Range ecology of Rocky Mountain bighorn sheep

by John G. Stelfox

Canadian Wildlife Service Report Series Number 39

Fisheries and Environment Canada
Pêches et Environnement Canada

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Issued under the authority of the
Minister of Fisheries and the Environment

Canadian Wildlife Service

Available by mail from
Printing and Publishing,
Supply and Services Canada,
Ottawa, Canada
K1A 0S4
or through your bookseller

Price:
Canada $2.25
Other countries $2.70
Price subject to change
without notice

Catalogue No. CW65–8/39
ISBN 0-660-00549-2

Design: Gottschalk+Ash Ltd.
Printing: Tri-Graphic Printing Ltd.
Contract No. OKT6-KL210-6-5978

Cover: A mature bighorn ram and ewe in winter pelage at Tangle Ridge, Jasper National Park. Photo by Danny On, US Forest Service.

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The author

John G. Stelfox is a wildlife and range ecologist with the Canadian Wildlife Service (CWS) in Edmonton, Alberta. After receiving a B.Sc. from the University of Alberta in 1952, he worked with the Alberta Fish and Wildlife Division for 11 years. During that period, he obtained an M.Sc. from Utah State University for his work on the effects of clearcut logging on a white spruce forest in western Alberta.

Dr. Stelfox joined the CWS in 1966 and has worked mainly on wild ungulates in the western Canadian national parks. His study of bighorn sheep ranges, reported here, led to his being awarded a Ph.D. from the University of Montana in 1975. He is currently developing a wildlife census program for the Warden Services, which includes preparing a system for recording wildlife data in a standardized and computerized form for use in the 14 western Canadian national parks.

Dr. Stelfox is married and has five children.

Acknowledgements

I am especially grateful to E. Eddleman, major advisor of this project, for assistance and guidance during the study and critical review of the manuscript.

Thanks are due to other committee members: W. L. Pengelly, B. W. O'Gara, J. R. Habeck, L. J. Lyon, and M. S. Morris. Each provided important advice and guidance throughout the study and a critical review of the manuscript.

This study would not have been possible without the joint cooperation of the CWS and the Warden Services of Jasper, Banff, Waterton Lakes, and Kootenay national parks. The cooperation and support of Warden Service personnel, often under severe weather conditions and on hazardous terrain, played a major role in the success of the study. I thank the CWS for financial support, encouragement, and field assistance. I appreciate the advice and support of W. E. Stevens, D. R. Flook, and J. P. Kelsall, and the significant contributions in the field and laboratory made by CWS wildlife technicians J. R. McGillis and H. J. Armbruster. J. Holmes, University of Alberta, and his staff conducted autopsy and endoparasite studies. A. W. Baily, University of Alberta, I. Sterling and T. J. Wood, CWS, reviewed the manuscript; their comments are gratefully acknowledged.

The patience and encouragement received from my wife, Betty, was a great help in seeing this study through to its conclusion.

Perspective

In 1966 a major die-off of Rocky Mountain bighorn sheep occurred in Kootenay National Park, British Columbia. This die-off created a three-fold concern within Parks Canada:

1. What was causing the die-off?
2. Would it result in the annihilation of the park herd?
3. Would the die-off extend to Jasper, Banff, and Waterton Lakes national parks?

Consequently, Parks Canada asked the CWS to conduct a complete ecological study of the bighorn sheep in these four parks. During the seven-year study (1967–1973), I investigated range ecology, population dynamics, disease, predation, interspecific competition, and climate on six winter ranges in Jasper, Banff, and Waterton Lakes parks and collected complementary data from Kootenay National Park. Detailed range studies were not conducted in Kootenay Park as the winter range lay outside the park and was being studied by provincial biologists.

The study showed that under natural conditions, Rocky Mountain bighorn sheep populations normally increased beyond range-carrying capacities. As a result, winter ranges were overgrazed and animal conditions deteriorated. Malnutrition, coupled with unusually severe winter conditions, made the animals susceptible to disease, particularly pneumonia–lungworm disease. Major die-offs consequently occurred approximately every 25 years. After each die-off, range condition gradually improved because of much-reduced pressure on the range, and sheep populations concurrently recovered to their pre-die-off numbers. These population fluctuations are strongly influenced by external and highly variable factors such as weather, predation, interspecific competition plus man-made influences; thus it is difficult to predict accurately future bighorn sheep populations.

Sheep often share their ranges with other ungulates, particularly elk and mule deer. These species also increased beyond the range-carrying capacity, but their numbers were not controlled by periodic die-offs. Only predation and severe winter conditions influenced elk and deer numbers to a significant but unpredictable degree. Thus elk and deer can be detrimental to the long-term well-being of bighorn sheep and their ranges by sustaining enough grazing pressure after the sheep die-off to prevent proper range rejuvenation.

I recommended little or no management of ungulate species in areas where human visitation is light. In heavily visited areas, where die-offs and denuded ranges would not be tolerated by visitors, I recommended some management to maintain total ungulate numbers at acceptable levels. This could be accomplished by maintaining a large and diverse predator population, by perpetuating critical winter grasslands through controlled burns, etc., and by trapping and transplanting surplus ungulates from heavily-grazed areas.

Abstract

The study was conducted from 1967 to 1973 on six winter grassland ranges to evaluate factors contributing to population fluctuations and die-offs of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis Shaw*) in Canadian national parks. Ranges stocked with 0.8 sheep-months/ha and 37% vegetation use were in good condition, while those with 1.5 sheep-months/ha and 46% use were in fair condition. Those supporting 2.0 sheep-months/ha and 61% use were in poor, overgrazed condition; 40% use of all vegetation, except *Juniperus* and *Arctostaphylos* spp. was proper use. Grazing capacities were highest on light–moderately grazed *Festuca scabrella* ranges, intermediate on moderate–heavily grazed *Elymus–Poa–Bromus* ranges, and lowest on overgrazed *Agropyron–Calamagrostis–Koeleria* ranges. *Potentilla fruticosa* and *Koeleria cristata* were more abundant on heavily grazed ranges. As forage utilization increased, forage production decreased, lungworm (*Protostrongylus stilesi*) burdens increased, sheep winter weight loss increased, and the number of yearlings per 100 ewes decreased. There was a positive correlation between winter barometric pressures and sheep numbers, and a negative correlation between snow depth and sheep numbers on winter grassland ranges. Severe winters were accompanied by a greater winter weight loss, increased lamb mortality, and a higher percentage of heavy lungworm burdens than during mild winters. Sheep populations followed eruptive fluctuation patterns and displayed no intrinsic self-regulating mechanism. Excess populations declined drastically from a pneumonia–lungworm disease complex initiated by malnutrition and unusually severe winter weather. Occasionally, severe winters temporarily checked population increases. Wolves did not prevent sheep, elk, and deer numbers from exceeding range carrying capacities. Elk were the major competitor for winter range forage and their numbers were not controlled by intrinsic or extrinsic limiting factors other than those imposed by man.

Résumé

L'étude, effectuée de 1967 à 1973, a porté sur six pâturages d'hiver dans le but d'évaluer les facteurs contribuant à la variation, tout particulièrement en cas de réduction soudaine, de l'effectif du mouflon des Rocheuses (*Ovis canadensis canadensis Shaw*) dans les parcs nationaux du Canada. L'état était bon des habitats de 0.8 mois-mouflon/ha, où la végétation

The author checks range conditions by the 10-point cluster method on Little Windy range in Jasper National Park. Photo by Ray Makowecki.

était utilisée à 37%, alors qu'était passable celui des aires de 1.5 mois-mouflon/ha, où la végétation était utilisée à 46%. Les habitats de 2.0 mois-mouflon/ha à 61% d'utilisation de la végétation, étaient surexploités et dans un état médiocre. Le taux optimum d'emploi, par le mouflon, de toute la végétation devrait être de 40%, exception faite des espèces *Juniperus* et *Arctostaphylos*. Les possibilités d'alimentation étaient élevées dans les pâturages de *Festuca scabrella* où la fréquence du broutement allait du léger au modéré, moyennes dans les pâturages d'*Elymus–Poa–Bromus* où elle allait du modéré à l'intensif et faibles dans les pâturages d'*Agropyron — Calamagrostis Koeleria* soumises à broutement excessif. Les espèces *Potentilla fruticosa* et *Koeleria cristata* étaient plus abondantes dans les pâturages assujettis à broutement intensif. A mesure qu'augmentait l'utilisation du fourrage, la production en diminuait cependant que s'accroissait la charge de nématodes (*Protostrongylus stilesi*), s'accentuait l'amaigrissement hivernal du mouflon et se réduisait le nombre de petits d'un an par cent femelles. Dans les pâturages hivernaux, la corrélation apparaissait positive entre pression barométrique hivernale et effectif des mouflons et négative entre ce dernier et l'épaisseur de la neige. A hiver rigoureux correspondaient un amaigrissement plus prononcé, une mortalité infantile accrue, un pourcentage plus élevé d'infestation par les nématodes qu'en cas d'hiver clément. L'effectif des mouflons présentait des variations soudaines et ne manifestait aucun indice du jeu d'un mécanisme auto-régulateur intrinsèque. L'excédent démographique déclinait radicalement du fait d'un complexe morbide de pneumonie et d'infestation aux nématodes, occasionné par la malnutrition et la rigueur anormale de l'hiver. Il est arrivé qu'un hiver rigoureux donne un éphémère coup d'arrêt à la croissance démographique. La présence de loups n'empêchait pas l'effectif des élans et des caribous de dépasser la capacité de charge des habitats. Le principal concurrent, pour le fourrage des pâturages d'hiver, était l'élan dont l'effectif n'était assujetti à la rétroaction d'aucun facteur limitatif intrinsèque ou extrinsèque hormis ceux qu'imposait l'homme.

Резюме

С 1967 года по 1972 год с целью оценки факторов, вызывающих текучесть поголовья и вымирание, наблюдающиеся в государственных парках Канады, обитающего в Скалистых горах снежного барана (Ovis Canadensis Shaw) проводилось исследование шести зимних луговых пастбиц. Пастбища, характеризующиеся 0,8 овце-месяцев/га и 37%-ным расходом растительности, находились в хорошем состоянии, в то время как пастбища, характеризующиеся 1,5 овце-месяцев/га и 46%-ным расходом, находились в удовлетворительном ссотоянии. Пастбища, характеризующиеся 2,0 овце-месяцев/га и 61%-ным расходом, находились в бедственном, чрезмерно стравленном состоянии; нормальным оказался 40%-ный расход всей растительности, за исключением Juniperus и Arctostaphylos spp. Эффективность выпаса была наиболее высокой на легко и умеренно стравленных пастбищах с Festuca scabrella, средней — на умеренно и сильно стравленных пастбищах с Elymus-Poa-Bromus и наиболее низкой — на чрезмерно стравленных пастбищах с Agropyron-Calamagrostis-Koeleria. Potentilla Fruticosa и Koeleria cristata были более обильными на сильно стравленных пастбищах. С ростом использования кормовых растений сокращалось их воспроизводство и усиливалась опасность заболевания легочной нематодой (Protostrongylos stilesi); кроме того, увеличивалась зимняя потеря веса у баранов и сокращалась численность годовалых животных на каждую сотню овец. Наблюдалось положительное соотношение между зимним барометрическим давлением и численностью баранов и отрицательное соотношение между глубиной снежного покрова и численностью баранов на зимних луговых пастбищах. Суровые зимы сопровождались большей зимней потерей веса, ростом смертности ягнят и более высоким процентом заболевания легочной нематодой, чем в мягкие зимы. Развитие поголовья барана происходило скачками, не подчиняясь никаким внутренним механизмам саморегулирования. Прирост поголовья резко сократился из-за комплексного заболевания воспалением легких и легочной нематодой, вызванного недостаточным питанием и необычно суровой зимой. Иногда из-за суровых зим временно прекращался рост поголовья. Сохранению пастбищ не способствовало и то положение, что волки уничтожили лишь небольшое число баранов, лося обыкновенного и оленей. Главным опустошителем зимних кормовых пастбищ были олени обыкновенные, причем никакие, внутренние или внешние, ограничивающие факторы, кроме человека, не влияли на изменение их численности.

Introduction and objectives

Four eruptive fluctuations in populations of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis Shaw*) were reported in the Canadian national parks of Jasper, Banff, Waterton Lakes, and Kootenay from 1936 to 1950. Hereafter these parks will be referred to as Jasper, Banff, Waterton, and Kootenay, and bighorn sheep as sheep. Each peak population terminated suddenly with the death of 75–85% of the population within a few months (Cowan 1945, 1950; Stelfox 1971) followed by a gradual increase in numbers. These die-offs had been attributed to pneumonia–lungworm, or verminous–pneumonia disease (Cowan 1945, Stelfox 1971).

When a fifth die-off occurred in September 1966 in Kootenay, Parks Canada initiated a study to determine the nature of the die-off and the importance of various environmental factors contributing to it.[1]

The objectives of this study were to compare the importance and interrelationships of the ecological factors as exhibited on sheep winter ranges in Jasper, Banff, and Waterton during the period 1967–71, and the effect these factors had in controlling sheep numbers, as follows:

1. range condition and trend;
2. summer and winter weather during a three-year period;
3. ungulate population dynamics, seasonal range use, disease parasite burdens, fecundity, and recruitment rates;
4. population trends and interspecific competition;
5. range grazing and carrying capacities;
6. population self-regulation in bighorn sheep, elk (*Cervus canadensis*) and mule deer *Odocoileus hemionus.*

It was hoped that the results obtained would help develop a management program for sheep in the Canadian national parks taking into account grazing capacity and physical and aesthetic carrying capacities.

The study also compares eruptive fluctuations of sheep with those reported for other wild ungulates, and examines the impact of all ungulates grazing on sheep winter ranges in respect to plant successional changes and the zootic disclimax concept. This concept refers to vegetational disclimaxes arising from animal influences such as heavy selective foraging by ungulates on specific plant species or communities.

I decided to conduct the study in three parks and over several years. This provided an excellent opportunity to study and compare the importance of various intrinsic and extrinsic factors in relation to population fluctuations of sheep. Range condition, range stocking rates and endoparasitic loads varied from park to park and forage production, winter weather, sheep production and mortality, and interspecific competition varied from year to year. I established two range study areas in each park; one low- and one high-elevation range. Information on population dynamics and disease-parasitism were to be obtained from as many areas within each park as feasible, including Kootenay. Other factors were recognized as possibly contributing to past sheep die-offs. These were:

1. predation from wolves and cougars (except during the period 1950–60 when these main predators were eliminated from many areas and held at low levels in others);
2. interspecific competition (since early 1940's) on winter ranges, particularly from elk;
3. severe winter and/or spring conditions which either directly cause die-off or predispose herds to die-offs;
4. the development of climax forests due to fire control which has reduced vital grassland winter ranges since about 1915.

The relative importance of each of these factors was not understood. Principal agents cited as responsible for past die-offs have been disease, disease-parasitism, range, weather, and interspecific competition.

Combined with a study of factors controlling sheep numbers, there existed a need to determine grazing and/or carrying capacities of critical ranges, i.e., the optimum number of sheep and other ungulates that a given range can support while still maintaining vegetation and soil in a productive state. Carrying capacities would have to be viewed in the light of park management objectives and fluctuating environmental factors in addition to grazing capacities. Consideration would have to be given to the combined effects of winter weather, reduced animal mobility, and forage availability, plus the constantly changing pressures of interspecific competition and predation as they relate to range carrying capacities.

A further consideration is that the harvesting of excessive numbers of wild ungulates in national parks is regarded as generally contrary to park management philosophies. It is therefore necessary to consider both the physical and aesthetic carrying capacities in relation to park policies and objectives. Because of the wide annual variations discussed above, a study of the range ecology of wild ungulates should span several years to encompass the major short-term variations in both the biotic and abiotic elements.

[1] This report is a summary of the results of the study carried out by the Canadian Wildlife Service. Complete data and results are given in Stelfox (1975) which can be obtained by writing CWS, Ottawa, K1A 0H3, or Regional Library, CWS, 1110-10025 Jasper Avenue, Edmonton, T5J 1S6. All appendices mentioned in this report are filed with Stelfox (1975) and can be obtained from the same addresses.

Literature review

Besides the five die-offs in the national parks between 1936 and 1950 mentioned previously, similar die-offs occurred on provincial ranges in the 1940s in Alberta and in the 1960s in British Columbia (Demarchi and Demarchi 1967, Bandy 1968, Stelfox 1971).

These eruptive fluctuations seemed to follow the pattern described by Riney (1964) and Caughley (1970) for eruptions of established populations whereby the eruption is triggered by the large discrepancy between the number of animals that the environment can carry and the number of animals actually present. An eruptive fluctuation in this study is considered to be an increase in numbers over at least two generations followed by a marked decline (Caughley 1970).

In the United States, die-offs occurred in parks in the 1920s and 30s (Marsh 1938, Buechner 1960) and throughout most of the sheep range on non-park lands in the United States in the 1920's. Similar declines occurred in the Rocky Mountain and California bighorns in British Columbia (Buechner 1960, Sugden 1961). The epizootic die-off in Colorado's Pike's Peak, Kenosha, and Tarryall herds during 1952-53 caused a population decline from 1,500 to 200–300. The Tarryall herd had previously crashed in 1923–24 and declined from 350 to 12 (Buechner 1960).

These die-offs were attributed to a lungworm–pneumonia complex, sometimes referred to as hemorrhagic septicemia. The lungworms involved were *Protostrongylus stilesi* in the lung parenchyma, and *P. rushi* in the bronchioles. Numerous pneumonia strains of *Pasteurella multocida* and *P. hemolytica* were believed involved in addition to other secondary agents such as *Corynebacterium pyogens* and *Clostridium* spp. (Marsh 1938, Cowan 1951, Buechner 1960, Bandy 1968).

Although less common than those dealing with population die-offs, several important range ecology studies have been written. Cursory range examinations were conducted in Banff and Jasper parks in the late 1930s and the 1940s (Cowan 1945, 1947*a*; Green 1949). A range study was conducted along the Athabasca Valley in Jasper in 1946–47 (Pfeiffer 1948) and in western Alberta in the 1950's (Wishart 1958). Since the beginning of the 1965–67 die-off in the East Kootenays of British Columbia, a series of range related studies have occurred (Demarchi 1965, 1968; Demarchi and Demarchi 1967; Hudson, Kitts, and Brink 1972; Hebert 1973). Prior to that die-off, Sugden (1961) studied range competition among bighorn sheep, mule deer, cattle, and domestic sheep in the Churn Creek area of British Columbia. In the United States, Buechner (1960) summarized the relationships between bighorn sheep and vegetation, while specific range ecology studies included Packard (1946), McCann (1953), Smith (1954), Buechner (1960), Schallenberger (1965), Oldemeyer, Barmore, and Gilbert (1971), Constan (1972), Hickey (1973), Matthews (1973). Briefly, the studies showed that in northwestern United States and southern Alberta and British Columbia, the two common winter range types are *Agropyron spicatum–Poa secunda*, and *Festuca idahoensis–Agropyron spicatum*. Other important winter range species included *Artemisia* spp., *Chrysothamnus* sp., *Purshia tridentata*, *Balsamhorhiza sagittata*, *Pseudotsuga* sp., and *Pinus ponderosa*.

Major range competition existed with elk, mule deer, cattle, and horses. Bighorn sheep generally ate a mixture of grasses, forbs, and shrubs on the winter ranges, whereas elk, cattle, and horses were primarily grazers and deer concentrated more on shrubs. In this report, grass and grasses refer to graminoids as they include *Carex*, *Juncus* and other grass-like genera. The greatest competition for grass occurred during the spring. Capp (1967) studied competition among bighorn sheep, elk, and deer in Rocky Mountain National Park, Colorado and concluded that forage competition by elk was the most significant reason for the decline in sheep numbers from 1925 to 1958. Smith (1954), Sugden (1961), and Capp (1967) experienced difficulty in determining food habits of bighorns by direct observations of feeding animals. Capp (1967) summarized the food habits of bighorn sheep as reported by various workers.

A few studies have been conducted on the blood chemistry and forage nutrition of bighorn sheep, including those on forage and serum phosphorus values (Hebert 1972), physiological values (Franzmann and Thorne 1970), chemical composition of winter forage (Demarchi 1968), and nutritive values of low- versus high-elevation forage (Hebert 1973).

Numerous studies were conducted on diseases and parasites. In Canadian national parks, studies were conducted by Cowan (1945, 1951), Blood (1963), Uhazy (1969), Uhazy and Holmes (1971), Uhazy, Mahrt, and Holmes (1971), Uhazy, Holmes, and Stelfox (1973), Stelfox (1974), Samuel *et al.* (1974). Outside of the national parks, several studies were conducted in British Columbia including Bandy (1968), Hebert (1970), Hudson (1970). In the United States, studies were conducted by Marsh (1938), Hunter and Pillmore (1954), Pillmore (1955, 1961), Allen (1960), Buechner (1960), Forrester and Senger (1963), Becklund and Senger (1967), Monson, McClinchy, and Nash (1970, 1971), Forrester (1971).

The only study dealing with the effect of snow cover on the social behaviour of sheep, that I am aware of, was conducted in Banff (Petocz 1973).

Study area

Figure 1 shows the locations of Waterton, Banff, and Jasper parks and the distribution of sheep and locations of the six study areas within the parks. The parks cover 18,116 km^2: 10,920 km^2, Jasper; 6666, Banff; and 530, Waterton. The herds in all six areas chosen for study occupied a total of 392 ha of grassland range during the winter. Of this total, I studied 151 ha intensively, i.e., more than one-third, to obtain data on forage production and utilization, climate, soils, ungulate densities, and seasonal range use. I did not include adjacent coniferous forested areas as they were not utilized appreciably during the winter months, contained little preferred winter forage and were generally inaccessible due to deep snow. Table 1 outlines basic characteristics of each of the areas studied.

1. Range and ungulate population conditions

1.1. Waterton Lakes

This area contained productive rough fescue (*Festuca scabrella*) winter ranges which appeared more productive than ranges in either Banff or Jasper. The low-elevation range no. 1 (Mt. Galwey) was moderately used by bighorn sheep and to a lesser degree by elk and mule deer. The high-elevation range no. 2 (Ruby Ridge) was lightly used by sheep and a few mule deer and elk. The sheep in Waterton normally came through the winter in good condition and exhibited a healthy appearance. Figure 2 shows the two ranges selected and the locations of range samples.

