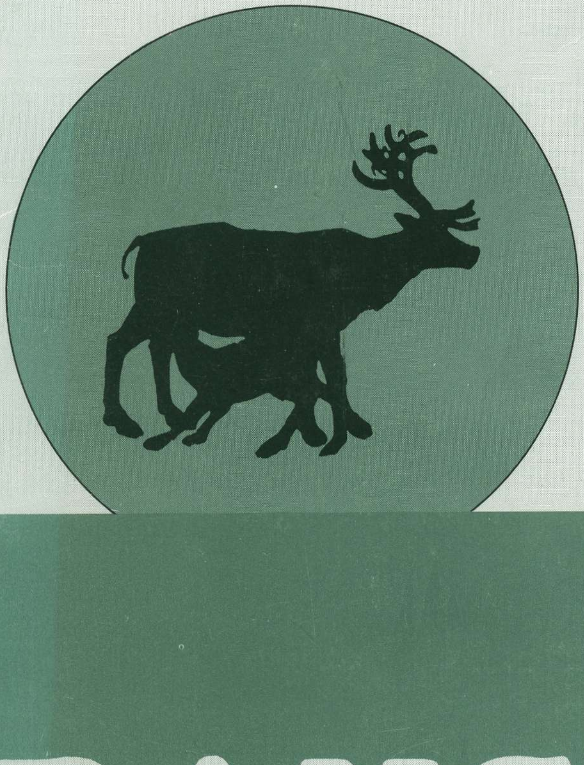
Proceedings of the Fourth International Reindeer/Caribou Symposium

Whitehorse, Canada
22 —25 August 1985



RANGIFER

Scientific Journal of Reindeer and Reindeer Husbandry

Special Issue No. 1, 1986

The Proceedings of the Fourth International Reindeer/Caribou Symposium
is in honour of Professor **Jack R. Luick** (1921 - 1983)

Special Issue No. 1

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Proceedings of the Fourth International Reindeer/Caribou Symposium

Whitehorse, Yukon, Canada
22 - 25 August 1985

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Frank L. Miller
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Published by Nordic Council for Reindeer Research (NOR)

Harstad, Norway, 1986

Rangifer

Published by:
Nordic Council for Reindeer Research (NOR)

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Printed by:
A/S Harstad Tidendes Trykkeri

ISSN 0801-6399

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EXXO Company USA, Anchorage, Alaska

Gulf Canada, Calgary, Alberta

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Rangifer — **World status report**

Session papers (these papers received peer review, two reviewers for each manuscript)

Special papers (these papers received limited editorial review after they were transliterated, but they received no peer review because we judged that no qualified reviewers were available to us)

Expanded abstracts & abstracts (these papers received only minimal editorial review and no peer review - much of the material in this section has been published elsewhere)

A Tribute to Jack Luick

Professor Jack R. Luick 1921 — 1983.

It is 1970 in Cantwell, Alaska. Early August, if memory serves. A borrowed bulldozer, pulling an ancient 2-wheel trailer, lumbers uphill toward 2 military surplus trailers and a rudimentary system of paddocks - in those days, the extent of our field facilities at the University of Alaska Reindeer Research Station. Perched precariously atop the trailer is a well-used outhouse «procured» from some abandoned cabin site in the Village surburbs.

An exciting day indeed, for we were about to install our very own convenience facility. Since placement of the bare essentials in 1967, the team had completed several batteries of field trials on reindeer, all of which required that some experiments be conducted in the dead of winter. The original field complex consisted only of an unheated handling barn and a drafty storage area. And if Mother Nature called unexpectedly, the recipient of the summons had but 2 choices, depending upon the degree of urgency. One could either hustle downhill to the automated equipment in the Village, or bare one's buttocks to the chill of the prevailing northerlies in a remote corner of the main paddock. Hence, the joyous anticipation on that particular summer day.

Jack, adorned in his colorful Lappish headpiece, supervises the caravan's progress with the sharp eye of a seasoned civil engineer, while Steve Person and Dan Holleman scurry about checking the ropes that secure the trailer's precious burden. Technician Dick Gau screeches commands and insults to yours truly whose incompetent hands are on the controls of the bulldozer. Bob White, our newly arrived token Australian, feigns participation, but maintains a safe distance from the crazy Yanks he has recently befriended, no doubt reflecting on the wisdom of his decision to relocate to Alaska. The only absentee is the amiable team greensleeve, Bob Dieterich.

Miraculously, the one-holer arrives on site more-or-less intact and is cautiously unloaded next to an excavation of the appropriate dimensions. At this point, an unexpected decision would have to be made. The unspoken assumption among most team members was that the entrance would have a southern exposure; on a clear day the occupant could then enjoy a spectacular, unobstructed view of Mt. McKinley. To Jack, however, the only logical choice was a northwest orientation toward the Village of Cantwell; that way, one might reflect on the past and contemplate the future of this quaint whistle-stop town along the Alaska Railroad, and note the comings and goings of its handful of friendly residents. Besides, he argued, one might spend an entire professional career on this remote hill and never be fortunate enough to synchronize the movement of bowels with a rare, cloudless view of the great mountain to the south.

Now you'd think that half a dozen scientists, having together braved the discomforts of frozen fingers and insect attack, as well as the frustrations of clogged catheters, hemolyzed blood, and malfunctioning field equipment, could make a unanimous decision on such a seemingly trivial matter. No such luck! Several arguments erupted and tempers flared. Compromises were formulated and promptly rejected. The negotiations reached an impasse, and heated exchanges continued while enroute to the local watering hole for the usual (or at least not unusual) pre-dinner cocktail hour(s). It is said that this was the worst argument in the 15-year history of the Reindeer Research Team. There never was a mutually acceptable solution.

This tongue-in-cheek anecdote illustrates the atmosphere of comradery that typified Jack's relationships with friends and colleagues. He wisely recognized that the quality of research, or any other endeavor for that matter, could be maximized by a cohesive team approach. It is unclear whether Jack had an instinct for assembling compatible folks or if his mere presence fostered that compatibility. Some of each, I suspect. The wide assortment of coauthors on his list of well over 100 publications testifies convincingly that his personal relationships and professional achievements were closely interwoven.

Jack will long be remembered for a unique sense of humor. Laughter was his antidote for everyday stress, and he seemed helplessly attracted to the extraordinary, the unconventional, the unusual. Seldom would he introduce a speaker, deliver a lecture, or even give a paper without first sharing a joke or humorous story with his audience. Who among those attending the conference banquet in Røros will forget Jack's hilarious account of a fictional exchange of letters with Eigil Reimers? A friendly, jocular informality was his trademark. In fact, if Jack's greeting didn't include a wisecrack, or at least a warm smile, one knew that serious trouble was afoot somewhere. In his personal and professional philosophy, there was always room for enjoying the task, as well as delighting in a quality product.

Jack's various experiences are enviable and his numerous accomplishments impressive. After serving as Captain, U.S. Army Air Corps, for 4 years during World War II, he enrolled at the University of California, Davis, and subsequently earned a B.S. in Animal Science. Following a second assignmenr in the military during the Korean Conflict, he retnrned to Davis to work under the brilliant Max Kleiber and emerged as a charter member of the famous Davis Tracer Team, pioneers in the use of radioisotopes in animal research. Jack distinguished himself by making the first measurements of calcium metabolism in the high-producing dairy cow using radio-tracer techniques. In 1956, Ph.D. in hand, he joined the faculty at Davis where he remained until 1964. He then expanded the application of his expertise in tracer methodology, first in Yugoslavia under IAEA sponsorship and, a year later, in Australia as a Fulbrigth Scholar.

Jack ventured to Alaska in 1966 at the invitation of Peter Morrison, then Director of the Institute of Arctic Biology, to initiate a research program in the nutritional physiology of large animals. Appropriately, Jack focused his attention on *Rangifer tarandus* and promptly secured a major grant from the U.S. Atomic Energy Commission to investigate the climatic and nutritional adaptations of this unique Arctic species. He initiated, or was closely involved in, numerous studies embracing a broad spectrum of research disciplines - from intermediary metabolism and body composition to animal capture and artificial insemination. He traveled frequently and extensively, notably to the Scandinavian countries and the Soviet Union, in conjunerion with his interests in *Rangifer*, and eagerly reciprocated with a special brand of hospitality to the many colleagues who visited Alaska. In the later years, Jack's research interests shifted somewhat toward reindeer husbandry and products marketing, with a specific interest in development of the industry in Western Alaska. However, he retained a keen interest in basic research, and was always quick with useful advice to colleagues and students alike.

Late in 1970, Jack pulled together a group of biologists, including Dave Klein and Peter Lent, to formulate plans for what was to become a series of international symposia on reindeer and caribou. The First, held at the University of Alaska, was extremely successful, but no more so than the Second in Norway, the Third in Finland, and now a Fourth in Canada. We all missed Jack's participation at the recent Whitehorse conference, as we will in Sweden in 1988.

The Cantwell Research Station is now famous throughout the circumpolar countries for a prolific output of research. To Jack, however, Cantwell represented a great deal more than an outdoor laboratory. He and his family spent many a vacation there, improving the station, hunting, fishing, and simply soaking up the casual village atmosphere. And the irony is bittersweet that Jack's last days were spent in the place he cherished. Perhaps he climbed that nearly hill and, with a wry smile at thickening clouds to the south, relaxed within a certain convenience facility to enjoy an unspoiled view of his favorite little town.

Ray Cameron

World status of wild *Rangifer tarandus* populations

T. Mark Williams and **Douglas C. Heard**

Abstract: We recognized 184 herds of wild *Rangifer tarandus*, 102 in North America, 55 in Europe, 24 in Asia and 3 on South Georgia. Seventy-five percent of the world population of 3.3 to 3.9 million animals occurred in nine herds. All seven herds larger than 120 000 animals were censused by some means of aerial photography and all were increasing. Herds between 20 000 and 120 000 were most often censused using aerial strip transect methods, while total counts were usually employed to census smaller herds. The most pronounced changes in *Rangifer* herd status between 1979 and 1985 occurred in North America where population estimates for five herds increased by a total of about one million animals. Part of this increase is attributable to a change from visual to photographic surveys. Eighty-three percent of North American, 88% of European, and 68% of Asian herds were stable or increasing.

Key words: *Rangifer tarandus*, caribou, reindeer, North America, Europe, Asia, census.

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Rangifer, Special Issue No. 1, 1986: 19 - 28

Introduction

This paper summarizes the most recent estimates of the size of the world's wild *Rangifer tarandus* herds and the trend in number since 1979 (Reimers *et. al.*, 1980).

Methods

Most of the data for this paper were supplied to us upon request by biologists from around the world. Addresses of those providing unpublished data are listed in the Acknowledgments. The data should be considered the most current available as of 1985.

Because many census techniques were employed, we lumped most methods into either total counts or sample counts and either direct visual counts or counts of animals on photographs. Total counts were attempts to enumerate all caribou in a herd, but they were usually increased, based on additional information, to account for missed animals. Strip and block sampling techniques may have covered a herd's entire range or may have been restricted to only part of it (e.g., the calving ground) and then extrapolated, usually on the basis of additional information, to a total population estimate. Except where noted, surveys were conducted by aircraft.

The ranges of many herds overlap. For the sake of clarity of the figures, areas of range overlap were not delineated. Also, where ranges overlapped jurisdictional boundaries, herds were arbitrarily allocated to one jurisdiction.

Trend refers to change in herd size since 1979. Date refers to the year when the survey was completed or when observations were collated to derive an estimate.

Results

There were 2.3 to 2.8 million wild *Rangifer* in 102 herds in North America (Table 1). The seven largest herds (George River, Bathurst, Beverly, Western Arctic, Kaminuriak, Porcupine and Northeastern Mainland) comprised 2 million animals or 80% of the North American population. Of the 71 herds for which a trend was known 49% were increasing, 34% were stable and 17% were declining. There were 2 135 000, 225 600 and 13 100 animals in increasing, stable and declining herds respectively.

Census techniques in North America have changed in recent years with the increased use of aerial photography to census calving or post-calving aggregations of caribou (Table 1).

There were 106 700 to 124 100 wild *Rangifer* in 58 herds in Europe and on South Georgia (Table 2). The largest herd (Hardangervidda) contained 20 000 animals or 17% of the European population. Of the 51 herds for which a trend was known 16% were increasing, 72% were stable and 12% were declining. There were 10 800, 86 800 and 15 600 animals in increasing, stable and declining herds respectively. The predominance of relatively small, stable populations reflects intensive management techniques.

There were 930 500 to 944 300 wild *Rangifer* in 24 herds in Asia (Table 2). The two largest herds (Taimyr and Yana-Indigir rivers) contained a total of 630 000 animals or 56% of the Asian population. Of the 22 herds for which a trend was known 18% were increasing, 50% were stable and 32% were declining. There were 575 900, 231 500 and 125 000 animals in increasing, stable and declining herds respectively.

Census techniques in Europe and Asia have also changed in recent years with the increased use of aerial photography in Norway and the Soviet Union. In Norway, censuses were total photo counts on winter or summer ranges. The Soviets used a total photo count method for the Taimyr population, and reported an increase in the use of aircraft to census, usually by strip samples, the remaining herds. Most other estimates of *Rangifer* herds in Europe were based on total counts.

No information has been collected on the three South Georgia herds (Table 2) since 1979 (Walton, pers. comm.).

Discussion

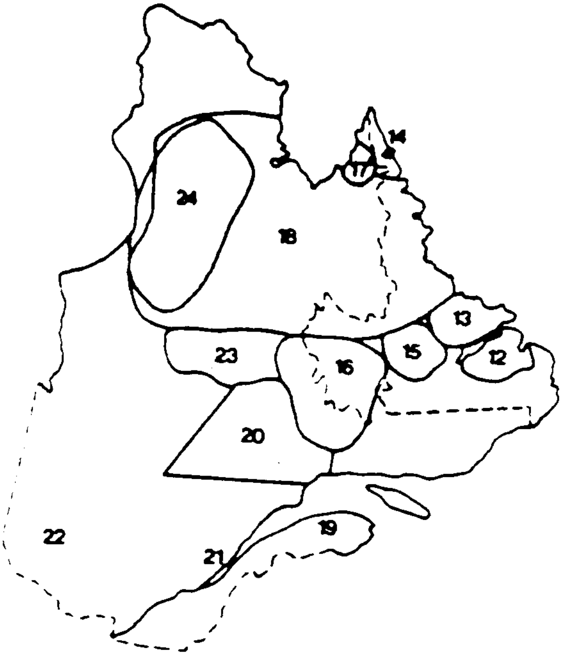
Nine herds made up 75% of the world population of 3.3 to 3.9 million animals. All seven herds larger than 120 000 were increasing and were censused by some means of aerial photography. The most pronounced changes in *Rangifer* numbers between 1979 and 1985 occurred in North America where the population estimates for five herds, the George River, Bathurst, Beverly, Kaminuriak and Western Arctic increased by a total of over one million animals. For the Bathurst, Beverly and Kaminuriak herds, part of the increase reflects greater accuracy in census results, attributable to a change from visual to photographic surveys, and part represents real population growth. This may also apply to the George River herd and to herds in Norway and the Soviet Union.

Large increases in the world's major caribou herds lead us to agree with Bergerud (Arctic 38:156, 1985) «...the great days of the caribou on the barren lands are here, at last». However, many animals in a few large herds would not compensate for loss of small herds that exist as isolated gene pools, i.e. the Gaspesie Park and Slate Islands herds (numbers 19 and 28, Table 1). With almost 20% of all herds declining, we must not become complacent with management of the world's wild *Rangifer* populations.

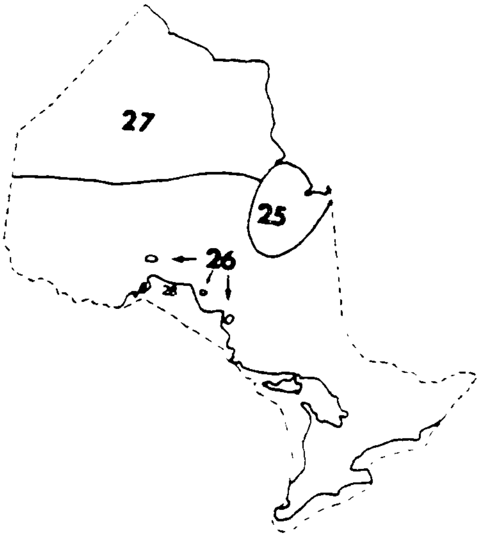
1a. Insular Newfoundland, Canada.

Fig. 1. Wild *Rangifer* herd ranges in North America. Numbers correspond to Table 1.

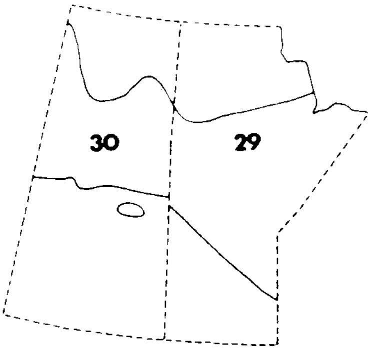
1b. Newfoundland and Quebec, Canada.



1c. Ontario, Canada.



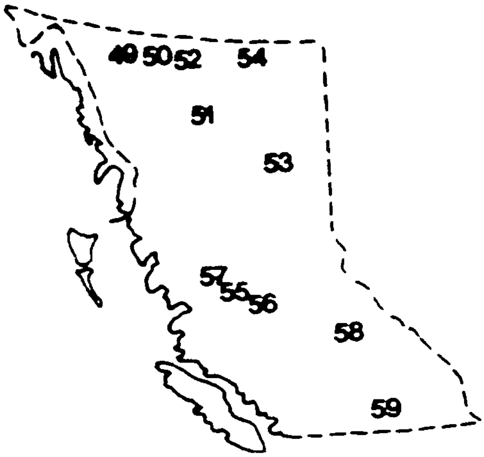
1d. Saskatchewan and Manitoba, Canada.



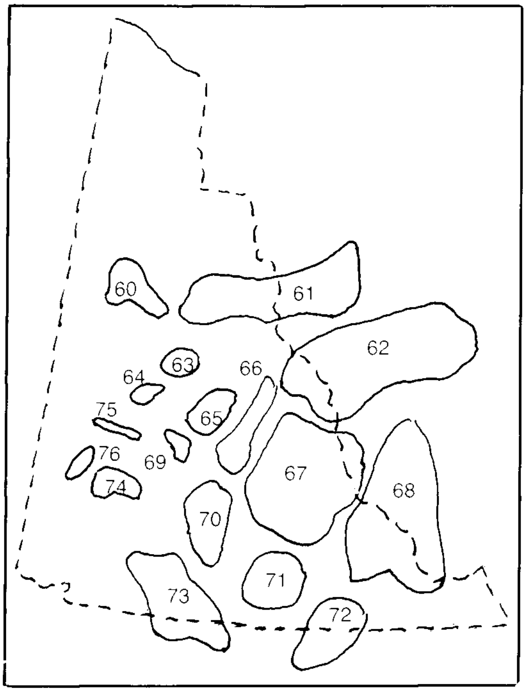
1e. Alberta, Canada.

1f. Northwest Territories, Canada.

1g. British Columbia, Canada.



1h. Yukon, Canada.



1i. Alaska, U.S.A.

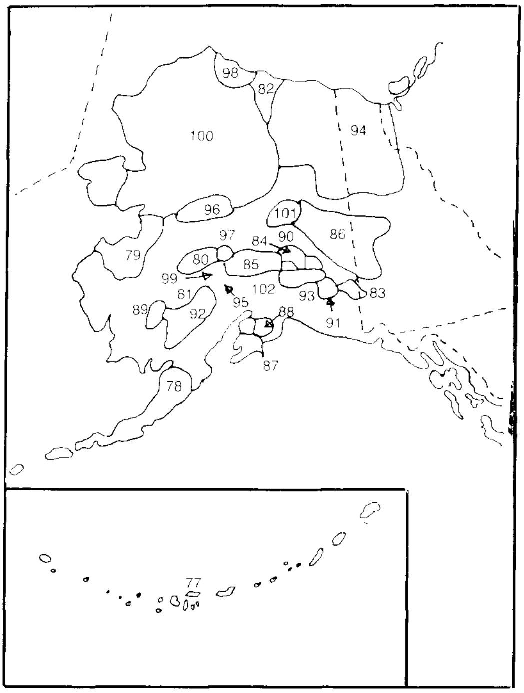


Table 1. Wild *Rangifer tarandus* herds in North America.

