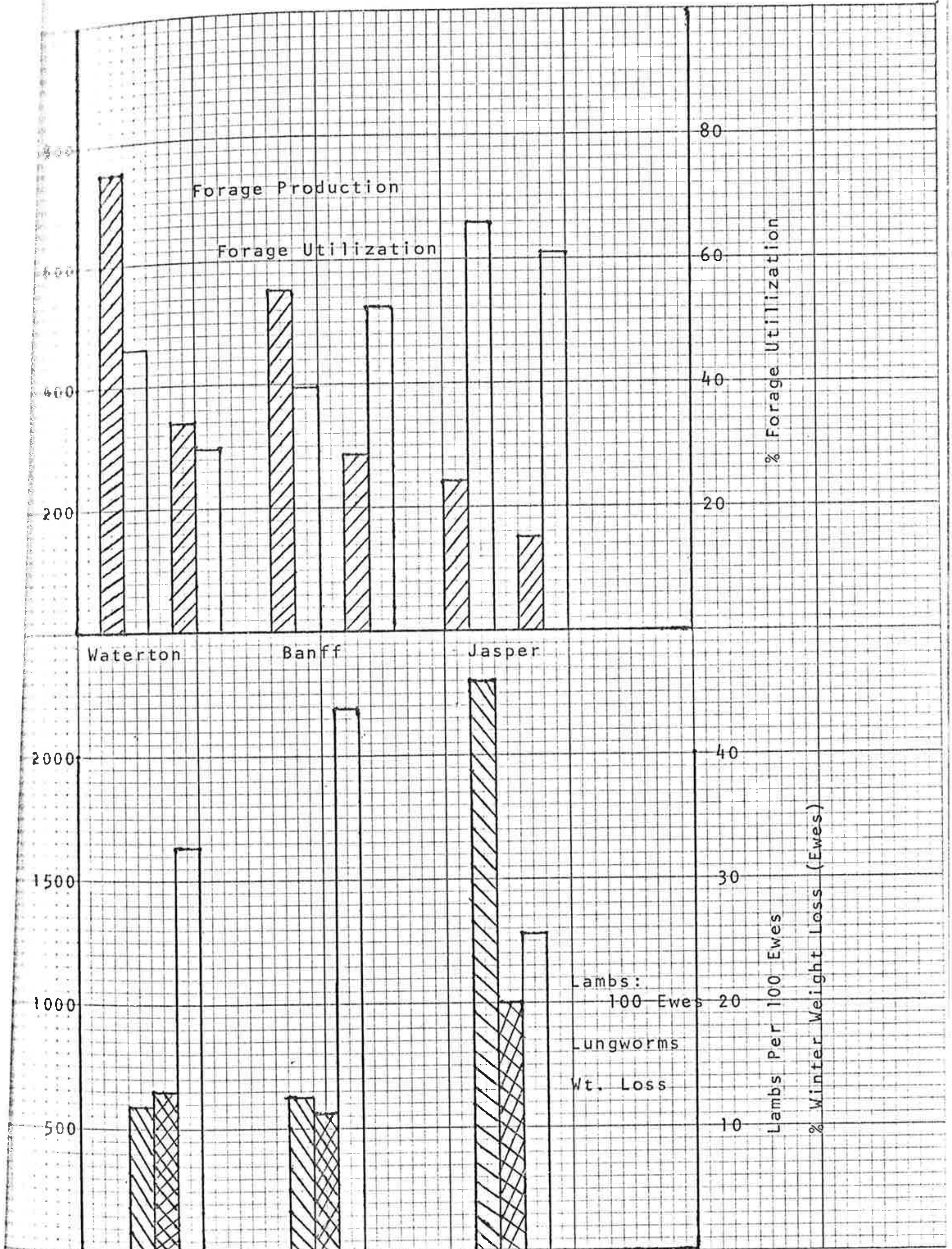

Figure 2. Correlations among forage production, forage utilization, winter weight loss, lungworm burden, and lambs: 100 ewes on bighorn sheep ranges 1967-71.

abundance of shrubby species, in particular shrubby cinquefoil, was much higher on ranges receiving over 50% forage utilization. Results indicate that shrubby cinquefoil can be used as an index to range condition and trend on sheep ranges in these parks. However, it will first be necessary to determine "normal" plant composition values under various grazing intensities for each major grassland community in each park. Present indications are that grasslands containing over 5%, and especially those with over 10%, foliage cover are being overgrazed.