1.2. Banff

This area contained moderately productive rough fescue–sedge (*Carex* spp.) sheep ranges which appeared less productive than Waterton but more productive than Jasper. The high-elevation range no. 3 (Palliser range) was moderately used by sheep, elk, and perhaps a few mule deer. The low-elevation range no. 4 (Mt. Bourgeau) was heavily used by sheep and a few mule deer and elk. Sheep usually overwintered in fair condition on Palliser, and

Figure 1

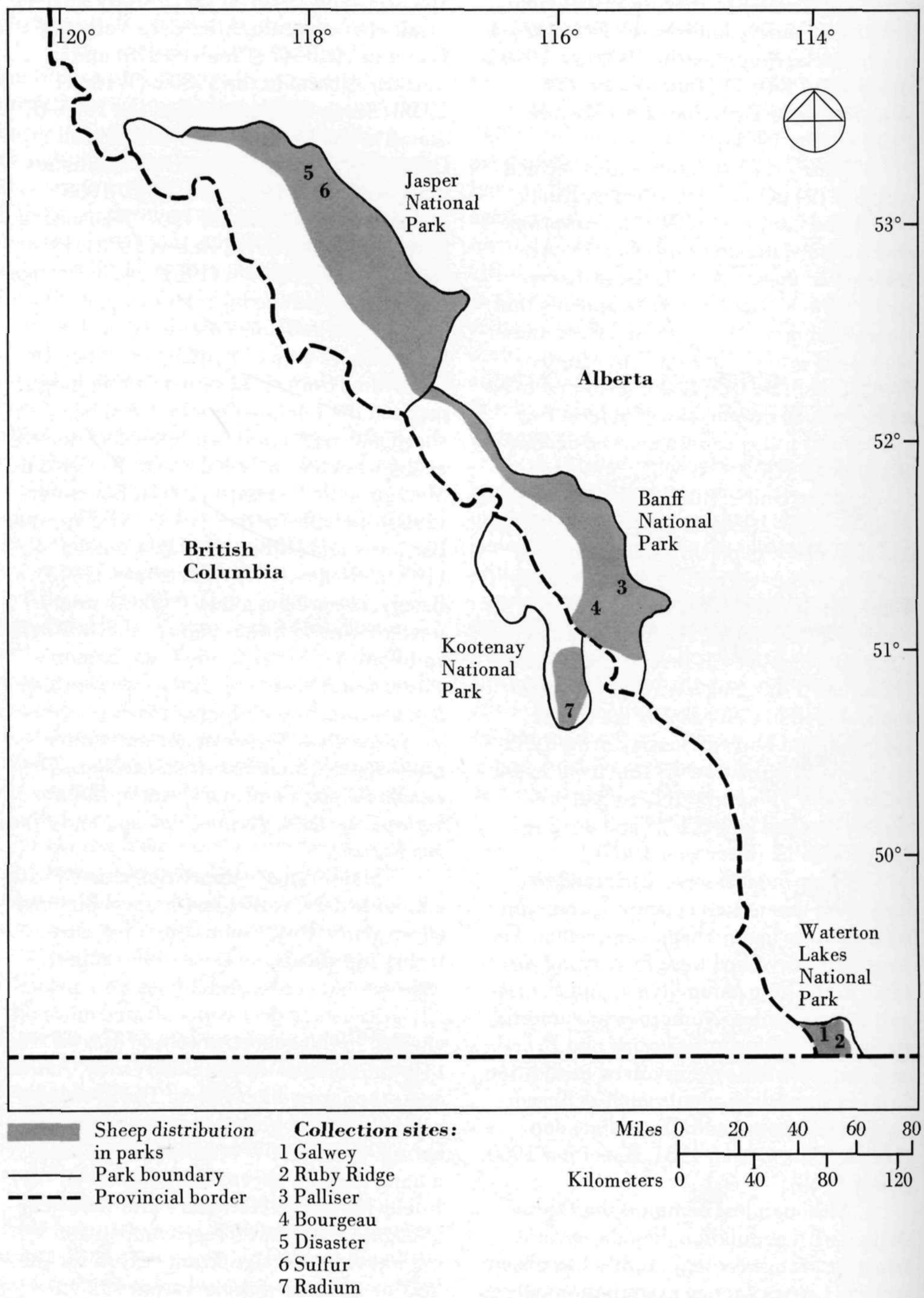


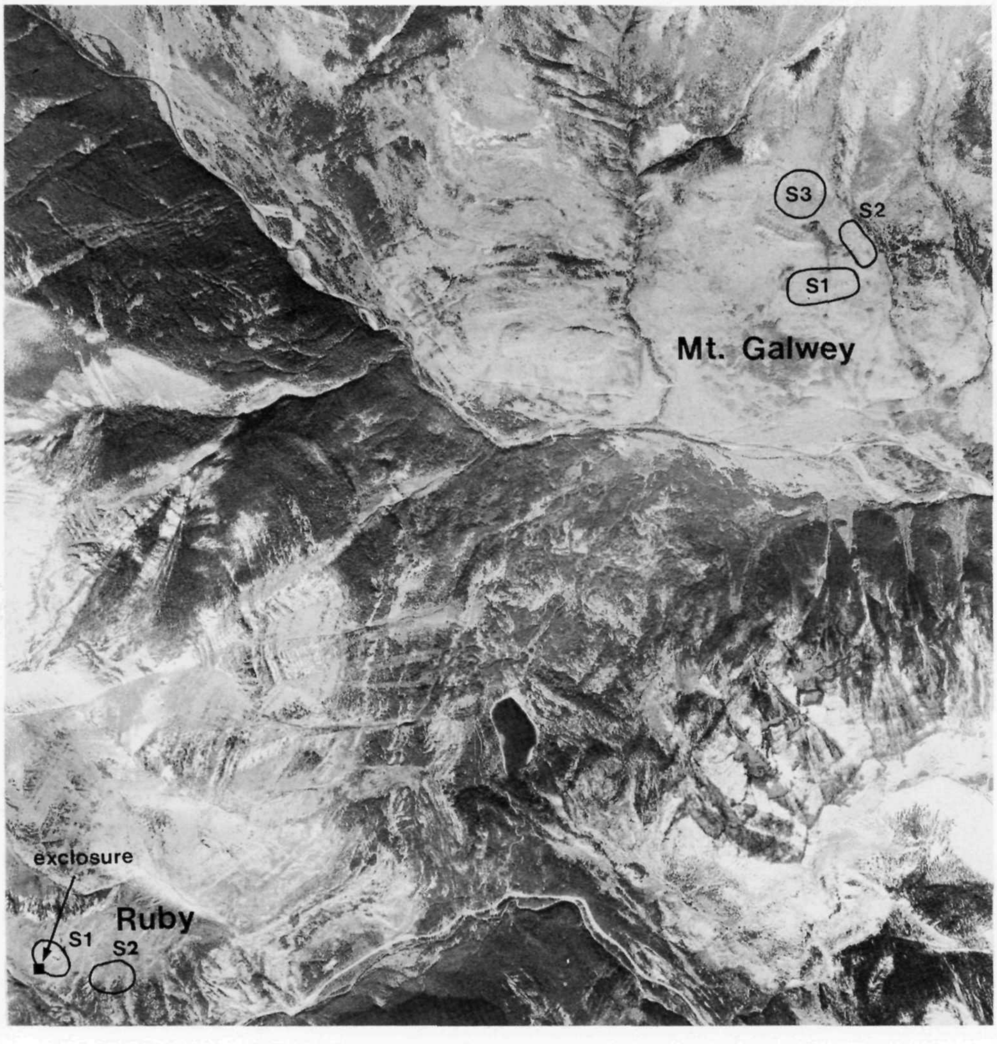
Figure 1
Locations of Waterton Lakes, Banff, Jasper, and Kootenay national parks, with bighorn sheep distributions and locations where samples were collected.

Figure 2
Mount Galwey and Ruby Ridge winter ranges, Waterton Lakes, showing locations of range samples, transects, and exclosures: 1967 air photo.

Table 1
Feature characteristics of six winter range study areas

Feature	Waterton		Banff		Jasper	
	Galwey	Ruby	Palliser	Bourgeau	Disaster	Sulfur
Elevation (m)	1525–1830	1830–2135	1891–2196	1830–2135	1068–1220	1617–1861
Exposure	S	S–SE	SW	S–SW	SW	SW
Dominant vegetation	Fescue–Wheatgrass–Bearberry–Oatgrass	Fescue–Sedge–Saskatoon–Wheatgrass	Fescue–Sedge–Cinquefoil	Junegrass–Wildrye–Bearberry–Wheatgrass	Bearberry–Juniper–Junegrass–Sedge	Cinquefoil–Wildrye–Sedge–Reedgrass
Area of grassland (ha)	52	38	77	23	114	50
Area sampled (ha)	30	19	18	23	42	17

Figure 2



in fair to poor condition on Bourgeau. Figures 3 and 4 show the two ranges selected and the locations of range samples.

1.3. Jasper

The two winter ranges studied appeared to be unproductive sedge–wheatgrass (*Agropyron* spp.)–wild rye (*Elymus innovatus*)–junegrass (*Koeleria cristata*) ranges. The low-elevation range no. 5 (Disaster Point) seemed less productive than the other five ranges and was heavily stocked with sheep plus some elk and deer. The high-elevation range no. 6 (Sulfur Ridge) was heavily utilized by sheep with little or no evidence of mule deer or elk use. Sheep normally came through the Jasper winters in thin condition. Figures 5 and 6 show the Jasper study areas and the locations of range samples. I will refer, hereafter, to the six winter ranges as Galwey, Ruby, Palliser, Bourgeau, Disaster, and Sulfur.

2. Geomorphology

Geologically, the study areas are characterized by pervious shale, sandstone, and limestone mountains with steep eastern escarpments and gentle westerly slopes (Mackay 1952). The winter ranges studied in Jasper and Banff lie within the Front Ranges of the Rocky Mountains. These are complex, folded, and faulted sheets of grey Paleozoic carbonates and shales often with exposed Mesozoic shales, sandstone, and carbonates. The ranges studied in Waterton lie within the Main Range of the Rocky Mountains, which is composed of older and

Figure 3
Palliser range, Banff, showing range sampling areas; 1967 air photo.

Figure 4
Mount Bourgeau winter range, Banff, showing range sampling areas; 1967 air photo.

harder strata — mostly red, green, and grey Precambrian and Cambrian sandstones, quartzites, shales, and limestones. Within all three parks, the ranges run in a northwest to southeast direction, thus exposing the gentle southwest slopes optimally in winter to the beneficial effects of solar action and the prevailing westerly winds. These slopes have developed the exposed grasslands essential for the winter survival of sheep.

I found grasslands along valley bottoms, on mountain summits and ridges, and on slopes ranging from 25° to 37° (47–75%). Below a 25° slope, coniferous and deciduous forests occur, whereas above 37° the grasslands fade into shale, scree, or rocky slopes with a sparse cover of shrubs, forbs and grasses. This is especially true on westerly and southerly exposures and at elevations from 1067 to 2134 m. On the more moist northerly, and to some extent the easterly exposures, forest vegetation generally succeeds on all slopes up to 37° with grasslands confined to disturbed slopes, *viz.* following fires, avalanches, and "blow-downs" from winds. Exposure has an influence on the moisture regime, and hence on the vegetation. The drier, warmer slopes facing south and west support more herbaceous and shrubby vegetation, while the more moist, cooler slopes facing east and north support more trees.

In general, the ranges to the east of the Continental Divide in Alberta have potentially high carrying capacity for wild ungulates. Variations in topography, altitude, geology and climate provide the necessary "edge-effect" between pasture and cover so important to all ungulate species.

3. Soils

The following soil information is from Stringer (1969). The soils of the *Festuca–Danthonia* Prairie of Waterton are Chernozems with many atypical features such as a very high gravel content, an ill-defined B horizon, and a disturbed A horizon due to heavy grazing by elk. The subalpine grassland soils in Banff are highly

Figure 3

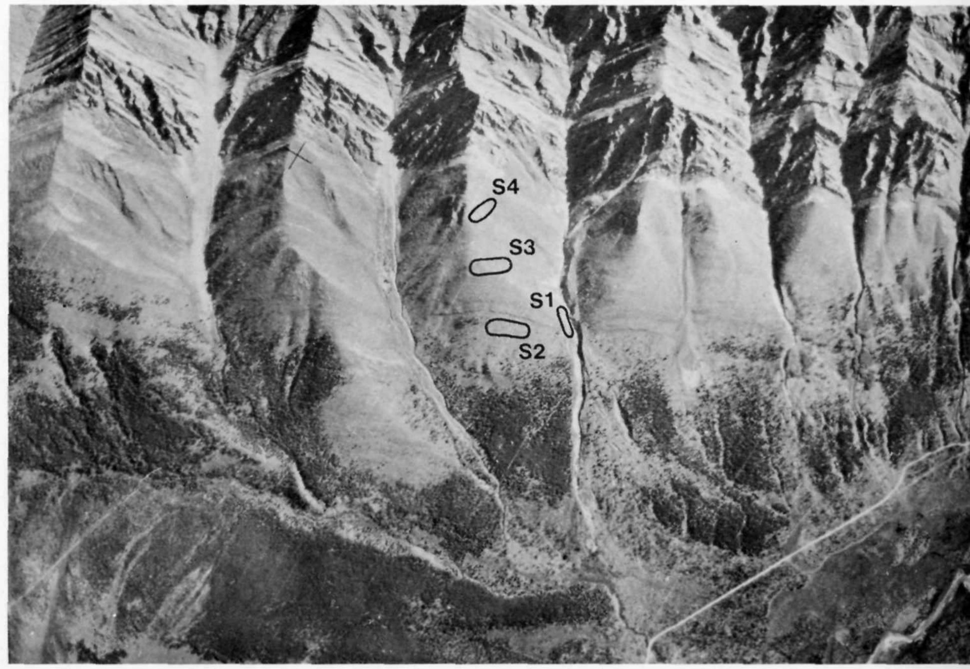


Figure 4

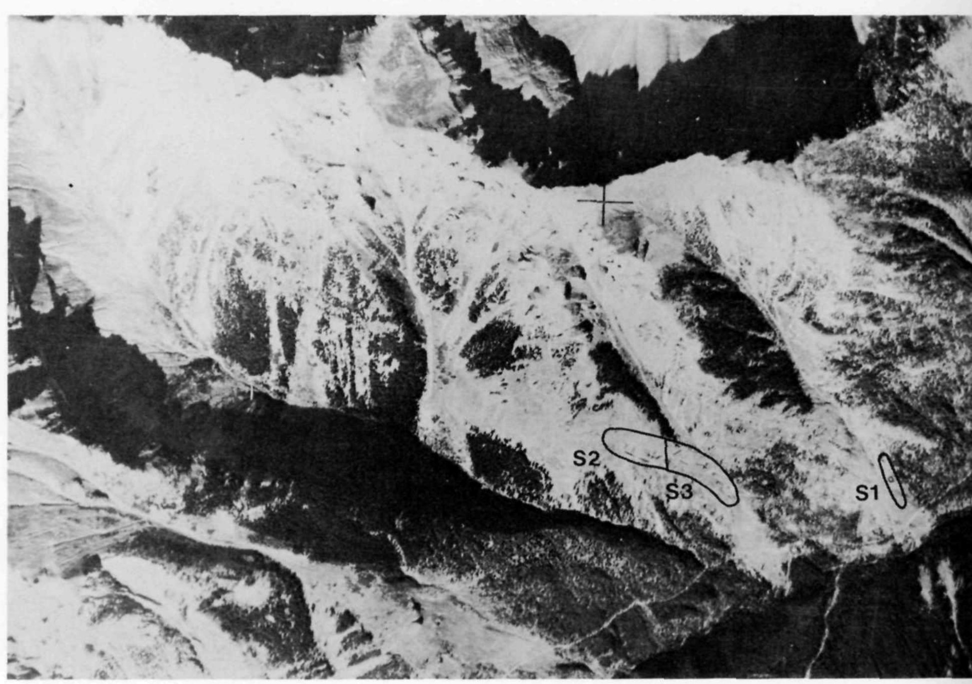


Figure 5
Disaster Point winter range, Jasper, showing range sampling areas; 1967 air photo.

Figure 6
Sulfur Ridge winter range, Jasper, showing range sampling areas; 1967 air photo.

Figure 5

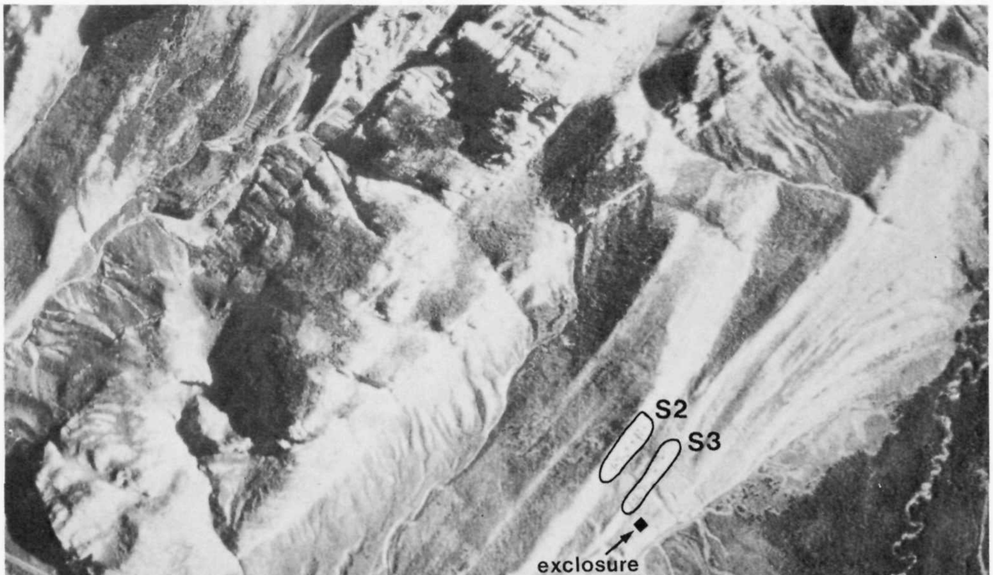
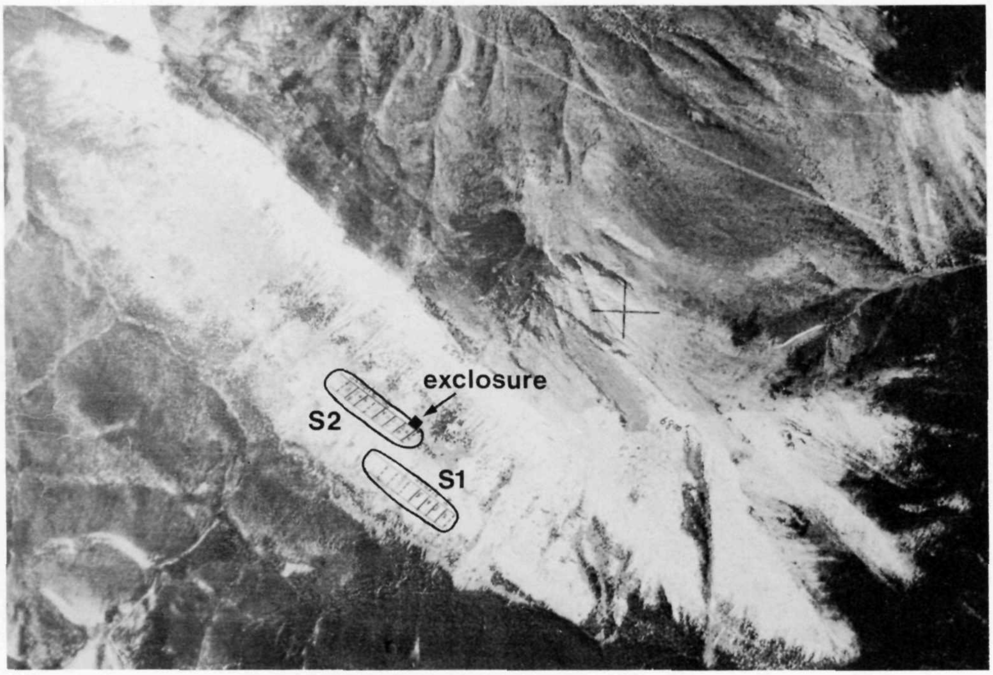


Figure 6



variable, consisting of Orthic Black Chernozem, Orthic Regosol, and Degraded Brown Wooded, plus some soils which do not fit into the National Soil Survey Committee (1968) classification.

The *Elymus innovatus* Sub-alpine Shrub Savanna soils at high elevations in Banff and Jasper are composed of large angular rocks and coarse gravel with no discernible horizons. The A horizon is dispersed among the rocks and gravel to at least 30 cm.

The *Koeleria–Calamagrostis montanensis* grasslands along the Athabasca Valley in Jasper have soils which are more xeric, undeveloped, and nutrient-poor when compared to other grasslands studied in Banff and Waterton. The soils are Orthic Regosol, Orthic Brown Wooded, Degraded Brown Wooded, and Orthic Black Chernozem. The Ah horizons are < 5 cm thick in most cases. There is very little litter and most soil surfaces appear to be very unstable. Most topsoils contain considerable amounts of wind-blown silt with a structureless accumulation of loose, grey-brown silt on the surface of some stands. Available nutrients are generally lower than for other grassland types.

4. Climate

The climates of the mountain valleys are transitional between three of six types of Canadian climate: the Prairie, Cordillera, and Northern Climatic regions (Anon. 1967). Climates are much different in the valleys than elsewhere in the mountains because of the effects of altitude, topography, and vegetation types on temperature and precipitation, and because of cold air drainage and valley winds, etc.

Table 2 summarizes Stringer's (1969) records of temperature and precipitation in the vicinity of the three study areas. For these three stations at Banff, Jasper, and Waterton townsites, the hottest month was July and the coldest, January. Waterton recorded very much higher precipitation values than did either Jasper or Banff. I also collected supplementary data from tem-

Table 2
Temperatures and precipitation at three meteorological stations in the study region, expressed as normals for period of 30 years (1931–60), Stringer 1969

			Temperature (°C)			Precipitation (cm)		
Station	Location	Elevation (m)	Mean annual	Mean daily July	Mean daily Jan.	Mean annual	Annual snowfall	Highest monthly snowfall
Waterton Park HQ	49°04′N 113°57′W	1295	5.0	17.4	−7.5	107.5	580	97
Banff	51°11′N 115°34′W	1383	2.1	14.5	−10.9	46.9	201	36
Jasper	52°53′N 118°04′W	1058	3.0	15.2	−11.4	40.6	125	28

porary weather stations at each study area (Appendices IV and VI, Stelfox 1975; see footnote 1).

5. Ungulate grazing patterns

In general, sheep summer above 2100 m. They may pass briefly through the winter ranges on their way to low-elevation natural licks or for water. During the summer, elk and mule deer move upwards from valley bottoms and may utilize the sheep winter ranges extensively from June to October.

As the September and October snows and cold temperatures freeze and partially cover the alpine forage, about two-thirds of the sheep drift downwards onto the winter grasslands below 2100 m. Of these, 50% winter in the 1800–2100 m zone (subalpine), about 21% winter at the 1050–1350 m zone (transition), and 29% winter on small grasslands within the 1350–1800 m coniferous zone. At this time, elk and deer generally migrate to the valley floor or lower mountain slopes. For all three species, there is a general constriction of range use towards the milder temperatures along the valley bottoms and the windswept grasslands (Stelfox and Taber 1969).

Mule deer use the mixed deciduous–coniferous forests extensively year-round and forage predominantly on browse species. They do, however, use a considerable amount of grasses throughout the year in these parks (Cowan 1947*a*). Elk use both deciduous and coniferous forests extensively year-round for shelter and some winter forage, although they generally forage on grasslands. Sheep remain almost exclusively on grasslands and rocky escarpments throughout the year, where they forage on a variety of grasses, forbs, and low shrubs (Cowan 1946, Stelfox and Taber 1969).

Methods and procedures

1. Range methods

1.1. Range condition and trend

Five main factors determine range condition: (1) plant composition, (2) plant density, (3) plant vigour, (4) soil chemical and physical characteristics, and (5) litter. Three factors indicate range trend: (1) plant vigour, (2) plant reproduction, and (3) erosion. To evaluate all those factors, I used the following inventory methods.