No.	Name	Estimate	Year	Method*	Trend**	Hunter Kill	Comment	Source***
1	Avalon	3300-6900	1982	BS	I			1
2	Middle Ridge, Mt. Peyton, Tolt	4600-9600	1982	BS	I			1
3	Pot Hill	450	1982	TC	I			1
4	Sandy Lake	200	1982	TC	I			1
5	Grey River	2500-8300	1982	BS	I			1
6	Gaff Topsails	1000-2100	1982	BS	I			1
7	Buchans	2000	1982	TC	I			1
8	LaPoile	6700-12100	1982	BS	I			1
9	Hampden Downs	400	1982	TC	I			1
10	Humber	450	1982	TC	I			1
11	Northern Peninsula	1500	1982	TC	I			1
12	Mealy Mtn.	660-740	1981	TC	I	Unknown		2
13	White Bear Lake	<100	1977	TC	D,TH	Unknown	May be viably extinct	2
14	Torngat Mtn.	5000-10000		G	I	500-1000		2
15	Red Wine Mtn.	720-780	1981	TC	S,V	Unknown	Range shared with inc.moose pop.	2
16	Lac Joseph	<600	1978	TC	D,TH	Unknown	Interprovincial, unprotected	2

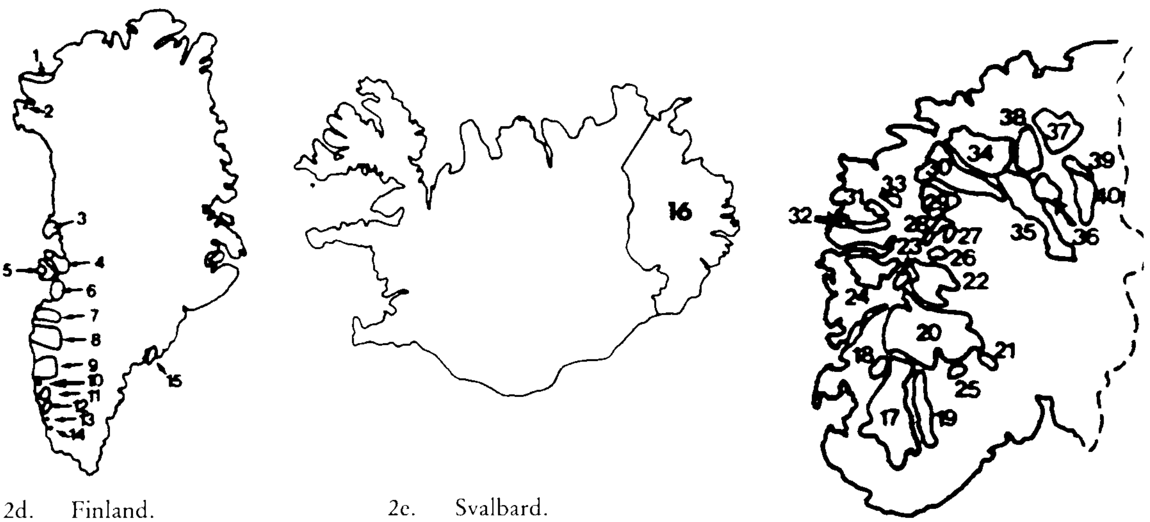
17	Koroc River	5000	1980	SS,TC				3
18	George River	600 000	1984	PS	I	15000	Calving ground survey	4
19	Gaspesie Park	250	1980	TC	D	Unknown	Range made into park in 1981	3
20	North Shore	2000	1977		D	Unknown		3
21	Grands Jardins	67	1982	TC	I	None Legal	Range made into park in 1982	3
22	Val d'Or	50		TC	S,TH		Logging threatens habitat	3
23	James Bay	4000-5000	1982		S	Unknown		3
24	Leaf River	65 000-70 000	1983		I	Unknown	Calving ground survey	5
25	NE Ontario	4500	1985	IO	S	Unk.native	No complete survey	6
26	N. Lake Superior	<200	1985	IO	S	None legal	Scattered remnant herds	6
27	NW Ontario	3100	1984	SS	U	2.4-3.6%		7
28	Slate Islands	600	1984	TC	I	None	Die-off expected	8
29	Manitoba herds	5000	1985	IO	S	2-300	Logging, Habitat loss	9
30	Saskatchewan herds	2500	1985	IO	D,TH	<100 legal	Logging, Roads	10
31	Alberta herds	1500-3000	1985	V	D,TH	<25 native	Logging, Poaching, Predation	11
32	Northeast Baffin	10000		G	U	1000	Never surveyed	12
33	North Baffin	>30 000		G	U	7000	Range expansion, not surveyed	12
34	South Baffin	>60 000	1984	SS	U	8000	Range expansion	12
35	Belcher Islands	287	1982	TC	I	32	Feral, introduced 1978	12
36	Coats Island	2100	1984	SS	S	300	Icing causes die-offs	13
37	Southampton Island	1100	1978	SS	I	70	Introduced in 1967	14
38	Northeastern Mainland	110 000-130 000	1983	SS	S	3900		15
39	Kaminuriak	180 -280 000	1983	PSS	I	10000	Calving ground survey	16
40	Beverly	250 000-420 000	1984	PSS	I	6000	Calving ground survey	17
41	Bathurst	320 000-450 000	1984	PSS	I	14300	Calving ground survey	13
42	Bluenose	50 000-80 000	1983	PSS	S	4000	Calving ground survey	18
43	Mackenzie Woodland	2000-5000		G	U	>150	No survey data	19
44	Boothia Peninsula	8900	1985	SS	U			20
45	Banks Island	5000	1985	SS	S	>500		21
46	Victoria Island	7000-9000	1980	SS	U	1100-1500		22
47	Somerset, Pr. of Wales	4400-5800	1983	SS	U	150-250		23
48	Queen Eliz. Islands	4200						
	eastern	1500	1961	SS	U	Unknown		24
	western	2700	1974	SS	U	Unknown		25
49	Atlin	500	1979		S			8
50	Kaudy-Level	800	1983	TC	D	11 males	Minimum count	8
51	Spatsizi-Lawyers Pass	1260	1982	TC	D	33 males	Minimum count	8
52	Horse Ranch	300	1982	TC	I	3 males	Wolf control	26
53	Pink Mountain	300	1978		S			26
54	Liard Plateau	125	1978	TC	S		Ground based	26
55	Telkwa	40	1977	TC	S		Radio-tracking	26
56	Tweedsmuir	200	1978	TC	I		Ground based	26
57	Itcha-Ilgachuz	700	1982	TC	I	59 males		8
58	Cariboo Mountains	1500	1984	MR	D		Predation, logging	27
59	Selkirk	25-30	1980	TC	S		Ground based	8
60	Hart River	1200	1978	TC	S	10		28
61	Bonnet Plume	5000	1982	TC	I	15-20		28
62	Redstone	5000-10000		G	U	45-50		28
63	Mayo				U	None		28

64	Ethel Lake	200	1977	TC	U,V	5		28
65	Anvil Range	300		G	U,V	15		28
66	Tay Lake	300		G	U,V	5-10		28
67	Finlayson	2500	1984	TC	I	250	Harvest reduction, Wolf control	28
68	Nahanni	2000		G	U,V	25-70		28
69	Glenlyon Range	350	1977	TC	U	5		28
70	Pelly Herds	1000		G	U	10-15		28
71	Wolf Lake	500		G	U	5-10		28
72	Little Rancheria	450		G	D,TH	20-25		28
73	Carcross Herds	600	1980	TC	S,V	10-15		28
74	Aishihik	1500	1981	TC	S	35-45		28
75	Dawson Range	250		G	U	5-10		28
76	Burwash	400	1982	TC	S,V	15-20		28
77	Adak	300	1982	TC	S	None	Preharvest count	29
78	Alaska Peninsula	>30 000	1984	TC	I	1454	Photo and visual	29
79	Andreafsky	400		IO	U	10-50	Not adequately censused	29
80	Beaver Mountains	1600	1983	TPC	U	25	Based on radio-collars	29
81	Big River	750	1982	TC	D	42-47	Based on radio-collars	29
82	Central Arctic	>12 500	1983	TPC	I	170		29
83	Chisana	1000	1981	TC	U	28	Ground based	29
84	Delta	8000	1984	TPC	S	694	Photo and visual	29
85	Denali(McKinley)	2100	1984	TC	S	None		29
86	Fortymile	16000	1984	TC,SS	I	250-300	Photo and visual	29
87	Kenai Lowlands	80-85	1983	TC	S	None	Based on radio-collars	29
88	Kenai Mountains	300	1982	TC	S	29	Based on radio-collars	29
89	Kuskokwim Mts.	600	1983	IO	U			29
90	Macomb	700	1981	TC	U	11	Based on 475 seen	29
91	Mentasta	3000	1983	TC	S	90	Photo and visual	29
92	Mulchatna	30 000-33 000	1984	TPC	I	1000-1500		29
93	Nelchina	25000	1984	TPC	I	969	Based on 22100 seen	29
94	Porcupine	150 000	1983	TC,SS	I	400	Photo and visual	29
95	Rainy Pass	1500	1984	IO	U	45-50		29
96	Ray Mts., Kokrines Hills	1000	1983	IO	U	25		29
97	Sunshine Mountains	525-750	1983	TC	D	None	Based on radio-collars	29
98	Teshekpuk	10 8000	1984	PSa		Unknown	Calving ground survey	29
99	Tonzona	<1000	1983	IO	U	10-15		29
100	Western Arctic	>200 000	1984	TC,SS	I	5000-12000	Photo and visual	29
101	White Mountains	800	1983	IO	U	6		29
102	Yanert	>500	1984	PSa	U	54	Yanert - Delta herd mixing	29

* BS=Block samples, TC=Total count, G=Guess, SS=Strip samples, PS=Photo strips, IO=Incidental observations, V=Various methods, PSS=Photo strip samples, MR=Mark resighting, TPC=Total photo count, PSa=Photo sample.

** I=Increasing, D=Decreasing, S=Stable, TH=Threatened, V=Vulnerable, U=Unknown

*** All sources are pers.comm. except those with a year citation.
1=Mercer, 2=Luttich, 3=Belanger and Le Henaff, 4=Anon. 1985, 5=Le Henaff and Messier, 6=Stefanski, 7=Darby, 8=Bergerud, 9=Kearney, 10=Trottier, 11=Edmonds and Rippen, 12=Ferguson, 13=Heard, 14=Kraft, 15=Heard et. al. 1986, 16=Heard and Calef 1986, 17=Gates, 18=Williams and Heard, 19=Decker, 20=Gunn, 21=Jingfors, 22=Jakimchuk and Carruthers 1980, 23=Gunn and Decker, 24=Tener 1963, 25=Miller et al. 1977, 26=Bergerud 1980, 27=Seip, 28=Farnell, 29=Davis.


2a. Greenland.
2b. Iceland.
2c. Norway.


2d. Finland.
2e. Svalbard.
2f. South Georgia.

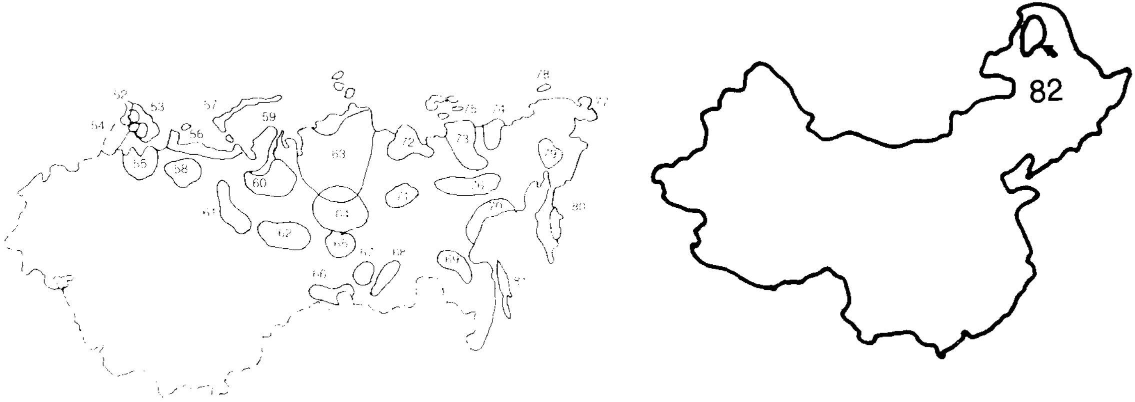

2g. Soviet Union.
2h. China.

Fig. 2. Wild *Rangifer* herd ranges in Europe, Asia and South Georgia. Numbers correspond to Table 2.

Table 2. Wild *Rangifer tarandus* herds in Europe, Asia and South Georgia.

No.	Name	Estimate	Year	Method*	Trend**	Hunter Kill	Comment	Source***
1	Inglefield Land	<100	1984		I,V	<10	Isolated, wild	1
2	Orlik Fjord	100-300	1978	TC	I,V	<10	Isolated, feral	1
3	Nunavik	<100	1980		D,TH		Isolated, wild	1
4	Nuussuaq	200-300	1980	IO	I	50	Wild, feral	1
5	Qeqertassuaq	150-250	1980	TC	I	35	Feral	1
6	Nassuttooq	400-600	1978	TC		100	Wild	1
7	Nassuttuup	1300-3300	1982	TC	D	700	Wild	1
8	Sisimut	2500-5500	1982	TC	D	2000	Wild	1
9	Nuuk	5200-10200	1982	TC	D	4000	Wild	1
10	Qoornoq	50-150	1982	TC	S,V		Feral	1
11	Ameralik	1000-2000	1983	TC	S	200	Wild	1
12	Sermilik	200-400	1982	TC	S	<50	Wild	1
13	Qassit	100-300	1982	TC	S	50	Wild	1
14	Neria	300-500	1980	IO	S	100	Wild	1
15	Tasiilaq	80-120	1980	IO	S.V	<10	Feral	1
16	Iceland	3000	1984	TPC	S,V	390	Aerial and ground; proposed hydro project	2
17	Setesdal Vesthei	2700	1978	TPC	S	352	Summer count	3
18	Saudafjella	75	1979	TPC	S	10		3
19	Setesdal Austhei	2000	1979	TPC	S	600	Summer count	3
20	Hardangervidda	20 000	1984	TPC	S	9200	Summer count	3
21	Blefjell	130	1979	TPC	S	50	Winter count	3
22	Hallingskarvet	2500	1984	TPC	S	1000	Winter count	3
23	Raudafjell	30	1978	TPC	S	0		3
24	Fjellheimen	850	1979	TPC	S	185	Summer count	3
25	Brattfjell-Vindeggen	600	1983	TPC	S	250	Winter count	3
26	Lærdal-Årdal	300	1979	TPC	L			3
27	Årdal-Tyin	100	1979	TPC	L			3
28	Vest-Jotunheimen	720	1977	TPC	S	88	Winter count	3
29	Ottadalen Sør	460	1980	TPC	S	81	Winter count	3
30	Ottadalen Nord	3100	1980	TPC	S	725	Winter count	3
31	Førdefjella	100	1978	TPC	S	14	Winter count	3
32	Sunnfjord	600	1978	TPC	S	20	Winter count	3
33	Svartebotnen	130	1979	TPC	S	25	Winter count	3
34	Snøhetta	2800	1984	TPC	S	1100	Winter count	3
35	Rondane	1200	1982	TPC	S	350	Winter count	3
36	Sølnkletten	530	1979	TPC	S	29	Winter count	3
37	Forelhogna	1800	1984	TPC	S	1000	Winter count	3
38	Knutshø	914	1984	TPC	S	350	Winter count	3
39	Tolga Østfjell	200	1979	TPC	S	9	Winter count	3
40	Rendalen	700	1984	TPC	S	125	Ground based	3
41	Finnish forest reindeer	600	1984	TC	I	0		4
42	Finnish	30-40	1984	TC	U	0	Introduced	4
43	Nordenskiöldland	4500	1985	TC	S	0		5
44	Reinsdyrflya	1000	1985	G	U	0		5
45	Nordaustlandet	500	1985	G	S	0		5
46	Edgeøya-Barentsøya	2500	1985	TC	S	0		5
47	Wedel-Jarlsbergland	300	1980	G	U	0		5
48	Brøggerhalvøya	50	1980	TC	U	0	Introduced; experimental	5
49	Busen	450	1976	TPC	D		Introduced	6

50	Barff	1000	1976	TPC	D		Introduced	6
51	Royal Bay	550	1976	TPC	S		Introduced	6
52	W. Kola Peninsula	230	1984	TC	I,TH	0	No contact with domestic reindeer	7
53	E. Kola Peninsula	2700	1984	TC	I,TH	0	Little contact with domestic reindeer	7
54	Karelia	7000-11000	1983	SS	S	0.7%		7
55	Archangel Forest	14000	1983	SS	S	<1.7%		7
56	Archangel Tundra	4000	1983	SS	S,TH	1%		7
57	Novaya Zemlya Isl.	6000-7000	1981	SS	I	3.3%	Recovered	7
58	Komi Forest	4000	1983	SS	S	1.3%		7
59	Yamal Tundra	2000	1983	SS	S,TH	<1.5%		7
60	Nadym-Pur Rivers	5000	1983	SS	D,TH	<1.5%	Close contact with domestic reindeer	7
61	Konda-Sosva Rivers	7000	1983	SS	D	<1.5%		7
62	W.Siberian Forest	5000	1983	SS	S,TH	<50	No contact with domestic reindeer	7
63	Taimyr	530 000	1984	TPC	I	13.8%		7
64	Evenkiysk	50 000	1982	SS	D	<2.0%		7
65	Upper Angara R.	10 000	1983	SS	D	<2.0%		7
66	Altai-Sayan Mntns.	10 000	1982	SS	S	<1.0%		7
67	Irkutsk	20 000	1983	SS	S	1.6%		7
68	E. Baikal	8000	1983	SS	S	<1.0%		7
69	Amur	3000	1983	SS	D	1.2%		7
70	W. Okhotsk	15 000-17 000	1983	SS	S	2.0%		7
71	Lena-Vilyui Rivers	20 000	1983	SS	D	<1.0%		7
72	Bulun	60 000	1983	SS	S	<11%	Interaction with reindeer husbandry	7
73	Yana-Indigir Rivers	100 000	1983	SS	S	<15%	Interaction with reindeer husbandry	7
74	Sundrun	30 000	1983	SS	I	<15%	Interaction with reindeer husbandry	7
75	Novosibirsk Isls.	7500-16 300	1980	SS	I	<1.0%	Two independent counts	7
76	Yukutsk Mntn. Taiga	30 000	1983	IO	D	<1.0%		7
77	Chukotsk Tundra	5000-6000	1981	SS	S	<10%		7
78	Wrangel Island	2000	1982	TC			Harvested to control population size	7
79	Chukotsk Forest	3000-5000	1981	SS	I			7
80	Kamchatka	4000	1983	SS	S,TH	1.8%		7
81	Sakhalin	3000	1983	IO	TH			7
82	Taxinganling	980	1982	TC	S,V	0	Wolves and disease	8

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* TC=Total count, IO=Incidental observations, TPC=Total photo count, G=Guess, SS=Strip samples

** I=Increasing, D=Decreasing, S=Stable, L=Lost, V=Vulnerable, TH=Threatened, U=Unknown

*** All sources are pers.comm. except those with a year citation.
1=Thing, 2=Thórisson, 3=Skogland, 4=Tunkkari, 5=Øritsland and Alendal 1985, 6=Leader-Williams 1980, 7=Kuzyakin, 8=Ma.

Acknowledgements

We thank the following people for providing us with unpublished data: *T. Bergerud*, Department of Biology, University of Victoria, Victoria, British Columbia, Canada, *M. Belanger*, Direction generale de la faune terrestre, Ministere du Loisir, de la Chasse et de la Peche, Quebec, Canada, *W. Darby*, Ontario Ministry of Natural Resources, Fort Frances, Ontario, Canada, *J. Davis*, Alaska Depaertement of Fish and Game, Fairbanks, Alaska, U.S.A., *R. Decker*, Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, N.W.T., Canada, *C. Gates*, Department of Renewable Resources, Government of the Northwest Territories, Fort Smith, N.W.T., Canada, *A. Gunn*, Department of Renewable Resources, Government of the Northwest Territories, Cambridge Bay, N.W.T., Canada, *J. Edmonds*, Department of Natural Resources, Government of Alberta, Edmonton, Alberta, Canada, *R. Farnell*, Department of Renewable Resources, Government of Yukon, Whitehorse, Yukon, Canada, *M. Ferguson*, Department of Renewable Resources, Government of the Northwest Territories, Frobisher Bay, N.W.T., Canada, *K. Jingfors*, Department of Renewable Resources, Government of the Northwest Territories, Inuvik, N.W.T., Canada, *S. Kearney*, Department of Natural Resources, Thompson, Manitoba, Canada, *P. Kraft*, Department of Renewable Resources, Government of the Northwest Territories, Inuvik, N.W.T., Canada, *D. Klein*, Alaska Cooperative Research Unit, University of Alaska, Fairbanks, Alaska, U.S.A., *V. Kuzyakin*, Central Resarch Laboratory on Wildlife Management and Nature Reserves, Moscow, U.S.S.R., *D. Le Henaff*, Direction generale de la faune terrestre, Ministere du Loisir, de la Chasse et de la Peche, Quebec, Canada, *S. Luttich* and *E. Mercer*, Department of Culture, Recreation and Youth, Wildlife Division, Government of Newfoundland and Labrador, Goose Bay, Labrador, Canada, *F. Messier*, Centre d'etude nordiques, Universite Laval, Ste-Foy, Quebec, Canada, *F. Miller*, Canadian Wildlife Service, Department of the Environment, Government of Canada, Edmonton, Alberta, Canada, *P. Tunkkari*, Department of Zoology, University of Oulu, Oulu, Finland, *C. Potvin*, Ministere du Loisir, de la Chasse et de la Peche, Gouvernement du Quebec, Saint-Cyrille, Quebec, Canada, *B. Rippen*, Department of Natural Resources, Government of Alberta, Edmonton, Alberta, Canada, *D. Seip*, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada, *T. Skogland*, Direktoratet for Naturforvaltning, Trondheim, Norway, *R. Stefanski*, Ontario Ministry of Natural Resources, Toronto, Ontario, Canada, *H. Thing*, Vildtbiologisk Station, Rønde, Denmark, *S. Thórisson*, Museum of Natural History, Reykjavik, Iceland, *T. Trottier*, Department of Tourism and Natural Resources, Government of Saskatchewan, la Ronge, Saskatchewan, Canada, *D. Walton*, British Antarctic Survey, Cambridge, England, *Y.-C. Ma*, Institute of Natural Resources, Harbin, China.

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Session papers

Macrominerals in free-ranging Swedish reindeer during winter

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Abstract: Samples of blood, rumen, and caecal contents were taken from 238 reindeer *(Rangifer tarandus)* slaughtered between September and March in two consecutive years. Levels of magnesium, calcium and phosphorus were measured to evaluate the extent to which levels of these minerals reflected changes in the grazing conditions through the winter. Twenty-one reindeer in poor conditon were included in the investigation and compared with normal animals with respect to the investigated minerals.

Serum values in September were within the normal range for domestic sheep *(Ovis* spp.) and cattle *(Bos* spp.) (Church, 1979). Magnesium was 0.9±0.1 mmol/l, calcium 2.8 ± 0.3 mmol/l and phosphorus 2.5 ± 0.5 mmol/l. Calcium values did not change very much through the winter while magnesium and phosphorus constantly decreased from September to February. Extremely low serum magnesium values (below 0.3 mmol/l in some animals were found in January and February. The majority of the animals in poor condition had low serum-magnesium values.

Key words: reindeer, *Rangifer*, nutrition, magnesium, calcium, phosphorus.

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Rangifer, Special Issue No. 1, 1986: 31 - 38

Introduction

An important part of the reindeer *(Rangifer tarandus* spp.) winter diet is lichens, which can be as much as 70-85% of the total food intake (Eriksson *et al.*, 1981). Lichens are low in protein and minerals compared with forage plants available to reindeer during other times of the year (Table 1). Even when the winter food supply is adequate to meet the need for energy, protein and mineral content can still be inadequate.

Since 1978, we have extensively studied field-slaughtered reindeer from northern Sweden. These studies have focussed on various topics, including reproduction (Inga, 1984), foetal growth (Mossing and Rydberg, 1982), muscle fibre composition (Kiessling and Rydberg, 1983), meat quality and slaughtering strategy. One of the main objectives has been to evaluate the influence of nutritional factors on the condition of the reindeer from chemical analysis of blood, organs and content of the alimentary tract.

In this report we show how magnesium (Mg), calcium (Ca), and phosphorus (P) content in different parts of the body change during the winter. We gave special attention to animals that were weak and in poor condition and compared them with animals in normal condition.

Material and methods

Samples were taken from 217 reindeer slaughtered in September to March in 1979/80

Table 1. Macromineral and crude protein content (g/kg dry matter) in some reindeer forage plants (Isotalo, 1971).

Plant	Mg	Ca	P	Crude protein
Lichens:				
Cladonia and *Cladina*	0.3-0.8	0.6-1.4	0.4-0.8	1 - 4
Alectoria and *Usnea*	0.2-0.3	1.1-2.0	0.6-0.8	6 - 7
Leaves:				
Betula	2.8	5.7	2.8	20
Shrubs:				
Vaccinium and *Empetrum*	0.9-1.5	3.6-5.1	1.1-2.6	6 - 14
Grass:				
Deschampsia etc.	0.7-2.2	1.2-4.2	1.6-2.1	8 - 18

and 1980/81 (Table 2). The animals were from the same area around Arvidsjaur, Sweden. The animals were considered by the herdsmen to be in normal condition - they showed normal activity and normal behaviour. In February/ March 1981, 21 reindeer in poor condition (hereafter referred to as weak animals) were selected (Table 2). These were animals which tired while running in the corral and could not keep pace with the others.

At slaughter we weighed the carcasses, the liver and the contents of the digestive tract. Weight of omentum was used as an index of body fat. Samples were taken of mixed arterial and venous blood when bleeding the animal, from the liver and from rumen-reticulum and caecum content. Before sampling, rumen-reticulum content (hereafter referred to as rumen content) was carefully mixed. Blood samples were kept in 10-20°C and centrifuged after 3-8 h. Blood serum and liver were stored frozen in -20°C until analysed. Samples of rumen and caecum content for mineral analyses were dried (to ca. 90% dry matter DM) and stored dry until analysed.