There was also a similar but lower positive correlation between increasing forage utilization and increasing coverage of junegrass (*Koeleria cristata*). This species also increases under heavy range utilization and increased stocking rates.

Rough fescue (*Festuca scabrella*) only occurred on the three ranges receiving less than 50% forage utilization and which produced more than 340 lbs./acre of dry weight forage.

The heavily grazed Jasper ranges contained an average of 33 plant species (19 and 47) compared to 66 plant species (60 and 72) on the two moderately grazed Waterton ranges.

An indication of the degree to which forage production potentials were lowered by overgrazing is revealed in Table 2 and Figure 5 which compare production within and adjacent to the large exclosures after 2 and 5 years of protection from grazing. On the heavily grazed Jasper ranges (64.0% utilization), forage production was 168% and 104% higher within the exclosures 2 and 5 years after protection from grazing than on adjacent grazed ranges that were only protected for the growing season in question. On the moderately grazed Waterton ranges (34.5% utilization), forage production was only 80% and 5.8% higher within the exclosures 2 and 5 years after protection compared to adjacent grazed ranges. Of interest is the fact that five years after protection from grazing, the moderately grazed and productive range at Galwey, Waterton park actually produced slightly less (0.4%) forage within the exclosure compared to the adjacent grazed range. This indicates that moderate grazing of productive ranges is beneficial in removing enough of the forage to prevent plants from being smothered by a heavy mantle of dead vegetation. Idaho fescue (Festuca idahoensis) especially seemed to be dying out under the heavy mantle of dead vegetation within the Galwey exclosure. Similar results were determined by Flook and Stringer (1974) on a productive (1,381 lbs./acre dry-wt.) low elevation grassland in Banff that was protected from grazing for 24 years. Forage production was 9.6% greater on the grazed range than within the exclosure.

Another benefit of moderate grazing is that it increases soil organic matter. Soils within the five exclosures averaged 12.6% organic matter compared to 14.5% for adjacent grazed soils.

The above results indicate that bighorn sheep and other grazing ungulates did not self-regulate their numbers in Jasper to a level optimum for range health and productivity. Their numbers increased to the level where forage production was reduced to less than one-half of its potential. This degree of range deterioration is not in the best long-term interests of either the range or its' grazing herbivores. If an effective density-dependent self-regulating mechanism was in operation, it should have limited animal numbers at a lower level when range conditions were better.

The long-term effect of periods of overgrazing followed by ungulate die-offs, on range productivity was determined on four sheep ranges along the Athabasca Valley that were studied in 1946 and again in 1970, 24 years later. In 1946, the ranges were severely overgrazed and in poor condition. A major die-off began the following winter which resulted in an 85% decline in bighorn sheep numbers. When the ranges were studied in 1970 the park population of sheep was similar to that in 1944 (Cowan 1945 and Stelfox 1971) namely 2,500 to 3,000. The die-off from 1947 to 1949 resulted from deteriorated winter ranges, pneumonia-lungworm disease and severe winter weather. As mentioned earlier, elk numbers declined during the same period although the reduction was relatively minor, and they did not suffer from disease. The slaughter of 697 elk along the Athabasca Valley during the period 1946 to 1949 was required to reduce grazing pressure and competition with bighorn sheep on the severely overgrazed ranges.

Figure 6 compares forage production, percentage vegetative cover, and ungulate range use in 1970 compared to 1946. It indicates that range conditions were just as good, in fact somewhat better, in 1970 than in 1946. Forage production was actually 3.6% higher and the amount of bare soil