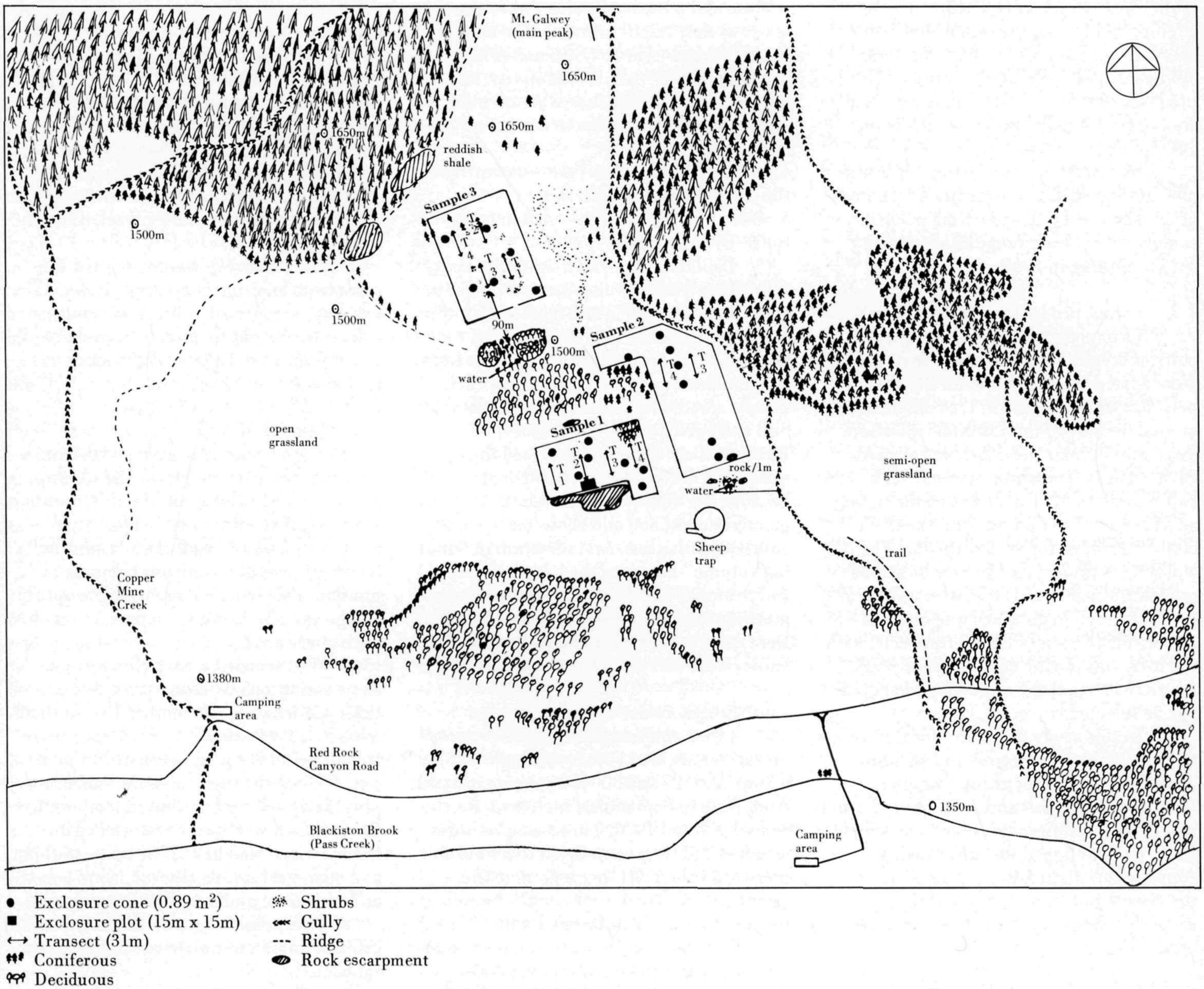
I divided each winter range into several sampling areas on the basis of variations in factors such as slope, exposure, and plant composition. Within these samples I established a total of 10 point-intercept transects, each 30 m long, using a restricted–randomized method for locating each transect. The number of points along each transect at which I sampled the vegetation was determined on the basis of vegetation heterogeneity. For each range I studied a minimum of 1000 and a maximum of 2000 ground coverage points. I used methods described by the United States Department of Agriculture (Anon. 1959) to determine vegetation composition, frequency, coverage, reproduction, and vigour.

Figure 7 shows the range sampling design for Galwey. To compare range condition and trend information from areas grazed with that from areas protected from grazing, a 13.5 x 13.5 m exclosure was established in each range in 1968. In 1970 and 1973, two and five years after the exclosures were built, I collected and compared vegetation data from a total of five 12-m point-intercept transects established within the exclosures and on the immediately adjacent grazed ranges. I also compared organic matter, nitrogen, calcium, phosphorous, and capillary-hygroscopic moisture potentials from exclosures with those from adjacent grazed plots to determine soil fertility and water-holding capacity of soils protected from grazing for five years.

In Jasper, the condition and trend of four additional winter ranges (Devona, Miette, Windy, and Talbot) in 1970 were

Figure 7
Mount Galwey bighorn sheep study area in Waterton Lakes National Park, 1968.

Figure 7



compared with results obtained 24 years earlier in 1946 (Pfeiffer 1948). In 1970 Pfeiffer and I reran the range plots using the same techniques on the same areas studied in 1946. We used a series of 10-point clusters at intervals along ten 15-m transects plus pellet group counts from 1000 plots.

To provide a visual record of gross changes in vegetation over time, I photographed two established points in each sample area of each range studied, every July beginning in 1968.

1.2. Forage production and utilization

I sampled the vegetation under 20 pairs of $0.9m^2$ portable exclosure cones and from adjacent grazed plots for a 3-year period, 1969 through 1971, to determine annual forage production and utilization. Vegetation under the cones was clipped each spring when winter use ended and before new plant growth was commencing and I sorted the clippings into the three classes: grasses, forbs, and shrubs. The cones were then placed in new locations predetermined by a restricted-random method which maintained one cone on either side of each of the 10 transects, with the locations during each of three years restricted so that the same location could not be selected twice.

In this study the term "forage" refers to all available herbaceous and shrubby vegetation except for ground juniper (*Juniperus communis* and *J. horizontalis*) and bearberry (*Arctostaphylos uva-ursi*) which could not be clipped without causing considerable disturbance to the soil and the survival of these species. It is more properly herbage (total annual herbaceous production).

1.3. Soil condition and profile

Soil samples were taken at depths of 0–15 and 30–45 cm and analyzed for:
1. organic content—used as an index to soil stability and litter carry-over;
2. macro-nutrients—the total nitrogen, phosphorus and potassium in grams per hectare is a broad measure of soil fertility; sodium and potassium values were also taken as they might influence the use of natural licks by sheep (Nocenti 1968);
3. soil reaction—pH, conductivity, and free lime determinations; these factors influence the ability of plants to extract nutrients from the soil;
4. soil texture and structure—measures of the soil's physical properties;
5. water holding capacity—taken from the 0–15 cm depth.

I obtained information on the above soil values from the unprotected ranges in 1968, 1969, and 1973 and from within the exclosures in 1973 after five years of protection from grazing. Soil samples were conglomerates of 6 to 12 points for each sample area. After collection, the Alberta Soil and Feed Testing Laboratory, Edmonton air-dried and analyzed the samples. I did not measure soil depths because the highly variable depth and conglomeration of soil and rocks made these values meaningless. An indication of "rooting volume" based on the proportion of soil to stones >2 mm diameter was deemed more appropriate and was obtained. Stones were removed from all samples and soil values were corrected to a stone-free basis.

1.4. Soil moisture and temperature

I took soil samples from 20 locations on each study area with a soil auger at depths of 0–15 and 30–45 cm twice-monthly from June to September, inclusive, for the years 1969 and 1970. These samples were weighed and then oven-dried to obtain soil moisture values. At the same time these samples were taken, I measured the soil temperature at 7 and 20 cm depths.

For purposes of analyzing the summer climatic data, moisture and temperature data were coded, resulting in a total of 34 variables per observation. In order to determine which of the 34 climatic variables had the most significant effect on forage production, I prepared a series of plots using seasonal averages of the variables (Appendix IV, see footnote 1).

As a second step, a complete correlation matrix was obtained showing the correlation of each of the previously defined 34 variables against every other variable. The correlation coefficient gives an indication of the linear dependence between two variables. For small sample sizes, the coefficient must be quite large before it is statistically significant. For a sample size of 12, the correlation coefficient must be larger than 0.576 at the 5% level of significance.

The third step was to conduct a regression analysis (step-wise) using 12 variables comprised of forage production, soil moisture and temperature, and precipitation. A total of five regressions were performed.

1.5. Climate

During summer, we recorded air temperature at ground level and 61 cm above ground twice monthly at 20 locations (where soil moisture and temperature readings were obtained). In addition we recorded the bi-monthly maximum and minimum air temperatures twice monthly at a permanent weather station set up on each study area.

We recorded winter climate and snow conditions twice monthly throughout three winters, i.e., November 1 to April 30, 1968–69, 1969–70, 1970–71. Data collected included snowpack distributions over the entire range, ambient temperatures plus maximum and minimum temperatures for each two-week period, snow depth, hardness and weight at 1–20 snow stations as avalanche hazards allowed, wind velocity and direction, and barometric pressure.

These data were correlated with information on ungulate distribution and range use.

1.6. Physiography

I described physiographic and other gross landscape features which included slope, aspect (exposure), landform, relief, elevation, and nature of soil-forming material. Aerial photographs, vegetative and relief maps were used to delineate various physiographic features while more detailed information was obtained from ground investigations.

2. Population dynamics

2.1. Ungulate populations

I determined the abundance and distribution of sheep and other ungulates on and adjacent to the winter ranges from ground and helicopter counts from 1967 to 1971. Classified ground counts were made bi-monthly for at least two years. Helicopter counts plus ground counts of animals on adjacent mountains were conducted as often as feasible to determine seasonal migration patterns and range use adjacent to the study area. I classified ungulates as to species, herd size, age, sex, and condition. Population densities were determined seasonally by relating total animal numbers of each species to a given area of range. Additional data on population size were obtained indirectly from fecal group counts of belt-transects (30 x 2 m) as described above.

Seasonal densities (stocking rates) of various ungulate species were determined from both ground and aerial surveys. Annual ungulate use, recorded as days-use per hectare (days/ha) was obtained by counting fecal pellet groups on 10 belt-transects 60 m^2 or 30 x 2 m for the period 1968–71. These transects were expansions of the 30 m point-intercept transects. Days/ha for each species were determined by dividing the number of pellet groups/ha by 13 (average daily defecation rate, Longhurst 1954, Mosby 1963). The belt transects were cleared of pellets each year after being counted with each count conducted in May or early June after snow-melt and prior to new plant growth. The days/ha values for each species were then converted to sheep-days/ha using the conversion values of 1 elk = 2.9 sheep, and 1 deer = 0.97 sheep (Stoddart and Smith 1955).

2.2. Animal condition

A 10-class condition scale, modified from Riney (1964) rated external animal condition for each season. I obtained fall and spring live weights plus chest girth measurements during live-trapping operations at Waterton and Jasper for a four-year period (1966–70). I correlated seasonal condition and weights by age and sex for these two parks with range conditions, forage production, stocking rates, winter climate, and internal parasite loads.

Fecal pellets were collected each month from June 1968 to June 1971 and analyzed for internal parasite loads (nematodes, cestodes, and coccidia). Road- and winter-killed specimens were autopsied, primarily to determine pneumonia–lungworm and gastrointestinal parasite infections.

2.3. Production and recruitment

I determined lamb production (lambs: 100 ewes) and yearling recruitment (yearlings: 100 ewes) rates from 1966 to 1971 for each of three seasonal periods; summer (July–August), late fall–early winter (November–January), and spring (April–May).

The summer period provided data on early post-natal production plus juvenile survival during the first year. Late fall–early winter values revealed the number of lambs and yearlings per 100 ewes entering the most severe stress period (January–April). Spring values provided a measure of both winter mortality of juveniles and recruitment rates (juveniles almost two years old).

I also recorded production and recruitment rates as a percentage of total herd values to determine herd increment rates.

Because the peak of lambing occurred about June 1, I used that date as the birth date for all sheep.

3. Grazing and carrying capacities

Grazing capacity is the number of hectares of forage required to support one animal-unit for a given period of time without inducing damage to vegetation or related resources (Severson, May, and Hepworth 1968). It is also "the maximum stocking rate possible without inducing damage to vegetation or related resources" (Huss 1964) expressed in terms of the number of animals (animal-units or animal-unit-months) on a specific area at a specific time. I used both definitions in this study with stocking rates expressed in terms of the "sheep-unit", which is equivalent to 0.2 animal-units (mature cow with calf). Elk and mule deer units were converted to sheep-units using the conversion factors of 2.90 and 0.97 respectively (Stoddart and Smith 1955).

Carrying capacities were evaluated by three methods :

1. the number of sheep-units the ranges supported during the period 1968 to 1971;
2. the optimum number (proper stocking) of sheep-units the ranges should support from a grazing capacity standpoint;
3. the optimum number of sheep-units from an aesthetic carrying capacity standpoint, i.e., that range carrying capacity commensurate with human acceptance, or preference, in terms of wild ungulate abundance and observability, plant community appearance, and the overall aesthetics of biotic–abiotic range components; the abiotic components should include such features as relatively stable land surfaces and naturally "pure" water qualities.

Results

A fine shot of a bighorn sheep taken by Danny On, US Forest Service, at Tangle Ridge, Jasper National Park.

1. Winter range condition and trend

Range condition is an expression of current range health relative to the potential for that site. This health is reflected through soil characteristics, plant species composition, species reaction to grazing, forage preference plus vegetation coverage and vitality.

Climatic, edaphic and biotic (especially grazing by animals) factors are directly important to range condition. Forest succession and fire are also important factors in mountain–foothills regions. Range condition will be discussed under the six headings of soil, plant composition and frequency, vegetative coverage and vitality, forage production and utilization, seasonal nutritive values, and effects of climate on forage production.

1.1. Soil

As soil is largely a product of climatic and vegetative effects upon rock material, it follows that on geologically young mountain soils the influence of parent material on soil nutrients and texture is considerable. Soil mineral deficiencies may result from deficiencies in the original parent material. Basically, soil is a function of climate, plants and animals, relief (topography and exposure), parent material, and time of soil formation (Jenny 1958). However, the influence of vegetation and grazing ungulates on soil development should not be overlooked.

Soils on the six ranges averaged 32.9 and 34.8% stones at the 0–15 and 30–46 cm depths, respectively. Rooting volumes (100%—stones >2 mm) were highest at Disaster and Galwey (99.7 and 85.9%), intermediate at Ruby, Bourgeau, and Palliser (66.4, 58.8 and 51.8%), and lowest at Sulfur (37.4%). Herbaceous roots penetrated to at least 53 cm on all six ranges with a dense rooting system down to at least 46 cm over most of each range. In the top 15 cm of soil, organic matter averaged 14.6% while the amount of nitrogen, phosphorus, and potassium averaged 4.9, 23.1, and 194.7 kg/ha respectively. Organic matter and nitrogen levels were highest in Banff and Jasper, while phosphorus and potassium levels were highest in Waterton, intermediate in Banff, and lowest in Jasper. Sodium values were light on all ranges. Free lime was nil on the Galwey, Ruby, and Palliser ranges, and light on Sulfur. It was moderate on Bourgeau and Disaster. High levels of free-lime may reduce nutrient availability to plants, and the comparatively high levels on Bourgeau and Disaster may have played a minor role in contributing to the poorer health of those sheep.

Soil textures were sand or loamy sand at the three ranges of Galwey, Ruby, and Sulfur. They were sandy loam at Bourgeau and sandy clay-loam at Palliser and Disaster.

I found no significant differences in the soil composition, texture, and water-holding capacities of four ranges under continuous grazing by sheep, deer, and elk when compared to exclosure areas protected from grazing for five years. However, organic matter levels were generally higher on the grazed ranges; 14.5% compared to 12.6% on ungrazed ranges. This higher level in grazed soils is probably due in part to the effects of ungulate trampling in crushing and compacting the vegetation into the soil. Part of the difference may be due to a greater proportion of the organic matter being tied up in new growth both above and below ground in the ungrazed vegetation compared to that on grazed ranges (Geiger 1965).

1.2. Plant communities

The six ranges are really a mixture of herbaceous and shrubby plants averaging 37.6, 34.3, and 28.1% basal coverage of graminoids, forbs, and shrubs respectively.

The types of rangeland Associations based on the two dominant genera, are:

Range		Association
Waterton	1. Galwey	*Festuca–Danthonia* Shrub Savanna
	2. Ruby	*Festuca–Carex geyeri* Shrub Savanna
Banff	3. Palliser	*Elymus innovatus–Festuca* Grassland
	4. Bourgeau	*Koeleria–Elymus innovatus* Shrub Savanna
Jasper	5. Disaster	*Koeleria–Juniperus* Shrub Savanna
	6. Sulfur	*Elymus–Potentilla* Shrub Savanna

The *Festuca–Danthonia* and the *Festuca–Carex geyeri* Shrub Savannas in Waterton are similar to the *Festuca–Danthonia* Prairie described by Stringer (1972) except that *Agropyron spicatum*, *Carex geyeri* and *C. richardsonii*, *Antennaria umbrinella*, *Cerastium arvense*, *Eriogonum umbellatum*, *Spiraea lucida*, *Amelanchier alnifolia*, *Arctostaphylos uva-ursi*, and *Rosa acicularis* are more prevalent in the former.

The *Koeleria–Juniperus* Shrub Savanna was similar to the *Koeleria–Calamagrostis montanensis* Grassland of the Athabasca River valley (Stringer 1972). In the former, *Agropyron dasystachyum*, *Carex filifolia* and *C. scirpoidea*, *Arctostaphylos uva-ursi*, *Juniperus horizontalis* and *Potentilla fruticosa* are more prevalent.

The *Elymus innovatus–Festuca* Grassland on the Palliser range contained more grasses and fewer shrubs than the *Elymus innovatus* Shrub Savanna of the subalpine *Picea–Abies* zone in Banff and Jasper (Stringer 1972). *Festuca scabrella*, *Bromus pumpellianus*, *Poa rupicola*, *Cerastium arvense*, *Hedysarum sulphurescens* and *Solidago multiradiata* were co-dominant on the *Elymus innovatus–Festuca* Grassland compared to *Hedysarum sulphurescens*, *Rosa acicularis*, *Amelanchier alnifolia*, *Fragaria virginiana*, *Galium boreale*, and *Rubus strigosus* on the *Elymus innovatus* Shrub Savanna ranges.

The *Elymus innovatus* Shrub Savanna on the Sulfur range occurred on a steep southwest facing slope in the subalpine *Picea–Abies* zone. It differed from the *Elymus innovatus* Shrub Savanna reported by Stringer (1972) by having *Carex scirpoidea*, *Poa rupicola*, *Achillea millefolium*, *Epilobium alpinum*, and *Potentilla fruticosa* as co-dominants, and by the absence or scarcity of *Amelanchier alnifolia*, *Rosa acicularis*, *Arctostaphylos uva-ursi*, *Hedysarum sulphurescens*, and *Symphoricarpos albus*. *Fragaria virginiana*, *Galium boreale*, and *Rubus strigosus* were common to both. The *Elymus innovatus* and *Koeleria–Elymus innovatus* Shrub Savannas occur on steep south and south-west slopes in the subalpine *Picea–Abies* zone and are frequently subjected to snowslides and rockfalls which prevent afforestation (Stringer 1972). The *Koeleria–Elymus innovatus* Shrub Savanna was similar to Stringer's *Elymus innovatus* Shrub Savanna except for the prevalence of *Koeleria cristata*, *Agropyron spicatum*, *Poa rupicola*, and *Arctostaphylos uva-ursi* which were probably the result of heavy grazing by bighorn sheep.

1.3. Plant composition and frequency

The use of plant composition to evaluate sheep range differs from that developed for cattle ranges. Forbs and shrubs appear nearly as important as grasses in providing the necessary year-round diet requirements for sheep, whereas on cattle ranges, shrubs and many forbs are considered range debits which should be minimized in order to maximize grass production. Native ungulates of the northern Rocky Mountain region must subsist year-long on native vegetation which is dormant for seven to nine months when herbaceous vegetation is often hidden under snow. Food preference information (Appendix I, see footnote 1) indicates that all three forage classes were utilized extensively, and in southeastern British Columbia the best year-long range for sheep was one having an assortment of grasses, forbs, and shrubs which provided the essential nutrient requirements during all seasons (Hebert 1973).

Table 3
Plant composition (basal cover) of three forage classes on six bighorn sheep winter ranges in Waterton Lakes, Banff, and Jasper national parks, 1968–70

Range		% composition (basal)			Total plant coverage (basal)
		Grasses	Forbs	Shrubs	
Waterton	Galwey	43.8	32.4	23.8	43.8
	Ruby	29.7	43.5	26.8	42.5
Averages		37.4	38.0	24.6	43.9
Banff	Palliser	46.6	42.9	10.5	47.6
	Bourgeau	46.7	24.0	29.3	30.0
Averages		46.6	36.1	17.3	38.8
Jasper	Disaster	19.7	17.5	62.8	42.2
	Sulfur	39.0	45.5	15.5	38.7
Averages		28.7	28.1	43.2	36.6
All parks (averages)		37.6	34.3	28.1	40.8

In general, ranges with the lowest forage production and the highest stocking rates had the least number of plant species. The light–moderately grazed Waterton ranges averaged 66 vascular species, the moderately grazed Banff ranges 60, and the heavily grazed Jasper ranges 33. Jasper averaged six grass species compared to 16 in Banff and 11 in Waterton. Trottier (1974) observed similar trends in the rough fescue grasslands of Manitoba. However, the lower number of plant species found in Jasper may have been due to more intensive glaciation in central compared to southern Alberta and a lack of refugia during glaciation (Moss and Campbell 1947).

The proportions of grasses and forbs to total vegetation were not higher in light–moderately grazed than in heavily grazed ranges (Table 3). Grasses refer to graminoids as they include grass-like genera such as *Carex* and *Juncus*. Conversely, shrubs formed a much higher proportion of the vegetation in heavily grazed ranges.

P. fruticosa was positively correlated to total forage utilization and stocking rates but negatively to forage production. Results showed that the proportion of *P. fruticosa* in the vegetation increased as forage utilization increased and as the numbers of ungulate days-use/ha increased, but decreased as forage production/ha increased. Thus, where *P. fruticosa* naturally occurs, it can possibly be used as an index to range condition on sheep ranges, provided that "normal" values are obtained for each community, based on soil, aspect, gradient, and climate. Results from this study indicate that grasslands containing over 5% and especially those with over 10% *P. fruticosa* (foliage coverage) were overgrazed.

The occurence of *Koeleria cristata*, also increased under heavy range utilization and increased stocking rates. *Festuca scabrella* only occurred on the three ranges receiving less than 50% forage utilization and which produced more than 374 kg/ha forage (dry weight). In any event, it is apparently not a natural component of Jasper ranges.

Artemisia and *Erigeron* species were common to all ranges except the one in excellent condition, Galwey, and there they were absent.

