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Recovery of Tundra Vegetation after Overgrazing by Caribou in Arctic Canada

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ABSTRACT. During the summer of 1987, 500–1000 caribou became stranded on Rideout Island in Bathurst Inlet, Northwest Territories. The 40 km^2 island did not have sufficient forage to support the animals until freeze-up, and the caribou eventually died from malnutrition after severely overgrazing the vegetation. In late July 1988, we found that most of the vascular vegetation on Rideout Island had recovered considerably. Vascular species composition and cover in the two major plant communities were comparable to those in similar communities on the adjacent, moderately grazed mainland. The willows (*Salix* spp.) and graminoid species were vigorous, and no differences were found in biomass allocation patterns of *Salix lanata* plants between the island and the mainland. However, essentially all of the macrolichen biomass was eliminated on the island, and full recovery could take more than 20 years.

Key words: caribou, caribou range ecology, overgrazing, Bathurst Inlet, arctic vegetation, *Salix* spp., *Betula* spp.

RÉSUMÉ. Durant l'été de 1987, de 500 à 1 000 caribous se sont retrouvés coincés sur l'île Rideout de l'inlet Bathurst situé dans les Territoires du Nord-Ouest. L'île de 40 km^2 n'avait pas suffisamment de plantes herbacées pour nourrir les animaux jusqu'à la prise des glaces, et les caribous ont fini par mourir de malnutrition après avoir brouté la végétation à un niveau extrême. À la fin de juillet 1988, on a trouvé que la plupart des plantes vasculaires sur l'île Rideout avaient largement récupéré. La composition et la couverture des espèces vasculaires dans les deux plus importantes communautés de plantes étaient comparables à celles, modérément broutées, des communautés semblables situées sur la terre ferme adjacente. Les saules (esp. *Salix*) et les espèces de graminées étaient vigoureuses, et on n'a trouvé aucune différence dans le schéma de répartition de la biomasse des plantes *Salix lanata* entre l'île et la terre ferme. Cependant, la biomasse des macrolichens a été pratiquement éliminée sur l'île et sa réintégration complète pourrait prendre plus de 20 ans.

Mots clés: caribou, écologie du territoire du caribou, broutage excessif, inlet de Bathurst, végétation arctique, esp. *Salix*, esp. *Betula*

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INTRODUCTION

The effects of overgrazing on arctic plant communities are virtually unknown, especially on the forage communities of barren-ground caribou. Overgrazing is the nearly complete removal of aboveground forage by grazing and associated trampling effects of high densities of herbivores. Klein (1968) described the irruption and crash of an introduced reindeer population on St. Matthew Island, Alaska, and attributed the decline to anomalously deep snow in one winter and overgrazing by the large reindeer population. The vascular vegetation recovered well, with a slight increase in the abundance of grasses (Klein, 1987). A similar irruption of reindeer on an Aleutian Island was reported by Scheffer (1951). Irruption of introduced reindeer on South Georgia Island caused extensive overgrazing in all plant communities, although grazing exclosures showed that the vascular and moss species were quite resilient once the grazing pressure was released (Leader-Williams, 1988). Most of the unsuccessful introductions of reindeer and caribou to islands have followed the same pattern of irruption, overgrazing and die-off (Leader-Williams, 1988).

During the summer of 1987, a group of caribou cows and calves estimated to number 500-1000 became inexplicably stranded on Rideout Island in Bathurst Inlet, Northwest Territories (N.W.T.). Caribou from the Bathurst herd regularly use the islands in Bathurst Inlet in summer (J. Tikhak, pers. comm. 1988), but there are no previous reports of animals becoming stranded. The N.W.T. wildlife guardian in nearby Umingmaktok (Bay Chimo) had noticed the caribou on the island in mid-July. By September, the N.W.T. Wildlife Service had become aware of the marooned caribou and a visit to the island was made in early October 1987. During the investigations, caribou were collected to confirm malnutrition mortality (D. Heard, pers. comm. 1988). All of the available vegetation was eaten by the caribou, and some areas were heavily trampled. Many caribou had died and survivors were weak. The caribou eventually died from malnutrition or were killed by wolves and bears.

In late July 1988, we visited Rideout Island to assess the recovery of the vegetation. In this paper we report on how the vegetation has responded one year after this rare circumstance of overgrazing by stranded caribou.