7.3% less in 1970 than in 1946. The abundance of ungulates on the ranges as reflected in the number of fecal groups per acre was slightly higher in 1970 compared to 1946. However, from an "animal-unit" basis the numbers were slightly less in 1970 because horse grazing had been eliminated in the 1950's and 1960's and because elk numbers were slightly less. However, bighorn sheep and mule deer numbers were 56% higher in 1970. The elk winter diet along this valley consists of 93% grasses, 6% Douglas fir and 1% bearberry, as opposed to 83% grasses, 10% forbs and 7% shrubs in the winter sheep diet (Cowan 1947a). The winter horse diet was probably almost exclusively grasses. These results show that the range trend did not continue downward between 1946 and 1970; in fact, the trend has been slightly upward. The big question yet unanswered is how far was the range condition reduced between the time the park was established in 1914, when elk numbers in Jasper were nil and sheep numbered not more than 450 (Millar 1915), and 1946 when elk numbered 4,000 and sheep 2,500 to 3,000. All we know for sure is that the range condition was poor and overgrazing severe prior to the 1947-49 die-off and that the condition in 1970 was still poor but slightly better. The results show that the bighorn sheep, elk and mule deer increased between 1914 and 1946 until their grazing pressure depleted the food supply to the point where the sheep died as a result of a pneumonia-lungworm disease plus the effects of three inclement winters. Elk and deer "winter-killed" to some extent from 1946 to 1949, but the basic cause of the decline of all three species was malnutrition due to overgrazed ranges and excessive numbers of animals. There was no evidence that any of the three species were employing a self-regulating mechanism to limit their numbers before their food supply was depleted. In fact they continued to increase and eat-out their food resource until starvation, assisted by inclement weather and disease, limited their numbers. The range evidently recuperated to some extent from 1950 to 1960 when ungulate numbers were reduced. However, their numbers once more increased to a level where the range was in a poor condition in 1970 and forage production was less than one-half the potential for the range. Again there was no indication that the ungulate species were exhibiting any significant self-regulatory mechanism to restrict numbers within the bounds of the range carrying capacities.

A final assessment of the self-regulating capabilities of bighorn sheep comes from an evaluation of reproduction and recruitment rates for the four parks. Table 3 presents the results obtained during the period 1966 to 1971.

This table shows that reproductive rates did not decline significantly in Jasper sheep herds where the range was in an unproductive state and stocking rates excessive. There were 35.7 lambs: 100 ewes compared to 32.8 lambs: 100 ewes in Waterton where the range was productive and only moderately overstocked. This indicates that the Jasper ewes did not exhibit any tendency to stabilize populations by reducing lamb production. Similarly, the Kootenay herd did not reduce reproductive rates in the face of serious range deterioration, excessive ungulate numbers and high endoparasite loads.

Table 3. Reproduction and recruitment rates of bighorn sheep in the four national parks, 1966 to 1971.

Park	Sample Size	LAMBS (1/2 Yr.) Per 100 Ewes	% of Population	YEARLINGS (1.5 Yrs.) Per 100 Ewes	% of Population	LAMB MORTALITY 0.5 1.5 Yrs.(%)
Jasper	4061	35.7	18.9	16.8	8.9	52.9
Banff	1884	44.1	16.1	21.5	7.9	51.2
Waterton	1285	32.8	14.0	21.0	8.9	36.0
Kootenay	1016	37.7	19.8	12.4	6.5	67.1
Averages	--	36.9	17.3	18.4	8.6	50.0

However, an examination of recruitment rates indicates a significant increase in lamb mortality on the overstocked and depleted ranges namely Jasper and Kootenay. The percent of yearlings: 100 ewes was 16.8 and 12.4 respectively, compared to 21.0 and 21.5 for Waterton and Banff. Lamb mortality, from the 0.5 yr. to the 1.5 yr. age classes, averaged 60.0% for Jasper and Kootenay, compared to 43.6% for Waterton and Banff. Lamb mortality was therefore 37.6% higher on overstocked, unproductive ranges than on productive, moderately stocked ranges.

DISEASE - PARASITISM

Endoparasite burdens were significantly higher in bighorns on depleted ranges as revealed by Table 1. Gastro-intestinal helminths per animal (excluding lambs) plus lungworm larvae/gm feces averaged 1,391 and 2,375 for Jasper, compared to 1,241 and 626 for Banff, and 1,214 and 594 for Waterton. Thus, endoparasite loads averaged 108% higher in Jasper sheep than in Waterton sheep.

Table 4 correlates endoparasite loads with range productivity, stocking rates, animal spring weights, and winter weight losses. The table clearly shows that as range productivity declines and stocking rates increase, that endoparasite loads rise with a corresponding decline in ewe spring weights and an increase in % winter weight losses. Animals below normal weight (15% below normal weight for that season) contained an average of 2,045 helminths compared to 885 for animals of normal weight.