Table 2. Numbers of animals by age, sex and condition slaughtered at different times.

Date of		Females		Males		Cast-	
slaughter	Calves	yearling	adult	yearling	adult	rates	Total
Animals in normal condition							
1979/80							
30 Aug — 26 Sept	-	-	-	2	30	3	35
23 — 26 Oct	2	-	6	-	-	-	8
19 Nov — 19 Dec	11	-	21	-	-	1	33
7 — 24 Jan	6	-	13	-	-	-	19
26 — 28 Feb	2	-	6	2	3	1	14
12 — 18 Mars	1	-	3	-	-	-	4
1980/81							
5 — 22 Sept	-	2	2	5	17	-	26
14 Nov — 17 Dec	4	10	9	13	1	3	40
8 — 26 Jan	6	4	5	6	2	-	23
9 — 27 Feb	1	3	6	3	-	2	15
Total	33	19	71	31	53	10	217
Weak animals in poor condition							
1981							
2 Feb — 17 Mar	6	3	-	11	1	-	21

Analyses of magnesium, calcium and phosphorus were made on blood serum and on acid digests of liver. Analyses of Mg and Ca were made on acid digests of rumen and caecum content. Mg and Ca were analysed on an atomic absorbtion spectrophotometer (Perkin Elmer 306). P was analysed according to Taussky *et al.*, (1953). On rumen and caecum content DM, pH and VFA (volatile fatty acids) were measured. The methods of sampling and preparing samples are described by Åhman and Åhman (1980).

Statistical analyses were carried out according to GLM (general linear models) procedure of the Statistical Analyses System (SAS Institute Inc., 1982). The model used tested effect of age and sex of animals, effect of time of slaughter and possible combined effect of these factors. When comparing weak and normal animals we used a model testing effect of conditon (weak - normal) and effect of age and sex. Only the animals slaughtered in February and March were used in the latter model.

Results and discussion

The four females slaughtered in September 1980 had the same body weights but lower omentum weights than those slaughtered in October to December (Table 3). No calves were slaughtered in September. Calves and females slaughtered in October to December weighed slightly more than those slaughtered later in the year. The omentum weights decrease relatively more than carcass weights. Males are known to

Table 3. Carcass weight (kg) and weight of omentum (% of carcass) in normal condition reindeer of different age and sex slaughtered at different times (mean±SD).

	Normal animals				Weak animals
	September	October - December	January	February- March	February- March
Calves					
n	-	17	12	4	6
Carcass, kg		21±2	18±4	19±4	15±2
Omentum, %		0.61±0.30	0.38±0.25	0.37±0.30	0.18±0.07
Yearling females					
n	2	10	4	3	3
Carcass, kg	24/29[1]	29±3	24±1	27±1	26±2
Omentum, %	0.57/0.55[1]	0.99±0.45	0.72±0.26	0.61±0.16	0.71±0.45
Adult females					
n	2	36	18	15	-
Carcass, kg	34/31[1]	35±5	33±4	33±4	
Omentum, %	0.44/1.09[1]	0.92±0.33	0.92±0.34	0.64±0.32	
Yearling males					
n	7	13	6	5	11
Carcass, kg	34±3	30±2	24±4	27±6	24±4
Omentum, %	0.48±0.16	0.35±0.23	0.54±0.40	0.34±0.23	0.46±0.32
Adult males					
n	47	1	2	3	1
Carcass, kg	55±10	36	39/31[1]	35±6	29
Omentum, %	0.83±0.18	0.04	0.45/0.46[1]	0.29±0.07	0.01
Castrates					
n	3	4	-	3	-
Carcass, kg	58±4	53±4		49±3	
Omentum, %	0.98±0.15	1.15±0.26		0.72±0.23	

[1] Sample values only.

loose up to 35% of their body weight during the 3-week rut in October (Rydberg, 1982) when they hardly eat at all (Skjenneberg and Slagsvold, 1968). As expected, males in this investigation had higher carcass weight and omentum weight in September, before the rut (Table 3). Later in the year weights for males were consederably lower.

The weak animals, except for yearling females, had significantly lower carcass weight ($P < 0.001$) than normal animals of the same age and sex at the same time of year (Table 3, the last two columns). Many of the weak animals, especially the weak calves, but also some of the normal animals had extremely low omentum weight, indicating that they had used almost all of their fat reserves. Dry matter and pH in rumen and caecum (15-20% DM and pH 5.5-7.0 in rumen and 15-19% DM and pH 6.0-7.0 in caecum) did not indicate any starvation or low intake of food prior to slaugther (Åhman and Åhman, 1980), nor did levels of VFA (80-180 mmol/l in rumen and 40-120 mmol/l in caecum). Weak animals did not differ from the other animals in this respect.

The changes in mineral values shown in Figs. 1, 2 and 3 through the winter differed between the two years. The first year there was a steady decline from September to February in the levels of minerals in serum and of Mg-levels in rumen and caecum. The serum values were higher in March. In the second year the decline came later and was less marked. Some of the differences between the two years could perhaps be explained by deeper snow in the area in late November and in December the first year (SMHI, 1979, 1980 and 1981). Snow deeper than 75 cm, as was the case in December 1979, could cause problems' for reindeer when digging for food (Eriksson, 1976).

Animals slaughtered at different times were not of the same age and sex (Table 2). The statistical analyses showed that in general there were no significant effects of age and sex on the levels of minerals but castrates had non-significantly higher caecum-Mg values than other animals ($P > 0.05$) and calves had lower levels in serum of Ca ($P < 0.01$) and P ($P < 0.05$). It proved that applying the statistical model, where the values are adjusted in relation to age and sex, did not significantly change the curves in Figs. 1-3.)

The levels we have found of Mg in rumen and caecum are similar to levels found in lichen-fed

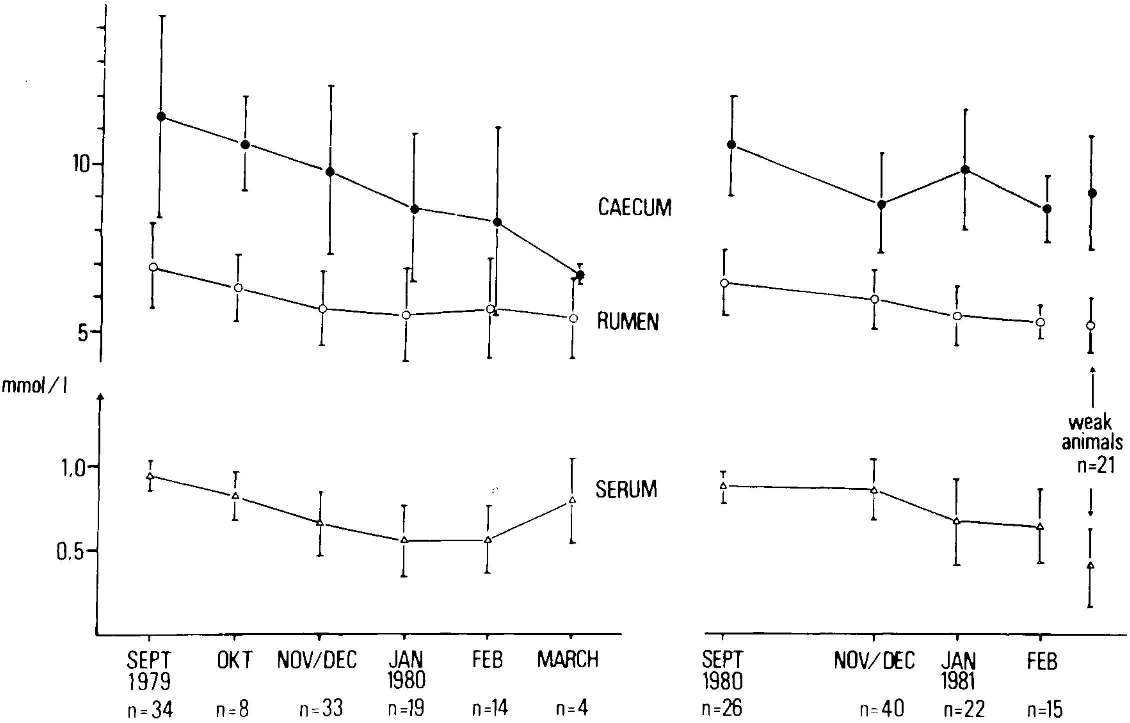

Fig. 1. Magnesium in serum (△) in rumen (○) in caecum (●) and content from free-ranging reindeer slaughtered at different times from September to March in 1979/80 and 1980/81 and from weak reindeer slaughtered in February/March 1981 (mean±SD).

Table 4. Magnesium levels in serum from reindeer slaughtered in February/March: comparision between animals in normal condition and weak animals (mean±SD).

	Normal animals			Weak animals		
	n	Mg mmol/l	no of animals with serum-Mg below 0.30	n	Mg mmol/l	no of animals with serum-Mg below 0.30
Calves	4	0.65±0.17	0	6	0.38±0.20	4
Yearling females	3	0.55±0.24	1	3	0.41±0.12	1
Yearling males	5	0.57±0.27	1	11	0.43±0.30	5
Adult males	3	0.52±0.28	1	1	0.29	1
Total	15	0.58±0.22	3(20%)	21	0.41±0.24	11(52%)

reindeer by Staaland *et al.* (1984). Their report also shows that Mg content of the digestive tract is markedly affected by mineral supplementation.

Serum Mg levels in reindeer in normal condition slaughtered in September of each of the two years (Fig. 1) were well within the normal range for sheep *(Ovis* spp.) and cattle *(Bos* spp.) (0.7 to 1.2 mmol/l, Church 1979). Among reindeer slaughtered in the first year, the values were lower from October and reached the lowest level (0.55 ± 0.20 mmol/l) in January and February. In the second year, the values stayed high throughout November and December (0.86 ± 0.18 mmol/l), but the values tended to be lower (0.66 ± 0.24 mmol/l) in reindeer slaughtered in January and February. The variation within groups was larger in the later part of the year. Most of the reindeer kept their serum-Mg values within the normal range while some had very low values (down to 0.2 mmol/l). In reindeer fed lichens for 4 months, Bjarghov *et al.* (1976) report similar Mg-levels. As in our study no symptoms of tetany were seen in the animals. Reindeer fed pelleted reindeer feed were reported by Bjarghov *et al.* to have serum-Mg values between 1.0 and 1.2 mmol/l.

The statistical analyses showed that weak animals had significantly lower serum-Mg values than normal animals ($P < 0.05$), with over one half of the weak animals having values below 0.30 mmol/l (Table 4). The animals did not show signs of tetany.

The levels of Ca in rumen (around 10-15 mmol/l) are somewhat higher than what Staaland *et al.* (1984) reports from four lichen fed reindeer, but lower than the values they report from reindeer fed mineral supplements (these had values above 20 mmol/l). In the caecum, we found varying levels of Ca during the first year (10-40 mmol/l). On the second year Ca levels increased from September to February, the mean value in September being 14 mmol/l compared to 31 mmol/l in February. An explanation for this could be mobilization of bone to meet the need for Mg and P when mineral content of the feed is low (Church, 1979). This could lead to excess of Ca in the blood and a secretion of Ca into the intestine, followed by high levels of Ca in caecum.

Serum Ca levels were very uniform throughout the year. There was a significant difference between the two years in the level of serum Ca ($P < 0.001$). This might be a genuine difference, or it could be due to some change in treatment of samples or method of analysis from one year to the next. Hyvärinen *et al.* (1977) and Nieminen and Timisjärvi (1983) report serum Ca values from reindeer slaughtered in October and February (2.3-2.8 mmol/l) that correspond well with the values we have from the winter 79/80. Serum Ca values reported by Bjarghov *et al.* (1976) from lichen-fed reindeer are at the same level. Our values from the second year, 80/81, are slightly higher with a maximum at 3.3 mmol/l. Normal values for domestic ruminats are 2.2 to 3.3 mmol/l (Church, 1979).

The consistent values for serum Ca through the year indicate a very good ability in reindeer to mobilize Ca from the bone to meet Ca requirements when Ca in the diet is low. Hyvärinen *et al.* (1977), however, claims that Ca deficiency at some times could be a problem.

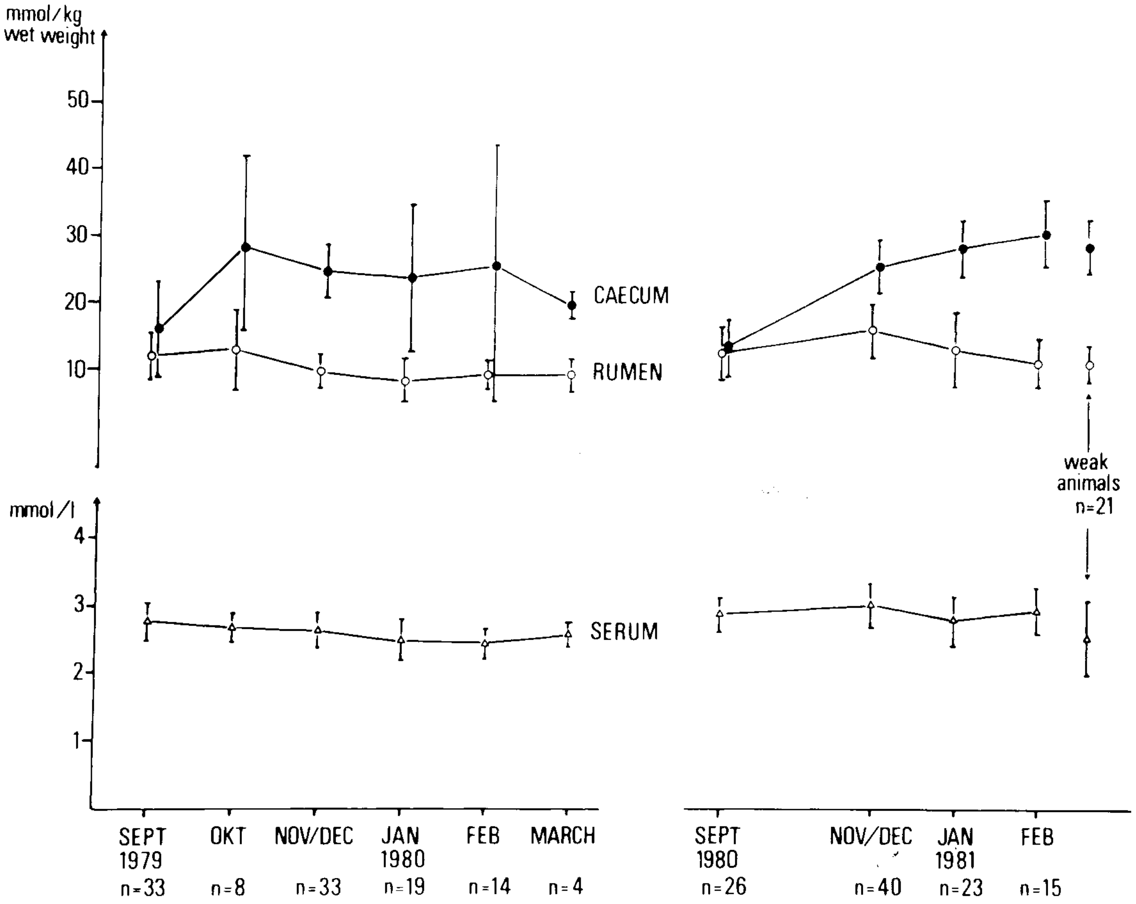

Fig. 2. Calcium in serum (△) in rumen (○) in caecum (●) and content from free-ranging reindeer slaughtered at different times from September to March in 1979/80 and 1980/81 and from weak reindeer slaughtered in February/March 1981 (mean±SD).

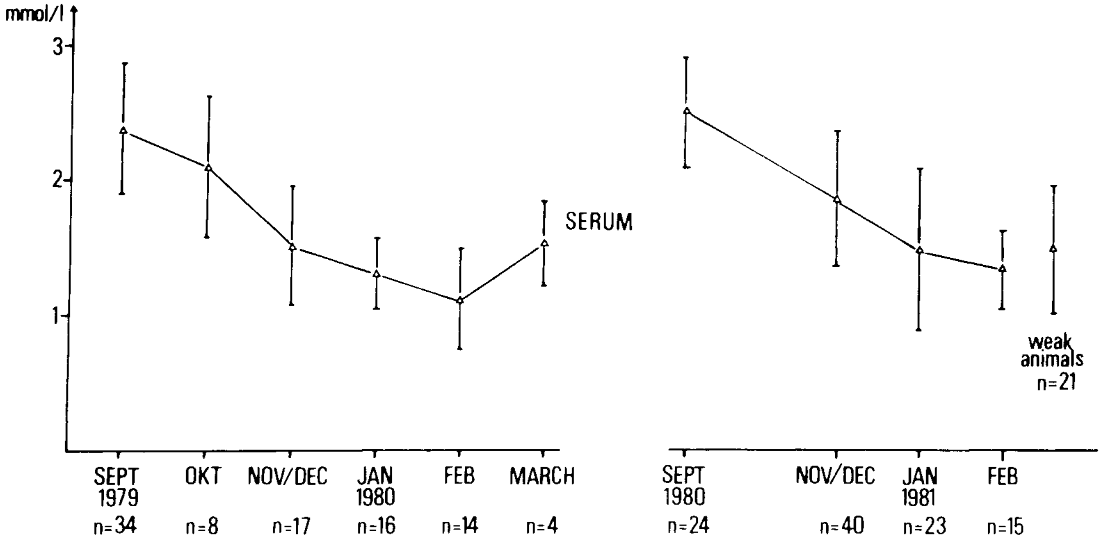

Fig. 3. Phosphorus in serum from free-ranging reindeer slaughtered at different times from Setember to March in 1979/80 and 1980/81 and from weak reindeer slaughtered in February/March 1981 (mean±SD).

They found extremely low serum-Ca values (1.7 ± 0.2 mmol/l) together with moderately low serum-Mg values (0.67 ± 0.12 mmol/l) in females living under poor nutritional conditions in February, and many reindeer from the same area died later and were reported to have had convulsions before death which indicates disturbances of grass tetany type.

The weak animals did not differ from animals in normal condition with respect to Ca-levels in rumen or caecum. In serum, the mean value of Ca was lower for weak animals: the difference was, however, not significant.

In serum-P there is a steady decline from autumn through winter. The same pattern was present in both years, though the values in January and February are slightly lower in the first year. P is often one of the most limiting minerals for many ruminants (Church, 1979) and probably also for the reindeer. This leads to low serum-P levels and a depletion of bone minerals (Church, 1979). No clinical signs of P-deficiency were shown in the reindeer investigated and the weak animals had serum-P values at the same level as animals in normal condition.

Our findings point to the conclusions that the winter conditions encountered in Scandinavia create difficulties for reindeer in meeting their mineral needs. This causes a magnesium and phosphorus deficiency and under the most difficult conditons a calcium deficiency. At some times Mg in serum drops to a level were the health of the animal is in danger.

Mg-deficiency along with deficiency in P and to some extent Ca are factors of considerable importance causing weakened condition in reindeer in the early spring.

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Reproductive performance of reindeer fed all-grain and hay-grain rations

Blanchard, J. M.[1] and **Hauer, W. E.**[1]

Abstract: Reproductive performance of grain-fed reindeer (*Rangifer tarandus*) was evaluated over a 2-year period. Groups of pregnant reindeer were fed one of three rations, (1) 100% whole-grain barley, (2) 98.9% whole-grain barley and 1.2% mineral and trace element supplement, and (3) 70% whole-grain barley and 30% finely-chopped bluegrass hay. Reindeer fed unsupplemented whole-barley failed to produce a single live calf. The addition of mineral and trace element supplement to the ration did not result in any significant improvement in reproductive performance. Eighty-five percent of the reindeer consuming unsupplemented and supplemented all-barley rations became pregnant; however, 76% of the pregnancies resulted in stillborn calves. One-hundred percent of the cows maintained on the grain/hay ration produced live calves. We speculate that reproductive failure in reindeer cows maintained on all-grain rations is most likely a result of a diet induced disfunction in maternal rumen and/or carbohydrate metabolism rather than a micro-nutrient deficiency. More research is neeeded to determine which metabolic pathways are affected.

Keywords: all-grain rations, reindeer, dystocia, stillborn.

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Rangifer, Special Issue No. 1, 1986: 39 - 41

Introduction

Reindeer (*Rangifer tarandus* spp.) herders in Alaska have always relied upon tundra rangeland as the only feed resource for their animals. Because of this dependency, feed availability and herd performance has often been affected by range quality, snow conditions and current competitive range-use by caribou (*Rangifer tarandus granti*). Alternate feeds could be invaluable to herders when used as a supplement to tundra rangeland. In addition, alternate feeds could also be utilized during emergencies caused by prolonged adverse weather or depletion of local grazing resources.

Experiments have been conducted to determine the feasibility of using Alaskan-grown livestock feeds as a supplement to tundra range and also as an alternative to grazing (Blanchard *et al.*, 1983). Due to the fact that cereal grain is the most available livestock feed in Alaska, initial studies focused on performance of reindeer fed all-grain rations (Blanchard, 1983). Initial trials showed that reindeer fed all-grain rations maintained considerable body finish throughout the winter months (Blanchard and Luick, 1980). However, preliminary findings also indicated that reindeer cows fed all-grain rations throughout gestation experienced a high incidence of reproductive failure (Blanchard *et al.*, 1983; Blanchard *et al.*, 1984).

The purposes of the feeding trials reported in this paper were to determine the extent of reproductive failure in grain-fed reindeer and to speculate on the role of nutrient imbalance or nutrient deficiency in reproductive failure.

Methods

Feeding trials were conducted during 1983 - 84 and 1984 - 85 using adult reindeer cows. Reindeer were placed on their respective rations 2 to 4 months prior to the fall rut and then maintained on these rations throughout gestation.

All-grain rations are typically low in several nutrients, including fiber and certain minerals and trace elements (National Academy of Sciences, 1971). In addition, unsupplemented

Table 1. Nutrient analysis (percent of dry-matter) of rations

Rations	NDF	ADF	Ca	P	K	Na
1984-WB[1]	26.9	10.4	0.08	0.42	0.74	0.04
1985-WB	40.9	8.5	0.13	0.36	0.57	0.06
1985-WB-MIN[2]	36.0	8.0	0.44	0.34	0.30	0.18
1985-WB+HAY[3]	50.6	17.3	0.22	0.32	0.83	0.06

[1] 100% whole-grain barley.

[2] 98.8% whole-grain barley, 0.55% limestone, 0.65% vitamin and mineral supplement.

[3] 70% whole-grain barley and 30% bluegrass hay.

all-barley rations (Table 1) have a relative imbalance of calcium to phosphorus (0.2:1.0) and sodium to potassium (0.05:1.00). To determine the effect of the level of micro-nutrient intake on reproductive performance, one grain-feeding group (1984-WB+MIN) was maintained during 1983 - 84 on an all-whole-grain barley ration supplemented with a mineral and trace element block (*ad libium*). The other 1983 - 84 group (1984-WB) served as a control and was maintained on an unsupplemented all-whole-grain barley ration.

