ARCTIC
VOL. 37, NO. 2 (JUNE 1984) P. 141-147

Productivity and Carrying Capacity of a Subarctic Sheep Winter Range

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ABSTRACT. Estimates of range composition and net primary productivity for a 10-year period are presented for the semi-arid grasslands of Sheep Mountain, Kluane National Park, Yukon, the winter range of a Dall's sheep (*Ovis dalli dalli*) population. Estimates varied among plots, depending on altitude and aspect, as well as among years, according to rainfall during the growing season. Extremes were 29.1 $g \cdot m^{-2}$ and 120.1 $g \cdot m^{-2}$. Over the 10-year assessment period, the vegetative composition did not change nor was there a grazing-related reduction in productivity. Winter range use by about 200 sheep was within the carrying capacity of the range. A 40% utilization rate of the winter range forage can evidently be sustained and provides a stocking rate of about 1.9 sheep-months$\cdot ha^{-1}$. A significant correlation is demonstrated between forage production of the winter range, lamb survival the following winter, and lamb production the following spring. This correlation indicates that a form of self-regulation of the sheep population is functioning.

Key words: productivity of subarctic, semi-arid grasslands; Dall's sheep, carrying capacity, Kluane National Park, Yukon

RÉSUMÉ. L'auteur présente des évaluations de la portée, de la composition et de la productivité primaire nette durant un période de 10 ans pour la prairie semi-aride de la montagne Sheep, dans le parc national Kluane, au Yukon, le terrain hivernal d'une population de moulfons de Dall (*Ovis dalli dalli*). Les évaluations varient selon les terrains, dépendent de l'altitude et de l'aspect, et aussi selon les années, par rapport à la précipitation durant la saison de croissance. Les extrêmes étaients de 29.1 $g \cdot m^{-2}$ et 120.1 $g \cdot m^{-2}$. Au cours de la période d'étude de 10 ans, la composition végétative ne changea pas et la pâturage n'occasionna aucune réduction en productivité. Le territoire d'hiver occupé par quelque 200 mouflons pouvait bien supporter ces derniers. Un taux d'utilisation de 40% du fourrage du territoire d'hiver peut évidemment être soutenu et peut fournir un taux de soutien d'environ 1.9 mois-mouflons$\cdot ha^{-1}$. Une corrélation importante est signalée entre la production du fourrage dans le territoire d'hiver, la survie des agneaux durant l'hiver suivant et la production d'agneaux au printemps suivant. Cette corrélation indique le bon fonctionnement d'un genre d'autoréglementation de la population de mouflons.

Mots clés: productivité dans les régions sub-arctiques, prairie semi-aride, mouflon de Dall, capacité de soutien, parc national Kluane, Yukon

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

An investigation of Dall's sheep and their habitat on Sheep Mountain, Kluane National Park, began in 1969. The sheep density was considered high and the winter range appeared overgrazed. Study objectives for 1969-1971 included documentation of Dall's sheep population dynamics, seasonal range use, forage selection and utilization rates, net productivity of winter range vegetation, and variations in vegetation productivity between years. Vegetative composition and distribution have been described in Hoefs *et al.* (1975), range productivity and utilization rates by sheep in Hoefs and Brink (1978), and various aspects of sheep demography and behaviour in Hoefs and Cowan (1979).

The establishment of Kluane National Park in 1972 and the designation of Sheep Mountain as a "Special Preservation Area" in the proposed park management plan led to a continuation of this study. To address primarily management problems, the demography of this sheep population was assessed annually (Hoefs and Bayer, 1983), and winter range productivity was reassessed after a 10-year period. The objective of this paper is to document a 10-year trend in productivity and vegetative composition of this winter range.

STUDY AREA

Sheep Mountain is located at Kluane Lake, southeastern Yukon Territory, in the centre of Kluane National Park (Fig. 1). The entire year-round range of the local Dall's sheep population, of which Sheep Mountain comprises the wintering area, is about 165 km² in size. The elevation of the Shakwak Trench, in which Kluane Lake is located, is about 775 m asl; the highest peaks of Sheep Mountain rise to 1950 m.

FIG. 1. Location of study area on Kluane Lake, southwestern Yukon Territory.