Endoparasite loads and disease infection are controlled by a complex of intrinsic and extrinsic factors such as immunilogical response, nutrition, psychological stress, and weather. A physiological relaxation of combativeness, which could be caused from malnutrition, may allow endoparasites, bacteria and viruses to increase in number and become prime agents in causing unthriftiness. The result would logically be a major population decline from a pneumonia-lungworm syndrome. The syndrome results from a reduction in host resistance due to adverse ecological conditions principally deteriorated range conditions, excessive ungulate densities, and malnutrition. The increased endoparasite loads and lungworm lesions make the weakened animals susceptible to the invasion of pneumonia bacteria, especially in the presence of severe winter and spring weather. Once the lungs become moderate-heavily infected with pneumonia-lungworm lesions the

Table 4. Correlations among forage production, grazing pressure, endoparasite loads, and animal condition of bighorn sheep in Canadian National Parks, 1966 to 1972.

National Park	lbs. Forage Per Acre	Grazing Pressure Animal Day-Use Per Acre	Endoparasite Loads: Total GI Helminth*	Endoparasite Loads: Lungworms Per Gm Feces	Endoparasite Loads: Lungworms % Heavy Loads	Animal Condition: Ave. Spring Ewe wt.	Animal Condition: % Winter Wt. Loss
	(1967-69)	(1967-69)	(1966-72)	(1967-69)	(1967-69)	(lbs)	(Ewes)
Jasper	133	71	1,201	2,375	48	135	20
Banff	205	75	2,553	626	17	141	11
Waterton	428	29	1,261	594	0	144	13
Kootenay 1965-66	--	--	--	3,580	92	--	--
1966-67	--	--	1,072	700	0	127	--
1972-	--	--	--	144	0	146	--

* Refers to average numbers per cadaver.

animal seems incapable of recovery and a die-off becomes apparent. It is important to realize that this population control mechanism is not initiated by any density-dependent self-regulating mechanism that is triggered as soon as stocking rates exceed range carrying capacities. Rather it is the simple result of malnutrition arising from excessive ungulates on an overstocked and declining food base that weakens the sheep to the extent that juvenile mortality rates increase. Under sufficient duress from adverse weather, endoparasites and disease a major decline is possible and population regulation achieved.

INTERSPECIFIC COMPETITION

The major competitors for bighorn sheep grassland forage in the parks have been elk and horses. The number of horses grazing in Jasper from 1934 to 1947 averaged 305 (Pfeiffer 1948). Most of these horses grazed along 20 square miles of the Athabasca Valley. Horses are the most selective of domestic animals in diet preference. They are primarily grass eaters, utilizing relatively small amounts of forbs and browse (Stoddart and Smith 1955). The years of heavy range use by horses along the Athabasca Valley from 1850 to the 1950's when horse grazing was curtailed, undoubtedly resulted in the initial decline in range condition. By the time elk became abundant in the 1930's, horses had already reduced the range to a poor condition. According to Pfeiffer (1948) "Considering the large numbers of horses present in the Park

[Jasper] and the fact that the horse consumes double the forage of the elk, it is apparent that those horses are maintaining themselves at the expense of the game population. It is also apparent that they have been a decided factor in the past years in hastening range deterioration."

Elk consume 93% grass in their diet compared to 83% grass in the bighorn sheep diet along the Athabasca Valley (Cowan 1944). In the 1940's, elk numbered in excess of 1,000 along the Athabasca Valley. Prior to 1935 their numbers were sparse (Pfeiffer 1948). By 1946 the nutritional condition of elk was poor and calf survival was low. At this time range conditions had become so poor and the numbers of elk, sheep and mule deer so high that the number of elk slaughtered annually was increased. Exclosures on three grasslands along this valley were producing 61% more forage annually, than the adjacent open-range, indicating that grazing by these three native ungulates plus horses was significantly reducing forage production capabilities of the ranges. Pfeiffer (op. cit.) concluded that "The ungulate chiefly responsible for the misuse of the area studied is the elk. This animal has increased greatly in a very short time on ranges that had been previously over-grazed as horse range." His results, plus those of Cowan (op. cit.) indicate that neither elk nor mule deer were exhibiting any sign of self-regulating their numbers on this denuded range. Their numbers continued to increase in a direct but inverse relation to a decline in range condition until malnutrition plus inclement winter ather caused a decline in their number from 1946 to 1949. ese two species lack the physiological control mechanism of isease which is effective in controlling sheep numbers, once anges are severely depleted. Elk in particular are not rone to lethal diseases and seem capable of maintaining their umbers at levels excessive to range carrying capacities. nless controlled by artificial means their numbers may stabilize or even decline somewhat in response to declining range condition, but they remain at levels which cause a continuing decline in range productivity and condition.