1.4. Range similarities

The six ranges showed considerable disparity even within the same park. The only genera common to all ranges (as observed in the plots) were *Agropyron*, *Carex*, *Campanula*, *Galium*, *Potentilla*, *Arctostaphylos* and *Rosa*. Other genera appearing on the plots of only five ranges but observed to some extent on all ranges were: *Bromus*, *Poa*, *Festuca*, *Koeleria*, *Artemisia*, *Erigeron*, *Achillea*, *Aster*, *Astragalus*, *Cerastium*, *Fragaria*, and *Solidago*.

Plant composition and frequency for the 17 major plant species and genera showed that *Agropyron* spp., *Festuca scabrella*, and *F. idahoensis* were the dominant grasses in Waterton compared to *Elymus innovatus* plus *Poa* and *Bromus* spp. in Banff, and *Koeleria cristata* plus *Calamagrostis* spp. in Jasper (Table 4). *Agropyron* and *Poa* spp. were present on six ranges; *Bromus* spp. and *Koeleria cristata* on five ranges. *Festuca idahoensis* was found only in Waterton, while *F. scabrella* also occurred on the Palliser range in Banff. Dominant forbs were *Campanula rotundifolia*, *Galium boreale*, *Solidago* spp., *Fragaria virginiana*, and *Aster* spp., while the three dominant shrubs were *Arctostaphylos uva-ursi*, *Potentilla fruticosa*, and *Rosa acicularis*.

Festuca scabrella, *F. idahoensis*, *Agropyron spicatum*, *Danthonia parryi*, *Carex richardsonii*, *Selaginella densa*, *Cerastium arvense*, *Lupinus sericeus*, *Arctostaphylos uva-ursi*, and *Amelanchier alnifolia* characterized the low-elevation *Festuca* grassland at Galwey. The higher elevation *Festuca* grassland at Ruby was also dominated by *F. scabrella*, but contained much less *F. idahoensis* and *Agropyron*, no *Danthonia*, and an abundance of *Carex geyeri* second only to *F. scabrella* in coverage. The dominant forbs on both grasslands were *Antennaria umbrinella*, *Eriogonum umbellatum*, and *Galium boreale* while the two dominant shrubs were the same except that *Amelanchier* was dominant compared to *Arctostaphylos* on the low elevation range.

The two *Elymus* grasslands occurred on high-elevation mesic ranges of Palliser in Banff and Sulfur in Jasper. *Poa rupicola* and *Bromus pumpellianus* were co-dominants in Banff compared to *Carex scirpoidea*, *P. rupicola*, and *Calamagrostis purpurascens* in Jasper. Dominant forbs

Table 4
Plant composition, sheep diet, and preference indices of common grasses, forbs, and shrubs on bighorn sheep winter ranges in Waterton Lakes, Banff, and Jasper national parks, 1968–70

		Diet			Range comp.			Pref.
Forage species	Range	% freq.	% comp.	Freq. x comp.(A)	% freq.	% cover	Freq. x cover (B)	index A/B
Agropyron spp.	Galwey	90	23.3	2097	90	21.8	1962	1.1
	Ruby	100	2.2	220	100	14.5	1450	0.1
	Palliser	30	0	30	30	0.9	28	1.1
	Bourgeau	90	0	90	90	9.9	691	0.1
	Disaster	100	21.0	2100	100	4.8	480	4.4
	Sulfur	56	1.4	78	56	2.6	148	0.5
Averages		78	8.0	624	78	9.1	710	1.2
Bromus pumpellianus	Galwey	0	0	0	60	0.8	51	0
	Ruby	—	—	—	—	—	—	—
	Palliser	0	0	0	90	7.0	630	0
	Bourgeau	0	0	0	70	3.6	252	0
	Disaster	29	2.9	84	43	1.1	47	1.8
	Sulfur	25	1.8	45	62	0.4	27	1.7
Averages		11	0.9	10	65	2.6	169	0.5
Calamagrostis spp.	Galwey	20	0.2	4	40	1.0	40	0.1
	Ruby	—	—	—	—	—	—	—
	Palliser	—	—	—	—	—	—	—
	Bourgeau	0	0	0	70	1.1	77	0
	Disaster	7	0.7	5	14	<0.1	0.6	8.7
	Sulfur	31	4.3	133	69	3.6	251	0.5
Averages		14	1.3	18	48	1.4	67	2.3
Festuca idahoensis	Galwey	80	17.2	1376	90	21.1	1899	0.7
	Ruby	20	8.6	172	90	8.0	720	0.2
	Palliser	—	—	—	—	—	—	—
	Bourgeau	—	—	—	—	—	—	—
	Disaster	—	—	—	—	—	—	—
	Sulfur	—	—	—	—	—	—	—
Averages		50	12.9	645	90	14.5	1305	0.5
Festuca scabrella	Galwey	100	29.8	2980	100	21.3	2135	1.4
	Ruby	80	80.1	6408	100	27.5	2745	2.3
	Palliser	0	0	0	90	12.7	1143	0
	Bourgeau	—	—	—	—	—	—	—
	Disaster	—	—	—	—	—	—	—
	Sulfur	—	—	—	—	—	—	—
Averages		60	55.0	3300	97	20.5	1988	1.2
Koeleria cristata	Galwey	70	3.2	224	90	4.6	419	0.5
	Ruby	0	0	0	10	0	0	0
	Palliser	0	0	0	80	5.8	464	0
	Bourgeau	0	0	0	90	13.2	1188	0
	Disaster	21	14.5	305	100	6.3	630	0.5
	Sulfur	—	—	—	—	—	—	—
Averages		18	3.5	—	74	6.1	451	0.2

cont'd on page 22

were *Cerastium arvense* and *Hedysarum sulphurescens* in Banff compared to *Galium boreale* and *Fragaria virginiana* in Jasper.

The two *Koeleria* grasslands were more mesic in the summer than the *Festuca* grasslands; they were as mesic as the *Elymus* grassland in Jasper but drier than the *Elymus* grassland in Banff. Co-dominant grasses on the *Koeleria* ranges were *Elymus innovatus* and *Agropyron spicatum* in Banff and *Agropyron dasystachyum*, *Carex scirpoidea*, and *C. filifolia* in Jasper. Dominant forbs were *Achillea millifolium*, *Hedysarum sulphurescens*, and *Aster sibircus* in Banff compared to *Erigeron caespitosus*, *Artemisia frigida*, and *Galium boreale* in Jasper. The dominant shrub was *Arctostaphylos uva-ursi* in both Banff and Jasper with co-dominants of *Potentilla fruticosa* in Banff and *Juniperus horizontalis* in Jasper.

1.5. Vegetation coverage and vitality

In general, the more foliage coverage relative to basal coverage on a range, the more productive the range, and conversely, the more equal the foliage coverage is to the basal coverage, the less productive the range. Thus the proportion of foliage to basal coverage, obtained by dividing the foliage values by the basal values, is a useful indicator of forage production and vitality.

For this study, I used the following ratings: foliage ÷ basal values greater than 2.5, good range; 1.5–2.5, fair range; less than 1.5, poor range. These production-vitality values varied considerably among the three parks studied: grass, forb, and shrub values were more than twice as high in Waterton as they were in Banff and Jasper. I rated range vitality in Waterton as good, Banff fair, and Jasper poor. Variation in plant species from park to park probably also accounts for some of the variation in range vitality.

Grass coverage (canopy) values were 92.1% in Waterton, 54.5% in Banff, and 30.6% in Jasper. Basal coverage values were less dissimilar with comparable total

Table 4, cont'd

		Diet			Range comp.			Pref.
Forage species	Range	% freq.	% comp.	Freq. x comp. (A)	% freq.	% cover	Freq. x cover (B)	index A/B
Elymus innovatus	Galwey	—	—	—	—	—	—	—
	Ruby	—	—	—	—	—	—	—
	Palliser	0	0	0	80	14.7	1180	0
	Bourgeau	0	0	0	90	12.9	1161	0
	Disaster	0	0	0	14	0.2	3	0
	Sulfur	50	2.9	145	87	5.1	441	0.3
Averages		12	0.7	—	68	8.2	558	0.1
Poa spp.	Galwey	0	0	0	20	0.1	3	0
	Ruby	0	0	0	10	1.3	13	0
	Palliser	0	0	0	100	9.3	930	0
	Bourgeau	0	0	0	90	6.0	540	0
	Disaster	0	0	—	7	0.1	0.3	0
	Sulfur	25	4.7	118	75	2.7	203	0.6
Averages		4	0.8	—	50	4.6	320	0.1
Aster spp.	Galwey	0	0	0	20	0.8	16	0
	Ruby	0	0	0	30	0.2	8	0
	Palliser	0	0	0	30	0.3	9	0
	Bourgeau	30	13.6	408	90	3.1	284	1.4
	Disaster	—	—	—	—	—	—	—
	Sulfur	6	1.1	6.6	31	<0.1	1	6.6
Averages		7	2.9	—	40	0.9	36	1.6
Campanula rotundifolia	Galwey	10	0.3	3	70	0.9	63	<0.1
	Ruby	50	7.0	350	90	4.4	396	0.9
	Palliser	0	0	0	60	0.5	33	0
	Bourgeau	0	0	0	20	0.2	4	0
	Disaster	21	2.9	61	86	1.6	138	0.4
	Sulfur	6	0.7	4	31	0	0	0
Averages		14	1.8	25	59	1.3	77	0.2
Fragaria virginiana	Galwey	0	0	0	10	0.1	2	0
	Ruby	0	0	0	30	0.6	18	0
	Palliser	0	0	0	70	4.1	291	0
	Bourgeau	0	0	0	20	0.3	7	0
	Disaster	—	—	—	—	—	—	—
	Sulfur	25	1.4	35	62	2.2	137	0.3
Averages		5	0.3	1	38	1.5	57	<0.1
Galium boreale	Galwey	0	0	0	100	4.4	440	0
	Ruby	0	0	0	90	5.3	482	0
	Palliser	0	0	0	10	<0.1	1	0
	Bourgeau	20	9.1	182	80	2.7	220	0.8
	Disaster	86	2.2	189	100	2.4	240	0.8
	Sulfur	12	1.1	13	94	2.5	235	<0.1
Averages		20	2.1	42	79	2.9	229	0.3
Phacelia sericia	Galwey	—	—	—	—	—	—	—
	Ruby	0	0	0	20	0.1	2	0

cont'd on page 23

Table 4, cont'd

Forage species	Range	Diet % freq.	Diet % comp.	Diet Freq. x comp. (A)	Range comp. % freq.	Range comp. % cover	Range comp. Freq. x cover (B)	Pref. index A/B
Phacelia sericia	Palliser	0	0	0	30	0.2	6	0
	Bourgeau	0	0	0	60	0.4	24	0
	Disaster	—	—	—	—	—	—	—
	Sulfur	19	1.4	27	19	1.1	21	1.3
Averages		5	0.4	2	32	0.5	16	0.3
Solidago spp.	Galwey	0	0	0	30	0.3	9	0
	Ruby	0	0	0	20	0.3	6	0
	Palliser	10	11.1	111	80	6.1	492	0.2
	Bourgeau	0	0	0	10	0.1	1	0
	Disaster	0	0	0	29	0.2	6	0
	Sulfur	12	1.1	13	19	0	0	0
Averages		4	4.1	16	31	1.2	37	<0.1
Arctostaphylos uva-ursi	Galwey	0	0	0	100	21.9	2190	0
	Ruby	0	0	0	90	14.4	1296	0
	Palliser	0	11.1	0	60	4.8	288	0
	Bourgeau	0	0	0	80	11.2	896	0
	Disaster	0	0	0	100	24.9	2490	0
	Sulfur	0	0	0	6	0.4	3	0
Averages		0	1.9	0	73	12.9	941	0
Potentilla fruticosa	Galwey	10	0.4	4	20	1.2	24	0.2
	Ruby	—	—	—	—	—	—	—
	Palliser	0	0	0	40	0.6	24	0
	Bourgeau	0	0	0	80	3.6	288	0
	Disaster	57	26.8	1528	100	5.4	536	2.9
	Sulfur	100	42.8	4280	100	7.7	770	5.5
Averages		33	14.0	462	68	3.7	252	1.8
Rosa acicularis	Galwey	0	0	0	70	2.8	196	0
	Ruby	0	0	0	90	4.2	378	0
	Palliser	0	0	0	30	0.5	15	0
	Bourgeau	10	4.5	45	80	3.6	288	0.2
	Disaster	14	1.4	20	29	0.7	21	1.0
	Sulfur	12	1.8	22	31	0.6	19	1.2
Averages		6	1.3	14	55	2.1	115	1.0

vegetation values of 43.9, 38.8, and 36.6% respectively.

Litter refers to dead vegetation that ultimately becomes organic matter and which influences soil fertility and structure. It is therefore a soil attribute and the amount present reflects plant production and utilization as well as range trend. On these ranges, litter coverage values were 47.1, 19.4, and 13.0% for Waterton, Banff, and Jasper respectively. Evidently, basic plant production and vigour were lower, and/or grazing heavier in Jasper compared with Banff and Waterton.

The inferior range condition in Jasper was also revealed in a higher percentage of bare soil, rock, and erosion pavement compared with Banff and Waterton (Table 5). At Jasper, 48.7% of the ground contained no organic covering compared to 39.5 and 8.4%, respectively, for Banff and Waterton. Although these values are in part soils-related, they do signify Jasper's inferior range condition.

1.6. Forage production and utilization

Table 4 gives diet values and preference index values based on plant utilization during or slightly prior to the July–early August period. The sheep diet value is the product of diet frequency (% transects on which the species were utilized) and diet composition (% all plants utilized of that species). These diet values, divided by range composition (% frequency x % cover) gave the preference index values.

Wheatgrasses provided the highest percentage of the diet throughout all ranges whereas rough fescue and Idaho fescue were the main diet species along with wheatgrasses in Waterton. Junegrass, brome, and blue grasses provided most of the grass diet on the heavily grazed Jasper ranges abetted by northern bedstraw, shrubby cinquefoil, and rose. The most preferred species during midsummer were reedgrasses, shrubby cinquefoil, asters, wheatgrasses, and rough fescue. Shrubby cinquefoil and asters were not noticeably preferred on the lightly grazed Waterton ranges.

A comparison of both production and utilization indicates that ranges producing the least forage, but with the greatest utilization, have the greatest proportion of forbs and shrubs to grasses (Table 6).

Forage production (dry wt.) increased as the stocking rate decreased and grass production was about four times greater on the light–moderate than on the heavily stocked ranges. The proportion of grass in the ungulate diet decreased as the stocking rate increased (Table 6).

Forb production was similar under the three rates of stocking, although the proportion both in the diet and in the forage composition increased directly with increased stocking rates. Shrub production was light on all ranges and neither this nor shrub utilization appeared correlated with stocking rates and range use (Table 6).

On all ranges studied forage production increased an average of 62.6% under two years of protection from grazing, but only 27.2% after five years of protection (Appendix 2, see footnote 1). Production within the five-year-old exclosure on the productive Galwey range was slightly less than on the adjacent moderately grazed range. The heavy mantle of dead vegetation appeared to smother and kill-out some plants, in particular Idaho fescue. This species is known to increase under heavy grazing (Johnston, Dormarr, and Smoliak 1971). Flook and Stringer (1974) reported similar results for a low-elevation grassland in Banff. Evidently, some grazing is important in maintaining maximum forage production, especially on grasslands producing at least 454 kg (green wt.) of forage.

Forage utilization averaged 47% for grass, 56% for forbs and 44% for shrubs with an average of 47% for all vegetation (Table 6 and Appendix VIII, see footnote 1). Use of the preferred forage species was probably closer to 75–100%. On the three ranges with the heaviest forage use (Disaster, Sulfur, and Bourgeau), deciduous vegetation was utilized 59, 63, and 48% respectively, indicating that these ranges were overstocked in the technical sense. The range damage evidenced on these three ranges was probably due not so much the 57% forage utilization as the repeated use of the same ranges during May and June of every year when the carbohydrate reserves of the plants were low. The range plants could probably withstand 70–80% use during the dormant fall and winter period. Maximum forage utilization values for foothill and mountain grassland ranges in Alberta are 55% of all forage (Lodge *et al* 1971), whereas optimum utilization in order to maintain a good proportion of preferred climax species should probably be closer to 30–40% utilization of all forage. Grass utilizations on these three ranges averaged 58.3% compared to an average forb utilization of 61.2%. Palliser and Galwey ranges received considerably less forage use (45% average) and could be considered moderately or

Table 5
Ground coverage, forage production index, and range vitality of bighorn sheep winter ranges in Waterton Lakes, Banff, and Jasper national parks, 1968–70

		% ground covered* by each element																
		Grasses			Forbs			Shrubs			Total veg.					Rock &		Range
Range		B	F	F/B	B	F	F/B	B	F	F/B	B	F	F/B	Litter	Bare soil	erosion pavement	Moss	vitality rating
Waterton	Galwey	19.2	81.4	4.2	14.2	32.2	2.3	10.4	26.7	2.6	43.8	140.3	3.2	45.3	6.6	1.7	0.1	Good
	Ruby	12.6	63.7	5.1	18.5	51.7	2.8	11.4	36.6	3.2	42.5	152.0	3.6	48.8	7.4	0.1	0.3	Good
Averages		16.4	75.7	4.6	16.7	42.1	2.5	10.8	31.8	2.9	43.9	149.6	3.4	47.1	7.0	1.4	0.2	Good
Banff	Palliser	22.2	35.4	1.6	20.4	32.3	1.6	5.0	4.7	0.9	47.6	72.4	1.5	20.0	12.5	19.5	1.6	Fair –
	Bourgeau	14.0	38.0	2.7	7.2	18.8	2.6	8.8	13.0	1.5	30.0	69.8	2.3	19.0	4.3	42.6	3.2	Fair+
Averages		18.1	36.4	2.0	14.0	25.7	1.8	6.7	9.4	1.4	38.8	71.5	1.8	19.4	8.4	31.1	2.4	Fair
Jasper	Disaster	8.3	8.6	1.0	7.4	3.7	0.5	26.5	7.2	0.3	42.2	19.5	0.5	14.9	37.8	4.7	0.1	Very poor
	Sulfur	15.1	23.5	1.6	17.6	13.9	0.8	6.0	7.5	1.2	38.7	44.9	1.2	3.6	4.4	41.1	4.8	Poor
Averages		10.5	20.1	1.9	10.3	11.6	1.2	15.8	7.4	0.4	36.6	39.1	1.1	13.0	21.3	27.4	1.6	Poor
Total averages		15.3	41.8		14.2	24.8		11.4	14.8		41.1	83.1		25.3	12.2	18.3	1.7	

* B = Basal hit, which refers to a crown hit or where a blade or stem enters the ground. F = Foliage hit, which is recorded only when the vertical projection of a point passes through foliage, but not the visible basal or crown portion of the plant. Values are absolute values from all samples and not averages from sample percentages.

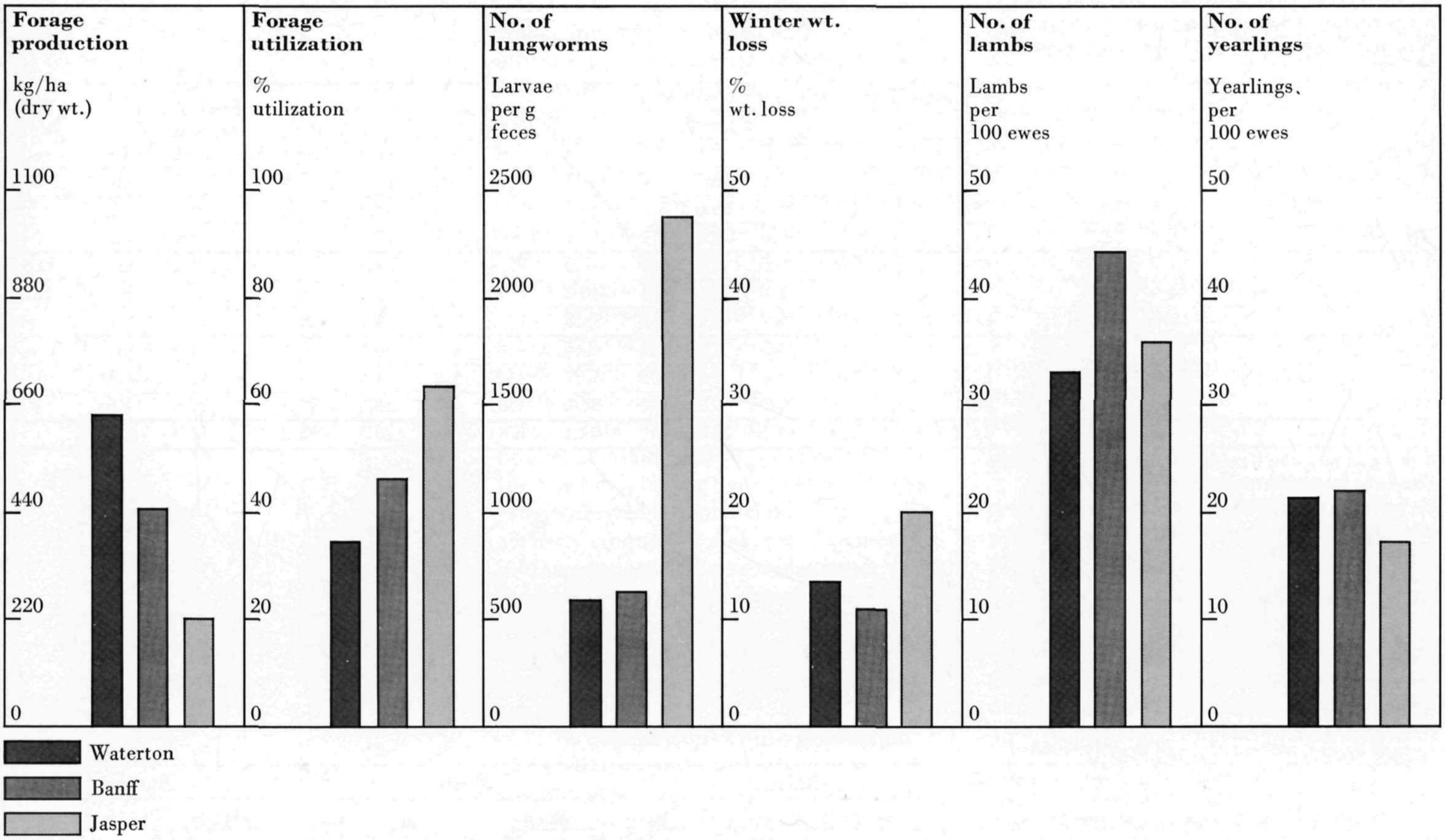
Table 6
Relationships between forage production, forage composition, and ungulate stocking rates and forage utilization on bighorn sheep winter ranges stocked lightly, moderately, and heavily, 1968–71

	Stocking	Forage	Forage	Grass‡				Forbs				Shrubs			
	rate	utiliz'n	prod.	kg/ha				kg/ha				kg/ha			
Range	sheep-days* per ha	as % all veg.†	kg/ha dry wt.	Prod.	Used	% of diet	% forage	Prod.	Used	% of diet	% forage	Prod.	Used	% of diet	% forage
Waterton	Lt. 20	Lt.-mod. 37	Good 619	510	176	77	82	86	42	18	14	22	11	5	4
Banff	Mod. 40	Mod.-hvy. 46	Fair 474	391	173	80	82	81	45	20	17	2	1	<1	<1
Jasper	Hvy. 65	Hvy. 62	Poor 225	130	86	63	58	77	45	32	35	17	7	5	7
Averages	42	47	439	344	145	74	74	82	44	23	22	13	7	4	4

* Sheep-days/ha refers to total ungulate use converted to sheep-days using the conversion of 1 elk = 2.9 sheep and 1 deer = 0.97 sheep.
† Conifer and Arctostaphylos vegetation not included.
‡ Grass includes sedges, rushes, and other grass-like plants.