Three vegetation zones are recognized in the area (Hoefs *et al.*, 1975). The boreal zone extends to about 1200 m and consists mostly of white spruce (*Picea glauca*). The subalpine

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shrub zone, composed mainly of dwarf birch (*Betula glandulosa*) and willow (*Salix* spp.), may reach 1550 m on favourable sites. Dry, south-facing slopes in the forested as well as in the subalpine zones are usually occupied by grasslands. These make up the winter range of the local sheep population and total about 365 ha in size. Frequently observed species in these zones are: *Artemisia frigida, Carex filifolia, Calamagrostis purpurascens, Agropyron yukonense, Arctostaphylos uva-ursi, Oxytropis viscida*, and *Erigeron caespitosus*. The alpine zone is the most extensive vegetation type in the area, covering about 80 km². *Dryas integrifolia, Festuca altaica* and *Cassiope tetragona* are dominant plants here. The altitudinal limit of vascular vegetation is reached at an elevation of 2150 to 2300 m. Permanent continuous snow cover is encountered above 2500 m.

The bedrock in the area comprises mainly metamorphic and sedimentary deposits of Triassic, Permian, and Cretaceous ages. Three glacial periods modified the physiography and left a thick layer of glacial till around the base of Sheep Mountain. The soils are juvenile and azonal. They are characterized, particularly at lower elevations, by recent loess deposits. The deposition of loess continues to this date, whenever strong down-glacier winds stir up the silt deposits of the Slims River flood plain at times of low water. Most soils are characterized by high alkalinity. More detailed descriptions are given for vegetation in Hoefs *et al.* (1975), geology in Muller (1967), and soils in Day (1962) and Douglas and Knapik (1974).

The Kluane area lies in the rainshadow of the St. Elias Mountains and the climate is semi-arid and continental. Annual precipitation averages 200 mm and the mean annual temperature is -2.5°C. The regional climate is modified by the proximity of Kluane Lake and the funnelling of drying down-glacier winds by the Slims River valley. Taylor-Barge (1969) elaborates in detail on the local climate and weather patterns.

The local sheep population, averaging 200 adults, is characterized by high density, mean values being 1.5 sheep·km^{-2} in summer and 6.8 sheep·km^{-2} in winter (Hoefs and Cowan, 1979); a short life expectancy of 12-13 years (Hoefs and Bayer, 1983); and a high incidence rate (75% in adult sheep; unpubl. data) of mandibular diseases that are collectively referred to as "lumpy jaw" (Glaze *et al.*, 1982). While sheep are the only abundant large mammal species in the area, they compete for forage with a large population of arctic ground squirrel (*Spermophilus parryii*) and on parts of the range with feral horses. Coyotes are the main predator on sheep. On the other hand, perhaps because of the proximity of the Alaska Highway, wolves are not often observed. Also, the impact of other potential predators, (bears, lynx, wolverine, cougar) appears to be negligible. A rich avifauna has been documented for the area (Theberge, 1978; Hoefs, 1973).

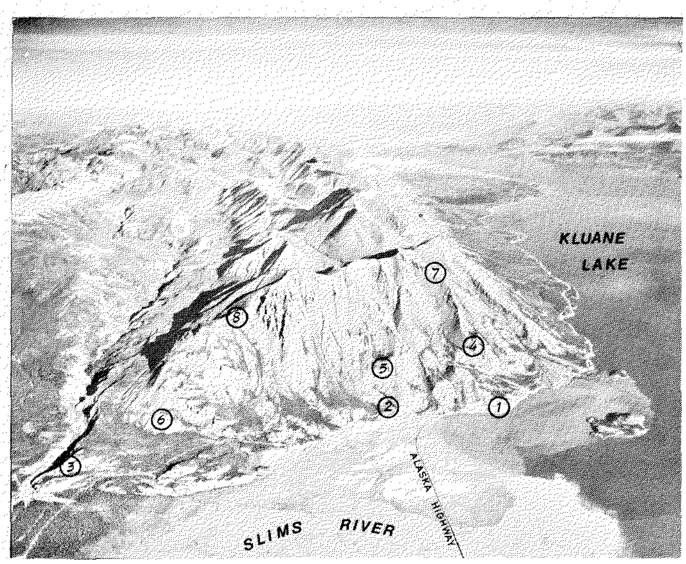

FIG. 2. Aerial photo of Sheep Mountain showing general physiography of study area and location of vegetation plots.