PREDATION

Wolves which were abundant in Jasper during the 1940's and early 1950's were ineffective in preventing wild ungulate numbers from increasing to the detriment of their range (Cowan 1947b).

SELF REGULATION

The study of range conditions, disease-parasitism and population dynamics of ungulates on bighorn sheep ranges in Jasper, Banff, Waterton and Kootenay from 1966 to 1972 in addition to the results from previous studies indicate the lack of an effective density-dependent, self-regulating mechanism in either bighorn sheep or elk. Five major population die-offs of sheep, plus population trends of sheep, elk and horses were reviewed and the evidence in all instances was similar. Bighorn sheep populations tend to increase in number until the condition of their winter ranges declines from overstocking. As the proportion of forage per sheep declines, endoparasite loads and juvenile mortality increases, while animal condition decreases. However, the ewes continue to produce lambs at a normal rate so that the population continues to increase, but at a decreasing rate. Increased parasitism is accompanied by increases in the incidence of lungworms which weaken the lungs and permit the invasion of pneumonia bacteria. As physiological stress increases under more pronounced malnutrition and increased parasite burdens the sheep becomes more susceptible to both the intrinsic pressure of disease-parasitism, plus the extrinsic pressure of weather. Severe winter and/or spring weather is then capable of initiating a pneumonia-lungworm syndrome which effects a major die-off, thus releasing the heavy grazing burden from the range.

Elk follow a similar pattern except that they are relatively intolerant to diseases or parasites which could cause a major die-off. Reproductive rates are evidently not significantly reduced as their forage supply diminshes and although their numbers may decline slightly or stabilize in the face of decreasing range conditions they remain high enough to maintain the range in poor condition or initiate a continued downward trend.

Certainly, bighorn sheep and elk do not exhibit any of the self-regulating mechanisms reported by Ardrey for primates (Ardrey 1961, 1966) or for certain carnivore species (Mech 1970, Hornocker 1970, Wynne-Edwards 1970). Sheep and elk

...dently do not exhibit self-regulation in the manner ...scribed by Wynne-Edwards (1970) for beaver. He contends ...at beavers restrict themselves in such a way as to "...use ...ly the annual income from their food resources and to not ...ig into the capital which is available and free for the ...aking."

My findings are more closely allied to those of Chitty (1964) as he does not imply thtt behavioural-genotypic ...haracteristics will prevent populations from increasing to ...he level where their food supply is damaged or an animal ...ie-off created. However, his suggestion that genetic change ...akes place rapidly enough to produce a different genotype ...uring a population ebb from that present during a population ...eak does not seem feasible for bighorn sheep or elk. As the ...ongevity of bighorn sheep can be 20 years and the period ...etween population cycles as short as 20 to 25 years (Stelfox ...971), some sheep will survive all, or most, of the population ...ycle. There is just not enough time for a major genotypic ...hange between the population peak and the following population ...bb which normally follows the peak by two to five years.

SUMMARY AND CONCLUSIONS

A six-year study of bighorn sheep range ecology, ...opulation dynamics and disease was conducted in the Canadian ...ational Parks of Jasper, Banff, Waterton Lakes, and Kootenay. ...he objectives were:

1. to determine the causes of population fluctuations, in particular die-offs in bighorn sheep.

2. to determine the interrelationships of various intrinsic and extrinsic factors in limiting sheep numbers. The intrinsic factors included disease-parasitism, animal condition, reproduction and recruitment. Extrinsic factors included range condition and trend, weather (in particular winter weather), interspecific competition by native ungulates (in particular elk) and by domestic ungulates (in particular horses) and predation.
3. to determine if any population-regulation 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 bighorn sheep populations and their ranges. Of particular interest was the possible existence of self-regulating mechanisms which could limit native ungulate populations before range condition and productivity were impaired.