SITE DESCRIPTION

Rideout Island, on the east side of Bathurst Inlet (Fig. 1), is a rocky island of *ca.* 40 km^2 separated from the mainland by a narrow channel of 2.5 km and from a larger island to the south by 1.5 km. Vegetation covers 50-60% of the island and is largely composed of two major plant communities: low shrub tundra and tussock tundra, with minor communities of wet sedge meadows and dry rock outcrop areas. The Bathurst Caribou Herd migrates through the region to calving grounds east of Bathurst Inlet and then returns through the area in late June–early July (Fleck and Gunn, 1982).

METHODS

We visited Rideout Island on 30 and 31 July 1988 and first surveyed the island from the aircraft for a general assessment of the vegetation. Vegetation measurements were made on 30 July in the two predominant plant community types on the island: 1) a low shrub tundra community, dominated by dwarf shrub species (e.g., *Betula glandulosa*, *Vaccinium uliginosum* and *Salix* spp.); and 2) tussock tundra, dominated by *Eriophorum vaginatum* (nomenclature follows Porsild and Cody [1980]). On 31 July, measurements were repeated in similar communities on the mainland, 3 km east of Rideout

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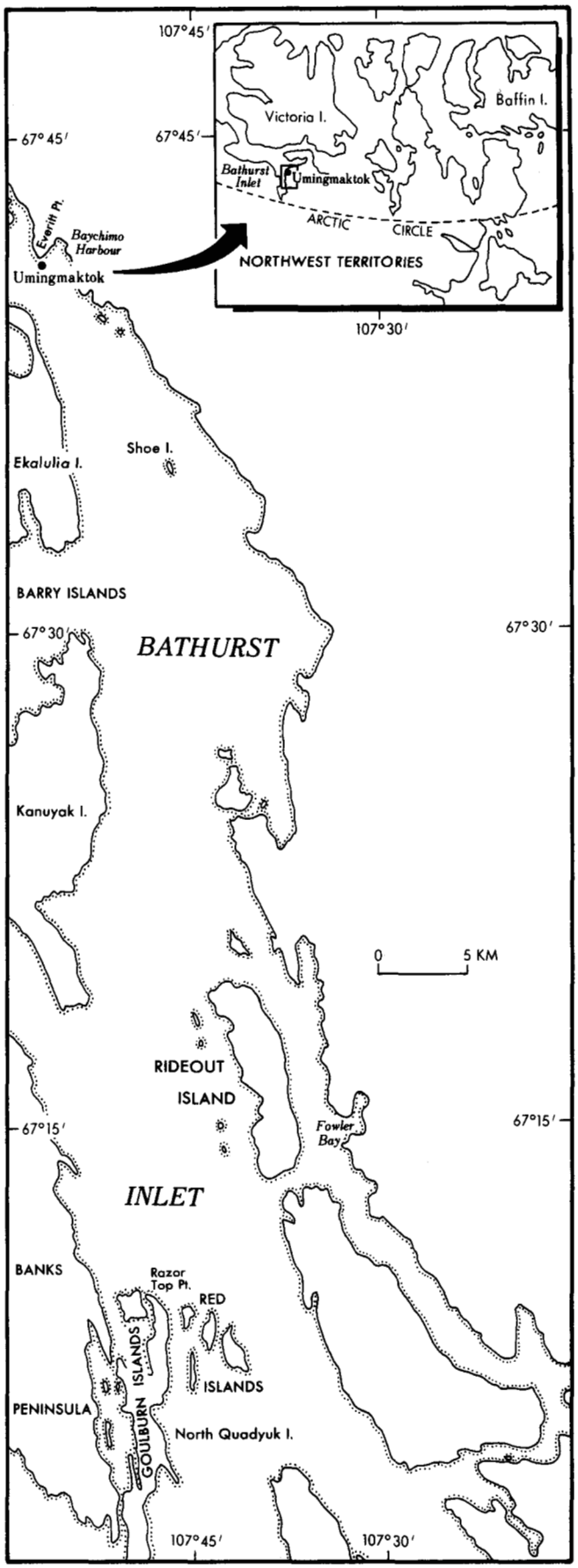

FIG. 1. Map showing location of Rideout Island, Bathurst Inlet, Northwest Territories.

Island. The mainland was considered to be a better control area than the larger island just south of Rideout Island because large numbers of caribou had been seen on that island during the same period they were observed on Rideout Island (J. Tikhak, pers. comm. 1988).

In large homogeneous areas of each community, plant cover was visually estimated for each vascular species, lichen growth form and moss from quadrats (100 × 50 cm). The quadrats were randomized by blindly throwing them over a shoulder. Within each quadrat, the number of browsed and unbrowsed shoots of the major shrub species were counted from three random 10 × 10 cm sections. The sections were chosen by blindly dropping a pencil into the quadrat. The number of browsed shoots per section was then averaged for each quadrat.