METHODS

Eight 15 × 15 m exclosures were established in 1969 on the southeast slope of Sheep Mountain at various altitudes and aspects (Fig. 2) in plant communities known to be used as winter range by Dall's sheep. Beside each exclosure was established an equally large control plot with comparable vegetation and physical characteristics. Each exclosure was protected from grazing by a 1.8 m high, seven-strand, barbwire fence (Fig. 3). The control plots were unfenced. In the selection of sites, an attempt was made to sample the three altitudinal vegetation zones (boreal, subalpine, and alpine), as well as the three aspects of the mountain that support grassland vegetation (south, southeast, and southwest). The plots were divided into 100 1-m² quadrats, arranged in 10 rows of 10 quadrats each. Species composition and foliage cover were determined to 1% accuracy, using a movable frame with a grid (Mueller-Dombois and Ellenberg, 1974). Foliage cover was preferred to basal cover because of the "bunch-like" growth

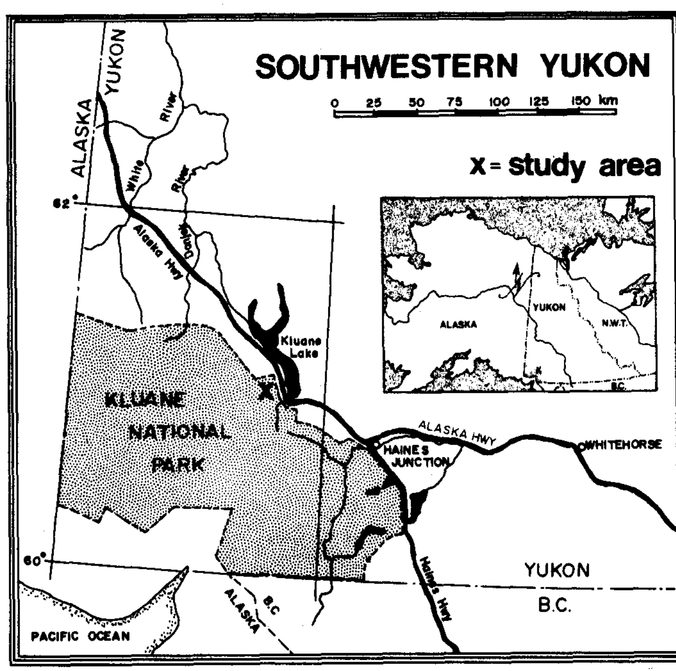

FIG. 3. Exclosure site #3 at west side of Sheep Mountain overlooking Sheep Creek.

TABLE 1. Physical characteristics, vegetative cover, and numbers of sheep pellets of plots at time of establishment, summer 1969

Plot Number	1		2		3		5		6		7		8	
Elevation (m)	800		815		940		1100		1050		1625		1600	
Aspect	120°		176°		240°		180°		236°		90°		226°	
Slope	20°		26°		26°		16°		20°		18°		26°	
Treatment	Open	Excl.	Open	Excl.	Open	Excl.	Open	Excl.	Open	Excl.	Open	Excl.	Open	Excl.
Vegetation cover (%)														
Vascular plants	21.7	22.0	20.5	16.8	18.0	17.5	28.6	31.5	24.2	21.6	42.3	44.2	38.2	33.1
Lichens	27.0	25.0	56.2	56.0	0.7	0.4	0.2	1.0	3.8	2.4	0.2	0.5	0.2	0.3
Mosses	0.5	0.1	0.5	0.6	0.4	0.5	P*	P*	5.7	1.3	P*	2.3	P*	0.1
Bare Soil (%)	49.8	52.9	22.8	26.6	80.9	81.6	71.2	67.5	76.3	74.7	57.5	53.0	71.6	76.5
No. of sheep pellets	42.3	63.3	6.2	5.2	93.0	79.8	81.2	88.8	93.8	68.2	89.6	78.0	82.6	82.6

*P = present in insignificant amounts

forms of many dominant plants in the area.