During 1984 - 85, three feed groups were established. One group (1985-WB) served as a control and received an, unsupplemented all-whole-grain barley ration (a repeat of 1983 - 84 control). During the 1983 - 84 trial, *ad libidum* mineral and trace element intake of the 1984-WB+MIN group was very low and therefore did not significantly increase micro-nutrient intake or change the low Ca:P and Na:K ratios significantly from that of the unsupplemented all-barley ration. A feed group (1985-WB+MIN) was created during the 1984 - 85 trial to again test the effects of mineral and trace element supplementation on the reproductive performance of reindeer fed all-barley rations. To assure sufficient intake, supplement was mixed directly with the grain producing a ration of 98.8% whole-grain barley, 0.65% limestone flour and 0.55% mineral and trace element supplement. This ration contained a Ca:P ratio of 1.3:1.0 and a Na:K ratio of 0.6:1.0.

A third feed group was established during the 1984 - 85 trial to determine the effect of adding a roughage source to all-barley rations. This group (1985-WB+HAY) was offered a ration (*ad libidum*) of 70% whole-grain barley and 30% finely-chopped bluegrass hay. This ration was not supplemented with micro-nutrients. The Ca:P ratio of 0.70 to 1.00 and Na:K ratio of 0.07 to 1.00 were considerably lower thant that of the supplemented all-barley ration (1985-WB+MIN).

Results

Reindeer fed unsupplemented all-whole-grain barley rations failed to produce a single live calf

Table 2. The reproductive performance of reindeer fed all-grain and grain/hay rations.

			Number of calves produced			Mean birth weight (kg)	
Feed group[1]	N[2]	Number pregnant cows	Live at birth	Live at 48 h	Stillborn	Live	Still
1984-WB	6	6/6[3]	0/6	0/6	6/6		8.3
1984-WB+MIN	7	6/7	1/6	0/6	5/6	4.8	5.8
1985-WB	3	2/3	0/2	0/2	2/2		2.3
1985-WB+MIN	4	3/3	2/3	1/3	1/3	4.1	2.7
1985-WB+HAY	4	4/4	4/4	4/4	0/4	6.6	

[1] WB=100% whole-grain barley (1984 & 1985); WB+MIN=100% whole grain barley plus mineral lick (1983 - 84) and 98.8% whole grain barley, 0.65% limestone flour, and 0.55% vitamin and mineral supplement (1984 - 85); and WB+HAY=70% whole grain barley and 30% choppel bluegrass hay.

[2] Number of reindeer in group sampled.

[3] 6/6=(number in this category) compared to (total number in this sample).

(Table 2). Reindeer consuming supplemented all-barley rations experienced only a slight improvement in reproductive success. The 1984-WB+MIN group produced one live calf that died within 48 hours of birth after failing to stand and nurse. Similar results were observed in the 1985-WB+MIN group where one calf died within 48 hours of birth and another weak and frail calf with a birthweight of only 2.3 kg lived for 7 days.

During the 1983 - 84 trial, 70% of the cows produced stillborn calves, of which all were malpresented at parturition. In all cases, malpresentation resulted in severe dystocia, and ultimately caused the death of two cows. During the 1984 - 85 trial, 33% of the stillborn calves were malpresented. All reindeer in the 1985-WB+HAY group produced live calves, which averaged 6.6 kg at birth.

Conclusions

The low absolute levels and relative imbalance of several micro-nutrients in barley may in part contribute to reproductive failure in reindeer cows fed all-barley rations. However, results from the present feeding trials indicate that factors other than micro-nutrient status alone are contributing to reproductive failure, since supplemented rations resulted in only a slight improvement in reproductive success. In addition, micro-nutrient status of reindeer consuming a 70% barley/30% chopped hay rations was not substantially improved over that of reindeer consuming an unsupplemented all-barley ration, yet, consuming the grain/hay ration resulted in high reproductive success.

Replacement of 30% of the grain (by weight) with hay increased neutral detergent fiber by 25% and doubled the acid detergent fiber content of the ration (all barley vs. barley/hay). This increase in fiber may have resulted in significant changes in rumen function, volatile fatty acid production, maternal carbohydrate metabolism and/or partitioning of nutrients between maternal and fetal tissues. More research is needed to determine the specific metabolic effects that occur when grain rations are fed to reindeer.

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The distribution and movement patterns of four woodland caribou herds in Quebec and Labrador.

W. K. Brown[1], J. Huot[2], P. Lamothe[3], S. Luttich[4], M. Paré[2], G. St. Martin[5] and J. B. Theberge[5]

Abstract: Recent studies of woodland caribou *(Rangifer tarandus caribou)* in northern Quebec and central Labrador have demonstrated similar patterns of seasonal movements and distribution among four herds. Aerial surveys and radio-telemetry indicated that animals occupied forest-wetland habitat at densities of 0.03 caribou km^{-2}, or lower, for most of the year. Although females were widely dispersed at calving individuals demonstrated fidelity toward specific calving locations, in successive years. Caribou did not form large post-calving aggregations. Movement was greatest in the spring, prior to calving, and in the fall, during or immediately after rutting. Caribou were generally sedentary during summer and winter, although some moved relatively long distances to late-winter range. Although the herds occupy continuous range across Quebec and Labrador, our data indicate that the herds are largely discreete and should be managed individually.

Keywords: woodland caribou, Quebec, Labrador, distribution, movements

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Rangifer, Special Issue No. 1, 1986: 43 - 49

Introduction

Most current understanding of seasonal movements, aggregation behaviour and habitat use by caribou (*Rangifer tarandus*) in North America is based upon studies of primarily tundra-dwelling barren-ground caribou (*R. t. groenlandicus*) or woodland caribou (*R. t. caribou*) in open or mountainous habitats (Bergerud, 1974; Bloomfield, 1980; Edwards and Ritcey, 1959; Freddy, 1979; Kelsall, 1968; Oosenbrug and Theberge, 1980; Skoog, 1968). The only detailed studies of caribou that occupy boreal-forest habitat in northern Canada year-around are from Alberta (Edmonds and Bloomfield, 1984; Fuller and Keith, 1981) and Manitoba (Darby and Pruitt, 1984; Shoesmith and Storey, 1977; Stardom, 1975). In this paper, we summarize and compare the movements, habitat use and herd discreeteness of four forest-dwelling herds in northern Quebec and central Labrador (Fig. 1).

The four populations are: the Lac Bienville herd (LBH); the Caniapiscau herd (CH); the Lac Joseph herd (LJH) and the Red Wine Mountains herd (RWMH). All four ranges lie on or within the southern periphery of the winter range of the much larger George River herd, currently estimated at >500 000 caribou (S. Luttich, unpublished data). The results of our studies have important implications for the management of these herds.

Study areas

The ranges of the four herds extend >1000 km from near Hudson Bay in northwestern Quebec to Lake Melville, Labrador (Fig. 1). The entire area is located on a series of adjacent, level to gently rolling, poorly drained plateaux. Uplands of low, rolling hills are interspersed throughout the region. Elevations on the plateaux range from 300 — 800 m and uplands extend to >1000 m.

The vegetation of the plateaux region is a mosaic of boreal forest and wetlands. Forests are primarily open lichen-woodlands, dominated by black spruce (*Picea mariana*), with tamarack (*Larix laricina*) common on wetter sites. Scattered stands of jack pine (*Pinus banksiana*) are found at the southern limit of the LBH range but do not extend further east or north. Deciduous forest, including trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*), occur uncommonly and only at lower elevations on some south-facing slopes and in major river valleys. The wetlands comprise a complex of fens, bogs and swamps interspersed with abundant lakes and rivers.

The uplands are dominated by tundra vegetation consisting of lichens, mosses, sedges and prostrate shrubs. Exposed bedrock and glacial erratics are common in upland areas.

Major predators of the caribou are wolves (*Canis lupus*) and black bears (*Ursus americanus*). Lynx (*Lynx canadensis*) are also present but are not numerous.

Human population centers in the region are sparse and located on the peripheries of the ranges (Fig. 1). The major industrial developments include iron-ore mines, near Labrador City and Schefferville, and the La Grande (in Quebec) and Churchill Falls hydroelectric projects. Transportation corridors include: a summer-use road across the southern portion of the range of the CH; a railway in western Labrador between the ranges of the LJH and CH; an «all-weather» road from the railway to Churchill Falls through the range of the LJH and a summer-use road through the range of the RWMH between Churchill Falls and Goose Bay.

Methods

In North America, caribou herds have been defined most often on the basis of the location of their calving grounds. The populations we report on calved over broad areas and did not use relatively confined calving grounds. However, they used these broad areas faithfully and displayed regular seasonal patterns of range use. As well, portions of each population aggregated during other critical life-history periods such as winter or rut. Thus we consider the populations to be relatively discrete and refer to them as «herds». All caribou of the Quebec — Labrador peninsula were classified by Banfield (1961) as the woodland subspecies (*R. t. caribou*).

In each study, radio-telemetry was used to monitor caribou movements and distribution, with emphasis on adult (>1-year old) females. Caribou were monitored at approximately monthly intervals from either fixed-wing aircraft or helicopters. Caribou habitat use was determined by observations made during aerial and ground-based surveys.

The herds and study periods are described below:

Lac Bienville herd (LBH)

Data from the LBH were collected between 1975 and 1980 by P. Lamothe. Seventeen female caribou were radio-collared in March 1977 and monitored through May 1979. During the study, the herd was estimated at approximately 1500 caribou. The range of the herd was >35 000 km^2 and winter densities were <0.03 caribou km^{-2}.

Caniapiscau herd (CH)

In 1981 and 1983, 42 female caribou of the CH were radio-collared (N=25 and 17, respectively). Data were collected from March 1981 through December 1984 by M. Paré and J. Huot. In 1977, prior to the study, the herd was estimated at approximately 600 animals. Because of winter ingress of caribou from the George River herd, the total herd size and density could not be estimated during the study. The entire range of the herd was not determined. The study area was approximately 41 000 km^2.

Lac Joseph herd (LJH)

Detailed study of the LJH, by G. St. Martin, S. Luttich and J. B. Theberge, began in April 1984 when 18 female caribou were radio-collared. Monitoring of the herd will continue through April 1986. In 1985, the herd was estimated at a minimum of 240 caribou. The herd's total range was >35 000 km^2 and caribou densities were estimated to be <0.03 caribou km^{-2}.

Red Wine Mountains herd (RWMH)

Data were collected for the RWMH from March 1982 through June 1985 by W. K. Brown,

S. Luttich and J. B. Theberge. In March 1982, 27 female caribou were radio-collared. Sixteen adult caribou (nine females and seven males) were radio-collared in March 1983. Herd size was estimated at approximately 800 in 1983 and the range of the herd, based upon the relocation of radio-collared caribou, was >25 000 km^2. Densities were <0.03 caribou km^{-2}.

Data were not collected in a standardized fashion among all studies and, therefore, some data are not available for all herds. Study of the LJH is ongoing and the information presented is based upon 13 months of monitoring, including two calving periods only.

Caribou distribution is described for the following seasons: spring (May — June; summer (July — August); fall (September — November); winter (December — February) and late-winter (March — April). The movements of radio-collared caribou in Fig. 2 are expressed as «mean kilometres moved per day» to standardize observations over variable survey intervals. These values are not intended to describe the actual daily movements of the caribou but represent indices to compare seasonal and herd variability in mobility.

Results

Spring

In spring, prior to calving, caribou in all herds dispersed widely from areas of late-winter aggregation. The greatest movements of radio-collared caribou between successive relocations occurred during this period (Fig. 2). Although individuals moved relatively long distances during this dispersal, the general area and extent of the ranges used remained the same as during winter and late winter.

In all herds, calving took place primarily during the first two weeks of June. Caribou were widely dispersed with estimated distributions of calving females of >12 000 km^2 for the LBH, >15 000 km^2 for the CH, >29 000 km^2 for the LJH and >12 000 km^2 for the RWMH. The

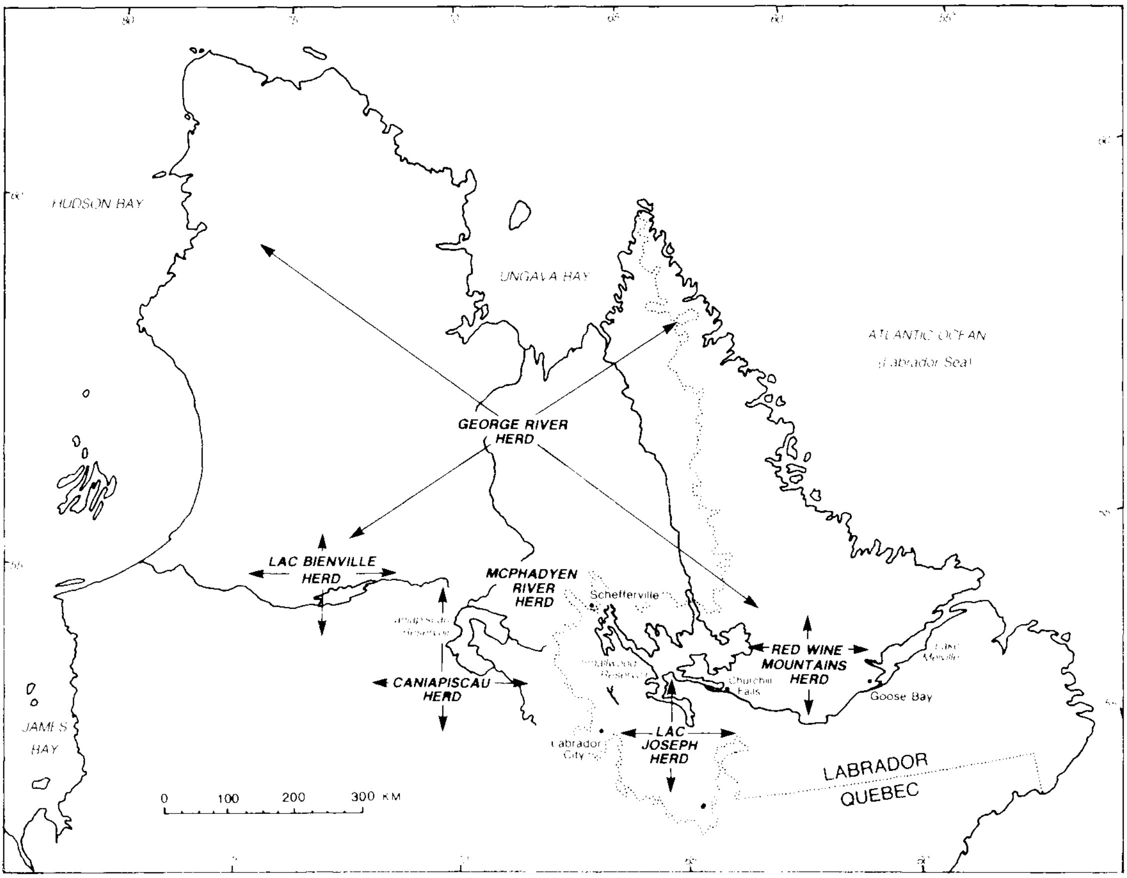

Fig. 1. Study areas in Quebec and Labrador.

estimated densities of calving females were <0.04 females km^{-2} in the LBH, LJH and RWMH. The mean group size, excluding newborn calves, in the RWMH in mid-June was 1.2 (SD=0.46, range=1 - 3, n=70).

Individual females displayed marked fidelity toward specific calving locations. During the calving period, >95% (n=70), 82% (n=9) and a minimum of 64% (n=23) of radio-collared females from the CH, LJH and RWMH, respectively, were located <10 km from their calving-period locations of the previous year. Of females in the LJH and RWMH, 33% (n=3) and 64% (n=16), respectively, were located <3 km from their former calving-period location. Several females were observed on the same island, peninsula or bog they had occupied the previous year. From their locations in March, some females of the CH travelled from 200 to >500 km (mean=75.3, SD=72.0, range=10 - 520, n=85) to return to the calving location they had used the previous year.

In the RWMH, there was no significant difference (G-test, P>0.99) between the fidelity of those females known to have had calves in successive years (n=15) and those whose reproductive status in successive years was unknown (n=8) (Brown and Theberge, 1985).

Not all females returned to their former calving locations. Two females of the LBH gave birth in successive years at sites separated by 120 and 139 km respectively. As well, two radio-collared CH females were located >250 km northeast of the study area, within the range of the George River herd, during calving in 1984; whether those individuals calved that year is unknown. Sixteen percent (n=6) of RWMH caribou were located during the 1983 and 1984 calving periods >30 km from their previous calving-season location (range=35 - 69 km). However, all remained within the recognized range of the RWMH. During the 1985 calving period, one RWMH female of unknown reproductive status moved >100 km east into the centre of the LJH range. That animal had been located on the western edge of the RWMH range during the previous 2 calving periods.

All observed calving sites of the LBH (n=29) and 82% (n=71) of the CH were located in small (<1 km^2), open wetlands, and usually only one

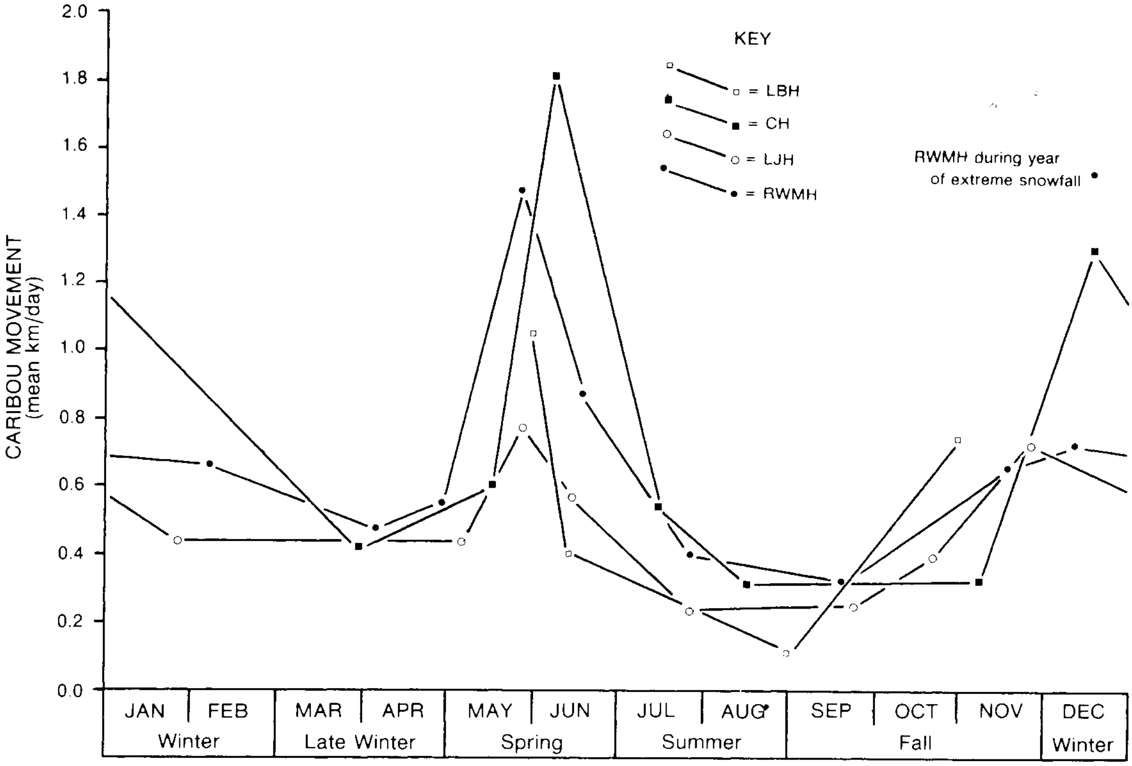

Fig. 2. Seasonal movements of caribou in the Lac Bienville, Caniapiscau, Lac Joseph and Red Wine Mountains herds.

female was observed per wetland. Caribou of the LJH and RWMH occupied similar forest-wetland habitats during the calving period but the specific habitat types used for calving were not determined. No radio-collared females of any herd were known to have calved in upland tundra, although this habitat type was available within each range.

Thirty-five percent (n=10), 41% (n=38) and <10% (n=5) of the calving sites of LBH, CH and RWMH females, respectively, were located on islands or peninsulas. The relatively greater proportion of LBH and CH caribou calving on these isolated topographic features compared with the RWMH may be due to a greater abundance of open water (approximately 20% in the LBH area and 21% in the Caniapiscau area after reservoir flooding, versus 13% in the Red Wine area).

Summer

Following calving, caribou did not form large post-calving aggregations. Females of the LBH, CH and RWMH remained alone with their calves or formed groups of two to three adult-calf pairs.

The caribou in all herds were relatively sedentary throughout the summer. Mean distances moved between calving and mid-summer were 10 - 20 km (Fig. 2). The animals remained in forest-wetland habitat; however, the relative use of forests versus wetlands was not determined.

Fall

Movements increased during the fall, probably due to breeding activity as the animals moved to form rutting groups, and caribou remained distributed over much of the total range of each herd. Rutting of the RWMH was estimated, based upon the timing of calving, to have peaked in mid- to late October (Brown and Theberge, 1985). Rutting appeared to take place in open wetlands, although quantitative data are lacking.

During the fall, group sizes increased but were variable among herds, ranging from 2.5 in the LJH (SD=1.46, range =1 - 5, n=17; late October) and 5.7 in the CH (SD=4.4, range=1 - 23, n=77; early November) to 15.5 (SD=13.9, range=2 - 60, n=22; early November) in the RWMH.

Winter and late-winter

Caribou movements varied among herds during winter and late-winter. Between November and early December, the distances moved by CH caribou increased substantially (Fig. 2). Other herds did not demonstrate a similar increase in movement at this time except for a distinct range shift by RWMH caribou between fall and early winter of 1983. That range shift was characterized by a synchronous northward movement of widely scattered animals, apparently made in response to extreme November snowfall (146.4 cm or 214% of normal snowfall at Churchill Falls). The direction of the winter movements of the CH caribou was not coordinated as was that of the RWMH, and the movement was not associated with greater than average snowfall.

Some caribou of the CH left the study area with caribou of the George River herd each winter, moving as far away as 520 km before returning during the calving period. In February and March 1984, >2000 George River caribou moved onto the range of the McPhadyen River herd (Fig. 2). Three of four resident caribou, which had been radio-collared in conjunction with the LJH study, associated with the George River animals at that time. However, they did not leave the McPhadyen area when the George River caribou migrated north in April.

Caribou of the LJH appeared to be the most sedentary of the four herds during winter and late winter. LJH caribou remained in localized areas of forest-wetland habitat, moving only short distances between surveys (mean=<26 km).

More than half of the RWMH made distinct range-shifts during the winter and late-winter from forest-wetland habitat to the upland-tundra regions of the Red Wine Mountains. Many of these movements were relatively long (range=16 - 86 km), and the caribou making them were generally sedentary both before and after. Caribou of the other herds remained primarily in forest-wetland habitat throughout the entire winter. LBH caribou used upland-tundra areas for loafing in late winter but returned to lichen woodlands to feed.

The mean group size in the LJH in February was 11.4 (SD=8.2, range=2 - 28, n=21). The mean group size in the RWMH in April was 11.1 (SD=8.8, range=1 - 43, n=53).

Discussion

Distribution and movements

The four study herds demonstrated similar patterns of seasonal dispersion and movements.