Figure 8
Correlations of forage production, forage utilization, lungworm burdens, percent animal winter weight loss, and animal productivity within three national parks, 1967–71.

Figure 8



optimally stocked. Grass and forb use averaged 41.8 and 58.0% respectively on these two ranges. On the lightly-stocked Ruby range, total forage use was 24.3%, while utilization of grasses and forbs was 24.2 and 24.5%.

Strong correlations existed between forage utilization and each of lungworm burden, yearlings: 100 ewes, winter weight-loss of ewes, and forage production, in decreasing order of significance (Fig. 8).

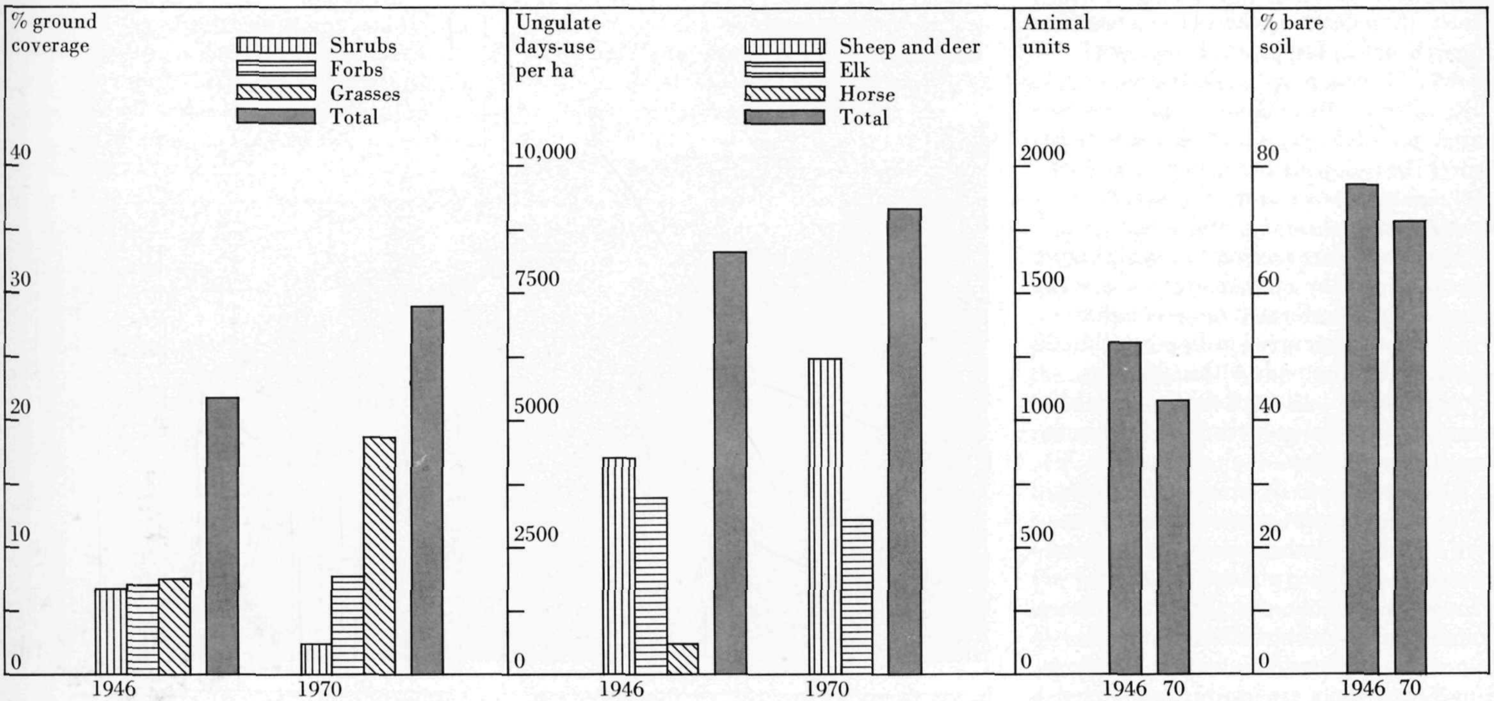
As forage utilization increased, forage production decreased, the lungworm burden increased, the winter weight-loss of sheep increased, and the numbers of yearlings: 100 ewes decreased. There was no significant correlation between forage utilization and the number of lambs: 100 ewes. Diet preferences for each forage type based on the relationship between forage produced and ungulate diet (% forage and % diet, Table 6) varies with the three rates of range stocking. On lightly and moderately stocked ranges the order of preference was forbs, shrubs, and grasses and on heavily stocked ranges, forbs, grasses, and shrubs.

Range production values must be further examined according to range site potentials as some ranges have higher potential for both forage production and utilization than others. For example, the lightly grazed (24.3%) Ruby range produced only 387 kg/ha of forage compared to 849 kg/ha for the moderately utilized (44.1%) Galwey range within the same park.

Based on differences in forage production within exclosures on ranges subjected to various intensities of grazing pressure, I derived approximate range potentials for the six winter ranges. Results showed that wild ungulate grazing on three heavily grazed ranges (Disaster, Sulfur, and Bourgeau) suppressed forage production 50, 50, and 28% respectively. Heavy grazing seemed to maintain these ranges as zootic disclimaxes. Although the productive Galwey range was moderately stocked, grazing did not significantly suppress forage production on this range, in

Figure 9
Correlations of plant coverage, ungulate use, and percent bare soil on winter ranges in Athabasca Valley, Jasper National Park, during two periods of peak ungulate populations, 1946 and 1970.

Figure 9



fact it may have slightly enhanced production. The Waterton ranges appeared to be close to climatic climax and the forage production of 849 kg/ha (dry wt.) for Galwey appears close to the maximum production potential for sheep ranges in the three parks. On the Palliser range, grazing suppressed forage production by about 20%.

A discussion follows which compares range conditions along the Athabasca Valley, Jasper in 1970 with that in 1946. In the 1940s grassland ranges along the Athabasca Valley were in a severely overgrazed condition (Cowan 1947*a*, 1950; Pfeiffer 1948; Flook 1964) with elk competing strongly with sheep for an inadequate supply of grassland forage. These deteriorated winter ranges, excessive numbers of native ungulates and horses, plus three unusually severe winters resulted in an 84% decline in sheep populations during the winters of 1946–49 (Stelfox 1971).

Range surveys of four sheep winter ranges along this same valley in July 1970 showed sheep numbers had increased by 1970 to levels similar to 1946, and grassland range conditions again appeared overgrazed.

The comparable studies during peak populations in 1946 and 1970 indicated that the overgrazed ranges of the 1940s recovered following the 1946–49 die-off so that they were able to support similar numbers of ungulates during the next population peak (Figure 9).

Plant coverage, especially grass, increased noticeably between 1946 and 1970 (Figure 9). Although total basal coverage increased only 32%, grass coverage increased 157%. During this period, forb and shrub coverage decreased 29 and 37% respectively. I believe this marked increase in grass coverage was due to:
1. the reduction of horse grazing in the 1950s and its elimination in the 1960s; since the mid-1800s large numbers of horses grazed year-long on these low-elevation grasslands (Moberly and Cameron 1929, Pfeiffer 1948); this would undoubtedly be more detrimental to these grasslands than seasonal (winter period only) grazing by native ungulates;
2. a 12% decrease in range use by elk in 1970 compared to 1946; stomach analyses of elk along this valley showed that their diet consisted of 97% grass compared to 83% for sheep and 15% for mule deer (Cowan 1947*a*).

Decreases in forb and shrub coverages were most pronounced in *Arctostaphylos uva-ursi*, *Lapula echinata*, *Artemisia frigida*, *Aster sibiricus*, and *Antennaria nitida*. Russian thistle (*Salsola pestifer*) continued to increase in coverage, while a marked decrease was observed in shrubby cinquefoil from 1946 to 1970. Figure 10 shows the general appearance of a heavily grazed range in Jasper, while Figure 11 shows a healthy range in Waterton.

The results obtained in 1970 compared to 1946 are significant because they reflect the following facts about the relationships between sheep population fluctuations and their winter ranges:

1. Sheep numbers recover following major die-offs caused by a pneumonia–lungworm disease and deteriorated range complex. This recovery occurred in Jasper within 20 years and in Kootenay within 25 years. Thus major die-offs attributed to the above complex do not always result in long-term population declines.
2. Range productivity recovers following periods of range deterioration and excessive ungulate numbers, providing grazing pressure is reduced at least 75% for about a decade following the die-off. Sheep numbers and range conditions are enhanced by a reduction in interspecific grazing competition, especially from horses and elk.

In conclusion, heavy grazing (398 sheep-days/ha and 61% utilization of all deciduous vegetation) noticeably suppressed forage production on winter grassland ranges. Light–moderate grazing (124 sheep-days/ha and 37% vegetation utilization) did not suppress, in fact, appeared to enhance production. Heavy grazing was associated with a significant decline in the grass and a corresponding increase in the forb component of forage. Following die-offs, precipitated by overgrazed ranges, both range productivity and sheep numbers recovered comparably to prior levels. No long-term deleterious effects on either the sheep or their winter ranges were indicated as a result of temporarily overgrazed ranges and population die-offs.

1.7. Forage quality and sheep preferences

Four factors are important to a discussion of seasonal forage qualities:

Figure 10

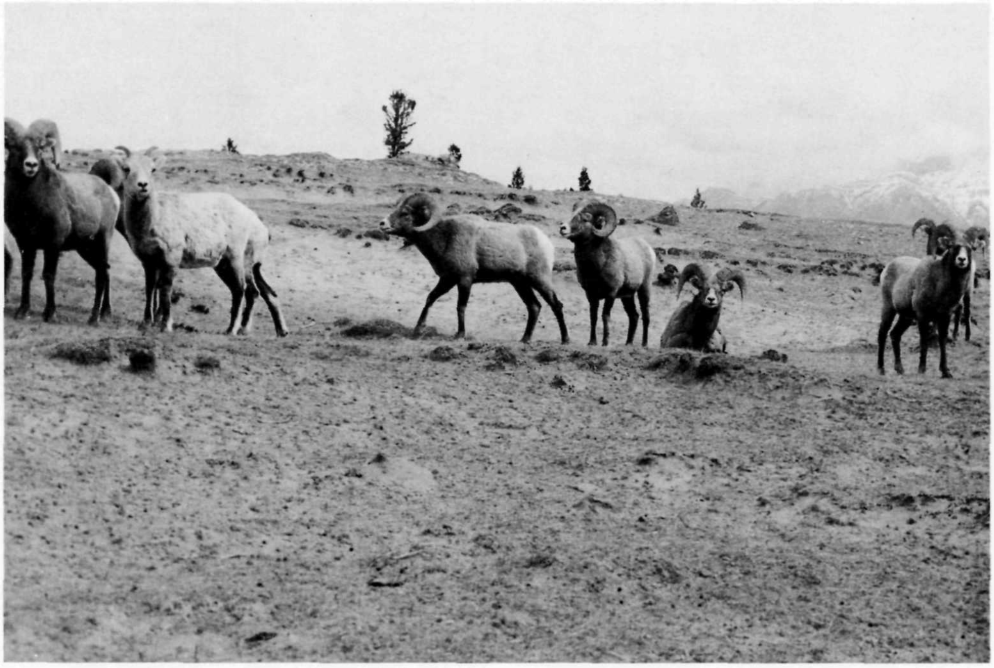


Figure 10
Heavily grazed Talbot range, Athabasca Valley, Jasper, January 1970.

Figure 11

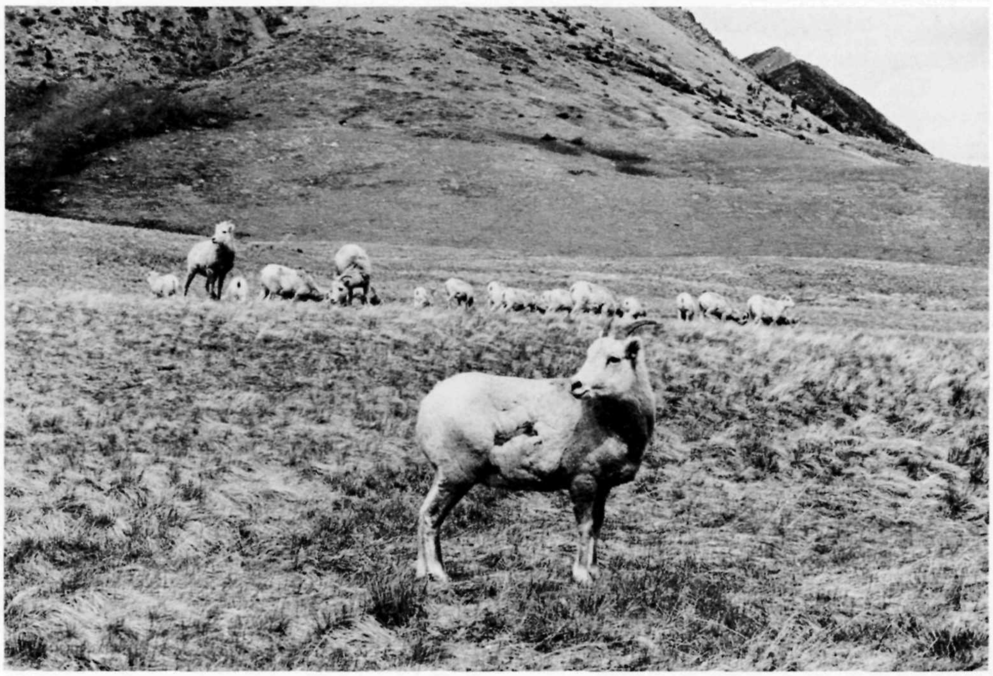


Figure 11
Bighorn sheep on good range at Waterton Lakes National Park, 1970.

1) green, young vegetation is more nutritious, palatable, and digestible than dormant, dry vegetation (Cook and Harris 1950, McCann 1956, Capp 1967, Dietz 1970, Hebert 1973); 2) alpine vegetation is nutritionally superior to low-elevation forage when similar species are compared (Johnston, Bezeau, and Smoliak 1968, Hebert 1973); 3) free-ranging sheep maximize nutrient intake by pursuing areas of "green-up" which occur on various exposures and elevations throughout a six-month growing season (April–September); 4) forage quality is strongly influenced by climate through its effects on plant nutrient content, the periods of commencement and cessation of growth, and the availability of forage.

High quality forage has high palatability, optimum levels of various nutrients, high digestibility of nutrient components, volatile fatty acids in optimum proportions for efficient energy production, adequate levels of minerals, vitamins, and trace elements, and efficient convertibility into components necessary for the animal body over sustained periods (Dietz 1970).

Sheep basically forage upward along slopes facing south and east in May and June until they reach the subalpine and alpine grasslands. In July and August they forage on south and west slopes at the highest vegetated elevations and along alpine valley bottoms as snow fields recede. By late August and early September, pasturing shifts towards north-facing grasslands and semi-open forests where snow melts the latest, and where herbaceous forage remains succulent and nutritious late into the fall. During cool-moist summers and falls, most foraging occurs within the south quadrants as forage remains succulent and more nutritious than on north-facing or shaded slopes (Stelfox and Taber 1969).

During winter months, sheep range on grasslands facing south and west at either high or low elevations depending on snowpack conditions. They lose considerable weight on dormant vegetation and their reproductive success is largely dependent upon the duration and intensity of winter and also on the rapidity of spring green-up. Valley-bottom and low-elevation south-facing slopes are evidently important to sheep in late pregnancy, and they influence lamb production and survival because they are the first areas to green-up and provide the high-protein forage necessary during late-pregnancy and early-lactation. If spring growth is retarded by cold weather, ewes are restricted to dormant forage which is lower in protein, phosphorus, energy, and carotene than green forage (Cook and Harris 1950). Without a high protein diet during late pregnancy, reproductive rates decline and juvenile mortality increases (Ransom 1964, Hebert 1973; see also section 3, Winter climate).

In this study, I evaluated forage quality by determining the nutritive values of 18 important range species, and by determining forage preference indices based on the comparative use of one species to another. High-elevation forage was significantly higher in protein, phosphorus and moisture, but lower in crude fiber and calcium than low-elevation forage. Forbs were highest in protein, calcium, and phosphorus while shrubs were highest in crude fiber. High-elevation ranges were Ruby, Palliser, and Sulfur, while low-elevation ranges were Galwey, Disaster, and Radium.

Diet composition data indicated that in the summer (July to early August) sheep utilized grasses more than forbs or shrubs (Table 7) and to a greater extent on the two productive Waterton ranges than on the overgrazed Jasper ranges. However, the degree of use of grasses was actually heavier on the unproductive Jasper ranges in the summer, indicating heavy use on a limited supply of grass with the more abundant shrubs and forbs forming a greater proportion of the diet (Tables 4 and 7). Grass use remained relatively constant throughout the year, with the heaviest use in winter (January–March) followed by less use in spring (April–June) and fall (October–December) and least use in summer (Table 7).

Four grasses which provided most of the July grass diet in decreasing order of use, were *Festuca scabrella*, *F. idahoensis*, *Danthonia parryi*, and *Agropyron* spp. The actual degree of summer use on individual grass plants was heaviest on *Agropyron dasystachyum*, *A. trachycaulum*, and *Koeleria cristata* for all three parks, with *A. spicatum* and *Festuca* spp. receiving somewhat less use. *Bromus* and *Calamagrostis* species received as much use as the above grasses on the Jasper ranges, but little or no use on Banff and Waterton ranges (Table 7). During mid-August, use of *F. scabrella* plants was spotty, ranging from nil to heavy. *F. idahoensis* received somewhat higher summer use, with 67% of the use being moderate and heavy. For both fescues plus *Agropyron spicatum*, use was noticeably heavier at the higher elevations. Use on *A. spicatum* was rated as nil–light near the valley bottoms compared to moderate–heavy midway up the mountain side. This difference was believed due to higher moisture and protein contents on the more mesic upper slopes, which undoubtedly increases palatability. *Koeleria cristata* was utilized heavily on all ranges whereas *Carex geyeri* was not noticeably used during the summer period.

Certain shrubs utilized heavily during midsummer were *Amelanchier alnifolia*, *Rosa acicularis*, and *Cornus stolonifera*. The low-preference shrubs, *Shepherdia canadensis* and *Potentilla fruticosa*, received moderate–heavy use during early June when new growth began. During the summer period these species received little or no use on the good-condition ranges (Galwey, Ruby, and Palliser) but moderate use on the poor-condition Jasper ranges. *P. fruticosa* in July provided 42.8 and 26.8% of the diet on the two poor-condition Jasper ranges compared to 0.4, 0, and 0% of the diet on the good-condition ranges. Another low-preference shrub, *Rosa acicularis*, received

Table 7
Percent utilization of major vegetation species by season on six winter ranges in Waterton Lakes, Banff, and Jasper national parks, 1967–72
(– = species not present, 0 = no utilization)

	Winter			Spring			Summer			Fall			Year-long		
Species	W'ton	Banff	Jasper	W'ton	Banff	Jasper	W'ton	Banff	Jasper	W'ton	Banff	Jasper	W'ton	Banff	Jasper
Grasses															
*Agropyron da**	30	75	0	0	60	20	25	27	27	20	50	10	19	53	14
Agropyron sp.†	75	75	0	25	25	10	10	10	37	50	50	0	40	40	12
Bromus spp.	0	0	0	0	10	10	0	0	35	0	0	0	0	2	11
Calamagrostis spp.	5	0	0	2	10	0	0	0	27	3	0	0	2	2	7
Carex spp.	75	0	0	25	0	25	0	0	2	50	0	0	37	0	7
Elymus in.	0	5	0	0	45	10	0	0	0	0	3	0	0	13	2
Festuca spp.	75	0	0	10	50	2	10	10	10	50	0	10	36	15	5
Koeleria cr.	30	75	0	0	60	20	25	27	27	20	50	10	19	53	14
Danthonia spp.	75	—	—	25	—	—	0	—	—	50	—	—	37	—	—
Juncus spp.	10	75	—	3	27	—	0	0	—	3	50	—	4	38	—
All grasses	37	34	0	9	32	12	7	8	21	25	23	4	19	24	9
Forbs															
Artemisia fr.	—	—	10	—	—	10	—	—	28	—	—	25	—	—	18
Achillea mi.	0	0	0	0	0	2	0	0	2	0	0	0	0	0	1
Anemone mu.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0.5
Astragalus spp.	0	0	0	0	0	0	0	0	35	0	0	0	0	0	9
Campanula ro.	0	0	0	0	0	0	25	0	37	0	0	0	8	0	9
Erigeron spp.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0.5
Fragaria vi.	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0.5
Galium bo.	0	0	0	0	0	10	0	2	0	0	0	0	0	0.5	2
Hedysarum spp.	0	0	0	0	25	25	0	35	10	0	0	0	0	15	9
Hieraceum spp.	0	—	—	0	—	—	10	—	—	0	—	—	2	—	—
Oxytropis spp.	—	0	0	—	50	50	—	10	27	—	0	2	—	15	20
Senecio spp.	0	0	0	0	0	10	0	0	0	0	0	2	0	0	3
Solidago de.	0	0	0	0	0	0	0	0	3	0	0	2	0	0	1
Taraxacum of.	—	0	0	—	0	10	—	0	25	—	0	10	—	0	11
Trifolium spp.	0	0	0	0	0	10	0	0	25	0	0	10	0	0	11
All forbs	0	0	1	0	6	9	3	4	14	0	0	4	1	2	7
Shrubs															
Amelanchier al.	60	0	0	50	0	0	10	0	2	20	0	0	35	0	0.5
Arctostaphylos uv.	2	0	3	3	0	3	0	0	0	0	0	0	1	0	2
Potentilla fr.	5	10	0	2	38	10	0	0	27	3	0	0	2	12	9
Rosa ac.	75	0	0	35	10	20	0	0	60	35	0	0	36	2	20
Prunus pe.	75	0	0	25	0	0	0	0	0	50	0	0	37	0	0
Salix spp.	2	75	0	0	50	2	0	0	35	0	50	10	0.5	44	12
All shrubs	36	14	0.5	19	16	6	2	0	21	18	8	2	18	10	7

* Includes some *Agropyron trachycaulum*.
† Includes some *Agropyron subsecundum*

heavier use on the three poor-condition ranges even though it was just as abundant on the better-condition ranges (Table 4).

Four forbs which provided most of the July forb diet were: *Silene parryi*, *Anemone* spp., *Oxytropis* spp., and *Hedysarum* spp. Forb use was primarily confined to the late spring–early fall period (May–October) whereas shrub use was common throughout the year (Table 7). A negative correlation existed between range condition and forb utilization with most forb use occurring on the heavily grazed Jasper ranges.