Individual fecal pellets of sheep were counted for each quadrat. Since the original work by Bennett *et al.* (1940), considerable use of fecal pellet counts has been made in wildlife investigations to assess parameters of range use and forage selection (Riney, 1957; Rogers *et al.*, 1958). Some of the problems involved with this technique have been discussed by Robinette *et al.* (1958) and Neff (1968). Its limitations are recognized. Nevertheless, in plots with comparable vegetation cover, slope gradient, and microclimate, it is still a worthwhile supplementary measure to assess range use intensity.

The physical characteristics, vegetation cover, and sheep pellet numbers of the plots are listed in Table 1. Site #4 was eliminated, since it could not be maintained till 1979.

The plots were established in July 1969, and productivity estimates were made in August 1969, 1970, 1971, and 1979.

TABLE 2. Vegetative composition of plots (%)

Plot Number	1				2				3				5			
Treatment	Open		Exclosure		Open		Exclosure		Open		Exclosure		Open		Exclosure	
Year	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979
Artemisia frigida	2.6	3.8	3.5	7.5	7.8	11.7	9.7	8.5	5.7	11.5	6.6	8.8	4.1	9.3	5.8	8.8
Carex filifolia	8.9	9.0	9.9	7.6	3.6	5.6	4.4	5.0	7.2	9.9	6.8	8.9	9.3	7.5	7.3	9.3
Agropyron yukonense	3.0	3.7	3.3	4.5	0.6	2.4	0.9	1.6	0.5	3.4	0.7	2.0	1.8	2.8	4.7	1.4
Calamagrostis purpurascens	1.3	1.2	0.7	4.7	—	—	P	—	0.3	1.4	0.5	0.9	6.7	13.4	4.1	5.1
Oxytropis viscida	0.1	—	P	—	1.2	0.5	1.9	0.5	0.1	0.5	1.7	1.2	3.1	2.1	1.2	3.2
Erigeron caespitosus	0.3	—	P	0.5	1.5	2.3	1.4	P	1.7	4.2	P	3.5	0.6	1.1	1.3	3.1
Artemisia rupestris	—	—	—	—	0.4	P	—	—	—	—	—	—	5.9	7.4	3.9	4.9
Poa glauca	0.2	0.1	0.3	—	—	—	—	—	—	—	0.1	P	P	P	P	—
Pentstemon gormanii	—	—	—	—	1.5	4.3	1.8	5.1	0.2	0.6	P	0.3	—	—	P	—
Potentilla hookeriana	—	—	—	—	—	—	—	—	0.1	0.3	—	—	P	—	—	—
Aster alpinus	—	—	—	—	P	P	P	—	—	—	0.3	—	P	—	—	—
Linum perenne	—	—	—	—	0.2	P	0.5	P	0.5	0.5	—	0.4	—	—	—	—
Plantago canescens	5.2	15.4	4.2	11.7	—	—	—	—	—	—	—	—	—	—	—	—
Artemisia hyperborea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pulsatilla patens	0.1	0.3	P	—	—	—	—	—	—	—	—	—	—	—	—	—
Minuartia rossii	—	—	—	—	—	—	—	—	—	—	—	—	—	P	P	—
Eurotia lanata	—	—	—	—	—	—	—	—	0.3	0.3	0.4	P	—	—	—	—
Lapulla mysotis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chamaerhodos erecta	—	—	—	—	—	—	P	—	P	—	—	—	—	—	—	—
Arabis holboellii	—	—	—	—	—	—	—	—	—	—	P	P	—	—	—	—
Senecio conterminus	—	—	—	—	—	—	—	—	—	—	P	—	—	—	—	—
Townsendia hookeri	—	—	—	—	—	P	P	—	—	—	—	—	—	—	—	—
Comandra umbellata	—	—	—	—	—	—	—	—	P	—	—	P	—	—	—	—
Total Vascular Vegetation Cover	21.7	33.5	22.0	36.5	16.8	26.8	20.5	20.7	17.5	32.6	18.0	16.0	31.5	43.6	28.6	35.8
Lichens	27.0	50.8	25.0	50.5	56.0	56.2	52.1	64.9	0.4	46.8	0.7	4.4	1.0	33.0	0.2	5.7
Mosses	0.5	1.0	0.1	2.2	0.6	1.9	0.5	1.8	0.5	3.3	0.4	1.8	P	P	P	P
Bare Soil	49.8	12.0	52.9	4.3	26.6	16.6	22.8	14.5	81.6	28.3	80.9	64.9	67.5	10.2	31.2	67.8
Sheep Pellets	42.3	58.4	63.3	9.0	5.2	1.6	6.2	3.8	79.8	28.1	93.0	53.5	88.8	35.1	81.2	76.7