Caribou were widely dispersed at calving, demonstrated calving-site fidelity and did not form large post-calving aggregations. Throughout the summer, they remained dispersed in small groups and were relatively sedentary. They increased their movements and group sizes during the rut, and then generally remained sedentary throughout the winter and late-winter. With the exception of the RWMH, the caribou did not extensively utilize available upland-tundra habitat.

These observations differ in some respects from the general patterns described for barren-ground caribou and tundra-dwelling woodland caribou (Bergerud, 1974; Kelsall, 1968; Skoog, 1968). None of the herds we report on migrated in large groups or followed «traditional» migration routes; the respective seasonal ranges of each herd largely overlapped; females did not aggregate on discrete calving grounds but still demonstrated marked calving-site fidelity; females did not utilize tundra habitat for calving although that habitat type was available; and caribou did not form large post-calving aggregations.

Movements similar to those of the herds we studied have been reported for other caribou and reindeer in forest habitats (Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984; Fuller and Keith, 1981; Helle, 1979, 1980; Pulliainen *et al.*, 1983; Shoesmith and Storey, 1977; Stardom, 1975). Thus, the patterns we observed may be typical of most forest-dwelling *Rangifer* populations.

Herd discreeteness and management implications

Our findings regarding caribou movements in northern Quebec and central Labrador have important management implications. The range fidelity displayed by caribou of the southern herds indicates that even with periodic, large influxes of George River caribou, the southern herds will persist and, therefore should be managed as discreete populations. More conclusive data concerning herd discreeteness may be obtainable through comparisons of body morphology and the electrophoretic analysis of globulin transferrins (*e.g.* Nadler *et al.*, 1967; Røed, 1985).

Some interchange of caribou between adjacent southern herds during our studies was expected because of the continuous distribution of caribou across the region. Our data indicate changes in the home ranges of some caribou in all herds, even during the calving period when range fidelity was greatest. However, interchange among the southern herds appeared to be a minor factor in the dynamics of the populations during our studies, based upon movement data from radio-collared caribou and empirical evidence collected during aerial surveys.

A more important factor was the periodic ingress by caribou of the George River herd. Since approximately 1980, large numbers of George River caribou have migrated through the ranges of the LBH and CH. In the winter of 1984 — 85, George River caribou were found at the northern and northwestern peripheries of the LJH and RWMH ranges.

The hypothesis regarding the persistence of southern herds will be testable if the range of the George River herd continues to expand. If the George River herd moves further south during future winters, and into the range of the LJH or the RWMH, our prediction is that such ingress will not substantially affect the distribution of those herds. The magnitude of the effect that such ingress may have on the population size of the southern herds cannot be predicted from our data. However, because of calving-location fidelity, a substantial shift in range affiliation by females of the southern herds should not occur.

Acknowledgements

We thank all of the individuals who participated in the field and analytical phases of the four studies. J. M. Barclay Brown prepared the figures. Constructive reviews by E. J. Edmonds and S. O. Mahoney improved the paper. Funding for the LBH study was provided by Hydro-Quebec and Quebec Ministére du Loisir, de la Chasse, et de la Pêche; for the CH study by the James Bay Energy Corporation, the La Grande Complex Remedial Works Corporation, Quebec Ministére du Loisir, de la Chasse, et de la Pêche and Université Laval; for the LJH study by the Newfoundland-Labrador Wildlife Division, Newfoundland-Labrador Department of Transportation, Canadian Department of Indian and Northern Affairs (DIANA), National Sciences and Engineering Research Council (NSERC), the University of Waterloo and Digital Equipment Corporation; and for the RWMH study by the Newfoundland-Labrador Wildlife Division, Lower Churchill Development Corporation, DIANA, NSERC, the University of Waterloo and Digital Equipment Corporation.

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Summer range fidelity of radio-collared caribou in Alaska's Central Arctic Herd

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Abstract: Sixty-four adult (2+ years) female caribou *(Rangifer tarandus granti)*, radio-collared in April or May 1975 - 82, were relocated during the following June and/or July within the summer range of the Central Arctic Herd (CAH). Relocations made during the following three summers were used to assess range fidelity. Cumulative relocations of radio-collared females in the Central Arctic region were equivalent to 91% of the projected availability based on transmitter life. A chronological analysis indicates that 98%, 91%, and 82% of radio-collared females were found there one, two, and three years later; most of the progressively lower relocation success is probably attributable to transitter malfunctions rather than emigration. These observations suggest that summer range fidelity of adult females in the CAH is at least 90%, and may approach 100%.

Key words: caribou, range fidelity, emigration, radio collars.

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Rangifer, Special Issue No. 1, 1986: 51 - 55

Introduction

Previously we reported a low frequency of emigration of collared female caribou *(Rangifer tarandus granti)* from the Central Arctic Herd (CAH) (Whitten and Cameron, 1983*a*). Of 127 females marked on winter range with transmitter and/or visual (numbered) collars between 1975 and 1978, seven (6%) were later observed in the Porcupine, Western Arctic, or Teshekpuk Herds (see Davis, 1980). It was concluded that these resightings constituted inter-herd movements.

In retrospect, it appears that some of the caribou collared in the Central Arctic region were within zones of overlap with the winter ranges of adjacent herds, and that our conclusions regarding the extent of emigration of CAH caribou may have been inappropriate. There is considerable evidence that variable numbers of caribou from the Western Arctic Herd, in particular, share a common winter range with animals from the CAH. In November 1976 and 1981, for example, we observed approximately 1200 and 400 caribou, respectively, in the Upper Itkillik River/Galbraith Lake area (Fig. 1), some distance from known CAH caribou to the north; tracks indicated that they had moved in from the west. Carruthers and Jakimchuk (1985) reported a steady increase in the numbers of caribou wintering in the western portion of the Central Arctic region since 1981. They estimated that 38 000 caribou occupied the area during winter 1984 - 85, some 23 000 more than the approximate size of the resident CAH. And, finally, recent Alaska Department of Fish and Game radiotracking studies indicate that some females from the Western Arctic and Teshekpuk Herds may winter as far east as the Sagavanirktok River (P. Valkenburg, pers. comm.).

Few specifics are available regarding overlap of the CAH and Porcupine Herd ranges. However, our recent observations of caribou distribution during summer, fall, and winter in the vicinity of the middle Canning River (Fig. 1) suggest that mixing of these two herds could also occur.

We report here on the summer range fidelity of CAH female caribou over a 10-year period. To avoid errors resulting from the inadvertent collaring of caribou from other herds, we first established CAH affiliation of radio-collared females based on use of the Central Arctic area during the first summer after collaring. Fidelity was then assessed by relocationg those individuals during the following three years.

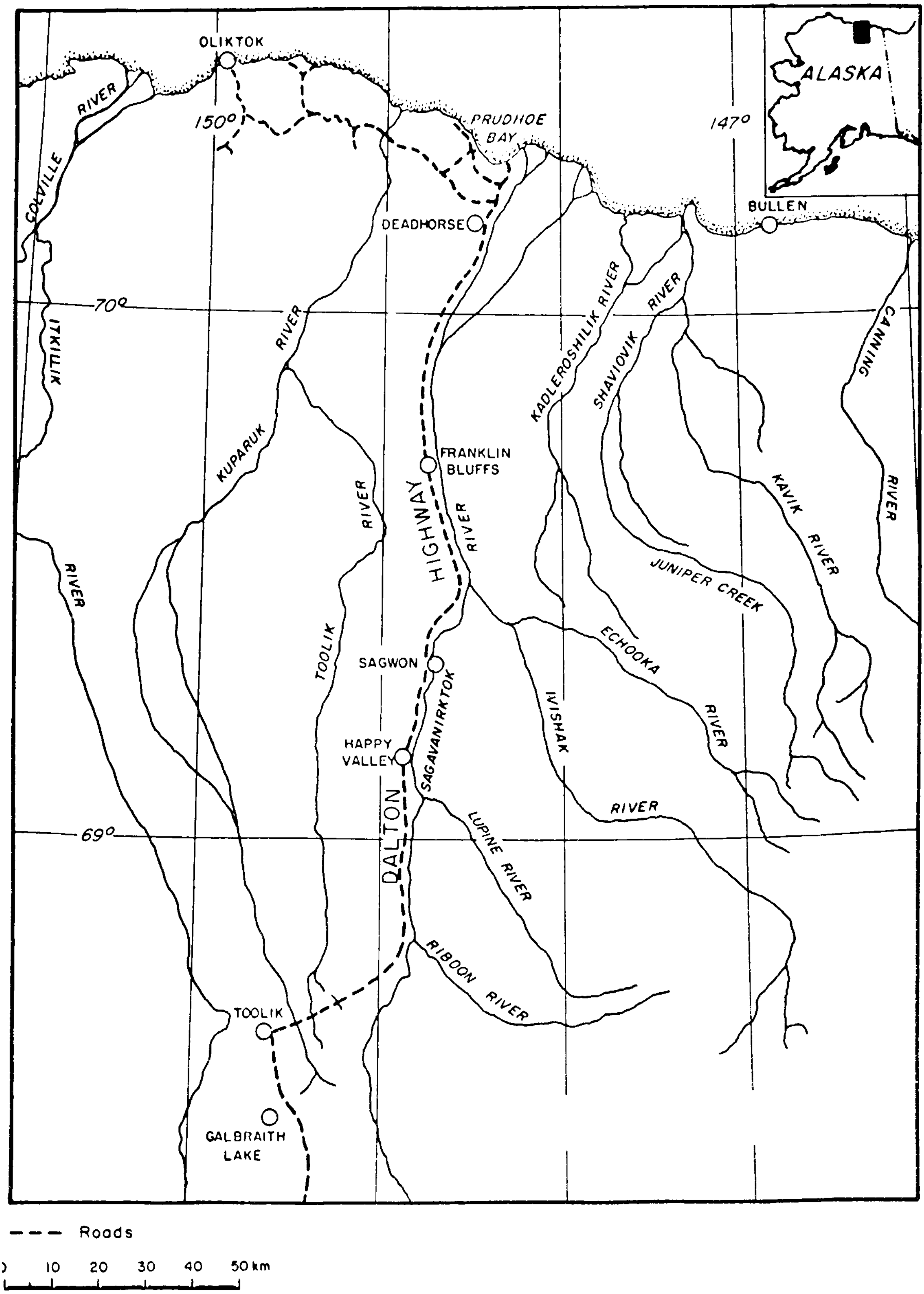

Fig. 1. The Central Arctic region of Alaska.

Table 1. Numbers of female caribou radio-collared, 1975 - 82, and the projected numbers of years that radio-collared caribou were available for tracking vs. years relocated in the Central Arctic region (Fig. 1), Alaska, during summer.

	Number of caribou		Number of collared caribou in Central Arctic, 1st summer[b]	Cumulative number of caribou-years	
Year	Collared[a]	Recollared[a]		Available for tracking[c,d] after 1st summer[b]	Relocated in Central Arctic[c] after 1st summer[b]
1975	8	1	5	4	4
1976	10	-	2	3	3
1977	12	1	9	22	22
1978	8	1	8	24	23
1980	13	-	8	9	8
1981	18	4	15	36	29
1982	21	-	17	44	40
Total	90	7	64	142	129 (91% fidelity)

[a] In late April or early May.

[b] June-July.

[c] Excludes known mortality, shed collars, and transmitter failures.

[d] Assuming 3.3 years transmitter life.

Methods

In April or May 1975 - 78 and 1980 - 82, 90 adult (2+ years) female caribou were equipped with radio-transmitter collars (Table 1) on the Central Arctic Slope of Alaska, generally within 20 km of the Dalton Highway (Fig. 1). Of these, seven were subsequently recollared (Table 1). Immobilization procedures, and the radio collars used through 1981, were described previously (Whitten and Cameron, 1983*a*). Transmitters used in 1982 were supplied by Telonics, Inc., Mesa, Arizona. All radio collars deployed after 1975 were equipped with a red and yellow numbered collar or coded with colored tape.

Radio-collared caribou were tracked and relocated using a fixed-wing aircraft equipped with a scanner/receiver and two dual element antennas (Telonics, Inc., Mesa, Arizona). Searches were conducted primarily within the area shown in Fig. 1. Each year through 1980, relocation attempts were made once in February or March, at approximately 10-day intervals between April and October, and again in November. For the period 1981 - 1985, we attempted relocations in March and/or April, at irregular intervals between May and August, and again in September and November. However, inclement weather and logistical problems occasionally prevented our completing radio-tracking flights as scheduled.

Radio-collared caribou observed between the Colville/Itkillik and Canning River drainages (Fig. 1) at least once during the first June or July after capture were considered members of the CAH. Fidelity to CAH summer range was evaluated one, two, and three years thereafter.

Mortalities of collared caribou and occurrences of shed transmitters were confirmed by visual inspection during routine tracking flights. Inoperative transmitters were identified through opportunistic sightings by air or from the ground, followed by verification that signal transmission had ceased. Radio-collared caribou not relocated in the Central Arctic region during the prescribed period and not otherwise accounted for (i.e., by confirmation of mortality, shed collar, or inoperative transmitter) were assumed to have left the area. However, such missing individuals were monitored for at least one year after the date of last relocation, both by us and by other biologists routinely tracking collared individuals from the other three Arctic herds. A radio-collared caribou observed on the summer range of another herd, after first being relocated on CAH summer range, was assumed to have emigrated to that herd.

Results

The cumulative relocation data indicate a high degree of repeated use of CAH summer range by radio-collared female caribou (Table 1). Between 1975 and 1982, 64 of the 90 females collared were observed in the study area during the first summer after collaring. Assuming the manufacturer's projected 3.3-year transmitter life and adjusting for mortality, shed collars, and confirmed transmitter failures, we calculated that known CAH caribou were potentially available for a total of 142 caribou-years of radio-tracking. Caribou were relocated in the Central Arctic region 129 of those years, indicating an overall fidelity of 91%.

An analysis across years yields similar results (Table 2). Of those radio-collared caribou located on CAH range the first summer after collaring, 98% were located in the Central Arctic area for an additional summer, 91% for two more summers, and 82% for three more summers (Table 2).

In a number of cases we were able to document CAH summer range fidelity for periods exceeding the 3.3-year standard operational life of transmitters. A few females were recollared (Table 1), some transmitters functioned longer than expected, and others with expired collars were sighted incidental to other activities. Eight radio-collared females were observed on CAH summer range for five consecutive years, one for five of six years, one for six of eight years, and one for seven of nine years.

Discussion

These data indicate a strong affinity of CAH female caribou to their summer range. Only seven radio-collared females accounted for all of the apparent range infidelity (Table 2; one in year 1, three more in year 2, and three more in year 3). Of these, only one was a confirmed emigration and another, with a weak transmitter, was eventually found dead on CAH summer range. The remaining five were never accounted for, and four of those were difficult to track because of weak or intermittent signals when last located.

The probability of a caribou with a failed transmitter remaining in the CAH undetected would have been high. Between 1975 and 1979, the likelihood of observing a collared caribou without the use of telemetry was only ca. 60% (Whitten and Cameron, 1983*a*). Since then, the proportion of collared caribou in the CAH has decreased with continued herd growth (Whitten and Cameron, 1983*b*; Smith, unpublished data), and general surveys of the CAH have been far less frequent and intensive.

Eleven transmitter failures were detected during the course of this study. That an additional six malfunctioned seems likely, especially considering that five were known to be weak or intermittent. Thus, transmitter malfunction was the probable cause of most of the supposed infidelity. Nevertheless, for the calculations in Table 2, individuals not accounted for during a given summer were considered

Table 2. Analysis across years of the fidelity of radio-collared female caribou to the Central Arctic region (Fig. 1), Alaska, during summer.

	Number of collared caribou					
Year	Total[a]	Unavailable for tracking[b]	Available for tracking	Leaving Central Arctic[c]	Relocated in Central Arctic during summer[d]	% Fidelity
0	90	17	73	4	64	—
1	64 (64)	13 (14)	51 (50)	0	50	98 (100)
2	51 (50)	7 (9)	44 (41)	1	40	91 (98)
3	44 (41)	6 (9)	38 (32)	0	31	82 (97)

[a] Number of caribou collared (year 0), or the maximum numbers of collared caribou initially available for tracking (years 1, 2, and 3).

[b] Visual confirmation of mortality, shed collar, or transmitter failure.

[c] Confirmed present on the summer range of the Porcupine, Western Arctic, or Teshekpuk Herd.

[d] During June and/or July.

NOTE: Values in parentheses are recalculations assuming six transmitter failures (one in year 1, two in year 2, and three in year 3). See text for details.

available for the projected 3.3 years of transmitter life. If the six missing female caribou are assumed to have been unavailable for tracking, the fidelity values increase to 100, 98, and 97% in years 1, 2, and 3, respectively (Table 2). We believe that the latter estimates are more realistic. Viewed from another perspective, the data indicate that emigration to the summer range of an adjacent herd was *confirmed* in only one of 64 cases.

Likewise, the available evidence indicates that little or no immigration into the CAH occurs. Since 1979, at least 200 adult female caribou have been radio-collared in the adjacent Western Arctic, Porcupine, and Teshekpuk Herds. However, not a single animal, having once been found on any of these herds' calving grounds or summer range, has been later observed on the summer range of the CAH.

Fidelity to a discrete calving area is the generally accepted criterion for assigning herd status to a particular group of barren-ground caribou (Skoog, 1968). Unfortunately, our data are insufficient to directly address the specific question of calving location. In most years, logistical complications or weather problems prevented our relocating all collared cows during the calving period in early June. When radio-tracking was attempted, however, all collared individuals found were on the CAH calving grounds (see Whitten and Cameron, 1985). Furthermore, our year-round relocation schedule (see Methods) provided fairly complete movement information on the majority of collared females. Caribou present on CAH summer range in late June and/or July, but not relocated at calving time, were known to have wintered in the Central Arctic region (Fig. 1). It seems highly unlikely that a pregnant female would move to the calving ground of an adjacent herd an then rejoin Central Arctic caribou on summer range (with a young calf) some 3 - 6 weeks later; in fact, no such movements have ever been documented. Hence, we believe that our estimates of *summer range* fidelity are a reasonably accurate reflection of *calving ground* fidelity.

Although patterns of range fidelity may differ among barren-ground caribou across North America, the preponderance of data on seasonal distribution and movements indicates that caribou occur as separate subpopulations or herds, each occupying a calving ground and summer range distinct from that of any other. Thus, censuses and composition counts conducted during summer provide the most reliable data on a given herd. In contrast, range overlap by adjacent herds during winter and/or spring is not uncommon, dictating that results obtained during those seasons be interpreted with caution.

Acknowledgements

This study was funded by Federal Aid in Wildlife Restoration Projects W-17, W-21, and W-22. Alyeska Pipeline Service Company and Northwest-Alaska Pipeline Company also provided logistical and financial support. We are grateful to J. R. Dau, P. Valkenburg, and D. D. Roby for expert technical assistance, and to W. L. Regelin, D. C. Heard, and S. Mahoney for their critical reviews of the manuscript.

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Distribution and habitat use of the Bluenose caribou herd in mid-winter

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Abstract: The mid-winter distribution and densities of the Bluenose caribou herd were compared with previous surveys over six years and were similar in all years except 1981 when exceptionally mild weather prevailed. Differences in group size, distribution and habitat use between sexes were noted in 1983. Caribou were distributed disproportionately to availability of vegetation types and used lakes significantly more than expected based on their occurrence. Male groups used conifer cover more than did female-calf groups which used open areas (lakes, fens, bogs) more than males. Cow-calf groups chose areas with a higher small lake density compared to lake density generally available. Generally caribou preferred habitat between 200 and 300 m in elevation with high densities of lakes less than 1 km^2 in size. Snow depths and hardness were greater in most unoccupied habitats than in occupied habitats. Wolves were associated with high densities of cow/calf groups.

Keywords: Barren-ground caribou, caribou winter habitat, distribution, Bluenose caribou herd.

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Rangifer, Special Issue No. 1, 1986: 57 - 63

Introduction

Nine aerial surveys of the winter range of the Bluenose caribou herd were conducted by Renewable Resources Consulting Services Ltd. between 1976 and 1983. Surveys conducted prior to 1982 were designed to describe the density and distribution of caribou on winter range. Surveys in 1982 and 1983 were designed to characterize habitats within winter range in order to predict caribou distribution in relation to petroleum exploration activity. This report presents the results of surveys conducted in January and February 1983, the objectives being:

1) to describe the distribution and density of caribou on winter range and compare these data with past surveys;
2) to describe caribou distribution in relation to vegetation types, elevation, the presence of lakes, snow conditions and wolf numbers.

Study area

The study area covers 63 000 km^2 within the region bounded by the Mackenzie river to the west, the Hare Indian River and Great Bear Lake to the south, and the Anderson river to the north and east (Fig. 1).

The area has a polar continental climate with long, cold winters and short, cool summers. The mean daily temperature for the coldest month (February) is —30°C and mean daily temperature for the warmest month (July) is 11°C (ALUR, 1977). The mean annual preciptation is 27 cm with an annual snowfall of 174 cm measured at Inuvik. Most snowfall occurs during September to December; June, July and August are the wettest months.

Much of the study area consists of rolling or undulating till plain, with numerous lakes and ponds. The major drainage systems in the region include the Anderson and Mackenzie rivers which drain northward into the Arctic Ocean. The area borders on the western extremity of the Precambrian Shield, referred to as the Mackenzie Uplands (Bird and Bird, 1961). Glacial features present in the study area include meltwalter channels, eskers, drumlins, hummocky moraine

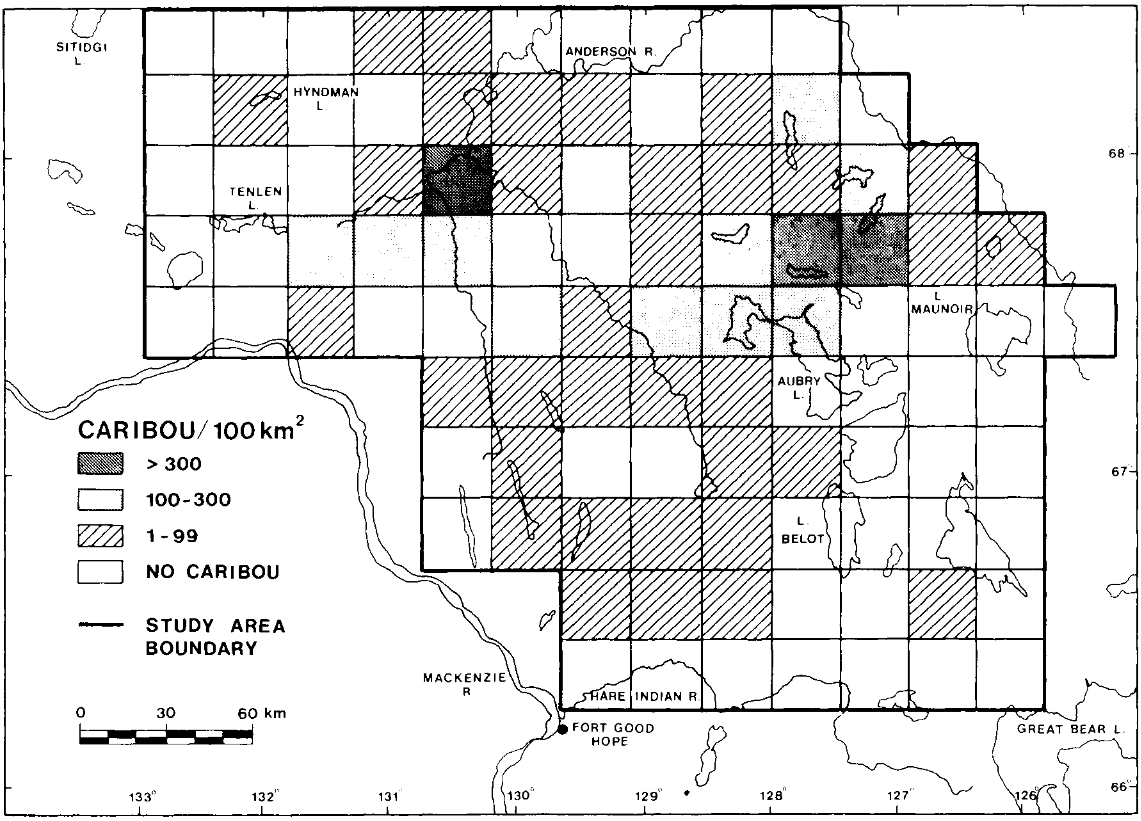

Fig. 1. Locations where caribou occurred in 4 years of 6 years during the mid-winter period (January through March) at different densities, 1976 - 1983.

and alluvial fans and deltas (ALUR, 1977). The most prominent uplands are the hills northeast of Lac Maunoir (maximum elevation = 550 m) and the Colville Hills (maximum elevation = 675 m) in the vicinity of Colville and Aubry lakes.