Bighorn sheep populations fluctuated sporadically during pristine times apparently as a result of severe winters, disease, and changes in range condition due to weather, fire, and interspecific competition. Their numbers were depleted between 1850 and 1910 by heavy indiscriminate hunting. The parks have existed at their present size of 7,511 square miles since 1915 and sheep have been protected from hunting. Numbers increased under this protection until 1937 when prolonged heavy range use by livestock and native ungulates in Waterton resulted in a major decline of bighorn sheep in the spring of 1937. Although the animals died of a "broncho-pneumonia" disease the underlying cause was evidently malnutrition due to an exhausted forage supply. The next die-off which occurred in Kootenay reduced the sheep population 85 percent in the fall and winter of 1940-41. The sheep died of a verminous pneumonia disease but the underlying cause was overgrazing of the winter range, interspecific competition, and the contraction of critical grasslands by forest succession. The third die-off occurred in Banff in 1941-42 with the population continuing to decline until 1950. Numbers declined from at least 1,100 to 350. Once more the cause of death was pneumonia-lungworm or "verminous" pneumonia but poor range conditions, heavy competition by elk for the declining food supply, plus forest succession which was reducing the acreage of grassland pastures.

The fourth die-off occurred in Jasper from 1946-49 when the sheep population declined by 85 percent. Although disease was not documented as the cause of death, pneumonia-lungworm was believed present during the die-off. Malnutrition due to severely overgrazed winter ranges, plus heavy competition from elk and horses for forage, and the stress of three severe winters, were responsible for the die-off. Elk and deer numbers declined to a small and insignificant proportion compared to sheep.

By 1950, the national parks contained only about 1,000 bighorns compared to 8,500 in 1936 and 2,500 in 1915. By 1966, sheep populations climbed to 4,425 prior to the fifth die-off which occurred in Kootenay in 1966 and 1967. Prior to the die-off the population was 135, similar to the previous peak population of 140 in 1940. The Kootenay die-off was again attributed to pneumonia-lungworm disease with range deterioration due to overgrazing being the primary cause. In 1973, sheep populations in Jasper were similar to those present in 1946 just prior to the 85% die-off. Range conditions were again poor and forage utilization excessive (64% utilization of all vegetation except ground juniper and bearberry). Endoparasite loads were approaching those present in Kootenay sheep prior to the 1966-67 die-off.

On the overgrazed Jasper ranges forage production was only 36% as high as that on the productive and moderately grazed Waterton ranges. Range-population-endoparasite relationships between the poor Jasper ranges and the good Waterton ranges were:

Park	Range Condition	Forage Produc./ Acre (dry)	Forage Util. %	Spring Ewe wts.	Winter Wt. loss	Lungworms/ Gm. feces	Lambs: 100 Ewes
Jasper	Poor	200 lbs.	64	135 lbs.	20	2,375	35.7
Waterton	Good	550 lbs.	34	144 lbs.	13	594	32.8

The sheep did not exhibit any density-dependent self-regulating mechanism to control their numbers in Jasper as range conditions continued to decline and endoparasite and disease loads increased. Lamb crops remained normal, although lamb mortality increased in proportion to that for sheep on good ranges (16.8 yearlings: 100 ewes in Jasper compared to 21.0 yearlings: 100 ewes in

Waterton) indicating weaker lambs on the inferior range.

The major extrinsic factors operating to limit sheep numbers after range utilization exceeds 50% are:

1. Endoparasites - in particular lungworms and gastro-intestinal helminths which stress the animal and evidently increase lamb mortality.
2. Pneumonia-lungworm disease - which is the proverbial "straw that breaks the camel's back", that culminates the physiological stress initiated by malnutrition and causes a 75% + decline in sheep numbers.
3. Range condition and trend - which is the primary extrinsic factor in limiting sheep numbers. It takes about a decade of overgrazing (50%+ utilization) to weaken both the range and the animals to the level where advanced symptoms of malnutrition (high endoparasite loads, high winter weight losses, and high lamb mortality) become apparent. At this stage pneumonia-lungworm lesions are prevalent in the lungs and the stage is set for a major die-oof once the weakened animals are subjected to the additional stress of severe weather conditions. Such a combination produces the lethal pneumonia-lungworm syndrome.
4. Winter weather - which combines with poor range conditions and malnutrition to produce the pneumonia-lungworm disease which causes the major die-offs. Occasionally, catastrophically severe

LITERATURE CITED

Anderson, P.K. 1961. Density, social structure and non-social environment in house-mouse populations and the implications for regulation of numbers. Trans. N.Y. Acad. Sci. Ser. 11, 23, (5): 447-451.