*P = present in insignificant amounts

(continued overleaf)

At each harvesting date 10 quadrats were clipped in each exclosure and control plot to 1 cm above ground level according to a "randomized block" design (Sokal and Rohlf, 1969). Quadrats which had been clipped in previous harvests were eliminated from selection. The clipped vegetation was stored, oven-dried, and weighed according to standard procedures (U.S. Dept. Agric., 1963).

RESULTS AND DISCUSSION

Foliage Cover and Species Composition

Table 2 gives the mean cover values of vascular plant species, lichens, and mosses as well as numbers of sheep pellets for 1969, when the experiment was initiated, and for 1979 when the plots were analyzed again to determine changes over a 10-year period.

In 1969 the mean vascular vegetation cover for the exclosures was 26.9% and for the open controls it was 27.1%. Paired t-tests of means revealed that these cover values were not significantly different. In 1979 the mean cover values for the exclosures were 38.6% and for the controls, 39.1%. This difference in vascular vegetation cover was highly significant for the exclosures and controls ($p = 0.001$). All abundant vascular plant species contributed to the increase in foliage cover in the exclosures, while in control plots, the increase was primarily of *Calamagrostis purpurascens, Artemisia rupestris, Pentstemon gormani, Erigeron caespitosus,* and *Plantago canescens*, species least preferred by sheep. Preferred forage species such as *Agropyron yukonense, Oxytropis viscida* and *Poa glauca* increased little (Hoefs, 1975).

Cover values doubled for crustose lichens in control plots and tripled in the exclosures during the 10-year period. These crustose lichens were mainly *Dermatocarpon hepaticum, Lecidea rubiformis, Lecanora lentigera, Caloplaca cirrochroa, Lecidea decipiens*, and *Parmelia taractis*, in decreasing order of abundance. There was a corresponding reduction in bare soil. The number of sheep pellets in the open control plots decreased from 69.8 in 1969 to 48.0 in 1979 ($p = 0.001$). This indicates a 31% reduction in grazing pressure.

Net Primary Productivity

Table 3 lists the mean productivity estimates for the initial August 1969 assessment as well as for the 1970, 1971, and 1979 harvests. While foliage cover of the range vegetation increased over this 10-year period, net productivity did not. The mean values in 1969 (68.7 $g \cdot m^{-2}$ in exclosures, 65.7 $g \cdot m^{-2}$ in

TABLE 2 (*continued*)