Three major forest types occur in the study area: upland spruce/feather moss, black spruce/sphagnum and black spruce/lichen (Forest Management Institute, 1974). Forest consisting of white (*Picea glauca*) and black (*Picea mariana*) spruce with abundant mosses and lichens, is the most common forest type (>80%) in the study area. Burns are also common in this type. Bog and forest consisting of black spruce, sedge meadows, willow sedge parklands and numerous shallow lakes and bogs, occurs in a limited area (<20% of study area) immediately north of the Hare Indian River and adjacent to the Mackenzie River (Jacobson, 1979).

Methods

Strip transects (1.0 km wide) spaced at 25 km intervals (4% survey coverage) were flown with a Cessna 185 fixed-wing aircraft during 21 to 28 January, and 22 February to 2 March 1983.

Caribou were classified as to the number of calves (young-of-year) and adults (includes all non-calf animals) whenever possible. Groups not classified as above were designated as predominantly male or female and calves where greater than two-thirds of either sex was classified. During aerial survey of the study area, vegetation type was recorded at 5 km intervals along transects based on military grid lines. During February and March, snow depth and hardness measurements (Ramsonde Penetrometer) were taken at 22 stations in the study area in cooperation with the Northwest Territories Wildlife Service.

The study area was divided into 101 cells, each 25 km square (625 km²) to accommodate transect spacing and to facilitate analysis of caribou distribution and density.

Lake density and area were measured from 1:250 000 scale topographic maps with a circular sample plot of 5 km radius (78.5 km²) centered on the vegetation sample points. The size of lakes within and partially within each plot was estimated based on diameter according to several classes.

Vegetation associations were evaluated using Ivlev's (1961) Electivity Coefficient:

$$E=(r_i - p_i) / (r_i + p_i)$$

Where: E=coefficient of electivity (preference index)

r_i=proportion of the variable used (use)

p_i=proportion of the variable occurring in the study area (availability)

Preference values indicate only the relative value (i.e., ranking) of a habitat component in comparison to others (Johnson, 1980).

Results

Caribou distribution and density
January — February 1983

Caribou occurred throughout most (57%) of the study area during the mid-winter period (January — February) in 1983. High (>300 caribou/100 km^2) density cells were present over 8% of the area in the northwest and northeast. Densities greater than 100 caribou/km^2 occurred over less than 22% of the area in January and less than 20% in February. Caribou were absent over 43% of the study area. The distribution in 1983 was similar to that reported over a 6 year period.

In January, high densities of caribou were found in the Aubry-Tedji lakes area and northeast of Tenlen Lake. In February, high densities were found from Aubry/Niwelin lakes northeast to the Anderson River, and near Tenlen Lake. Generally, the distribution was similar during January and February except that more caribou occupied the northeastern portion of the study area in February.

Males and females were segregated on the range with most male groups occupying the southwestern half and females the northeastern half of the area. Female groups were three times larger ($\bar{x}$=20.6, n=224) than male groups ($\bar{x}$=7.2, n=207, Z=5.1, $P<0.05$) and contributed most to high caribou density areas. Males were much more dispersed than females and rarely occurred at densities exceeding 100 caribou/100 km^2.

Between late January and early March female caribou groups moved eastward while male groups exhibited no discernible direction of movement. Females were concentrated in an area surrounding Tedji Lake in February, whereas males were dispersed over the area between Travaillant Lake and Lac Belot. Subsequent movement by females in mid-March was north to the area between Simpson Lake and the Anderson River (Williams, pers. comm.).

Table 1. Caribou numbers and density for mid-winter aerial surveys within the study area, 1976 — 1983.

	Survey date								
	1983		1982		1981		1980	1977	1976
Observation	Feb.	Jan.	Feb.[1]	Jan.[1]	Feb.[2]	Jan.[3]	Mar.[2]	Feb./ Mar.[4]	Feb.[5]
Total caribou	4047	5269	3179	2989	2060	3107	6945	4079	845
Caribou on transect	1745	2191	2235	2708	1966	1361	3759	2875	
Caribou/ 100 km^2	94.55	118.6	94	120	86	85	90	90	88
Survey area (km^2)	46 175	46 175	60 000	56 500	57 000	40 000	67 000	80 000	64 000
Percent sample	4	4	4	4	4	4	6.25	4	4

[1] Carruthers and Sopuck (1982)

[2] Carruthers and Jakimchuk (1981).

[3] Carruthers (1981).

[4] Wooley and Mair (1977).

[5] Data for survey by Hawley, in Decker (1976); all caribou assumed to be on transect.

Winter 1976 — 1983

Data from nine aerial surveys in six winters (January — March) were used to analyze caribou distribution in the study area (Table 1). High densities (>300 caribou/100 km^2) of caribou consistently used the northern half of the study area (Fig. 1). Between January and March there was a decrease in the dispersion of different density classes and a shift to the north and east.

Caribou distribution in relation to winter range physiography

Vegetation type

The distribution of caribou in relation to the availability of six vegetation types appears in Table 2. Caribou used lakes and rivers four times more frequently than their occurrence. Open conifer was used in proportion to its occurrence and all other types were used less than their occurrence.

No significant relationship was found between group size and vegetation type (F=0.503, df=678, P>0.05). Group size on lakes ($\bar{x}$=15.6, n=368) was the same as off lakes ($\bar{x}$=12.0, n=310, t=—1.36, P>0.05). However, group composition (age and sex) varied significantly with vegetation type (x^2=15.2, P<0.05). Male groups used open conifer forest more than female-calf groups which used open areas (lakes, fens, bogs) more than did males.

Table 2. The availability of six vegetation types and their use by caribou ranked by a preference index (+1.0=most preferred; —1.0=least preferred).

Vegetation	Availability		Caribou groups[1]		
Type	No.	%	No,	%	Preference
Lake/River	59	14.5	368	54.4	+0.5791
Open conifer	226	55.5	254	37.4	—0.1948
Herbaceous	66	16.2	40	5.9	—0.4685
Closed conifer	15	3.7	11	1.6	—0.3962
Burned forest	38	9.4	4	0.6	—0.8800
Shrub	3	0.7	1	0.1	—0.7500
Total	407	100.0	678	100.0	

[1] Group chi-square = 895.0, df = 5, p<0.001

Elevation

Elevation was considered to be an important physiographic feature influencing caribou distribution. Caribou were found at a mean elevation of 250 m above sea level (asl) which was the average for the study area (t=0.08, n=678 318; P>0.05) (Fig. 2). Differences related to sex of groups (t=2.26, n=207 224; P<0.05) and survey data (t=2.98, n=377 301; P<0.05), although statistically significant, were small (<12 m) and probably not biologically significant.

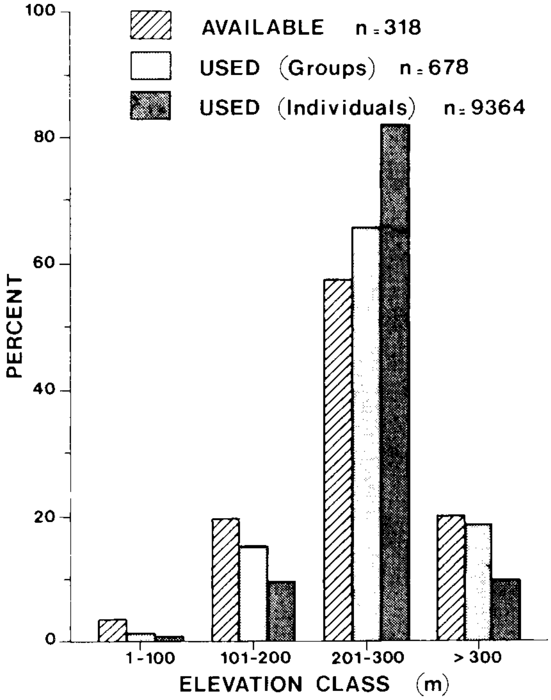

Fig. 2. The distribution of elevation classes and their use by caribou, January - February 1983.

Lakes

Open areas represented by lakes, rivers, fens and bogs were the most preferred of six vegetation types deemed available. To clarify this observation we examined the size and location of lakes in the study area.

Caribou preferred lakes less than 1.0 km^2 in area (Fig. 3). They selected locations with a large number of small lakes ($\bar{x}$=0.53 lakes/km^2, n=678) compared to lake density generally available ($\bar{x}$=0.41 lakes/km^2, n=318, t=7.55, P<0.05). Large lakes were not used by caribou as frequently as areas with high densities of small lakes. Preferred locations contained many small lakes which comprised a total area of 2 - 30 percent of the landscape.

These patterns of selection were evident for all caribou groups but there were differences related to the sex of groups. Female-calf groups were observed on lakes more often (54.3%, n=204) than male groups (45.7%, n=172) ($x^2=4.07$, df=1, $P<0.05$) and female groups were observed in areas of higher lake density ($\bar{x}=0.57$ lakes/km^2, n=343) more than males ($\bar{x}=0.49$ lakes/km^2, n=329, t=—4.94, $P<0.05$).

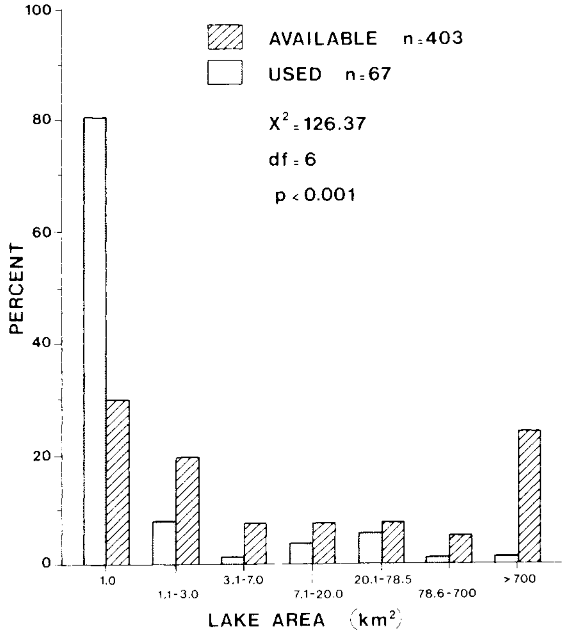

Fig. 3. Use of different sizes of lakes by caribou groups, January - February 1983.

Snow Depth

In 1982, snow depth and hardness were measured at 64 stations throughout the study area. Mean snow depth was highest in forest >300 m asl (68.4 cm) and lowest in forest <300 m asl (62.2 cm). Snow depth in areas of high caribou density (>300 caribou/100 km^2) averaged 62.2 cm. Snow was of similar hardness at low elevations but significantly harder at elevations >300 m asl.

Wolves

Wolves were found in areas with high densities of caribou. Caribou density in cells containing wolves ($\bar{x}=167$ caribou/100 km^2, n=23) was significantly higher than in cells without wolves ($\bar{x}=73$, S.E.=12, n=188, t=2.05, $P<0.05$). This relationship was stronger for female-calf groups where their density in cells with wolves was much higher ($\bar{x}=19$ groups/100 km^2, n=23) than in cells without wolves ($\bar{x}=4$ groups/100 km^2, n=233, t=2.49, $P<0.05$). Wolves were observed only in the northern half of the study area.

Discussion

The distribution of caribou observed in January and February 1983 was consistent with the pattern recorded over the previous 5 years (Wooley and Mair, 1977; Carruthers and Jakimchuk, 1981; Carruthers and Sopuck, 1982). The consistent use and size of winter range and similar densities since 1976 corroborate census results that suggest the Bluenose herd has been relatively stable in numbers in recent times and suggests a strong affinity for particular habitat types.

Caribou were segregated on the winter range by sex which typifies most seasonal distributions and reflects differing adaptive strategies of males and females (Jakimchuk and Ferguson, unpublished data). Cows and calves were found in forested areas with high snow depths and high densities of small lakes whereas males occupied forested areas with often lower snow depths and fewer small lakes.

Burned forest was one of the least preferred vegetation types available to caribou. In 1983, 0.2% of caribou were found in burned forest, and a maximum of 3.3% (0.0 — 3.3%) was observed in the previous winters. Results from all winters showed that about 90% of all caribou were located in unburned areas below 300 m asl.

Snow depths and hardness were greater at high elevations than elsewhere and we believe that these conditions inhibit the use of such areas by caribou (Carruthers and Sopuck, 1982). Under normal or above-normal snow conditions in mid- and late-winter, caribou avoid high elevations. However, in the absence of a sufficient snow stimulus, such as in January 1981, and in the fall and early winter, caribou were dispersed through otherwise unfavourable mid-winter habitats. This pattern was reflected by the greater dispersion of caribou and wolves in January 1981 (Carruthers and Jakimchuk, 1981).

The selection of open habitat (lakes, fens and bogs) by caribou in mid-winter has been previously noted by Miller (1974, 1975, 1976) and Pruitt (1959). The use of small lakes allows caribou to visually locate wolves and provides a sufficiently large, shallow, often wind-packed snow surface for escape by running (Nasimovich, 1955; Pulliainen, 1965).

Wolves can visually check large lakes for caribou rather quickly, whereas in areas of large densities of small lakes it takes longer for wolves to locate caribou since they have to check each lake individually. Also, individual caribou, fleeing across a large lake can be readily followed by wolves whereas caribou running from lake to nearby lake may make it more difficult for wolves to locate and follow individual animals.

The proximity of other lakes and open areas allows shorter movements in deep snow and efficient exploitation of the more extensive feeding sites on lake margins, adjacent forest and in bogs and fens (Riewe, 1979). These characteristics allow caribou to forage and escape predators even in the presence of deep snows. As snow depths increase through the winter, caribou, especially cows with calves, move into areas with these characteristics and away from areas which lack preferred habitats.

Bluenose caribou used their forested winter range in a consistent manner during winters of normal snow conditions. The pattern of use was consistent over 6 years and reflects the efficient response of caribou to snow conditions that gradually reduce forage and predator avoidance options though the winter. Caribou associate with habitat features that are most imortant to their survival.

Acknowledgements

The 1981 to 1983 aerial surveys were funded by Petro-Canada Ltd. We appreciate the assistance and support of Dr. Wayne Speller of Petro-Canada. Jim Perreault of Fort Good Hope assisted with the 1983 field survey. George Collin of Petro-Canada reviewed the report. The 1980 and February 1981 aerial surveys were funded by the Polar Gas Project of Toronto. M. Tate typed the manuscript and I. Szabo drafted the figures.

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Caribou of the Central Arctic Region of Alaska in relation to adjacent caribou herds

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Abstract: There was an unusual increase in numbers of caribou *(Rangifer tarandus granti)* in the Central Arctic region of Alaska from 1981 to 1985. In fall and winter numbers were up to five times greater than at the onset of calving in June. Numbers appeared to double during the month of June each year, then remain relatively stable over the summer period with a further increase in the fall. Ingress of caribou from outside the region in fall was observed in all years and egress in the early spring is postulated. We conclude that a small resident herd inhabits the region year round with numbers increasing through ingress of caribou from the Western Arctic herd possibly beginning as early as June. Increases or decreases in the size of adjacent herds probably will affect the numbers of caribou occupying the Central Arctic region.

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Rangifer, Special Issue No. 1, 1986: 65 - 71

Introduction

In 1976, Cameron and Whitten (1979) identified caribou in the Central Arctic region of Alaska between the Colville and Canning rivers as the Central Arctic caribou herd (Fig. 1). Since then caribou numbers in the region have increased at a rate of 12 to 20% per year to 13 000 in 1983 (Whitten and Cameron, 1983; Smith, 1985). The current view that these caribou represent a «distinct unit» is based on the concept of fidelity to a calving ground and synchronous, uniform movements (Cameron and Whitten, 1979:630).

Prior to 1976, caribou in the region were sometimes described as a herd although specific calving grounds were not described (Child, 1973; Roseneau *et al.*, 1974; Gavin, 1979). Skoog (1968:356) concluded that Central Arctic caribou made up a «remnant» herd occurring outside «centers of habitation» of the Porcupine and Western Arctic herds (Fig. 2).

During the course of monitoring caribou in the Central Arctic region from 1981 through 1985, we noted changes in numbers and movements which suggested an overlapping of range with the adjacent Western Arctic herd. Our observations are consistent with the views of Skoog (1968) and raise questions concerning range relationships of caribou in the region. We discuss the results in relation to the current concept of a caribou herd and implications to research and management of caribou in the region. The objective of this paper is to provide more data on the changing numbers of caribou in the Central Arctic Region of Alaska and to show that more than one herd occurs in the region.

Study area

The study area, located in north-central Alaska, covers 46 000 km^2 (Fig. 1). The area is treeless and ranges in elevation from 0 to 1500 m above sea level. The physiography of the area was described by Roby (1978).

Methods

The area was sampled by aerial survey at 10% coverage with 20 to 30% coverage along a coastal strip 100 km wide during Mid-June. Most caribou in the area are within this 100 km zone between late May and July. Standard strip

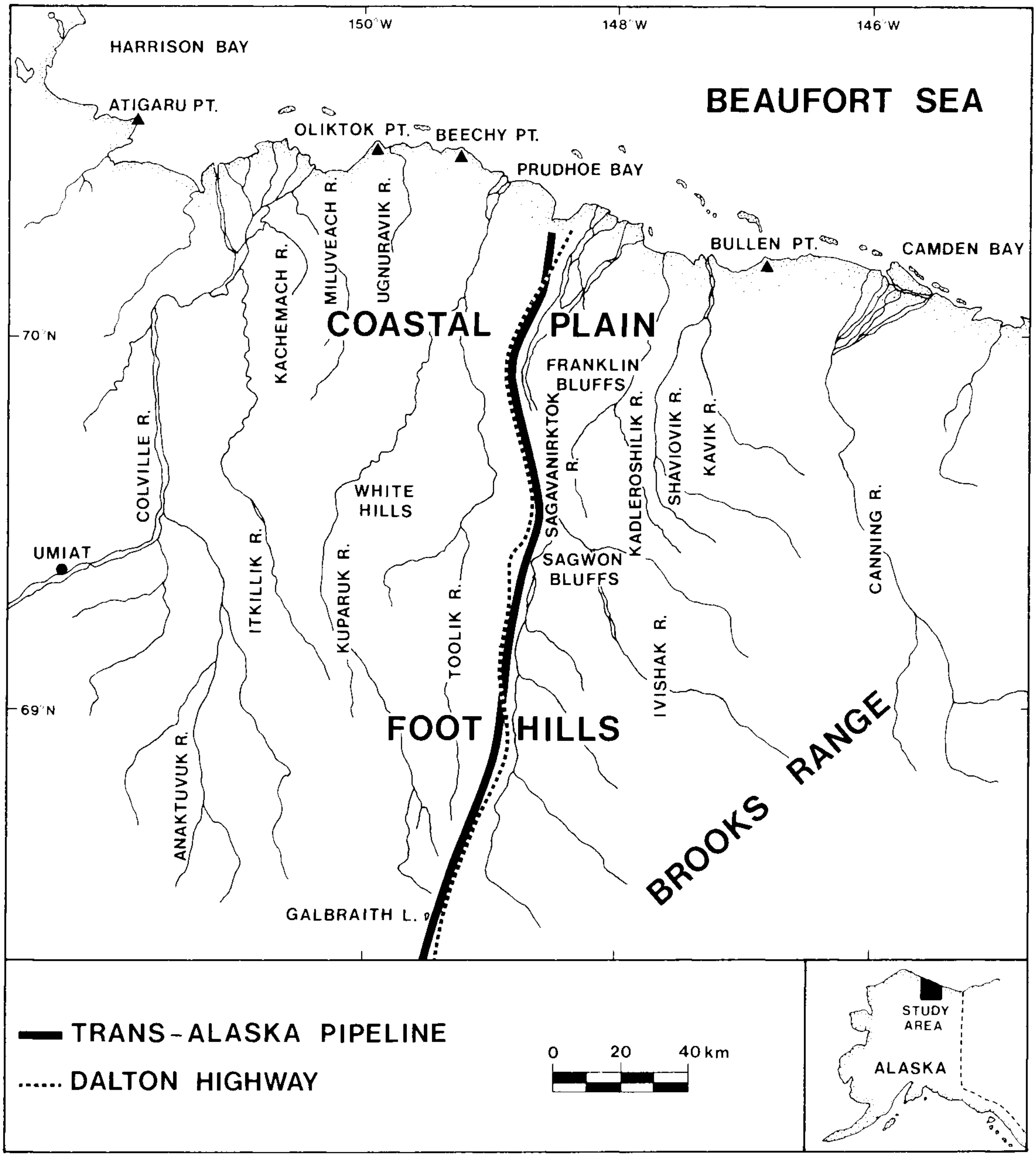

Fig. 1. The Central Arctic region and study area bounded by the Colville and Canning rivers.

transects (Caughley, 1977; Eberhardt, 1981) oriented north to south were systematically located and consistently sampled from May to March. Helio Courier and Cessna fixed-wing aircraft were flown at 120 m agl at 160 kmph. Two experienced observers were used in all surveys with the pilot as navigator.