To assess the response of the major shrub species to overgrazing, random shoots of *Salix lanata* and *Betula glandulosa* were harvested from the low shrub tundra communities on both the island and the mainland. The shrubs were transported to the lab, sorted into green leaves, live woody tissue, flowers and attached dead matter and oven-dried (80°C) before weighing. The component dry weights of the harvested shrubs were used to calculate percent biomass allocation.

Data for browsed shoots and biomass allocation were tested for normality using Kolmogorov-Smirnoff and standardized skewness and kurtosis measures, and for heterogeneity of variances with Bartlett's and Cochrane's tests (Sokal and Rohlf, 1981). Analysis of variance was used to detect differences between Rideout Island and the mainland control sites.

RESULTS

General Overview

From the aircraft, the plant communities had apparently recovered from the overgrazing. Some heavily used trails could be seen through wet areas, but there were no obvious signs of permanent damage. However, wet areas were heavily trampled with >50% bare ground in some places. In these communities the major invading species was *Equisetum arvense*. There was also evidence that the caribou had been digging for roots in most communities. Most deciduous shrubs had numerous dead shoots, a consequence of being stripped of leaves the previous summer. There was also a nearly complete lack of fruticose and foliose lichens.

Community Response

In the low shrub tundra community, the cover of dwarf shrub species was generally lower on Rideout Island than on the mainland (Table 1). This was especially true for the evergreen species *Arctostaphylos alpina* and *Ledum decumbens*, whose cover was significantly lower on Rideout Island. One curious exception to the trend was *Vaccinium uliginosum*, which had greater cover ($P < 0.1$) on the island than the mainland. Cover of forbs and grasses and sedges was similar in both sites ($P > 0.1$) and constituted minor components of the community. There was a noticeable lack ($P < 0.05$) of foliose and fruticose lichens in the low shrub tundra of Rideout Island. Much of the lichen cover on Rideout Island consisted of broken pieces of thalli that had been grazed by the caribou. Moss cover was greater ($P < 0.1$) on the island than on the mainland, but there was little difference in cover of litter and bare ground.

TABLE 1. Mean cover (% ± SE) of major species from low shrub tundra communities on Rideout Island and the mainland site

Species	Rideout Island (n = 7)	Mainland (n = 7)
Arctostaphylos alpina	5 ± 2	14 ± 4**
Betula glandulosa	10 ± 3	9 ± 4
Cassiope tetragona	4 ± 1	12 ± 5
Empetrum nigrum	4 ± 3	9 ± 2
Ledum decumbens	2 ± 1	7 ± 2**
Salix lanata	7 ± 2	4 ± 1
Salix reticulata	4 ± 1	9 ± 8
Vaccinium uliginosum	16 ± 4	7 ± 2*
Hedysarum alpinum	<1	1 ± 1
Pyrola grandiflora	<1	2 ± 1
Grasses and sedges[a]	3 ± 1	1 ± 0.5
lichen - foliose + fruticose	2 ± 1	9 ± 2**
lichen - crustose	<1	1 ± 0.5
moss	34 ± 7	18 ± 4*
litter	15 ± 3	11 ± 1
bare ground	1 ± 1	1 ± 0.5

[a] Major species include *Poa arctica*, *Eriophorum angustifolium* and *Carex aquatilis stans*.
* Means significantly different (ANOVA; $P<0.10$).
**Means significantly different (ANOVA; $P<0.05$).

In the tussock tundra community, the cover of the dominant sedge species (*Eriophorum vaginatum*) was slightly less ($P<0.1$) on the island than the mainland site (Table 2). However, there was little difference between the sites in cover of the other sedge species (*Carex aquatilis stans* and *Eriophorum angustifolium*). The differences in cover of the dwarf shrubs between the sites was not as pronounced as in the low shrub community. Only the deciduous species *Betula glandulosa* had significantly lower cover on the island. However, as in the low shrub tundra community, *Vaccinium uliginosum* had greater ($P<0.05$) cover on the island than on the mainland. Forbs were slightly less prominent on the island but were a minor component of the community in both sites. Although lichens are relatively infrequent in tussock tundra communities, there were virtually no lichens, including crustose lichens, present in the site on Rideout Island. Moss cover was greater ($P<0.1$) on the island than the mainland, although litter and bare ground cover were similar in both sites.

Shoots of *Betula glandulosa* and *Vaccinium uliginosum* were more heavily browsed ($P<0.05$) in the low shrub community of Rideout Island than on the mainland (Table 3). *Salix lanata* was heavily browsed on the island but showed great variability. *Ledum decumbens* was essentially ungrazed in both sites.