Plot Number	6				7				8				Means			
Treatment	Open		Exclosure		Open		Exclosure		Open		Exclosure		Open		Exclosure	
Year	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979	1969	1979
Artemisia frigida	10.1	16.3	8.1	11.7	14.9	15.3	6.6	19.4	5.1	10.2	3.0	5.2	7.2	11.2	6.2	10.0
Carex filifolia	1.3	1.9	4.0	3.3	6.7	7.8	11.0	9.1	20.7	24.2	13.0	18.9	8.2	9.4	8.1	8.9
Agropyron yukonense	3.4	4.6	2.5	2.5	—	—	—	—	P*	0.8	—	—	1.6	3.0	1.7	2.4
Calamagrostis purpurascens	1.3	3.1	4.1	4.7	5.1	7.2	9.8	17.5	2.0	8.3	3.4	13.2	2.8	5.8	3.8	7.7
Oxytropis viscida	4.9	7.3	4.4	8.4	13.1	11.8	9.7	17.3	1.6	5.3	1.8	5.4	3.4	3.9	3.0	5.1
Erigeron caespitosus	0.6	0.9	1.1	1.0	—	—	P	P	0.7	1.4	0.4	0.7	0.8	1.4	0.6	1.2
Artemisia rupestris	—	—	—	—	—	—	—	—	4.4	8.2	9.2	11.1	3.6	5.2	6.6	8.0
Poa glauca	—	—	—	—	1.2	2.7	1.0	2.5	3.7	2.1	2.3	1.7	1.0	1.0	0.8	1.2
Pentstemon gormanii	—	—	—	—	—	—	—	—	—	—	—	—	0.8	2.5	0.9	2.7
Potentilla hookeriana	—	—	—	—	0.3	—	0.4	0.4	P	P	P	—	N/A			
Aster alpinus	P	P	—	—	—	—	—	—	—	—	—	—	N/A			
Linum perenne	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Plantago canescens	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Artemisia hyperborea	—	—	—	—	0.8	0.3	3.3	3.5	P	0.7	P	0.4	0.4	0.5	1.7	2.0
Pulsatilla patens	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Minuartia rossii	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Eurotia lanata	—	—	—	—	0.2	P	2.4	—	—	—	—	—	N/A			
Lapulla mysotis	—	—	P	P	—	—	—	—	—	—	—	—	N/A			
Chamaerhodos erecta	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Arabis holboellii	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Senecio conterminus	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Townsendia hookeri	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Comandra umbellata	—	—	—	—	—	—	—	—	—	—	—	—	N/A			
Total Vascular Vegetation Cover	21.6	34.1	24.2	31.6	42.3	45.1	44.2	69.7	38.2	61.2	33.1	56.6	27.1	39.5	26.9	39.6
Lichens	2.4	43.3	3.8	31.9	0.2	0.4	0.5	1.0	0.2	9.8	0.3	21.6	12.6	24.0	12.2	35.5
Mosses	1.3	2.0	5.7	5.8	P	0.5	2.3	1.0	P	P	0.1	P	1.0	1.7	0.7	1.5
Bare Soil	74.7	28.6	76.3	32.5	57.5	24.2	53.0	23.3	71.6	15.3	76.5	10.8	61.4	33.0	61.8	17.7
Sheep Pellets	68.2	22.0	93.8	25.4	89.6	52.1	78.0	68.4	82.6	66.3	82.6	33.1	69.8	48.0	79.8	27.9

*P = present in insignificant amounts

controls) were not statistically different. In 1979 the net productivity of the controls was only 52.7 $g \cdot m^{-2}$ ($p = 0.05$), while that of the exclosures remained essentially stable (69.8 $g \cdot m^{-2}$). The overall mean value of all plots (61.7 $g \cdot m^{-2}$) was the lowest of the four assessments. Variations in net productivity during the 1969-1971 period were related to precipitation during the growing season (Hoefs and Brink, 1978). We concluded that the low productivity in 1979 also reflects primarily this environmental parameter rather than the impact of grazing. Forage yields in the exclosures as well as in Plot #2a, which is not grazed by sheep, were already significantly higher in 1970, only one year after protection.

production from one year to the next, which can be considerable, are brought about primarily by variation in rainfall during the growing season ($r = 0.952$), a relationship documented for many other semi-arid grasslands (Blaisdell, 1958; Dahl, 1953; Rogle and Hess, 1947).

Sustainable Range Use Rate

Based on forage production estimates, acreages of grasslands on the winter ranges (Hoefs *et al.*, 1975), and known sheep forage consumption rates (Palmer, 1944; Hebert, 1973; Seip, 1983), it was estimated that this winter range can support

TABLE 3. Net primary productivity in $g \cdot m^{-2}$ (oven dry weight) and rainfall during the growing season (mm)