The numbers of caribou were derived as a raw ratio estimate using 10% survey coverage (Jolly, 1969), with the variance estimated according to the formula of Miller *et al.* (1977). All estimates were corrected for visibility bias by multiplying by 1.25 based on convention and recent work by Heard (1985). However, this correction assumes equal bias over all survey periods. We believe that visibility bias can be higher during late May surveys because of snow melt conditions which varied considerably over the 4 years and because new born calves are not easily seen. Bias was not measured during any survey but estimates of

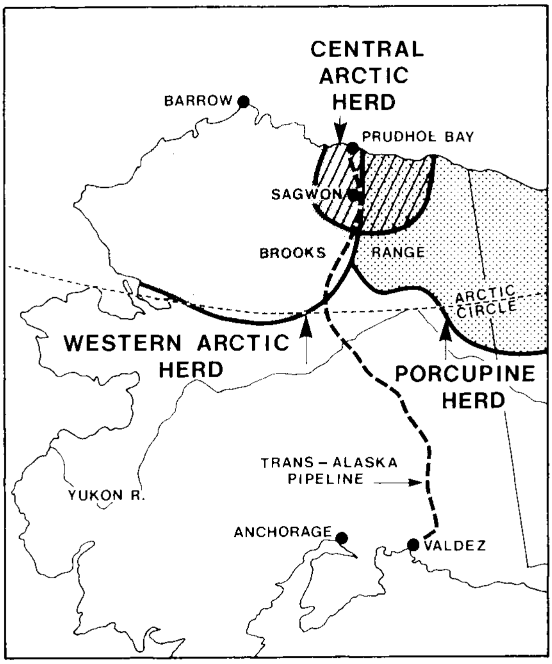

Fig. 2. General ranges of the Central Arctic, Western Arctic and Porcupine caribou herds in Alaska (Western Arctic and Porcupine ranges after Hemming, 1971).

numbers during June were similar to those reported by Whitten and Cameron (1983) and Smith (1985).

Average annual rate of increase (r) was measured by regressing log e of population size on time (Caughley and Birch, 1971).

Results

Estimates of numbers of caribou in the study area were made for 26 surveys conducted between June 1981 and June 1985 (Table 1). The average annual rate of increase (r) was variable depending on the time of year the data were collected. The highest estimate of r was obtained for late winter (r = 0.56) and rut periods (r = 0.52), and the lowest in the spring (late May) (r = 0.04). During the post-calving period in mid-July (r = 0.20) caribou were highly aggregated and estimates are qualified by high variances. Our best estimate of numbers based on the lowest variance (CV = 0.18) was during the calving period in mid-June. Numbers increased at r = 0.31 from 1981 to 1985 based on the calving period estimates. These observations suggest an ingress of caribou during the pre-rut in 1982 and during the rut in most years. Egress appears to occur during the early spring.

There were three times the number of caribou in the study area in fall and late-winter compared with May and June. By May the numbers declined to less than 25% of the March estimate. However, 3 weeks later, in Mid-June, the numbers more than doubled in size. In 1985 we sampled the study area at 10% coverage twice from 30 May to 17 June. The estimated number of caribou in the study area almost tripled during this period from an estimated 6400 (SE = 1000) to 17 000 (SE = 2900). From 1982 to 1984 a further 3 to 4-fold increase in numbers occurred between calving and the rut. The greatest

Table 1. Estimate of Caribou numbers in the study area based on 10% survey coverage.

Life cycle phase	Estimate of numbers ± SE[1]										Average annual rate of increase
	1981		1982		1983		1984		1985		
Late winter	—		5300	1200	16600	3900	—		33000	8300	0.56
Spring	—		3900	1300	5600	1300	1900	500	6400	1000	0.04
Calving	4700	700	6600	1100	9400	1700	10900	1800	17000	2900	0.31
Post-calving	6400	2600	10000	4300	3700	2000	30200	12400	—		0.20
August dispersal	7700	3100	6200	1700	11400	5000	—		—		0.20
Pre-rut	5000	1300	13500	2500	9400	4600	—		—		0.32
Rut	6300	1400	27300	5000	29000	7200	35700	10100	—		0.52

[1] Rounded to the nearest 100.

Table 2. Ratio of adult males: 100 females in various seasons from 1981 to 1985.

Year	Late winter	Spring	Calving	Post calving	August dispersal	Pre-rut	Rut
1981	—[1]	—	32.5	117.9	23.3	52.2	175.4
			(1350)[2]	(427)	(502)	(280)	(168)
1982	22.8	21.7	47.8	42.9	67.7	76.8	61.2
	(124)	(146)	(683)	(140)	(317)	(442)	(574)
1983	36.2	23.7	32.4	40.4	35.4	39.5	54.8
	(531)	(245)	(886)	(1414)	(562)	(413)	(1184)
1984	—	55.9	55.5	118.5	—	—	71.4
		(212)	(1454)	(118)			(744)
1985	129.4	195.3	108.4	—	—	—	—
	(1670)	(685)	(1384)				

[1] Dash indicates no sample.

[2] Number of adults classified.

increase occurred in the fall while numbers were relatively stable during the summer.

The ratio of adult males to adult females was highly variable both within and between years (Table 2). No consistent changes in sex ratios were observed during periods of ingress/egress. Although seasonal biases in classification are possible, consistent methodologies were employed on all surveys.

The increase in numbers in the fall resulted from an ingress of caribou from the west. In all years in September or October we observed large numbers of caribou (2500 — 15 000) moving into the region from the northwest up the Itkillik River Valley and in the Anaktuvuk River area. In the fall and late winter of 1985, a relatively high proportion of these animals were males (Table 2). The apparent increase in numbers (from late May to July) occurred in all years but no obvious movement of caribou from outside the study area was detected.

Discussion

Our observations of caribou in the study area and review of recent and historical data strongly support the view of Skoog (1968) concerning the origin of caribou in the area. There appears to be a small number of resident caribou (6400 in 1985) that remain in the study area throughout the year. During the calving period, caribou from outside the study area move into the area to calve along with caribou resident year round in the study area. By fall there is a larger ingress of caribou that overwinter in the area. We suspect that most of these animals move to the west and northwest in the spring leaving behind a resident herd that calves along the coastal zone each spring.

This resident herd is analogous to the Central Brooks Range herd described by Skoog (1968) as a relict of previous population highs in the adjacent Western Arctic and Porcupine caribou herds. This view is corroborated by observations made by Child (1973), Gavin (1979) and Roseneau *et al.* (1974). During the early 1970s when the adjacent Western Arctic and Porcupine herds were large (Davis *et al.*, 1980; Bergerud *et al.*,1984), Child (1973) described a small, distinct resident «Central herd» of about 3000 animals in the region with periodic large influxes of caribou from other herds during the summer and fall (White *et al.*, 1975). Roseneau *et al.* (1974) described a similar situation referring to a remnant «Central Arctic herd».

Coincident with the decline of the Western Arctic herd during the early 1970's (Davis *et al.*, 1980) the number of caribou in the study area also declined at the same rate (see Gavin, 1979). Ingress and egress in the east and west during the fall and spring, respectively, ceased during this period. In 1975, Whitten and Cameron (1983) estimated only 5000 caribou in the study area and designated them the Central Arctic herd (Cameron and Whitten, 1979).

Since 1975 the Central Arctic herd has increased at a rate of 13 to 20% per year (Whitten and Cameron, 1983; Smith, 1985). The Western Arctic herd has increased since 1976 an average of 11 — 14% annually (Davis *et al.*, 1980;

Anderson and James, 1984) and the Porcupine herd at 10 — 12% since 1981 (Whitten, 1984). In fall 1976, 1200 Western Arctic caribou were observed in the Central Arctic region (Whitten, in Roby, 1978) but subsequently, fall movements of the Western Arctic herd into the area were not documented until 1981 and have accelerated since then (this study; Valkenburg *et al.*, 1983).

Caribou that moved into the area in the fall probably wintered in the region in 1983 and 1985 and perhaps in other years. Historically, when caribou numbers north of the Brooks Range were high, caribou have wintered in the region (Skoog, 1968; Roseneau *et al.*, 1974; Valkenburg *et al.*, 1983). Olson (1959) reported 150 000 caribou wintering in the Central Arctic in 1958.

Caribou presumably moved out of the area between late winter and spring. Roseneau *et al.* (1974), Skoog (1968), Gavin (1979) and Valkenburg *et al.* (1983) reported movements to the west and east by caribou that wintered in the foothills of the study area. These movements occurred in late April and May and involved much larger numbers of caribou than those moving north at that time. Surveys during this period are required to confirm these movements.

The apparent increasing male: female ratio from calving to the rut suggests a movement of male caribou into the study area during the summer and an exodus during the spring consistent with changes in overall numbers. Previous researchers speculated that an ingress of males occurred in the study area during summer (Gavin, 1979; Whitten and Cameron, 1983). This observation is common for other caribou herds where males move slowly from winter to summer ranges along similar but broader routes than those used by migrating females (Kelsall, 1968; Parker, 1972).

The definition of a caribou herd centers on seasonal range use and association with specific calving grounds (Skoog, 1968; Thomas, 1967). The Central Arctic herd was described on this basis (Cameron and Whitten, 1979). However, the mobility of caribou confounds herd identification. If we measured the size of the herd at the onset of calving we would derive an estimate quite different from that obtained a week or two later. The most recent estimate of 13 000 in 1983 was based on a photo census in late July (Smith, 1985). This estimate is consistent with previous estimates and extrapolations (Whitten and Cameron, 1983) but probably includes a substantial number of caribou that originated from outside the study area.

The overall range of caribou censused in July 1983 is quite different than previously reported (Cameron and Whitten, 1979). When we extended our surveys west of the Colville River and east of the Canning River we continued to encounter calving caribou, indicating a continuum of calving beyond the boundaries previously established for the herd. The numbers of caribou within the artificially established boundaries include those from other «herds» for at least 10 months of the year. The numbers within the study area are variable throughout the year but can reach a total in late fall and winter which is up to five times that of late May and calving populations. These differences have a bearing on virtually all aspects of understanding the ecology of caribou within the region. For example, there are significant considerations in such diverse areas as range use studies, disturbance studies, harvest allocations and in interpretations of herd demography.

Large changes in the size of some herds (e.g., Kaminuriak, George River, Bathurst, Beverly), the discovery of «new» herds (e.g., Lorillard, Wager Bay, Melville, Teshekpuk, Central Arctic) and the extinction of others (e.g., Dolphin and Union, Arctic Islands) demonstrates the importance of understanding the mobility of caribou (Bergerud, 1980). «Unusual» movements of caribou (e.g., Fortymile, Bluenose, Nelehina, Western Arctic) have significance to the animals and we should strive to incorporate their meaning into our understanding of caribou biology. What might be considered to be an aberrant or unusual distribution or movement may reflect events which have significant adaptive value. These may involve re-occupation of unused or predator free ranges or may reflect population size, characteristics and trends.

The Central Arctic herd appears to be manifesting itself once again according to the incomplete scenario constructed by Skoog (1968) almost 20 years ago. In 1984, Bergerud *et al.* (1984) reiterated that change within the study area was imminent. Based on Skoog's hypothesis (1968), there could be many more caribou occupying the study area if the adjacent Western Arctic and Porcupine herds continue to increase and expand their ranges into the Central Arctic Region. Alternatively, a decline in numbers might be associated with a major range shift or decline in the numbers of adjacent herds. We must be prepared to recognize and document the occurrence of these events if and when they occur.

We believe that researchers and managers should acknowledge the variable status of caribou in the Central Arctic region which are currently considered to be a distinct herd (Cameron and Whitten, 1979). If this variability is ignored, interpretation of research conducted in the region may be in serious error. The dynamic nature of the population must also be considered in management decisions affecting caribou found in the Central Arctic region.

Acknowledgements

Alyeska Pipeline Service Company sponsored most of this study with additional sponsorship provided by ARCO Alaska, Inc., Exxon Company, U.S.A., Chevron U.S.A. Inc., Sohio Alaska Petroleum Company, Conoco Inc. and Amerada Hess Pipeline Corporation. P. Bente, D. Masiak, D. Volsen, D. Vernam, C. Linkswiler and S. Ferguson assisted with data collection and analysis. S. Ferguson, D. Thomas and L. Sopuck reviewed the manuscript.

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Evaluation of a satellite telemetry system for monitoring movements of caribou

James A. Curatolo[1]

Abstract: A cow caribou from the Central Arctic Herd was collared with a satellite-monitored radio transmitter in the Kuparuk Oilfield, Alaska, in 1984. From 19 June to 17 August, the radio transmitted 18 hours per day. A total of 346 locations were recorded, for a mean of 5.8 locations per day or one location every 3.1 hours of transmission time. The location of 13 direct observations of the radio-collared cow averaged less than 1 km from the nearest satellite-fixed location. The satellite-fixed locations of the radio-collared cow provided detailed data on movement patterns during the three seasons studied. The cow traveled an average of 8 km day^{-1}, 23 km^{-1}, and 14 km day^{-1} during the post-calving season, mosquito season, and oestrid fly season, respectively.

Key words: caribou, telemtry, satellite, movements, petroleum development.

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Rangifer, Special Issue No. 1, 1986: 73 - 79

Introduction

Conventional radio telemetry, in which radio-collared animals are tracked from the ground or from aircraft, is an effective, widely used technique for monitoring animal movements. In recent years, advances have been made in the use of satellites for receiving transmissions from radio-collars (Gandy, 1982; Kolz *et al.*, 1982). Satellite-based receivers offer several advantages over aircraft- or ground based receivers: animals can be tracked in all weather conditions, the cost per location may be lower, the risks to personnel are greatly reduced and additional information can be gathered from auxiliary sensors. The last two considerations are important when comparing satellite telemetry to aircraft telemetry in remote areas. The major disadvantages of satellite telemetry are that the precision and accuracy of the locations can vary, transmissions can only be monitored when a satellite is passing overhead, and the availability of transmitters and satellites is limited.

Satellite telemetry is based on the Doppler effect; as the satellite passes overhead, changes in radio-wave frequency are measured and used to calculate the location of the transmitter. The accuracy of this technique depends on oscillator stability, which is affected by temperature. The transmitter will not function below —40°C. Calculation of locations assumes that elevation of the transmitter is constant. Location accuracy declines as the difference between the actual and assumed elevations increases.

The only satellite system available to the private sector for location information is the TIROS-N Series satellites, using the ARGOS (Centre National d'Etudes Spatiales, France) Data Collection System. Two satellites were in operation during this study; plans call for the use of two satellites until at least 1990 (ARGOS Bulletin, October 1984).

Telonics, Inc. (Mesa, Arizona) recently developed a satellite-compatible transmitter suitable for use on caribou (Pank *et al.*, 1985). The availability of that transmitter provided the impetus to pursue a study of caribou movements using satellite telemetry.

This study was intiated to determine the effectiveness of satellite telemetry for monitoring the late-spring and summer movements of a caribou in the Central Arctic Herd (CAH) of Alaska. Two specific objectives were addressed:

1) to determine the daily movement patterns of a caribou, and
2) to determine the reliability and accuracy of satellite-fixed locations of the radio-collared caribou.

Study area

The study area was bounded by the Colville River on the west and the Kuparuk River on the east, and extended inland approximately 32 km. This area encompasses the Kuparuk Oilfield and the western portion of the Prudhoe Bay Oilfield. Detailed informatin on physiography, climate, and vegetation is prestented by Walker *et al.* (1980).

Methods

Field work began on 19 June 1984, when biologists from the Alaska Department of Fish and Game and Alaska Biological Research placed a collar with conventional and satellite transmitters on a cow caribou near Milne Point. The cow was accompanied by a calf.

The frequency of the satellite transmitter was 401.650 MHz (UHF). The transmitter duty-cycle was 18 h day^{-1}, from 0400 to 2200 Alaska Daylight Savings Time; this transmission schedule corresponded to the maximal number of overpasses by the satellite. A pulse of data was transmitted to the satellite once each minute. These data were relayed to a ground station and then transferred to the ARGOS Service Center (Toulouse, France) for decoding and compilation. Monthly computer print-outs were mailed from the ARGOS Service Center to our office. Data could also be transferred daily between ARGOS and our computer via a telephone modem.

The data received included the date, time, and latitude and longitude (to the nearest thousandth of a degree) of each location, the temperature of the collar, and an activity count. The distanee traveled by the cow was determined by measuring the straight-line distance between consecutive locations. The collar temperature and activity count did not correlate with ambient air temperature and behavior, respectively (Pank *et al.*, 1985), and are not discussed in this paper.

The standard beacon transmitter was used to locate the caribou through standard radio-telemetry techniques. The caribou was located periodically from a Piper PA-18 "Super Cub" aircraft to obtain accurate locations for comparison with satellite fixes.

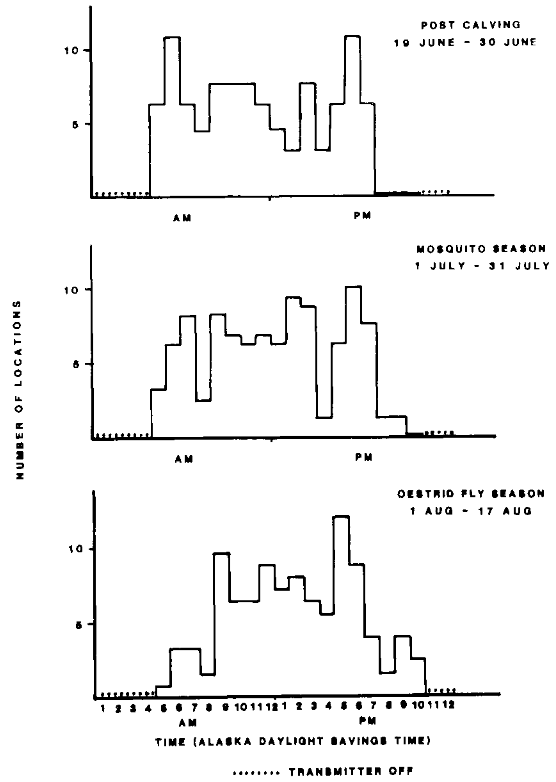

Fig. 1. Diurnal distribution of satellite-fixed locations of a cow caribou in the Central Arctic Herd, Alaska, 1984.

Prior to being placed on the caribou, the radio-collar was placed at several sites in the Kuparuk Oilfield between 21 and 26 May to compare the satellite-fixed locations with known locations. Locations of the radio-collar and the caribou were determined from 1:63 360-scale U. S. Geological Survey topographic maps.

Results and discussion

Life of the satellite transmitter

The satellite transmitter functioned from 19 June to 17 August 1984 for a total of 1080 h, 80 h (8%) longer than expected. The next generation of transmitters, built in 1985, are expected to last 20% longer due to stronger batteries and reduced electrical drain from the transmitter (D. Beaty, pers. comm.).

Number of locations

A total of 346 locations were recorded, for a mean of 5.8 (SD=2.5) locations per day, or one location every 3.1 h of transmission time (Table 1). Additional locations would probably have been recorded if the NOAA-8 satellite had not stopped working in late June, leaving only one satellite for the remainder of the project. The diurnal distribution of locations fixed was consistently low during certain periods (Fig. 1). Few locations were collected during 0400 - 0500 and 1900 - 2200 because few satellite passes occurred during those periods and because some satellite orbits made reception difficult (e.g., low angle of elevation during the pass). During 0700 - 0800 and 1500 - 1600, few locations were collected due to the pattern of satellite passes, which created a gap in coverage. These results indicate that radio transmissions should be timed to coincide with periods when satellite passes are most frequent (based on satellite orbit predictions), to maximize the number of locations fixed. Three hours of continuous transmission should be adequate to fix one location on a regular basis.

Accuracy of locations

Two procedures were used to determine the accuracy of the locations fixed by the satellite. First, the radio-collar was placed at five sites in the study area during late May. Thirteen satellite fixes were obtained for those five sites. The mean difference between the satellite-fixed locations and the known locations was 1.0 km (SD=0.74). Second, 13 locations of the radio-collared cow were obtained from direct sightings during aerial and ground surveys in July. During those surveys, we were unable to locate the cow at precisely the same moment that the satellite did. The sighting locations averaged less than 1 km from the nearest satellite-fixed locations.

The differences between known and fixed locations indicate that the accuracy of locations obtained by satellite should be satisfactory for the purposes of many studies. Indeed, even locations plotted from direct observations contain some error, depending on the type of map used and the ability of the observer to record an accurate location.

Movements patterns

The movement patterns of the radio-collared cow differed among the post-calving, mosquito, and oestrid fly seasons (Fig. 2, 3 and 4). During most of the post-calving period the cow remained between the Oliktok Point and Milne

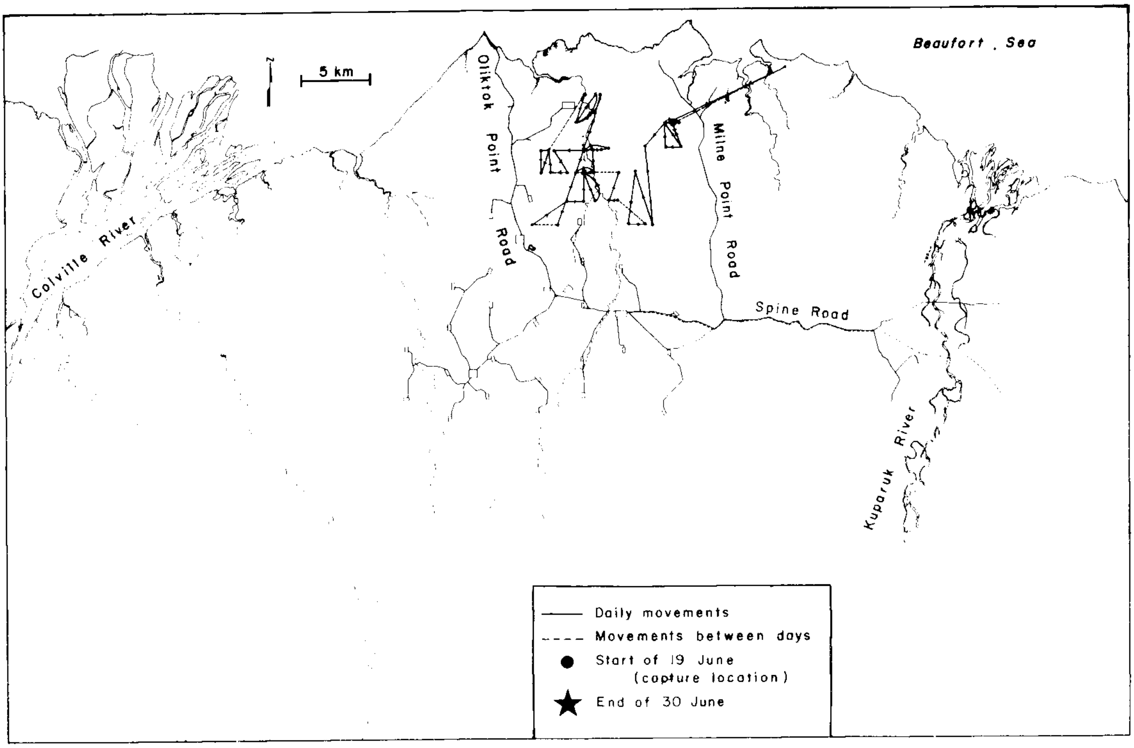

Fig. 2. Movements of a satellite-radio-collared cow in the Central Arctic Herd, Alaska, during the post-calving period, 19-30 June 1984.