In the tussock tundra community, the shoots of *Betula glandulosa* and *Salix lanata* were more heavily browsed ($P<0.05$) on Rideout Island (Table 3). This also appeared to be the case for *Vaccinium uliginosum* on the island; however, sample sizes prevented statistical testing. A small proportion of the shoots of *Ledum decumbens* was eaten in the tussock tundra community on the island, while those on the mainland were ungrazed.

Species Responses

Biomass allocation to leaves, stems and flowers was not different in shoots of *Salix lanata* harvested from Rideout Island or the mainland (Table 4). In addition, the percentage of attached dead biomass did not differ between the sites. Many *Salix* plants on the island had numerous new shoots produced from the base of the main shoot or from roots near the soil surface. In some cases, these shoots had grown as much as 30 cm. Leaves were produced from older branches, the top portions of which were usually dead, with evidence of browsing.

In contrast, biomass allocation in shoots of *Betula glandulosa* was different between Rideout Island and the mainland (Table 4). Allocation to leaves and flowers was significantly lower in the shoots harvested on Rideout Island. The smaller amount of biomass in leaves and flowers resulted in the percent biomass in stems being greater in shoots from Rideout Island than on the mainland. *Betula* plants did not produce "compensatory" shoots from the base as in *Salix*, and the leaves appeared to be smaller in size relative to the mainland plants.

TABLE 2. Mean cover (% ± SE) of major species from tussock tundra communities on Rideout Island and the mainland site

Species	Rideout Island (n = 10)	Mainland (n = 5)
Eriophorum vaginatum	20 ± 2	27 ± 3*
Arctostaphylos alpina	3 ± 2	5 ± 3
Betula glandulosa	3 ± 1	9 ± 3**
Dryas integrifolia	<1	1 ± 1
Empetrum nigrum	2 ± 1	2 ± 2
Ledum decumbens	6 ± 2	4 ± 2
Salix lanata	6 ± 2	10 ± 2
Salix reticulata	2 ± 1	4 ± 2
Vaccinium uliginosum	9 ± 3	2 ± 1**
Forbs[a]	<1	2 ± 1
Carex aquatilis stans	2 ± 1	1 ± 0.5
Eriophorum angustifolium	2 ± 1	1 ± 1
lichen - foliose + fruticose	<1	1 ± 0.5**
lichen - crustose	0	1 ± 0.5**
moss	16 ± 2	11 ± 1*
litter	8 ± 1	7 ± 1
bare ground	3 ± 1	1 ± 1

[a] Major species include *Polygonum viviparum*, *Pyrola grandiflora* and *Saussurea angustifolia*.
* Means significantly different (ANOVA; $P<0.10$).
**Means significantly different (ANOVA; $P<0.05$).

TABLE 3. Mean percent (± SE)[a] of browsed shoots of dominant shrub species in low shrub and tussock tundra communities on Rideout Island and the mainland site

Species	Rideout Island	Mainland
Low shrub tundra		
Betula glandulosa	52 ± 7 (4)	6 ± 6 (4)*
Salix lanata	51 ± 21 (4)	4 ± 13 (3)
Vaccinium uliginosum	30 ± 8 (5)	3 ± 3 (6)*
Ledum decumbens	0 (3)	0 (6)
Tussock tundra		
Betula glandulosa	36 ± 10 (5)	7 ± 4 (4)*
Salix lanata	37 ± 7 (8)	8 ± 8 (4)*
Vaccinium uliginosum	23 ± 6 (10)	0 (2)
Ledum decumbens	5 ± 3 (8)	0 (4)

[a] Value in brackets is sample size: the number of cover quadrats in which the species was present.
*Means significantly different (ANOVA; $P<0.05$).

TABLE 4. Mean biomas allocation (% of total weight ± SE) in *Salix lanata* and *Betula glandulosa* shoots harvested from low shrub tundra communities on Rideout Island and the mainland site

Component	Rideout Island	Mainland
Salix lanata	(n = 45)	(n = 16)
% leaves	19.4 ± 1.5	23.5 ± 1.6
% stems	63.1 ± 1.9	64.3 ± 2.5
% flowers	0.2 ± 0.2	0.1 ± 0.1
% attached dead	17.3 ± 2.1	12.2 ± 1.8
Betula glandulosa	(n = 31)	(n = 11)
% leaves	12.5 ± 1.3	21.5 ± 1.3*
% stems	70.4 ± 1.9	62.9 ± 2.0*
% flowers	0.1 ± 0.04	1.3 ± 0.3*
% attached dead	17.1 ± 1.9	14.4 ± 2.1

*Means significantly different (ANOVA; $P<0.05$).