Plot No.	Treatment	1969	1970	1971	1979
1	Control	59.0 ± 19.0	57.5 ± 6.9	37.3 ± 9.8	43.5 ± 16.9
	Exclosure	56.9 ± 6.5	70.4 ± 13.1	51.3 ± 10.0	56.9 ± 21.5
2	Control	58.8 ± 21.1	75.4 ± 18.4	45.8 ± 15.3	47.8 ± 29.5
	Exclosure	65.9 ± 19.9	72.3 ± 19.7	49.8 ± 14.9	53.9 ± 21.1
3	Control	45.9 ± 12.9	61.1 ± 31.7	29.1 ± 9.4	47.7 ± 28.9
	Exclosure	41.0 ± 9.4	70.2 ± 16.2	58.6 ± 35.8	56.9 ± 28.8
5	Control	90.5 ± 32.8	58.9 ± 27.7	51.4 ± 14.7	54.2 ± 15.4
	Exclosure	85.0 ± 29.8	96.6 ± 23.4	98.5 ± 42.3	75.3 ± 38.2
6	Control	45.5 ± 9.1	53.8 ± 9.2	37.5 ± 5.5	42.8 ± 14.7
	Exclosure	59.7 ± 14.6	99.3 ± 35.7	62.0 ± 22.5	69.7 ± 38.8
7	Control	45.0 ± 5.1	97.1 ± 12.8	87.3 ± 13.5	80.1 ± 22.7
	Exclosure	52.5 ± 9.4	103.2 ± 20.2	89.9 ± 21.9	92.9 ± 24.1
8	Control	115.2 ± 72.5	86.3 ± 36.0	88.4 ± 11.7	52.9 ± 21.3
	Exclosure	120.1 ± 79.5	99.9 ± 20.4	104.5 ± 18.4	88.8 ± 34.9
Means (95% confidence limits)		67.2 ± 24.4	78.7 ± 20.8	63.9 ± 17.6	61.7 ± 25.5
Precipitation (sum of May, June & July)		71.0	90.2	54.4	60.4

The increase in foliage cover resulted from a reduction in grazing pressure in the mid-1970s due to a sheep population decline of more than 20% between 1971 and 1977 (Hoefs and Bayer, 1983). Reduction in grazing pressure is also obvious from the increase in crustose lichen cover, which is easily destroyed by trampling (Hoefs and Brink, 1978) and the reduction in sheep fecal pellet numbers. While sheep numbers declined, horse use of the area increased (6 horses in 1969-71, 11 horses in 1976-77; Hoefs and Bayer, 1983). However, horses were prevented from interfering with the plot assessments by fences that did not exclude the sheep. The data obtained from the plots reflect only sheep use of the area. The winter range as a whole was open to horse grazing.

The sheep population built up again in the late 1970s to a size similar to that of 1971-72 (201 adult sheep in 1979; Hoefs and Bayer, 1983), while horse use of the area declined to a negligible level. Drought and restored grazing pressure by sheep explain the low forage production for 1979. Increased foliage cover did not translate into improved yield, since individual plants were low and lacked vigour.

Considering the 10-year trend, we can conclude that the sheep population, which averaged 200 during winter, did not have a long-range negative influence on either productivity or species composition of its winter range. Fluctuations in forage

a population of about 200 sheep over winter. This estimation is supported by population data. A review of historic data (Hoefs, 1975) and recent population statistics (Hoefs and Bayer, 1983) revealed that a herd size of about 200 in winter was not exceeded even in years of predator control, or after National Park establishment when poaching was largely prevented and the removal of sheep for zoos, game farms, or scientific purposes was disallowed. Prior to National Park establishment, this removal of sheep through human activities was the single most important adult mortality factor (Hoefs, 1975). Further evidence of a capacity-filled winter range comes from the sensitive relationship between forage production on the winter range and lamb survival over the following winter ($r = 0.966$), as well as forage production and natality rates the following spring ($r = 0.826$), and the trend in sheep population performance and horse use of the area during the past decade (Hoefs and Bayer, 1983).

In 1970 (9.02 cm ppt.) about 30% of the available forage was removed by sheep. The total removal rate would climb to 40% if use of the area by horses were included (Hoefs and Brink, 1978). In 1971, a year with less favourable rainfall conditions (5.44 cm ppt.), 20% less forage was produced, but 5% more sheep were on the mountain (1970: 195 adult sheep; 1971: 206 adult sheep). For that year the forage removal rate by sheep was estimated at 38%. Together with that by horses, it exceeded 50%. A utilization rate in excess of 50% was considered too high (Scotter, 1975; Stelfox, 1976), and a decline in the sheep population was predicted, should the presence of horses on the range be allowed to continue. Such a decline did indeed take place, and paralleled an increase in horse use of the area. By 1977 up to 11 horses used Sheep Mountain and the sheep population had dropped to 165 adults. Subsequently horse use of the area was "discouraged", and in recent years, only five horses have occasionally inhabited the range. The sheep population built up again and in 1979 and 1980 reached levels (199 and 191 adults, respectively) similar to those observed in the early 1970s.