Ardrey, R. 1961. African genesis. New York, Atheneum.

---------. 1967. The territorial imperative. Dell Publishing Co.

Andrewartha, H.G. and L.C. Birch. 1954. The distribution and abundance of animals. Chicago, Univ. of Chicago Press.

Bandy, J.P. 1968. Rocky Mountain bighorn sheep losses in the East Kootenay Region of B.C., 1965-67. Unpub. paper presented at the Northwest Section, Wildlife Society Meeting. Edmonton, Alberta 19 pp.

Buechner, H.K. 1963. Territoriality as a behavioral adaptation to environment in Uganda kob. Proc. 16th Int. Congr. Zool. 3, 59-63.

Cauley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51(1): 53-72.

Chapman, R.N. 1928. The quantitative analysis of environmental factors. Ecology, 9: 111-122.

Chitty, D. 1952. Trans. Roy. Soc. London B 236. 505.

---------. 1960. Population processes in the vole and their relevance to general theory. Can. J. Zool. 38, 99.

Chitty, D. 1964. Animal numbers and behaviour. In: Fish and Wildlife, a memorial to W.J.K. Harkness, ed. by J.R. Dymond, Longmans Canada Ltd., Don Mills, Ontario.

Christian, J.J. 1963. Endocrine adaptive mechanisms and the physiologic regulation of population growth. In: Physiological Mammalogy. W.V. Mayer and R.G. Van Gelder, Eds. Academic Press. New York.

Christian, J.J. and D.E. Davis. 1964. Endocrines, behavior, and population. Science, N.Y. 146(3651) 1550-60.

Clarke, C.H.D. 1941. Wildlife investigations in Banff and Jasper National Parks. Typewritten report in files of Canadian National Parks Branch, Ottawa. 21 pp.

-------------. 1949. Fluctuations in populations. J. Mammal. 30(1): 21-24.

Cole, G.F. 1969. Elk and the Yellowstone ecosystem. Research Note, Yellowstone National Park.

Cottam, W.P. 1961. Our renewable wild lands - a challenge. Univ. of Utah Press, Salt Lake City.

Cowan, Ian McT. 1944. Report on wildlife studies in Jasper, Banff and Yoho National Parks in 1944. Typewritten report in files of Canadian National Parks Branch, Ottawa. 83 pp.

-------------. 1945. Report of wildlife studies in 1944 and parasites, diseases and injuries of game animals in the Rocky Mountain National Parks 1942-1944. Typewritten report in files of Canadian National Parks Branch, Ottawa. 147 pp.

Cowan, Ian McT. 1947a. Range competition between mule deer, bighorn sheep and elk in Jasper Park, Alberta. Trans. N.A. Wildlife Conf. 12: 223-227.

--------------. 1947b. The timber wolf in the Rocky Mountain National Parks of Canada. Canadian J. of Research. D. 25: 139-174.

--------------. 1950. Some vital statistics of big game on overstocked mountain range. Trans. N.A. Wildlife Conf. 15: 581-588.

Darling, F.F. 1937. A herd of red deer. London and New York, Oxford Univ. Press.

Davis, D.E. 1953. The characteristics of rat populations. Quart. Rev. Biol. 28, 373-401.

Demarchi, R.A. and D.A. Demarchi. 1967. Status of the Rocky Mountain bighorn. Wildlife Review 4(4): 10-14.

Eddleman, L. and A. McLean. 1969. Herbage - its production and use within the coniferous forest. In: Coniferous forests of the Northern Rocky Mountains, ed. by R.D. Taber. Univ. of Montana Foundation, Center for Natural Resources. pp. 179-196.