1.8. Effects of climate on forage production.

Under conditions of moderate grazing, climate is the major factor modifying plant cover, while under heavy grazing climate is often less important (Coupland 1958). Most grassland range studies agree that the worst depletion in forage associated with drought occurs on overgrazed ranges. Precipitation during the months of May and June had the greatest effect of any weather factor on forage yield of short-grass prairies in one growing season (Smoliak 1956). Seasonal mean temperature, hours of bright sunlight, and wind velocity had a negative effect on forage production in the study. The start of continuous spring growth on sheep ranges in British Columbia coincided with the date when daily air temperature rose to 5.6°C, whereas the date growth ceased coincided closely with the date when available soil moisture supplies were exhausted (Harper 1969).

My study showed a general positive correlation between forage production and both spring soil moisture and spring precipitation, although the results were not completely consistent for the six ranges (Tables 8 and 9). There also appeared to be some interrelationships between soil moisture and precipitation both in the spring and the previous winter. Soil temperature did not appear to be positively correlated with forage production.

Water-holding capacity is approximately the percent difference between soil moisture values at the wilting point and field capacity, 15 and ⅓ atm. respectively. Water-holding capacities (%) for four of the ranges were Disaster 18.5, Palliser 11.7, Galwey 11.2, and Ruby 1.4. Although the Disaster soil had the highest water-holding capacity, it produced the least forage. The Ruby soil had a water-holding capacity only 8% as great as the Disaster soil, yet it produced more than twice as much forage. This must be largely due to the fact that precipitation on the Ruby range amounted to 34.5 cm during the spring period (April–June) compared to only 8.6 cm at Disaster during the same period. The Galwey range also received 34.5 cm of precipitation during the spring period and had a high water-holding capacity, which largely accounts for the high forage production of 849 kg/ha of dry forage.

Results obtained from correlation analysis on the effects of 34 climatic variables on forage production suggested that spring, summer, and previous winter data should be used in the step-wise regression analysis using the 12 variables of forage production, soil moisture and temperature, and precipitation.

The results from five regressions performed on these 12 variables showed that spring precipitation was the single most important variable and typically explained 40% of the variation in forage production. Spring soil moisture explained a further 33% of the variation, with all subsequent variables in the regression each accounting for 2 to 3% of the total variability. A formula was produced for predicting forage production from the regression analysis. The formula states that:

Forage Production = − 1117.9 + 169.3 x (spring precipitation) + 22.3 x (spring moisture 0–15 cm) − 68.4 x (previous winter precipitation) + 26.4 x (20 cm spring temperature) + 34.1 x (summer moisture 0–15 cm) − 15.9 x (summer precipitation).

In summary, spring soil moisture and spring precipitation appear to be the two most important factors affecting forage production.

1.9. Range condition summary

Based on the above evaluations of plant composition, plant density, plant vigour, soil, and litter, the conditions of the six ranges studied were determined to be:

Range		Condition
Waterton		Good
	Galwey	Good
	Ruby	Good
Banff		Fair
	Palliser	Fair-good
	Bourgeau	Poor-fair
Jasper		Poor
	Disaster	Poor
	Sulfur	Fair-poor

1.10. Range trend

Range trend is determined by evaluating three factors: plant vigour, plant reproduction, and soil erosion. Because I did not measure plant reproduction in this study, I based trend primarily on plant vigour and soil erosion. Plant vitality (vigour), based on the difference between foliage and basal coverage values, gives a reasonable index to range trend. These differences indicate that plant vigour was good in Waterton, fair in Banff, and poor in Jasper (Table 5). On the poor and fair condition ranges, vigour was lower for shrubs and grasses than for forbs. For example, a comparison of Jasper and Waterton foliage ÷ basal values showed 0.4 and 2.9 for shrubs, 1.9 and 4.6 for grasses, 1.2 and 2.5 for forbs respectively. Similar differences existed between Banff and Waterton indicating that shrubs were reduced to the lowest vitality on heavily grazed ranges, grasses reduced somewhat less, and forbs least.

Soil erosion proved to be a useful indicator of range trend in some areas. Plant pedestals and plant disturbance by pawing and trampling were the main form

Table 8
Forage production, soil moisture, soil temperature, and precipitation on six bighorn sheep winter ranges, 1968–71

Park	Range & Year	Forage prod'n (kg/ha dry wt.)	Soil moisture (%)*		Soil temp. (°C)*		Precipitation (cm)†				
			Spring	Summer	Spring	Summer	Spring	Summer	Spring, summer	Previous summer	Previous winter
Waterton	**Galwey**										
	1968	884									
	1969	734	7.7	3.3	16.6	17.8	37.0	6.5	44.2	29.5	54.4
	1970	930	6.3	7.1	13.3	13.1	37.8	38.3	77.2	6.6	48.0
	1971						27.3	12.5	40.4	38.9	53.1
	Averages	849	7.0	5.2	15.0	15.5	34.0	19.0	53.8	24.9	51.8
	Ruby										
	1968	314									
	1969	447	5.6	2.0	16.4	18.1	37.0	6.5	44.2	29.5	54.4
	1970	399	5.3	5.0	10.2	14.2	37.8	38.3	77.2	6.6	48.0
	1971						27.3	12.5	40.4	38.9	53.1
	Averages	387	5.4	3.5	13.3	16.2	34.0	19.0	53.8	24.9	51.8
Banff	**Palliser**										
	1968	320									
	1969	922	24.0	8.4	11.7	15.4	21.8	15.3	37.6	13.7	21.6
	1970	614	19.9	8.7	11.2	13.2	13.8	6.5	20.6	15.5	11.2
	1971						12.5	8.5	21.3	6.6	20.8
	Averages	619	21.9	8.5	11.4	14.3	16.0	10.0	26.4	11.9	17.8
	Bourgeau										
	1968	131									
	1969	461	15.4	6.6	14.8	13.7	21.8	15.3	37.6	13.7	21.6
	1970	396	10.2	6.8	14.9	18.4	13.8	6.5	20.6	15.5	11.2
	1971						12.5	8.5	21.3	6.6	20.8
	Averages	330	12.8	6.7	14.9	16.1	16.0	10.0	26.4	11.9	17.8
Jasper	**Disaster**										
	1968	249									
	1969	120	13.7	18.8	17.9	10.4	5.0	19.3	24.3	15.0	10.7
	1970	151	13.2	7.0	16.5	14.0	7.5	5.3	12.9	19.6	9.4
	1971						13.0	12.3	25.6	5.3	19.6
	Averages	174	13.4	12.9	17.2	12.2	8.5	12.3	21.1	3.2	13.2
	Sulfur										
	1968	358									
	1969	184	14.6	15.5	12.3	7.5	7.3	19.8	27.4	13.0	10.7
	1970	281	10.7	8.4	14.4	9.9	11.0	8.0	19.3	20.1	9.3
	1971						12.3	14.3	26.9	8.1	19.6
	Averages	274	12.6	11.9	13.3	8.7	10.3	14.0	24.6	13.7	13.2
Averages (all ranges)	Waterton	617	6.2	4.3	14.2	15.9	34.0	19.0	24.9	53.6	51.8
	Banff	474	17.3	7.6	13.2	15.2	16.0	10.0	11.9	26.4	17.0
	Jasper	228	13.0	12.4	15.3	10.5	9.3	13.0	13.5	22.8	13.0
	All	439	12.2	8.1	14.2	13.9	19.8	14.0	16.8	34.3	27.7
	1969	478	13.5	9.1	15.0	13.8	21.8	13.8	19.1	36.1	29.0
	1970	461	10.9	7.2	13.4	13.8	20.3	17.3	14.0	38.1	22.9

* Soil moisture and temperature values are averages of four values (two each for June and July at the two depths). Wilting point values: Galwey 24.4, Ruby 20.0, Palliser 38.3, Disaster 10.7. Soil moisture is based on a "total" soil basis including stones. Spring = June, July; summer = Aug., Sep., except in precipitation.

† Spring precipitation = April, May, June. Summer precipitation = July, Aug., Sep.

Table 9
Forage production associated with soil moisture on six sheep winter ranges, summers of 1969 and 1970

Range	Year	Forage prod'n (kg/ha dry wt.)	Soil moisture values (%) at 0–15 and 30–45 cm depths*							
			June		July		Aug.		Sep.	
			0–15	30–45	0–15	30–45	0–15	30–45	0–15	30–45
Galwey	1969	734	10.7	8.8	6.0	5.2	3.8	3.0	3.2	2.8
wilting point = 20.8	1970	930	7.7	6.9	6.0	4.7	3.1	3.0	12.1	10.2
field capacity = 30.4										
% stones = 14.7										
Ruby	1969	447	8.7	7.1	3.6	3.5	2.1	1.9	2.0	2.0
wilting point = 9.6	1970	400	5.6	5.7	6.2	4.0	2.0	1.9	9.1	6.9
field capacity = 10.3										
% stones = 52.0										
Palliser	1969	923	24.5	22.0	25.0	24.7	9.9	9.7	7.3	6.8
wilting point = 23.6	1970	614	16.0	15.2	24.1	21.2	6.9	6.7	12.7	8.6
field capacity = 30.7										
% stones = 38.5										
Bourgeau	1969	462	14.0	15.4	16.8	15.5	7.4	7.6	6.2	4.7
	1970	396	12.3	11.6	8.5	8.5	4.5	4.7	9.2	9.0
Disaster	1969	121	5.6	8.5	21.5	19.2	19.9	20.7	17.2	15.9
wilting point = 10.7	1970	152	21.9	14.0	8.1	8.7	5.8	6.5	8.5	7.3
field capacity = 29.2										
% stones = 0										
Sulfur	1969	184	10.6	11.3	18.2	18.4	13.6	15.6	16.7	16.3
	1970	281	16.4	16.8	4.4	5.1	3.3	3.8	15.2	11.5
All ranges	1969	478	12.4	12.2	15.2	14.4	9.5	4.4	8.8	8.1
	1970	463	13.3	11.7	9.6	8.7	4.3	4.4	11.1	8.9

* Soil moisture values determined on a "total" soil basis, including stones.

of erosion on Disaster and Palliser and to a lesser extent on Sulfur and Bourgeau. They were not evident on the Waterton ranges.

Range trend is best determined by comparing present and past vegetation and soil values. Such information was gathered along the Athabasca Valley in Jasper on four sheep ranges from range data obtained in 1946 and again in 1970. Vegetative coverage was 6.9% and forage production 3.6% higher in 1970 than in 1946, while bare ground was 7.3% less in 1970 than in 1946. These three values indicate an upward trend in range condition along the Athabasca Valley in Jasper between 1946 and 1970. It was not possible to obtain comparable trend information in Banff and Waterton because of the lack of previous range studies.

Although quantitative data were not obtained on plant reproduction, cursory examination indicated poor reproduction on Disaster and Bourgeau, fair reproduction on Sulfur and Palliser, and good reproduction on Galwey and Ruby. These values were based on an estimate of the abundance of seed heads and young plants observed during the field study. A general evaluation of range trend for each park was

Waterton:
trend stable; no evidence of active erosion; reproduction of plants adequate;

Banff:
trend downward; definite evidence of active soil slumping, hillside terracing, disturbed and dislodged plants on Palliser and to a lesser extent on Bourgeau;

Jasper:
trend stable or slightly downward on Disaster and Sulfur although slightly upward on four other sheep ranges; there was some evidence of active soil disturbance and terracing although the major trend symptom was poor regeneration, with a preponderance of older and dead-decadent plants.

1.11. Evaluation of sampling methodology

The point-intercept method appeared to be a poor choice for sampling vegetation but it was chosen as it was the standard grassland range sampling technique used in the Canadian national parks. The method is time-consuming and less accurate than several other methods. One of the major difficulties lies in the large number of sample points required to sample minor species adequately and the time required for sampling. The 1000–2000 sample points used in my study were undoubtedly insufficient to sample minor vegetation species adequately.

The area-coverage method for sampling has given satisfactory estimates of coverage (Daubenmire 1959; Eddleman, Remmenga, and Ward 1964). I believe some area-coverage method such as the 400 cm² rectangular plot should be used to replace the point-intercept technique in grassland range sampling in the national parks. However, a comparison of the accuracy of both methods should be made before abandoning the point-intercept method.

2. Ungulate use of range and climate

The variables affecting ungulate use of the range, particularly in winter, are mainly temperature, wind velocity, average snow depth, snow resistance, and barometric pressure.

I averaged data from 20 snow stations on each of six ranges to give an indication of overall weather conditions after testing the justification of this by the Spearman Rank Correlation test.

Rank correlations obtained when comparing numbers of bighorn sheep using winter ranges with the climatic variables showed a small significant positive correlation with present temperature, a highly significant positive correlation with barometric pressure, a significant negative correlation with snow depth, and a small significant negative correlation with wind velocity and snow resistance.

2.1. Barometric pressure and temperature

Sheep movements frequently occur prior to winter storms and well before the temperature drops, the winds increase or change, and the storm actually occurs. These movements are probably in response to another environmental variable — dropping barometric pressures. Results show a large positive correlation between sheep numbers and barometric pressure.

Table 10
Chest height and two-thirds chest height measurements of bighorn sheep in Jasper and Banff national parks

	Adults		Yearlings		Lambs	
	Rams[5]*	Ewes[14]	Rams[3]	Ewes[1]	Rams[20]	Ewes[3]
Chest height (cm)	53.9	48.6	47.7	49.2	43.8	44.3
2/3rds chest ht. (cm)	35.9	32.4	31.8	32.8	29.3	29.5

* Sample size.

It is advantageous for sheep herds to leave the west-facing grasslands before storms arrive, as these grasslands are exposed to the prevailing westerlies and violent snowstorms. Therefore a movement of sheep herds from the main winter range, triggered by falling barometric pressures preceding winter storms, reduced the number of animals observed on these ranges. Conversely, sheep moved back to the exposed major wintering slopes as barometric pressures rose with the end of storms. A similar response of caribou to changing barometric pressures has been observed (Pruitt 1960).

2.2. Snow depth and hardness

A significant negative correlation between snow depth and numbers of sheep existed, i.e., there were fewer animals on winter ranges as snow depth increased. Ungulate mobility is noticeably impaired when snow depths become two-thirds as great as the animal's chest height (Telfer and Kelsall 1971). The situation becomes critical when snow depths reach chest height and the animal is forced to plow through the snow. Measurements taken in 1970 and 1971 showed these two critical snow depths for sheep to be 30 and 44 cm for lambs, 32 and 48 cm for yearlings and ewes, and 36 and 54 cm for adult rams (Table 10, Fig. 12).

Sheep therefore will generally avoid snow depths in excess of 30 cm and I used the "<30 cm" depth to determine that portion of each range available for grazing each winter. This information is required to correct range carrying capacity values based only on forage production and proper use.

Monthly snow depth data during the three winters of 1968–71 revealed great disparities among years. The winter of 1969–70 had the least snow, 1970–71 was intermediate, and 1968–69 had the most snow (Fig. 12).

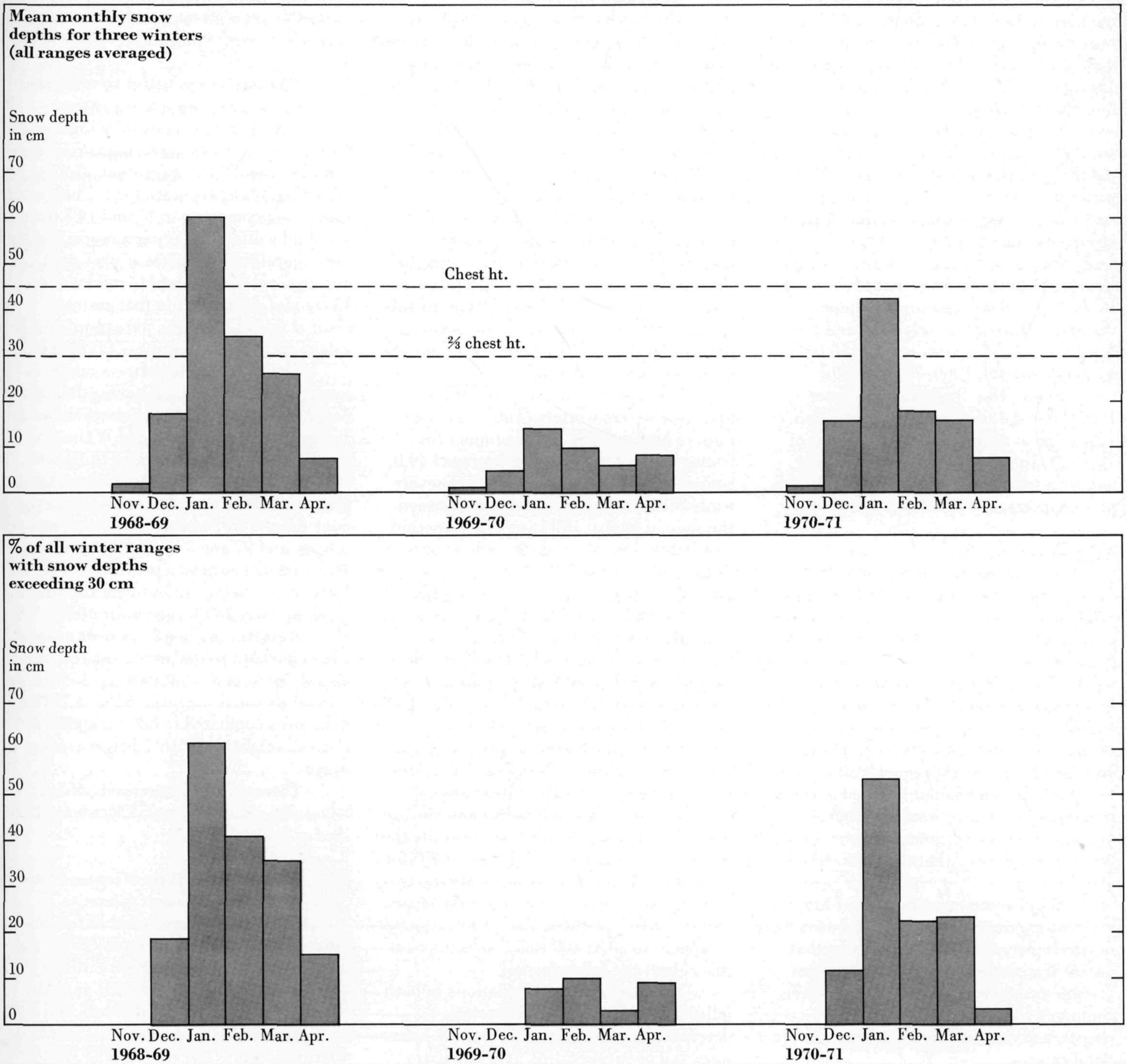
During the severe winter, an average of 28.3% of the range was unavailable in the six months of November–April, with 39.0% unavailable during the worst four months of December–March. Conversely, during the following mild winter only 4.7 and 4.9% of the ranges were unavailable during the six-month and four-month periods respectively. Taking averages for the three winters, 17.2% of the range was unavailable throughout the six-month period, and 23.7% during the four-month period. The four-month period of December through March is the critical bottle-neck for winter survival imposed by excessive snowpack conditions, and range grazing capacities should be reduced an average of 25% to account for that portion of the winter forage unavailable during the winter because of snow depths exceeding 30 cm.

Average percentages of each range covered by >30 cm of snow during the four months of December through March, for the three winters 1968–71 were

Range		% covered
Waterton		29.6
	Galwey	20.2
	Ruby	39.0
Banff		42.2
	Palliser	53.0
	Bourgeau	31.4
Jasper		6.0
	Disaster	12.1
	Sulfur	0.0

Figure 12
Snow depths during two severe and one mild winter, 1968–71.

Figure 12



These results indicate that grazing capacities of Waterton ranges should be reduced by 30%, Banff ranges by 42%, and Jasper ranges by 6% to take into account those portions of winter ranges unavailable during the critical four-month period of December–March.

The period of most severe snow resistance (depth-hardness) occurred during the three month period of January–March, with the latter month recording the greatest snow resistance. Considerable disparity occurred among winters, with an average snow resistance during the winter of 1968–69 more than three times that of the winter 1970–71. Cumulative snow resistance values for the winter period November–April were 19,141, 3796 and 35,150 for the winters 1968–69, 1969–70, and 1970–71 respectively. The "light-snow" winter of 1969–70 had a snow resistance value only 10% as great as that during the winter of 1970–71. In other words, some winters impose a snow severity 10 times as great as other winters.

2.3. Wind velocity

A negative, but not statistically significant, correlation occurred between wind velocity and sheep numbers on winter ranges, indicating that sheep preferred light winds but were equipped to cope with strong winds. They winter on grasslands exposed to prevailing westerly and southerly winds which often bare all or portions of the range of snow. Because of this behaviour they must be able to tolerate considerable wind. I suspect they endeavour to avoid a combination of excessive wind and cold, moving to the lee of mountains and/or upward to a warmer thermal layer, when able.

Wind velocity averaged 15.7 km/h with the greatest amounts of wind occurring in November, April, and January in that order. Waterton ranges had the greatest average amounts of wind (26.2 and 19.7), compared to 12.5 and 13.4 for Jasper ranges, and only 7.8 and 13.8 km/h for Banff ranges.

3. Winter climate, sheep production, and survival

The two harsh winters of 1968–69 and 1970–71 were accompanied by a greater weight-loss of sheep, increased lamb mortality, and a higher lungworm burden than during the two mild winters of 1967–68 and 1969–70 (Table 11). I obtained weight losses by pooling data from Jasper, Banff, and Waterton for each year except 1970–71, when only Jasper data were available.

Lamb mortalities and ewe weight losses were 2.7 and 5.0 times greater, respectively, during the harsh as opposed to the mild winters. Lamb mortality refers to the decline of lambs:100 ewes from the fall period (October–November) to the spring period (April–May). Ewes refers to females of two years and older.

Lamb production did not decline following severe winters (Table 11). The ratio of lambs: 100 ewes in summer following the two mild winters averaged 49.0, compared to 49.5 following the two severe winters. However, the difference between the ratio of lambs: 100 ewes for the period November–January and the ratio of yearlings: 100 ewes the following fall was always greater when a severe winter intervened between these two periods. For example, in Jasper and Waterton, the numbers of lambs: 100 ewes were 50.8 and 48.6 (49.7–av.) in the fall of 1970 at the beginning of a severe winter. The next fall (1971) these cohorts had been reduced to 38.1 and 0 (19.1 av.) respectively, as revealed in the number of yearlings: 100 ewes. This reduction in juveniles was 30.6: 100 ewes or 61.6% of the 1970 production. The average juvenile mortality during and following the two severe winters was 66.4% for the 0.5 to 1.5 year period. Conversely during the two mild winters the lamb: ewe ratio for Jasper and Waterton averaged 42.7: 100 in the fall compared to 20.4: 100 (52.2% decline) for this cohort the following fall.

Because of annual variations in both fall and spring ratios it is impossible to determine juvenile mortality by only examining fall or spring ratios. It is necessary to compare fall lamb: ewe ratios with similar ratios the next spring or with yearling: ewe ratios the next fall to provide an accurate measure of winter mortality.

4. Parasitism related to climate, range, and stocking rates

Lungworm burdens were higher during severe winters. During two severe winters 41 and 23% of fecal samples contained high lungworm loads (>1400 larvae /gm feces) compared to 17 and 14% during two mild winters. Heavy lungworm burdens were therefore 2.06 times as prevalent during severe as opposed to mild winters. There was no indication that gastrointestinal (g.i.) helminths were more prevalent during severe winters (Table 11).