Little is known about sustainable winter forage utilization rates of subarctic, semi-arid grasslands. While a removal rate in excess of 50% appears to be too high, one of about 40% was suportable. Making allowance for the use of horses, a forage utilization rate of 40% in 1970 allowed for a high winter survival rate of lambs (71%) and an above average natality rate the following spring (47 lambs: 100 ewes). Such a utilization rate of sheep winter ranges in semi-arid areas is supported by Stelfox (1976), who writes: "Ranges stocked with 2.0 sheep-months/acre and 37% vegetation use were in good condition, those with 3.7 sheep-months per acre and 46% use were in fair condition, while those supporting 5.0 sheep-months per acre and 61% use were in poor, over-grazed condition. Proper use was 40% use of all vegetation, except junipers and bearberry."

Considering range size, productivity, and utilization rate, as well as sheep numbers and range use period, the 1970/71 stocking rate amounted to 1.92 sheep-months$\cdot$ha^{-1} (0.8 sheep-month$\cdot$acre^{-1}).

Relation Between Forage Production of the Winter Range and Vital Statistics of the Sheep Population

The question of whether or not ungulates have intrinsic mechanisms to regulate their numbers within the limits imposed by the carrying capacity of their range is an intriguing and highly controversial one. Geist (1971) suggested that the numbers of native ungulates that are associated with climax vegetation types (such as sheep) are self-regulated. Buechner (1960), however, reported that sheep are subject to wide fluctuations in numbers, although not all populations show this trend. Those that live under severe environmental conditions tend to be relatively stable. In support of Buechner's (1960) position, large population fluctuations caused by severe die-offs have been reported for bighorn sheep in Alberta and British Columbia (Cowan, 1945; Edwards, 1956; Demarchi and Demarchi, 1967; Bandy, 1968; Stelfox, 1971); in Montana (Marsh, 1938); and in Colorado (Buechner, 1960).

Subarctic sheep populations that are exposed to more uniformly severe environmental conditions tend to be relatively stable (Geist, 1971; Hoefs and Bayer, 1983). This stability appears to be brought about by predator pressure and severe winter weather conditions. On the other hand, parasites and diseases, which often cause drastic fluctuations in sheep numbers in southern areas, are of little importance in subarctic herds (Palmer, 1941; Murie, 1944; Leopold and Darling, 1953; Nichols and Smith, 1971; Heimer, 1981).

TABLE 4. Relation between forage production on winter range and vital statistics of sheep population

Year	Forage production* ($g\cdot m^{-2}$)	Lamb survival the following winter (%)	Lambs born the following spring (Lambs/100 ewes)
1969	67.2	60	41
1970	78.7	71	47
1971	63.9	61	41
1979	61.7	56	30

*These values differ somewhat from those listed in Hoefs and Brink (1978), because of the exclusion of Plot #4, which could not be maintained to 1979.

On Sheep Mountain, forage production on the winter range, lamb production the following spring, and the survival rate of lambs the following winter are significantly correlated (Table 4). The four years during which range productivity assessments were conducted were years in which the population was at high levels (200 adults). The largest amount of forage (78.7 $g\cdot m^{-2}$) was produced in 1970, the year with the most favourable rainfall conditions during the growing season (Hoefs and Brink, 1978). During the following spring (1971) the highest natality rate (47:100) was documented. Of the lambs born during the spring of 1970, 71% survived the winter. During the summer of 1979 the average forage production was only 61.7 $g\cdot m^{-2}$. During the following spring, lamb production was poor (30:100) and only 56% of the lambs born in the spring of 1979 survived the winter.

The data presented lend support to the concept of population self-regulation in northern sheep. They argue against the hypothesis presented by Stelfox (1971, 1976) that sheep cannot maintain their numbers at "safe" levels but build up to peaks that exceed the carrying capacity of their range and are therefore subject to periodic die-offs of perhaps 25- to 30-year intervals.

ACKNOWLEDGEMENTS

The author is grateful to Parks Canada and the Yukon Wildlife Branch for supporting this investigation. This paper is an abbreviated version of a much larger report submitted to Parks Canada and is published with permission of that agency.

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