Edwards, R.Y. 1956. Snow depths and ungulate abundance in the mountains of Western Canada. J. of Wildl. Manage. 20(2): 159-168.

Elseley, L. 1961. Darwins Century: evolution and the men who discovered it. Doubleday and Co. Inc., New York.

Elton, C. 1942. Voles, mice and lemmings. Clarendon Oxford.

Errington, P.L. 1956. Factors limiting higher vertebrate populations. Science, N.Y. 124, 304-7.

Flook, D.R. and P. Stringer. 1974. Hillsdale exclosure (24 yrs. old) standing crop production compared to adjacent grazed range, July 16, 1968. Preliminary unpublished results. Canadian Wildlife Service files, Ottawa.

Flook, D.R. 1964. Range relationships of some ungulates native to Banff and Jasper National Parks, Alberta. In Grazing in terrestrial environments. Blackwells Scientific Publications 1964. pp. 119-128.

Fosberg, F.R. 1967. A classification of vegetation for general purposes. In Guide to the check sheet for IB Pareas. IBP Handbook no. 4. By G.F. Peterken. Blackwell Scientific Publications, Oxford.

Green, H.U. 1949. The bighorn sheep of Banff National Park. Typewritten report in files of Canada. Parks and Historic Sites Service. Ottawa. 53 pp.

Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monograph no. 21. The Wildlife Society, Inc.

Houston, D.B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton Natnl. Hist. Assoc. Bull. no. 1.

-------------. 1971. Ecosystems of national parks. Science, Vol. 172, pp. 648-651.

Klein, D.R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. In: Animal populations in relation to their food resources. ed. by A. Watson. Blackwell Scientific Publ.

Kurt, F. 1968. Das Solialverhalten des Rehes (_Capreolus capreolus_ L.). Mammalia Depicta, 102.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press.

-------. 1970. Introduction. _In_: Animal populations in relation to their food resources. ed. by A. Watson. Blackwell Scientific Publ.

Leslie, P.H. and R.M. Ransom. 1940. J. Animal Ecology. 9: 27.

Lowdermilk, W.C. 1953. Conquest of the land through 7,000 years. U.S. Dept. of Agric., Agriculture Information Bull. no. 99. Soil Cons. Serv. Washington, D.C.

Malthus, T. 1960. Thomas Malthus 1830. _In_: Three essays on population: Thomas Malthus, Julian Huxley, and Frederick Osborn. The North American Library of World Literature Inc., New York, pp. 13-62.

Martinka, C.J. 1969. Ungulate winter ecology studies in Glacier National Park. Annual Report, 1969. Office of Natural Science Studies, National Park Service 1970, pp. 74-75.

Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, New York.

Millar, W.N. 1915. The big game of the Canadian Rockies. Conservation of fish, birds and game. Proceedings of Committee Meeting, Nov. 1-2, 1915. The Methodist Book and Publishing House, Toronto. pp. 100-124.

Milne, A. 1962. J. Theoret. Biol. 3:19.

Morris, M.S. 1956. Elk and livestock competition. J. Rge. Manage. 9(1): 11-14.

Nicholson, A.J. 1958. Ann. Rev. Entomol. 3: 107.

Pengelly, W.L. 1963. Thunder on the Yellowstone. Naturalist 14(2): 18-25.

Pfeiffer, E.W. 1948. Some factors affecting the winter game ranges of Jasper National Park. Abstract of M.S. thesis. Univ. of British Columbia, Vancouver, B.C. 46 pp.

Rasmussen, D.I. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11: 229-275.

Riney, T. 1964. The impact of introduction of large herbivores on the tropical environment. IUCN Publications new series. no. 4: 261-73.

Stelfox, J.G. 1971. Bighorn sheep in the Canadian Rockies: a history 1800-1970. The Canadian Field-Naturalist 85(2): 101-122.

Stoddart, L.A. and A.D. Smith. 1955. Range Management. McGraw-Hill Book Co. New York.

Watson, A. and Robert Moss. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: Animal populations in relation to their food supply, ed. by A. Watson pp. 167-220.

Wynne-Edwards, V.C. 1965. Self regulation systems in populations of animals. Science 147: 1543-1548.

------------------. 1970. Feedback from food to populations. In: Animal populations in relation to their food resources, ed. by A. Watson. Blackwell Scientific Publ.