Sheep on poor-condition ranges in Jasper averaged 1391 g.i. helminths compared to 1241 and 1214 for sheep on fair and good ranges in Banff and Waterton. Corresponding stocking rates (ungulate days-use/ha) and forage utilizations for the period 1968–71 were 345 and 61% for the poor ranges, 177 and 46% for the fair ranges, and 97 and 37% for the good ranges. These results suggest a positive correlation between g.i. helminth burdens and both stocking rates and forage utilizations.

Results obtained from necropsies of 73 complete or partial carcasses revealed that sheep in poor condition (>15% below normal seasonal weight) averaged 3237 g.i. helminths compared to 880 for sheep of normal weight, or <15% below average weight.

Diseased sheep averaged 3463 g.i. helminths compared to 953 for sheep classified as healthy.

5. Population dynamics and health

5.1. General population dynamics

I obtained information on the population dynamics of sheep from 7230 classified ground counts from 1966 through 1971. These counts consisted of 4061 animals observed in Jasper, 1884 in Banff, and 1285 in Waterton. I classified animals as lambs, yearlings, rams, and ewes (Table 12).

Table 11
Comparisons of winter weather conditions, lungworm and gastro-intestinal helminth loads, winter weight losses, lamb mortality, and reproduction the following summer in Jasper and Banff national parks, 1966–71

Event		Winter (November–March) 1966–67 Severe	1967–68 Mild	1968–69 Severe	1969–70 Mild	1970–71 Severe
Mean temperature (°C).		−8.8	−4.9	−10.2	−5.2	−7.7
Mean snow depths (cm)	Banff and Jasper	11.2	2.4	23.1	9.4	38.1
	Banff	13.0	3.4	31.0	10.2	42.2
	Jasper	9.4	1.4	15.2	8.6	34.0
G-I helminths (md)		732	1650	1076	1084	1176
Lungworms	Lesions (M-H/tot) (lungs)	3/3	5/10	6/13	3/10	5/9
	% over 1400 l/g (fecal samples)	—	17	41	14	23
	Larvae/gram (log mean)	—	508	789	493	474
Winter wt. loss (%) (adult ewes)		+4	2	18	6	22
Winter lamb mortality (%)	Banff	—	7	54	15	67
	Jasper	—	34	72	33	67
Production next summer (lambs: 100 ewes)	Banff (July–Aug.)	—	62	60	49	—
	Jasper (July–Aug.)	32	37	40	48	48
	(Nov.–Jan.)	47	42	40	51	38

Table 12
Bighorn sheep productivity and juvenile survival in four Canadian national parks, 1966–71*

	Park	Total sheep	Ewes	Rams	Lambs Total	Lambs :100 ewes	Lambs % of herd	Yearlings Total	Yearlings :100 ewes	Yearlings % of herd	Juvenile mortality† (%)
July–Aug.	Waterton	432	215	106	72	33.5	16.7	39	18.1	9.0	45.8
	Banff	560	261	138	112	42.9	20.0	49	−18.8	8.7	56.2
	Jasper	915	468	163	176	42.1	19.2	108	23.1	11.8	38.6
	Kootenay	145	68	32	42	61.7	29.0	3	4.4	2.1	92.9
Totals & averages‡		1907	944	407	360	38.1	18.9	196	20.8	10.3	45.6
Nov.–Jan.	Waterton	37	17	11	5	29.4	13.5	4	23.5	10.8	20.0
	Banff	486	182	167	94	51.6	19.3	43	23.6	8.8	54.3
	Jasper	1581	807	279	360	44.6	22.8	135	16.7	8.5	62.5
	Kootenay	438	260	68	77	29.6	17.6	33	12.7	7.5	57.1
Totals & averages*		2104	1006	457	459	45.6	21.8	182	18.1	8.6	60.3
Apr.–May	Waterton	818	318	325	103	32.4	12.6	72	22.6	8.8	30.1
	Banff	838	246	438	98	39.8	11.7	56	22.8	6.7	42.9
	Jasper	1565	876	339	231	26.4	14.8	119	13.6	7.6	48.5
	Kootenay	433	205	116	82	40.0	18.9	30	14.6	6.9	63.4
Totals & averages*		3221	1440	1102	432	30.0	13.4	247	17.2	7.7	42.8
Yearlong totals and averages	Waterton	1285	548	442	180	32.8	14.0	115	21.0	9.0	36.1
	Banff	1884	689	743	304	44.1	16.1	148	21.5	7.9	51.3
	Jasper	4061	2151	781	767	35.7	18.9	362	16.8	8.9	52.8
	Kootenay	1016	533	216	201	37.7	19.8	66	12.4	6.5	67.2
Totals & averages*		7230	3388	1966	1251	36.9	17.3	625	18.4	8.6	50.0

* Aerial survey data not included. Ewes and lambs consist of animals of two years and older.

† Juvenile mortality = $\frac{\text{lambs}-\text{yearlings} \times 100}{\text{lambs}}$

‡ Kootenay excluded.

I tabulated observations for three periods: summer (July–August), early winter (November–January), and spring (April–May) prior to lambing. Although one lamb was observed as early as May 11, only a very small percentage of lambs arrived before June.

The summer period provided data on early post-natal production, although lamb: ewe ratios underestimate total productivity as some ewes are not yet readily visible with their lambs. Thus, observed lamb: ewe ratios are usually higher in the early winter period, which probably provides the best estimate of productivity.

I determined annual variations in production during three seasons over a five-year period. Summer averages for the three parks were 38.1 lambs: 100 ewes and 20.8 yearlings: 100 ewes compared to respective early winter ratios of 45.6:100 and 18.1:100. Spring ratios were 30.0:100 and 17.2:100 respectively (Table 12).

Lamb production was highest in Banff, slightly lower in Jasper, and noticeably lower in Waterton. Conversely, lamb mortality was negligible in Waterton while in Banff and Jasper it averaged 22.9 and 40.8% respectively. Over-winter mortality of yearlings was relatively light except in Jasper, averaging 3.8, 3.4, and 18.6% for Waterton, Banff, and Jasper respectively.

Juvenile mortality values for the 21–22 month period from July–August of the first year to April–May of the third year, when juveniles were almost two years old, were 32.5, 46.8, and 67.7% for Waterton, Banff, and Jasper respectively, with mortality in Jasper twice as great as in Waterton and 1.4 times as great as in Banff.

These results suggest that the Jasper population appeared to be compensating for high juvenile mortality by maintaining a high reproductive rate (Inversity Principle, Errington 1956). Conversely, production and juvenile mortality of the Waterton population was considerably less (Table 1, Appendix VII, see footnote 1).

There was a strong negative correlation between the degree of forage utilization and recruitment rates, but no significant correlation between percent utilization and lamb production.

Figure 13

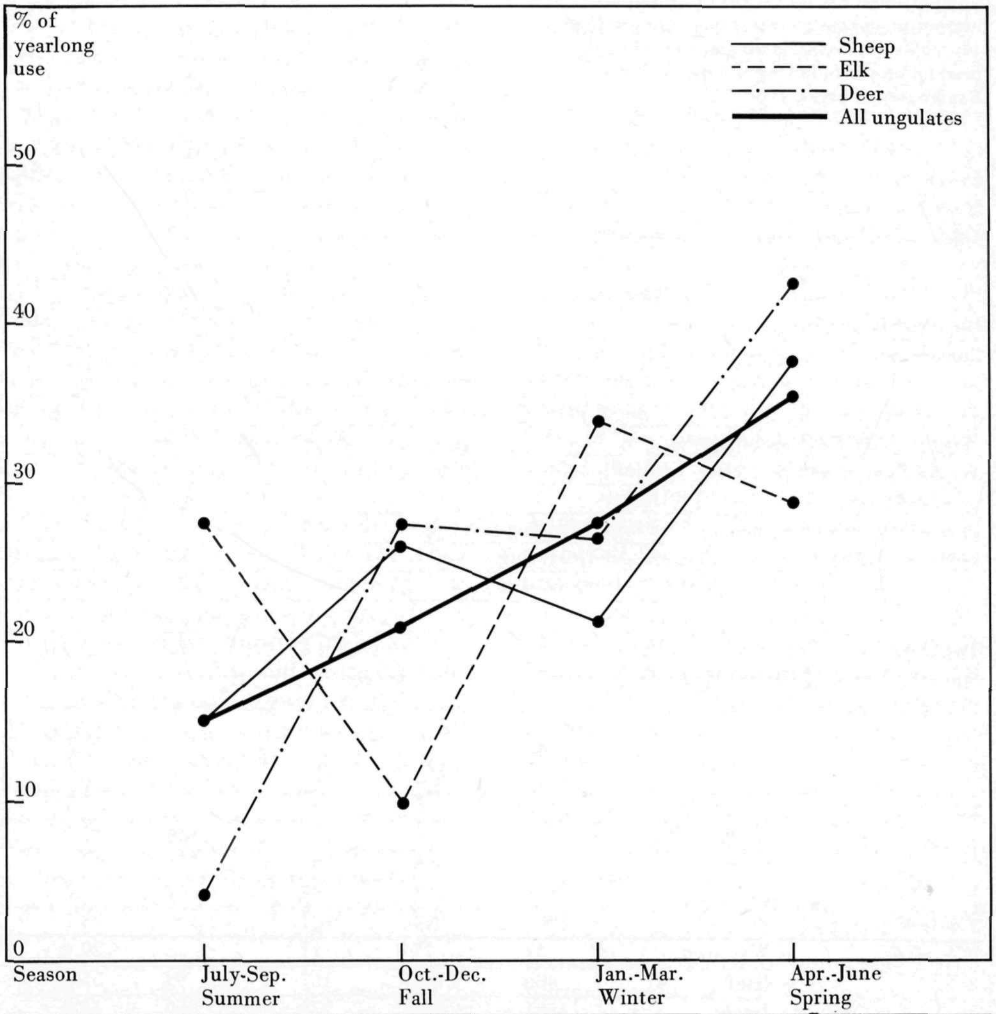


Figure 13
Seasonal use of six bighorn sheep winter ranges by sheep, elk, and mule deer based on 2492 sightings for three years, 1968, 1969, and 1970.

5.2. Seasonal use of winter ranges

A total of 2035 sheep, 231 elk, and 226 deer sightings were made during the three-year period 1968–70, in which sightings were made during 432 observation-days consisting of two days per month.

The heaviest use by both sheep and deer occurred during the spring, followed next by fall, winter, and summer in decreasing order of use. During the nine-month period October–June, 84.8% of the sheep use occurred. Elk use was greatest during winter, somewhat less during spring and summer, and considerably less during fall.

For all three ungulates, 63.4% of the use occurred during the winter and spring periods, with spring use the heaviest (36.3%). The seasonal distribution of use was similar for sheep and deer but dissimilar for sheep and elk (Figure 13). Total ungulate use increased from summer through fall and winter, reaching a peak in spring.

Herd size varied by season with the largest average sheep herds occurring during the spring (20.5) and winter (19.2) periods. Smallest herds occurred in summer (10.5) with a year-long average of 16.3 and a range of 2 to 74 sheep per herd.

5.3. Population trends and die-offs, 1800 to 1973

For the period 1890 to 1966, sheep populations fluctuated sporadically due to severe winters, disease, and changes in the condition of their ranges due to weather, fire, and interspecific competition. Between 1860 and 1910, their numbers were depleted to one-fourth of their former level because of year-long hunting from an influx of miners, loggers, traders, railroad workers, settlers, and resident Indians (Stelfox 1971).

Between 1910 and 1915, 19,529 km² of sheep country were established as national parks. This action, in addition to increased grasslands resulting from extensive wildfires during the late 1800's and early 1900's, and improved range conditions due to low sheep and elk numbers, tripled the number of sheep by 1936 (Stelfox 1971).

Between 1936 and 1950, a series of die-offs in all four parks and adjacent provincial lands reduced sheep numbers from 4500 to 1000. Pneumonia–lungworm disease and severe winter weather were 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 by malnutrition made the sheep vulnerable to the effects of disease–parasitism and inclement weather.

From 1950 to 1966, sheep numbers in the parks increased from 1000 to 4425. This increase was attributed to improved range conditions due to light stocking rates of sheep, elk, and livestock following the previous die-offs, annual elk reduction programs, predator-control programs in the 1950's, and near-normal winters (Stelfox 1971).

In Kootenay, from September 1966 to the spring of 1968, sheep numbers declined 75% because of deteriorated winter range, excessive ungulate populations, and a pneumonia–lungworm disease. This disease was evidently initiated by the severe winter of 1964–65 (Demarchi 1967, Bandy 1968, Stelfox 1971).

There was a correlation between population density, range condition, and animal weight. In Kootenay, when the die-off was in progress during the spring of 1967, adult ewes averaged 53.1 kg. In the spring of 1972, when the population was less than one-half the peak population of 1965, adult ewes were 13.2 kg heavier (66.3 kg av.). In Jasper, where population densities were higher and range conditions poorer than in Banff and Waterton, ewes averaged 61.3 kg in spring compared to 64.1 kg in Banff and 65.4 kg in Waterton.

Between 1966 and 1973, populations either increased slightly or stabilized in Jasper, Banff, and Waterton. There was some evidence that populations were stabilizing in Jasper and Banff because of the two severe winters in 1968–69 and 1970–71 and perhaps from increased predation by coyotes, wolves, and cougars. The 1973 sheep population was approximately 4000, of which 2000–2500 were in Jasper, 1000–1500 in Banff, 350–425 in Waterton, and 70–80 in Kootenay. Native ungulate densities were very high in Jasper where range conditions were the poorest between 1966 and 1969. Along the Athabasca Valley in Jasper, an estimated 820 sheep, 600 elk, and 200 mule deer wintered on 5180 ha (0.32 per ha). In Waterton, during an aerial survey in February 1967, at least 350 sheep, 264 elk, 235 mule deer, and 14 mountain goats were observed wintering on 5857 ha or 0.15 per ha (Stelfox 1971).

6. Interspecific competition

The major competitors for sheep grassland forage were elk and horses. The number of horses grazing in Jasper from 1934 to 1947 averaged 305 (Pfeiffer 1948); most grazed 5120 ha of the Athabasca Valley. Horses are the most selective feeders of domestic animals, eating primarily grass and 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 1950s, when horse grazing was curtailed, undoubtedly caused the initial decline in range condition. By the time elk became abundant in the 1930s, horses had already reduced the range to poor condition.

Along the Athabasca Valley, grass comprises 93% of the elk diet compared to 83% of the sheep (Cowan 1944). During the 1940s, more than 1000 elk wintered along the Athabasca Valley, whereas prior to 1935, their numbers were sparse (Pfeiffer 1948). By 1946, the condition of elk was poor and calf survival was low. At that time, range conditions were so poor and numbers of elk, sheep, and mule deer so high that the annual elk slaughter was increased. Exclosures on three grasslands along the valley were producing 61% more forage annually than the adjacent open-range, indicating that grazing by native ungulates, particularly elk and horses, was significantly reducing forage production. The results of Pfeiffer (1948) and those of Cowan (*op. cit.*) indicated 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 relationship to a declining range condition until malnutrition plus inclement winter weather caused their numbers to decline from 1946 to 1949. These two species lack the physiological control mechanism of disease, which is effective in controlling sheep numbers once ranges are severely depleted. Elk, in particular, are not prone to lethal diseases and seem capable of maintaining their numbers at levels excessive to range carrying capacities. Unless controlled by predators or artificial means, their numbers may stabilize or even decline somewhat in response to declining range condition, but they seem to remain at levels which cause a continuing decline in range productivity and condition.

7. Predation

Wolves, which were abundant in Jasper during the 1940's and early 1950's, were ineffective in preventing wild ungulates from increasing to the detriment of their range (Cowan 1947*b*). During the early 1940's, the winter ranges in Jasper harboured 11.6 to 15.5 wild ungulates compared to 0.04 wolves per km^2, and sheep were not an important prey species (Cowan 1947*b*). In Jasper, they were present in small numbers north of the Athabasca Valley from 1966 to 1968. In 1969, they moved into the Athabasca Valley and since then have increased their pressure on sheep and other wild ungulates. A wolf study in Jasper from 1968 to 1973 showed that sheep occurred in 2 and 4% of the summer and winter wolf scats respectively, even though sheep were the second most abundant wild ungulate on wolf winter ranges. During that study, elk were the most abundant ungulates on both summer and winter ranges and the species most prevalent in summer wolf scats. Mule deer were as abundant as sheep, but only one-eighth as abundant as elk on the winter range of wolves; yet they occurred in 66% of the scats compared to 11 for elk and 4 for sheep (Carbyn 1974). There was some evidence that wolf predation along the Athabasca Valley in the late 1960s was having the beneficial effect of dispersing sheep and elk numbers and grazing pressure more equitably throughout the valley.

Coyotes (*Canis latrans*) and cougar took a small number of sheep in all parks studied from 1966 to 1973. During deep-snow winters, larger numbers of kills by coyotes and cougars were reported. The annual harvest of sheep by the three main predators as determined from Warden Services records was judged to be less than 10%. There was no report of bald or golden eagles (*Haliaëetus leucocephalus* and *Aquila chrysáetos*) taking any sheep during this study, although occasionally they were sighted harrassing sheep.

8. Range grazing and carrying capacities

8.1. Grazing capacities

Grazing capacities must involve the plant community composition desired, forage production, proper use, and season of use. Proper use is that portion of the current year's growth that can be grazed year after year without causing damage to that plant, important associated plants, or the soil (Cook *et al.* 1962). Concerning the plant composition desired, grazing capacity was based on the existing community composition. Information presented earlier showed that on heavily grazed ranges the number of grassland species averaged 33 compared to 60 species on moderate and 66 on light–moderately grazed ranges. The proportion of shrubs, in particular that of shrubby cinquefoil, increased significantly in a community under heavy grazing, while the proportion of grasses decreased correspondingly. Tall grasses such as rough fescue decrease or disappear under heavy sheep grazing, while short grasses such as junegrass increase under heavy grazing (Smoliak 1974). If land-use objectives of the national parks include maintaining a diverse, productive community, then it would be necessary to reduce grazing capacities below 40% forage use on overgrazed ranges until the desired plant composition was attained and then to increase use to 40% to maintain this desired composition. For the three overgrazed ranges, forage use of 25–30% for 10 to 20 years should produce a significant upward trend in range condition and result in more diverse and healthy plant communities.

Forage production in relation to grazing capacity was based on existing forage production rather than potential production. The three overgrazed ranges had their production potentials decreased 50, 50, and 30% by heavy grazing. Grazing capacities of these ranges would increase as forage production approached site potential through decreased grazing pressures.

Proper use must be determined on the basis of either demonstrated proper use on that range from results of various stocking rates, or from proper use values determined from similar ranges in that general region. For the Fescue grasslands of the Prairie–Foothills region of southwestern Alberta, 55% forage use has been considered proper use (Lodge *et al.* 1971). For the *Stipa–Bouteloua* Prairie in southeastern Alberta, a stocking rate of at least 0.4 ha per ewe per month was recommended for sheep grazing on a nine-month basis (Smoliak 1974). A 40% proper use value was used in this study because Jasper ranges were rated as heavily overgrazed under 61% total vegetation use, Banff ranges were lightly overgrazed under 46% use, and Waterton ranges optimally grazed at 37%. "Use" values were based on total vegetation or herbage, rather than just on forage. Once adequate diet preference information is obtained, it will be possible to identify forage species and determine proper use for forage only, rather than for all vegetation. The approximate percentage of total vegetation that was actually forage was determined from both the percentage of canopy coverage of species eaten in relation to the total vegetation coverage and also the percentage which each forage class contributed to total vegetation production. Results indicated that on the overgrazed Disaster range, 76.7% of the vegetation clipped, weighed, and used in determining forage production values was actually forage, the other 23.3% was non-forage. On the moderately grazed Galwey range, 86.9% of the vegetation clipped was forage. By excluding species of low preference ($>20\%$ of the plants utilized) then only 34.2% of the Disaster vegetation was forage compared to 73.0% for the Galwey vegetation. These calculations indicated that 59% use of Disaster herbage was virtually total use of preferred species. On the other hand 44.2% use of the Galwey vegetation was equivalent to about 60% use of preferred forage species.

Concerning season of use, these ranges were primarily winter and spring ranges with 63.4% of the use occurring during the winter and spring periods of January–June, and 84.5% of the use occurring during the nine-month period October–June. However, elk and deer use was heavy during the spring as was elk use during the summer. These ranges could support heavier grazing than similar ranges used primarily in summer because the vegetation and land surface are less vulnerable to damage from grazing and trampling in the winter. This potential for increased grazing pressure is offset, however, by physiographic and edaphic conditions on the steep mountainous terrain (av. slope 32.7°) which make both the vegetation and land surface more susceptible to damage from grazing ungulates than ranges of the Prairie and Foothill regions.

Season of use influences both grazing and carrying capacities because of reduced forage availability during the seven-month period (October 15–May 15) when snow normally covers at least a portion of the range. During this period, the wild ungulates forage on bare or shallow-snow areas. The number of hectares required per sheep-unit must be increased proportionately to the amount of the range covered by snow depths >30 cm during the critical winter period. Results presented earlier indicated that grazing capacities of Waterton ranges should be reduced 30%, Banff ranges 42%, and Jasper ranges 6% to account for those portions of the winter ranges covered by >30 cm snow during the winter.

Grazing capacity must also involve both the herd composition and the relative forage intake per age–sex class of animal. Forage requirements for adult ewes, on a dry-weight basis, are 1.0 kg/day, 29.9 kg/month, 179.6 kg/year for the six-month grazing period in Waterton and 239.5 kg/year for the eight-month grazing period in Jasper and Banff (Hebert 1973). Palliser, Ruby and Galwey ranges were used predominantly by rams, whereas Sulfur, Disaster, and Bourgeau were primarily ewe ranges. On the basis of average body weights per age–sex class it was possible to determine the degree of grazing pressure each animal class exerted on the range. Adult ewes (>2.9 yr.) averaged 64.0 kg in the spring and were considered 1.0 sheep-unit. Rams (>2.9 yr.) averaged 87.6 kg and were considered 1.37 sheep-units. Yearlings (1.9 yr.) averaged 56.3 kg and were considered 0.88 sheep-units, while lambs (0.9 yr.) averaged 34.0 kg and were considered 0.53 sheep-units. Sheep on the Waterton ranges comprised an average of 1.11 sheep-units compared to 0.93 sheep-units for each sheep on the Jasper ranges.

An average of 430 kg/ha of forage was produced on the six ranges. Using a 40% proper use value, and a monthly forage requirement of 30 kg, it required 0.17 ha to support 1 sheep-unit per month. By adjusting the animal units actually on the range on the basis of herd composition, each sheep averaged 1.05 sheep-units indicating a predominance of rams on the ranges studied. Each sheep on the range therefore required 31.4 kg of forage per month which reduced the average grazing capacity of the ranges to 0.18 ha to support 1 sheep per month.

Grazing capacities were highest in Waterton and lowest in Jasper (Table 13). The highest grazing capacity was on the Galwey range (0.10 ha/sheep-month) and the lowest on Disaster (0.42 ha/sheep-month).

Considering a grazing year to be six months in Waterton and eight months in Banff and Jasper, it required 0.81 ha to support 1 sheep per year in Waterton, compared to 1.42 ha in Banff and 2.51 ha in Jasper.