DISCUSSION

The stranding of large numbers of caribou on islands has not been previously reported. The reasons why 500-1000 caribou stayed on Rideout Island are unknown, but Inuit believe high winds discouraged the caribou from swimming away, and lack of leadership among the group was an important factor (J. Tikhak, D. Kaomayok, pers. comm. 1988). The density of animals (13-25·km^{-2}) was much higher than the vegetation could support for any length of time and is well beyond estimated carrying capacities for island populations of *Rangifer* spp. (Leader-Williams, 1988). Densities of caribou cows are high on calving grounds, and 50 animals·km^{-2} over 1000-2000 km^2 is not unusual (D. Heard, pers. comm. 1988). However, the high densities are temporary and the caribou move within a week. The caribou were on Rideout Island for 8-12 weeks.

Despite the severe overgrazing, the vascular vegetation on Rideout Island appeared to have recovered quite well within a single growing season. Cover of most species was lower on the island than on the mainland, but the vigour of the graminoids and deciduous shrubs, especially *Salix* spp. and *Vaccinium uliginosum*, indicate that the plants should recover from this unique episode. However, the lichens were heavily damaged and could take 20 years or more to recover to normal levels (Klein, 1987). In addition, Klein (1987) reported that the lichen species most frequently found in the recovering forage communities of St. Matthew Island were not highly preferred species (e.g., *Cladina* spp., *Cetraria* spp. and *Cladonia* spp.) found in abundance on a nearby ungrazed island. This seems to indicate a successional sequence must occur before the most desired lichen species regain prominence. The increased moss cover in disturbed areas may play a role in the succession, since the common macrolichens are strongly associated with moss cover on hummocks in both major plant communities.

The lack of lichens on Rideout Island will probably discourage caribou from using the island for some time. In a recent census of the Bathurst caribou herd, some tracks were seen on the island but no animals were sighted, while many animals were seen on the mainland and on the larger island directly south of Rideout Island (D. Heard, pers. comm. 1990).

The very high incidence of browsed shoots on the island clearly shows the degree of overgrazing. The mainland site had many well-used trails, but the relatively low degree of browsing is more likely the typical situation for this region. Although there was some evidence the caribou were using evergreen Ericaceous species known to be of low palatability and digestibility (e.g., *Ledum decumbens* and *Cassiope tetragona*) (White and Trudell, 1980), it appears that they continued to avoid these species, despite the shortage of more desirable forage. In contrast, *Empetrum nigrum*, also an evergreen dwarf shrub, was the most frequent component of rumen contents found with the reindeer carcasses on St. Matthews Island (Klein, 1968). *Empetrum* is a minor component of the tundra communities in the Rideout Island area but was not noticeably browsed on the island.

The rapid recovery of *Salix* spp. is consistent with results of studies of disturbance in the Subarctic. Members of the genus are well known for their ability to produce biomass through coppice sprouting, which is important in biomass production for energy (Pearce, 1984) and for browse (Bryant and Chapin, 1986; Wolff, 1978). Kershaw *et al.* (1988) have shown that shrubs of subarctic *Salix arbusculoides* recovered to 75% of original size in one growing season after cutting all shoots to ground level. In similar experiments, de Grosbois (1989) found *S. arbusculoides* shrubs attained dry weights equal to controls in just two growing seasons. *Vaccinium uliginosum* also showed relatively rapid recovery, with higher cover values on the island, primarily due to increased leaf production. These responses are analogous to the compensatory growth response to grazing found in many graminoid species (McNaughton, 1983). The other shrub species did not show this compensatory response.

Klein (1987) reported that graminoid plants (grasses and sedges) and willows had increased in abundance after most of the lichen mat was removed by reindeer. Graminoid density and willow cover continued to increase with increasing grazing pressure. Similarly, Leader-Williams (1988) found that certain grasses increased in abundance in heavily grazed areas of South Georgia and that the introduced reindeer utilized graminoids as the major winter forage in the absence of lichens. Neither of these responses was found on Rideout Island after one growing season, although the major graminoid species did not appear to have been affected by the intense grazing. Henry and Svoboda (1989) have found that high arctic sedge meadows show increased net production in response to moderate grazing by muskox.

In summary, low arctic vascular vegetation is resilient to a single episode of overgrazing by caribou. Recovery of lichen biomass will undoubtedly require many more years. Subsequent studies are planned to document the long-term recovery of the vegetation on Rideout Island.

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