Using the Galwey range as a general guide to proper use, reducing forage use from the current 44% to the recommended 40% and making further adjustments based on snow-pack conditions, realistic grazing capacities varied from 0.42 ha per sheep-month on Disaster to 0.11 ha per sheep-month on Galwey, or an average of 0.21 ha per sheep-month for the six ranges. Corresponding values for a sheep-year ranged from 3.40 ha on Disaster to 0.68 ha on Galwey, or an average of 1.54 ha per sheep-year for the six ranges (Table 13).

Stated another way, the realistic grazing capacities become 5.9, 4.2, and 3.2 sheep-months per ha in Waterton, Banff, and Jasper or 1.0, 0.5, and 0.5 sheep-years per ha respectively.

In summary, actual grazing capacities were 78, 78, and 99% as great as the potential grazing capacities in Waterton, Banff, and Jasper respectively. "Actual" refers to grazing capacity adjusted for local snow-pack conditions, whereas "potential" is based strictly on vegetation grazing capacity assuming all forage is available.

8.2. Carrying capacities

Carrying capacity is the maximum number of animals that can survive the greatest period of stress each year on a given land area (Huss 1964).

Stocking rates, i.e., the number of sheep-units the range supported in 1968–71, in terms of sheep-months/ha as calculated from the pellet-group-count method were:

Jasper—9.9 for Disaster, 14.3 for Sulfur, 12.1 av.

Banff—12.8 for Palliser, 6.2 for Bourgeau, 8.9 av.

Waterton—7.2 for Galwey, 2.7 for Ruby, 4.9 av.

The average stocking rate for the six ranges was 9.1 sheep-months/ha. Stocking rates on the two Jasper ranges were 4.4 and 3.6 (4.0 av.) times greater than recommended for proper use. Banff stocking rates were 2.7 and 1.7 (2.2 av.) times greater than proper use, while Waterton ranges were only stocked 0.8 and 0.8 (0.8 av.) times as great as suggested proper use (Table 13). These results suggest that optimum sheep-months/ha based on 40% proper use were:

Table 13
Grazing capacities of sheep ranges based on 40% proper use and a monthly forage requirement of 29.7 kg per sheep unit

		Waterton			Banff			Jasper			
		Galwey	Ruby	Ave.	Palliser	Bour-geau	Ave.	Disas-ter	Sulfur	Ave.	Ave., 3 parks
Forage/ha (dry. wt.)		1890	863	1378	1378	735	1055	388	610	500	978
Ha/sheep-unit-month		0.10	0.19	0.12	0.12	0.22	0.16	0.42	0.27	0.33	0.17
Sheep-unit-months/ha		11.50	5.30	8.30	8.30	4.50	6.50	2.30	3.80	3.00	6.00
Based on age-sex composition of populations	Sheep-units per sheep	1.11	1.11	1.11	1.26	0.97	1.12	0.97	0.89	0.93	1.05
	Ha/sheep-month	0.10	0.21	0.13	0.15	0.22	0.18	0.41	0.24	0.31	0.18
	Sheep-months/ha	10.50	4.80	7.50	6.50	4.80	5.80	2.30	4.30	3.30	5.80
	Ha/sheep-year*	0.60	1.30	0.80	1.20	1.70	1.40	3.30	2.00	2.50	1.30
	Sheep-years/ha	1.70	0.80	1.30	0.80	0.60	0.70	0.30	0.53	0.40	0.77
Based on snowpack limitations per grazing year	% ranges unavailable in winter†	13.30	30.70	22.00	28.40	16.40	22.40	1.90	0	0.90	15.20
	Ha/sheep-month	0.11	0.30	0.17	0.21	0.26	0.23	0.42	0.24	0.31	0.21
	Ha/sheep-year	0.68	1.80	1.00	1.70	2.10	1.80	3.40	2.00	2.50	1.54
	Sheep-months/ha	9.00	3.30	6.00	4.80	3.80	4.30	2.30	4.00	3.30	4.80
	Sheep-years/ha	1.50	0.50	1.00	0.50	0.50	0.50	0.25	0.50	0.50	0.75
Carrying capacities	Sheep-days/ha	60	65	62.5	123	120	120	305	493	398	193
	Elk-days/ha	40	2.5	20	63	20	43	2.5	0	<2.5	21
	Deer-days/ha	20	2.5	10	2.5	13	8	0	0	0	6.3
	Sheep-unit-days/ha	195	73	133	308	190	248	310	493	403	263
	Sheep-units per sheep	1.11	1.11	1.11	1.26	0.97	1.12	0.97	0.89	0.93	1.05
	Actual sheep-days/ha	218	80	148	388	185	278	300	438	375	275
	Sheep-months/ha	7.3	2.8	5	13	6.3	9.3	10	15	13	9.3
	Sheep-years/ha	1.3	0.5	0.8	1.5	0.8	1.30	1.30	1.80	1.5	1.3
	Ha/sheep-month	0.14	0.36	0.2	0.08	0.16	0.11	0.10	0.07	0.08	0.11
	Ha/sheep-year	0.8	1.8	1.2	0.6	1.28	0.88	0.80	0.56	0.64	0.80

* A sheep-year = 6 months in Waterton and 8 months in Banff and Jasper.
† Based on a sheep-year in relation to % of each range covered in excessive snow depths (> 30 cm) during six-month period, Nov.–Apr.

Jasper—Disaster 2.2, Sulfur 4.0; 3.2 av.
Banff—Palliser 4.7, Bourgeau 3.7; 4.2 av.
Waterton—Galwey 8.9, Ruby 3.2; 5.9 av.

In order to induce an upward trend on the overgrazed Jasper ranges, the 40% proper use value should be reduced to 30%, which would be Disaster 1.7 and Sulfur 3.0; 2.3 av. sheep-months/ha.

On the Disaster range, 97.7% sheep-units were sheep, whereas only 30.1% of the Galwey units were sheep with the remainder being elk and deer; indicating considerable variation in the ungulate composition of "sheep-units" of grazing pressure (Table 13).

In summary, a 30% proper use value for the poor-condition Jasper range and a 40% proper use for the fair–good and good-condition Banff and Waterton ranges would be required to induce an upward range trend in Jasper and Banff and to maintain the existing range condition in Waterton. These values would require stocking rates of 5.9, 4.2, and 2.5 sheep-months/ha for Jasper, Banff, and Waterton ranges respectively. This would mean a 51% decrease in the Jasper stocking rate, a 13% decrease in the Banff stocking rate, and would permit a 7% increase in the Waterton stocking rate.

In determining grazing and carrying capacities of winter ranges, it is necessary to consider the effects of summer alpine ranges in conditioning the animals for winter survival and for reproductive success. The ability of the poor-condition Jasper winter ranges to support more animals than grazing capacity calculations indicate as possible must be at least partly due to large protein stores accumulated on summer ranges. Bighorn sheep in British Columbia have shown that they supplement the winter range diet from rumen reserves of bacterial protein obtained from the summer range, combined with possible urea recycling and a reduction in urine nitrogen during periods of low nitrogen availability (Hebert 1973). Klein and Schønheyder (1970) demonstrated the ability of deer species to compensate for low nitrogen levels in the forage by recycling nitrogen through the saliva and further conservation of ruminal nitrogen by recycling it through successive generations of the microbial population.

Alpine forage in Alberta and British Columbia is more nutritious and digestible than similar forage at low elevations (Johnston *et al.* 1968, Hebert 1973). Jasper ewes were in prime fall condition and weighed slightly more than Waterton ewes (76.7 kg compared to 75.3 kg) when they descended from the summer alpine range. This indicated an adequate, high quality alpine forage. This prime fall condition undoubtedly enabled higher densities of sheep and other ungulates to winter on the unproductive, low-elevation Jasper ranges than the grazing capacity data indicated, even though the winter weight loss for ewes was 20% compared to 13% for ewes on the productive Waterton ranges. This prime fall condition in Jasper was also associated with a high ratio of 35.7 lambs: 100 ewes compared to 32.8 lambs: 100 ewes in Waterton despite the poorer spring condition of ewes in Jasper (61.3 kg compared to 65.3 kg in Waterton). Summer range has been shown to play an important role in the late winter survival of sheep and in providing the nutrients necessary to maintain reproductive condition (Hebert 1973). The unproductive Jasper winter ranges (224.6 kg/ha) supported 398 sheep-days/ha compared to 131 sheep-days/ha for Waterton ranges which produced 2.5 times more forage. This was largely due to an abundance of high quality summer forage in Jasper.

Fires and forest succession strongly influenced the carrying capacity of national parks for sheep. Wildfires burned extensive areas of western Canada during the droughts of the 1830s, 1860s, 1890s, and 1930s (Rowan 1952). There was little brush on the foothill rangelands of southwestern Alberta in the late 1800s. The result of brush and forest invasion in the 1900's was a marked decrease in herbaceous forage. The aspen groves yielded about 449 kg/ha compared to 1348 on adjacent fescue prairie (Johnston and Smoliak 1968). During the period 1907–69 the rate of brush invasion onto grasslands in south-central Alberta averaged 0.05% per year and 0.75 in the Porcupine Hills of southwestern Alberta. Annual herbage production averaged 528, 518, and 2012 kg/ha in the willow, aspen, and rough fescue commøunities respectively (Bailey and Ulroe 1974).

Within the Canadian national parks, fire suppression and forest succession along the "wintering" grasslands of the Athabasca Valley were severely reducing the grasslands and subsequently the carrying capacity of this valley to support wild ungulates by the 1940s (Cowan 1946, Pfeiffer 1948). In Banff, in 1921, the south end of the Sawback Range, which had been burned at the turn of the century, was an open grassland with a few scattered, mature Douglas firs that supported 375 sheep (Hewitt 1921). By 1953 the area was thickly covered with a young forest of Douglas fir and few sheep were present (Banfield 1958).

Wildfires not only create new grasslands to feed sheep and other grazing ungulates, but also periodically redistribute biomass. Following wildfires, minerals released from organic storage are taken up rather quickly by herbaceous plants and resprouting shrubs which are likely to be more nutritious and productive, as well as more available than are pre-fire plants (Lyon and Pengelly 1970). Although logging of at least 40,500 ha of forest land annually in the northern Rockies is partially replacing fires in the role of creating seral habitat (Lyon 1969), it has no role in the Canadian Rocky Mountain parks. The carrying capacity of these parks for sheep will undoubtedly continue to diminish in direct proportion to the rate of forest encroachment onto grasslands unless wildfires are permitted to run their course, except where a definite threat to settlements and commercial structures exists. Fortunately, Parks Canada officials are becoming more aware of the beneficial role of wildfires and are adopting a broader philosophy towards wildfire management.

Another important point to consider when comparing grazing and carrying capacities and proper use is the plant community composition preferred by the ungulate in question. The poor-condition Jasper ranges with their relatively high proportion of shrubs and forbs to grass actually supported three times as many sheep-units per hectare as the good-condition Waterton ranges. The heavy grazing pressure and higher proportion of shrubs and forbs appeared to be synonymous with higher carrying capacity. A study of wild sheep ranges in southeastern British Columbia concluded that optimum sheep range was one having a good mixture of grasses, forbs, and shrubs (Hebert 1973).

There are two main considerations in determining optimum densities of sheep and allied ungulates within national parks from an aesthetic standpoint:

a. the importance which park visitors place on the opportunity to view sheep, elk, and deer compared to other important park features;

b. the importance visitors place on viewing ungulate ranges in good condition with a diversity of productive plant species, compared to overgrazed, unproductive ranges with a paucity of floral species, and a general eroded appearance of both the plant community and soil base.

This study showed that carrying capacities were considerably higher on unproductive, overgrazed ranges which contained relatively few plant species, but which contained a higher proportion of shrubs and forbs to grasses. This fact suggests that more sheep will be available for viewing when their numbers are not controlled by man and temporary periods of overgrazing are permitted. For the past

15 years the greatest number of accessible sheep available for viewing has been along the Athabasca Valley in Jasper. People come to view, photograph, study, and write about these sheep. Park visitors will drive by many spectacular abiotic park features, but seldom fail to stop when sighting a herd of wild sheep.

In Waterton, sheep populations are considerably lower than in Jasper, but are still adequate to provide numerous observation opportunities for park visitors. The productive rough fescue grasslands on which the sheep forage are floristically more appealing than the unproductive and eroded Athabasca Valley grasslands.

Public reaction to denuded grasslands is another consideration. People are becoming conscious of the emaciated appearance of severely "hedged" shrubs and "barked" poplar and pine trees on ranges where ungulate populations are allowed to exceed range carrying capacities.

Considering all the above information, it appears that optimum numbers of sheep are those similar to present densities in Waterton. Such densities permit frequent observation by the public without protests concerning starving, diseased animals, and overgrazed ranges. This *decision in no way implies that the parks* should adopt a management plan to limit sheep stocking rates to 4.9 sheep-months/ha on winter ranges.

Another vital consideration is the optimum numbers of elk and deer sharing the sheep ranges, and the effects which uncontrolled numbers will have both on the sheep and their ranges. No solution to this dilemma appeared from this study *except that uncontrolled elk numbers* have in the past led to declines in numbers of other associated ungulates and their ranges in Jasper, Banff, and Elk Island parks. This situation has generally been unacceptable to both the public and park managers. However, the basic philosophy of leaving park ungulates unmanaged and unaffected by man to the greatest degree possible prevails and is one which I support. Control measures should not be implemented except for those areas frequented by large numbers of humans and only during periods when natural mortality factors, such as weather and predation, are unable to contain elk densities to a level where critical ranges are maintained in at least fair condition.

9. Population regulation

Each of the five die-offs was associated with deteriorated winter ranges caused by excessive ungulate numbers. Prior to each die-off, and as the amount and quality of forage per sheep declined, endoparasite loads and juvenile mortality increased while animal condition decreased. Ewes continued to produce lambs at a normal rate, however, thus increasing the population but at a decreasing rate due to *increased juvenile mortality*. The heavier endoparasite burdens increased the physiological stress, making the sheep more susceptible to both the intrinsic pressure of disease–parasitism plus the extrinsic pressures of weather and predation. At this point, severe winter and/or spring weather was capable of initiating a pneumonia–lungworm disease complex which caused a major die-off and which permitted range *rejuvenation*.

Elk seemed to follow a similar pattern except that they were relatively immune to diseases and parasites capable of causing a major die-off. Reproductive rates were not significantly reduced as their forage supply declined because their numbers remained high enough either to maintain the range in poor condition or to produce a further decline in range condi*tion. Neither sheep, elk, nor deer exhibited* any of the self-regulating mechanisms for primates reported by Ardrey (1961, 1967) or for certain carnivores by Hornocker (1970), Mech (1970), and Wynne-Edwards (1970). To be valuable to both the animal and its environment, a self-regulating mechanism must limit the population before a density is reached which causes serious range deterioration.

Presently, the Jasper ranges are in a poor, overgrazed state and another sheep die-off appears imminent unless ungulate numbers are significantly reduced by severe winter weather predation. These deteriorated conditions appear both on ranges utilized almost exclusively by sheep and on ranges used also by elk and deer. Results indicate that the interactions of several extrinsic factors, notably winter weather, the quantity and quality of winter forage, and predation regulate sheep, elk, and deer populations. Intrinsic factors of parasites and disease combine with the above extrinsic factors to provide the terminal regulating mechanism "pneumonia–lungworm" disease.

The inability of elk, sheep, deer, and moose to self-regulate their numbers in the Canadian national parks before inflicting serious damage to their range has also been clearly demonstrated by Cowan (1947*a*, 1950), Pfeiffer (1948), Green (1949), and Flook (1964).

Summary and conclusions

Five eruptive fluctuations occurred in populations of bighorn sheep between 1936 and 1967 in the Canadian national parks. Each fluctuation terminated in a rapid die-off; the population declining by at least 75%.

This study from 1967 to 1973 was designed to determine the role which winter grassland ranges, subjected to various stocking rates, played in limiting sheep numbers. Specifically, the study included:

1. range condition, trend, and carrying capacities;
2. summer and winter weather influences;
3. ungulate population dynamics, seasonal range use, disease–parasite burdens, fecundity, and mortality;
4. population trends and interspecific competition;
5. self-regulation in sheep, elk, and mule deer.

Two winter ranges, one low- and one high-elevation, were studied in each of Waterton, Banff, and Jasper parks. Point-intercept transects, portable exclosure cones ($0.89 m^2$) and permanent exclosures (13.7 x 13.7m) were used to obtain data on vegetation composition, density, frequency, production, and utilization. Two-dimensional ordination and linear regressions were used to compare ranges and to correlate plant species with range condition. Forage and soil samples were analysed to determine forage nutritive values and composition. Soil moisture and temperature readings were taken from 20 locations per range. Climatic data were obtained from one weather and 20 snow stations per range. Results were correlated with forage production, forage availability, and ungulate use of winter ranges by the association coefficient and step-wise regression analysis techniques.

Sheep herds were classified seasonally to determine rates of production and recruitment and to provide an index to sheep-unit grazing pressure per animal. Sheep were weighed in the fall and spring to determine over-winter weight losses. Chest-height measurements were associated with the ability of various age and sex groups to cope with different snow depths. Disease–parasite information was obtained from carcasses and fecal samples.

The Waterton ranges were productive *Festuca–Danthonia* grasslands, light–moderately grazed. They produced 619 kg/ha (dry wt.) of vegetation comprised of 82% grasses, 14% forbs, and 4% shrubs. The Banff ranges were moderately productive *Elymus–Koeleria* grasslands that were moderately grazed. They produced 474 kg/ha of vegetation comprised of 82% grasses, 17% forbs, and 1% shrubs. The Jasper ranges were unproductive *Koeleria–Elymus* grasslands that were heavily grazed. They produced 225 kg/ha of vegetation comprised of 58% grasses, 35% forbs, and 7% shrubs. *Potentilla fruticosa* and *Koeleria cristata* were negatively associated with forage production and positively with forage utilization.

Litter coverage values were 47 and 13% on the light–moderate and the heavily-grazed ranges respectively, while corresponding non-vegetation coverage values were 8 and 49%.

As forage utilization increased, forage production decreased, lungworm burden and overwinter weight loss increased while the number of yearlings: 100 ewes (recruitment rate) decreased. However, lamb production did not decline as population density and forage utilization increased.

Forage production increased 268 and 204% on the heavily grazed and unproductive ranges, which were protected from grazing for two and five years respectively. Conversely, on the most productive and light–moderately grazed range, forage production increased 220% under two years of protection from grazing, then declined to −0.4% of the value on adjacent grazed ranges under five years of protection. The heavy mantle of dead vegetation smothered some species, notably Idaho fescue, making the range less productive when not grazed.

The three ranges with the heaviest use (Disaster, Sulfur, and Bourgeau) received 57, 58, and 61% utilization of total vegetation, grasses, and forbs respectively, and were considered overgrazed. Forage production on these ranges was suppressed an average of 43% by grazing. Vegetative composition was altered in favour of forbs and shrubs, erosion was prevalent and plant vigour low. Grass production averaged 174 kg/ha on these three heavily grazed ranges compared to 591 for the moderately-stocked Palliser and Galwey ranges.

Range stocking averaged 12.4, 9.1, and 4.9 sheep-months/ha for Jasper, Banff, and Waterton respectively, with an average of 9.1 sheep-months/ha for the six ranges. On the basis of 40% utilization of all vegetation being proper-use, grazing capacities averaged 3.0, 6.4, and 8.2 sheep-months/ha. When these values were corrected for those portions of the ranges unavailable due to excessive snow depths, realistic grazing capacities became 3.2, 4.2, and 5.9 sheep-months/ha. On a grazing-year basis (8 months for Jasper and Banff and 6 months for Waterton) these values became 0.5, 0.5, and 1.0 sheep-years/ha for Jasper, Banff, and Waterton. Stocking rates in Jasper were 3.8 times greater than those recommended for proper use. Banff stocking rates were 2.2 times greater than proper use, while Waterton rates were only 0.8 as great as proper use. Optimum stocking rates were 3.2, 4.2, and 5.9 sheep-months/ha for Jasper, Banff, and Waterton respectively.

A comparison of four winter ranges along the Athabasca Valley in Jasper in 1970 with 1946 indicated that sheep numbers, following an 85% die-off in the 1940's, recovered to former peak populations within 25 years. Neither winter ranges nor sheep populations were permanently impaired by the temporary overgrazing and high endoparasite burdens associated with peak populations. A decline of at least 75% of the sheep population appears essential to provide the necessary decrease in grazing pressure required for proper range recovery.

Forage species on alpine ranges were significantly higher in protein, phosphorus, and moisture, but lower in crude fiber and calcium than they were on low-elevation grasslands in August.

Grass used by sheep remained relatively constant throughout the year with slightly heavier use in winter and lighter use in summer. Grasses receiving the heaviest use were *Agropyron dasystachyum*, *A. trachycaulum*, and *Koeleria cristata*, however, this was largely influenced by species composition on heavily versus lightly-grazed ranges.

Forb use occurred primarily during May–October, with heavier use occurring on the heavily grazed Jasper ranges. Shrub use was common throughout the year on all ranges.

There was a highly significant positive correlation between barometric pressure and numbers of sheep on the exposed winter grasslands. Conversely, there was a significant negative-correlation between snow depth and numbers of sheep on these ranges. The mobility of lambs, yearlings, ewes and rams was noticeably impaired when snow depths reached two-thirds of chest height or 29.3, 31.8, 32.4 and 35.9 cm respectively. During the four-month period of December–March, 24% of the grassland area was unavailable for grazing due to snow depths exceeding 30 cm although the year-to-year variation was high. The period of greatest snow resistance (depth x hardness) occurred during January–March.

Some winters imposed a snow severity 10 times greater than other winters. Severe winters were accompanied by a greater overwinter weight loss (5.0 times greater), by increased lamb mortality (2.7 times greater) and by a higher percentage of heavy lungworm burdens (2.1 times greater) than during mild winters. However, lamb production was not reduced following severe winters. The difference between the ratio of lambs: 100 ewes in the fall and the ratio of yearlings: 100 ewes the next fall was always greater when a severe winter intervened between those two periods.

Although there was no evidence that gastrointestinal helminths were more numerous during severe winters, there was a positive correlation between g.i. helminth burdens and both stocking rates and forage utilizations. Sheep in poor condition averaged 3237 g.i. helminths compared to 880 for sheep of normal weight. Diseased sheep averaged 3463 g.i. helminths compared to 953 for healthy sheep.

Interspecific competition by elk and deer, and on some ranges horses, plus a decline in the extent of grassland ranges by forest encroachment significantly influenced park carrying capacities for sheep.

Sheep populations increased until winter ranges became overgrazed, at which time both endoparasite burdens and lungworm infection increased. Eventually, the lungs became heavily infected with pneumonia–lungworm lesions. Malnutrition and severe winter weather, combined with heavily infected lungs, terminated in a pneumonia-lungworm disease and the rapid mortality of at least 75% of the population.

Neither sheep, elk, nor deer displayed any effective self-regulating mechanism to control their numbers before winter ranges became overgrazed and forage production noticeably impaired. Elk and deer were not vulnerable to any diseases which would result in heavy mortality. Predation by wolves, cougar, and coyotes did not prevent sheep, elk, and deer numbers from increasing beyond the carrying capacity of the winter ranges.

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