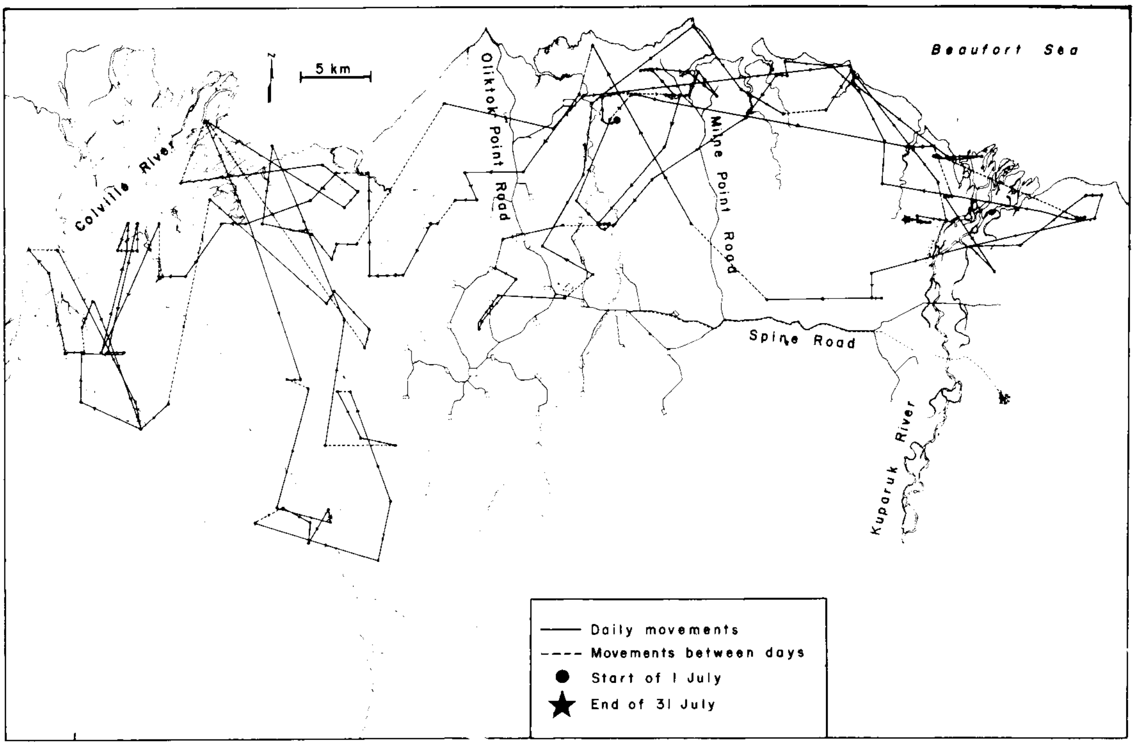

Fig. 3. Movements of a satellite-radio-collared cow in the Central Arctic Herd, Alaska, during the mosquito season, 1-31 Juli 1984.

Point roads, moving an average of 8 km day^{-1} (Table 1). The cow remained within an area that had a relatively high density of caribou during the calving season (Cameron *et al.*, 1983).

The cow crossed the Milne Point Road at least twice, but tended to be located at least 1.6 km from any road during this period (Fig. 2). Cows may be more wary when their calves are very young (Lent, 1966), which may account for this distribution. In the future it may be possible to determine if structures such as pipelines and roads are being avoided by caribou by using relatively few satellite-radio-collared animals, because of the high number of locations fixed.

The movement pattern of the cow changed considerably after the emergence of mosquitoes (Fig. 3). During mosquito season the cow traveled a mean distance of 22.5 km day^{-1}, moving as far west as the Colville River and at least 10 km east of the Kuparuk River, and crossing the Milne Point and Oliktok Point roads a minimum of six and four times, respectively.

The movements of this cow generally fit within the entire summer range used by caribou in the Kuparuk Oilfield in 1983. (Lawhead and Curatolo, 1984), and illustrate three important characteristics of CAH movements during mosquito season. First, mosquito-harassed caribou travel into the wind until they reach mosquito-relief habitat at or near the coast (White *et al.*, 1975); river deltas are favored as relief habitat (Cameron, 1983; Lawhead and Curatolo, 1984). Because the prevailing summer winds in the study area are from the ENE (Walker *et al.*, 1980), caribou in the Kuparuk Oilfield often use the Kuparuk River delta during the mosquito season (Lawhead and Curatolo, 1984). In 1984, however, the frequency of westerly winds was abnormally high (Lawhead, 1984), causing caribou to seek relief from mosquito harassment in the vicinity of the Colville River delta. This occurrence accounts for the number of locations near the Colville River (Fig. 3). Second, in response to severe mosquito harassment, CAH caribou usually travel east or west near the coastline (depending on wind velocity and direction), which is cooler and windier than inland areas; the movements of the collared cow reflect this tendency. Third, as mosquito harassment subsides during cool, windy weather, CAH caribou move inland (White *et al.*, 1975; Curatolo and Murphy, 1983); the collared cow moved relatively far inland (Fig. 3) only during prolonged periods of cool weather.

During oestrid fly season, the radio-collared cow left the areas of the coastal plain used during mosquito season and moved inland (Fig. 4). The mean minimum distance traveled per day decreased to 14.5 km during this period (Table 1), probably due to the long periods of standing typically engaged in by caribou during oestrid fly season (Espmark, 1968). The cow was found near the Spine Road-Kuparuk Pipeline corridor in three separate areas (Fig. 4). This association may have resulted from oestrid fly harassment, because CAH caribou sometimes select roads and pipelines as fly-relief habitat (Curatolo and Murphy, 1983). The collared cow was observed standing under a pipeline on 1 August (S. Murphy, pers. comm.).

Conclusions

The satellite transmitter used in this study worked well under summer field conditions and allowed intensive monitoring of the movements of a cow caribou in the CAH. The caribou was located an average of about six times per day, which far exceeded the results of standard ground or aerial telemetry studies of this species. In addition, locations were obtained regardless of weather conditions, allowing a continuous record of the animal's movements during a 2-month period. Locations fixed by satellite were within 1.0 km of the true locations, which is accurate enough for the purposes of most movement studies.

The high number of location fixes potentially available through satellite telemetry can provide the data necessary to answer important management questions regarding caribou. Examples of further applications worth pursuing include documentation of caribou responses to man-made structures, segregation by sex due to selection of different habitats, and clarification of range-use patterns. As satellite telemetry is refined, the data needed to address such issues will become more accessible, thereby allowing greater cost-effectiveness of research funds and increasing the amount of information available for making management decisions.

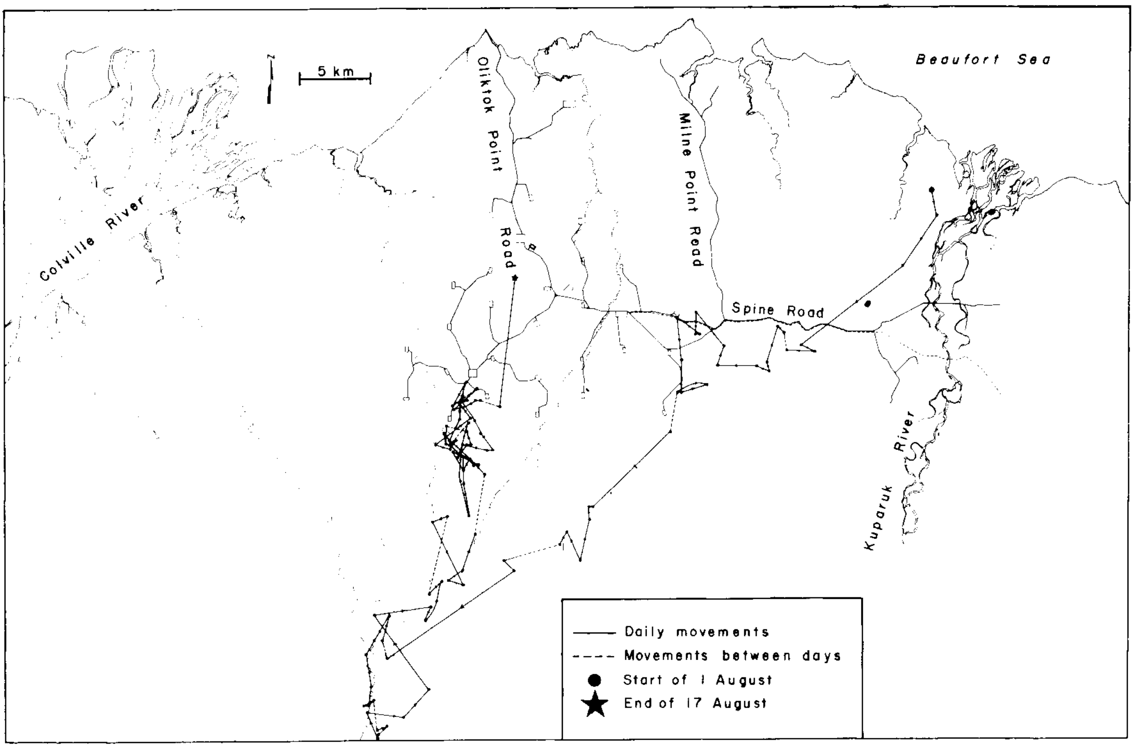

Fig. 4. Movements of a satellite-radio-collared cow in the Central Arctic Herd, Alaska, during the oestrid fly season, 1-17 august 1984.

Table 1. Seasonal means for locations, number of locations, and distances traveled, for a cow caribou monitored by satellite telemetry, 1984.

Season	Mean location		Mean number of locations per day	Mean minimum distance traveled per day (km)	N[a]
	Latitude	Longitude			
Post-calving (16-30 June)	70.42 (0.04)[b]	149.62 (0.09)	4.7(2.1)	8.5(3.5)	59
Mosquito (1-31 July)	70.38 (0.09)	149.76 (0.54)	5.9(1.7)	22.8(9.5)	184
Oestrid fly (1-17 August)	70.22 (0.08)	149.79 (0.27)	6.2(3.5)	14.5(6.1)	106
Overall (19 June-17 august)	70.34 (0.11)	149.75 (0.43)	5.8(2.5)	17.7(7.4)	346

[a] n=total number of locations

[b] Number in parentheses is one standard deviation.

Acknowledgements

This project was funded by ARCO Alaska, Inc. I thank Dr. Robert Newell, Senior Environmental Coordinator, ARCO Alaska, Inc., Anchorage, and Dr. June Lindstedt-Siva, Manager of Environmental Services, Atlantic Richfield Co., Los Angeles, California, for their interest and support during this project. I especially thank Dave Beaty and Stan Tomkiewicz of Telonics, Inc. (Mesa, Arizona), for their enthusiasm and expertise in dealing with the technical aspects of the satellite radio-collar. Jim Dau and Ray Cameron, Alaska Department of Fish and Game, Fairbanks, collared the caribou. Arnie Dresselhaus, North Pole Air Service, provided competent aerial support. Amy Reges, Rich and Peggy Rohleder, Brian Lawhead, and Steve Murphy helped with field work and editing. Mary Moran and Karen Kincheloe draftet the figures and Betty Anderson typed the report.

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Seasonal variations and responses to normal activity of the deep body temperature in the Svalbard reindeer *(Rangifer tarandus platyrhynchus)*

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Abstract: Deep body temperature was recorded in two female Svalbard reindeer during summer and winter. The reindeer were subjected to naturally occurring weather, photoperiod and stimuli in outdoor pens on Svalbard. A telemetry system was employed using transmittors ingested into the rumen. Mean deep body temperature was 0.3°C higher in winter and while the animals were lying down. This suggests a different strategy for thermoregulation than that employed by other reindeer subspecies.

Key words: reindeer, deep body temperature, seasonal changes, resting means, normal activity means.

Rangifer, Special Issue No. 1, 1986: 81 - 85

Introduction

The Svalbard reindeer is found on the high arctic Svalbard Archipelago, between 77° and 81° N.Lat. Mean monthly air temperatures are below 0°C for most of the year, strong winds are common and the sun is below horizon for over 4 months. To maintain a constant deep body temperature (T_{db}) in this cold climate these reindeer employ various means for reducing heat loss. Morphological adaptations such as their small appendage size and thick pelt, as opposed to other reindeer races have been described by many and may assist in reducing heat loss. Still, relatively little is known about the T_{db} of these animals.

The T_{db} of caribou calves (*R. t. tarandus*) was studied by McEvan *et al.* (1965) and observed to be 39°±0.78°C. Later the T_{db} for non-exercising and exercising adult reindeer (*R t. tarandus*) was recorded by Hammel *et al.* (1972) as 38.4°±0.2°C and 39.2°±0.1°C respectively. Yousef and Luick (1975) reported T_{db}'s between 38.4° and 38.8°C from yearling reindeer (*R. tarandus*) in ambient temperatures of 10° to 30°C. Segal (1983) and Segal and Ignatov (1974) investigated the T_{db} of adult reindeer (*R. t. tarandus*) and found a 0.3°C reduction during winter. Cermnych and Visneveckaja (1980) studied adult reindeer (*R. t. tarandus*) during late winter and reported T_{db}'s of 38.3°±0.01°C, with fluctuations from 38.0 to 38.8°C. They also stated that the T_{db} of 16 animals dropped to 37.7±0.02°C in response to a 16°C decrease in ambient temperature, which occurred over 12 hours. This suggests an inertia in the regulatory system's response to decreased T_{db}'s. Also, the above information indicates that there are seasonal deep body temperature differences, differences between calves and adults and from rest to exercise.

Since there was no published literature on T_{db} in Svalbard reindeer (*R. t. platyrhynchus*), a study seemed warranted. The present work investigated for seasonal variations in T_{db}, and the possible relationship between T_{db} and their normal lethargic movements and resting.

Methods and materials

Seasonal variations and responses to normal activity of T_{db} were investigated by the remote monitoring of two tame female reindeer, F_1 and F_2, subjected to naturally occurring weather, photoperiod and stimuli in outdoor pens.

Activity observations recognized only two activity levels 1) resting and 2) active. «Resting» meant lying down. During the winter resting was always in the curled up, legs under, round ball posture. «Active» included all activities where the reindeer were on their feet, eg. standing, walking, grazing. All such movement was usually lethargic.

Measurements of T_{db} and observations of activity were recorded hourly for a minium of 96 continuous hours during an observation period. Observation periods were in February, March and December for both F_1 and F_2, while for F_2 July and August were also included. In addition, during December, February and March, the animals were continually observed between measurements to ascertain the length of time they spent resting.

Deep body temperature was actually rumen temperature, measured using SINTEF temperature sensitive radio transmitters (SINTEF Reguleringsteknikk, 7034 Trondheim) which were ingested. These thermistor temperature sensors had an accuracy of ±0.2°C and were Teflon coated cylinders, with length 50 mm and diameter 20 mm. The transmitters responded to changes in temperature by altering signal-pulse frequency, which was detected by an FM radio. A stop watch was used to measure the time taken to record 50 signals. The T_{db} was then read from the calibration chart for that transmitter. Calibration of transmittors before use was done by the SINTEF office. Body temperatures were always measured at least three times. The mean from these three was taken as the T_{db} for that measurement.

Traditionally deep body temperatures are measured by rectal probe. To help evaluate this study's results to those of previous studies, comparison measurements of rectal and rumen temperature were taken simultaneously at 5 different ambient temperatures (—20°, —2°, 5°, 11° and 23°C).

Comparison of sample means was done by computing "t" for unpaired series of samples from two populations, a "t" test with no assumptions made as to equality of the variance (Snedecor and Cox, 1967). All temperature means are given with their standard error of the mean. The ±0.2°C accuracy error of the sensors became intrinsic within the standard deviation for individual measurements and standard error of the mean due to the volume of samples.

Results

Mean T_{db} for F_1, at age 4 months, was 39.14±0.07°C, (mean ambient temperature —3°C). The mean T_{db} for F_1 and F_2, from 12 to 18 months of age, was 38.83±0.05°C.

T_{db}'s changed seasonally. For F_1 T_{db} rose from a combined mean for activity and resting of

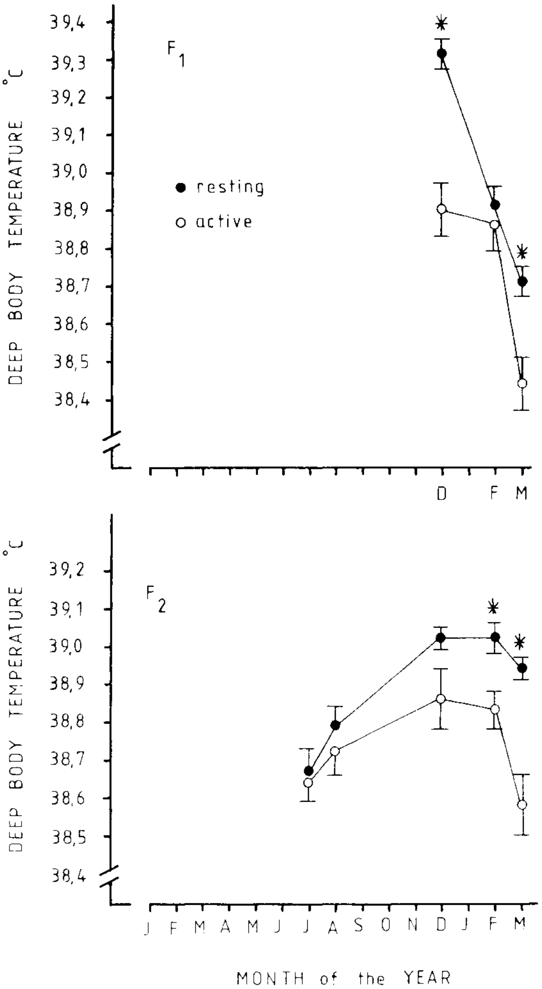

Fig. 1 Deep body temperature means for normal activity and rest in July, Aug., Dec., Feb. and March. Animals F_1 and F_2 are shown separately (mean±se). Months in which the difference between the two means was significant are marked with an asterix.

38.65±0.04°C in July (n=107) to 38.96±0.04°C in December (n=108). This difference in the means from July and December was significant ($P<0.001$).

The mean of all resting values for F_1 and F_2 combined was 38.92±0.02°C(n=530). Similarly the mean for all activity values was 38.73±0.02°C (n=360). The difference between these means was also significant ($P<0.001$).

Examined each month, the mean T_{db}'s for resting are higher than mean T_{db}'s for activity (Fig. 1), but the difference was not always statistically significant. For F_1 there was a significant difference between the mean T_{db}'s for resting and activity, in the months of December and March ($P<0.001$ and $P<0.002$ respectively). For F_2 significant differences occurred in February and March ($P<0.01$ and $P<0.001$ respectively) (Fig. 1).

During December, February and March significant differences between resting and active T_{db}'s were found when the animals rested continuously (no activity between the hourly observations) for 1 or more hours. The mean T_{db} for rest and activity combined was 38.83±0.05°C. However the mean T_{db} for activity occurring in the hour just prior to continuous rest was 38.68±0.07°C (Fig. 2). After one hour of continuous rest, the mean T_{db} was 39.01±0.04°C (Fig. 2). The 0.3°C difference between the initial active T_{db} and the T_{db} following continuous rest of 1 more hours was statistically significant ($P<0.001$). There were no significant differences ($P<0.05$) among the resting means shown in fig. 2, though each by itself, was significantly different from the initial active T_{db} ($P<0.001$ for 1, 2, and 3 hours rest; $P<0.02$ for 4 hours and $P<0.05$ for 5/6 hours).

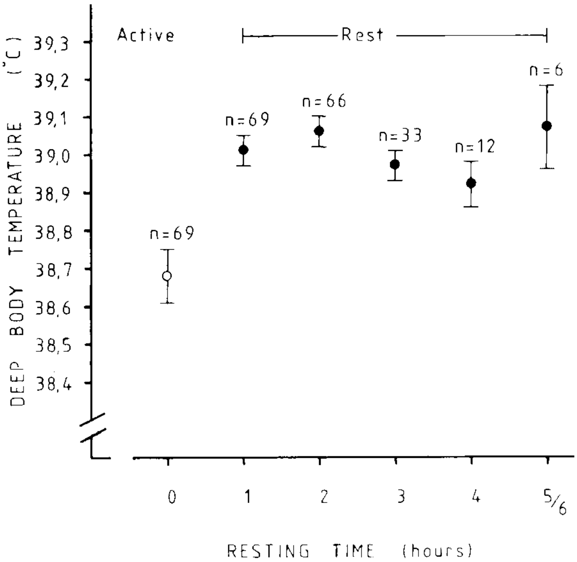

Fig. 2 Deep body temperature differences between resting for 1 or more hours and normal activity prior to rest during the Dec., Feb. and March observation periods (mean±se).

The mean rectal T_{db} was always lower than mean rumen T_{db} at all 5 ambient temperatures tested. The difference between the two was least, 0.3°C, at ambient temperatures above 0°C. At ambient temperatures of —2° and —20°C the temperature difference was 1.0° and 1.6°C respectively. All differences were significant ($P<0.05$).

Discussion

Deep body temperatures measured were rumen temperatures. When rumen and rectal measurements were compared mean rectal T_{db} was always lower than mean rumen T_{db}. The temperature difference perhaps can be accounted for by rumen microbial activity providing a fermentation heat increment thereby elevating all T_{db} measurements. Heat production of rumen ingesta can be as high as (0.09kcal/hr)/kg body wt. (Hammel *et al.*, 1962). However, the temperature difference between rumen and rectal means was not constant (being greater at ambient temperatures below 0°C) suggesting that rumen microbial activity may not be the only factor operating.

Snow ingestion affected only 9 out of the 100's of individual measurements within the study and were considered insignificant in affecting overall temperature means.

Mean T_{db} was 38.83°±0.05°C for normal activity and resting combined, in reindeer aged 12 to 18 months. These results were higher than the 38.4°C for adults from the study by Hammel *et al.* (1972). The presence of a fermentation increment might account for some of this difference. However, Yousef and Luick (1975), reported T_{db}'s of 38.4 to 38.8°C for yearlings (Table 1).

F_1 at 4 months of age had a mean T_{db} of 39.14±0.07°C similar to McEwans's *et al.* (1965) 39.0±0.78°C for caribou calves (Table 1).

Observed deep body temperatures were surprisingly higher when the animals were resting than when active. Mean deep body temperature rose 0.3°C and stabilized at

Table 1. Mean body temperature (°C) of reindeer/caribou, *Rangifer tarandus*

Subspecies	Adult/Subadult Summer	 Winter	 Rest	 «Active»*	 Exercise	Calf	Reference
tarandus	-------------	-------------	-------------	-------------	-------------	39 ±0.78°	McEwan *et al.* (1965)
tarandus	-------------	-------------	-------------	38.4 ±0.2°	39.2 ±0.1°	---------	Hammel *et al.* (1972)
tarandus	-------------	-------------	-------------	38.3 to 38.8°	-------------	---------	Yousef and Luick (1975)
tarandus	38.7	38.4	-------------	-------------	-------------	---------	Segal and Ignatov (1974)
tarandus	38.7 ±0.4°	38.4 ±0.2°	-------------	-------------	-------------	---------	Segal (1983)
tarandus	-------------	38.3 ±0.01°	-------------	-------------	-------------	---------	Cermnych and Visneveckaja (1980)
platyrhynchus	38.65 ±0.04°	38.96 ±0.04°	38.92 ±0.02°	38.73 ±0.02°	-------------	39.14 ±0.07°	This study
	mean (rest + normal activity) 38.83±0.05°						

* «active» for this study was all normal lethargic activity; for other studies «active» meant non-exercise.

≈39.0°C (Fig. 2) when lying down for 1 or more hours in winter (unfortunately summer data concerning lying down was not available). This increase was probably due to a reduction in total conductance as a result of the «round ball» resting posture. Thus small T_{db} increases, within the ranges measured, seen to be tolerated without any metabolic adjustment being made to keep T_{db} strictly constant. The T_{db} rise indicates an inertia in the regulatory system. Cermnych and Visneveckaja (1980) also found indication of inertia within the system, but in their study it was for T_{db} decreases.

Mean T_{db} was highest in winter and lowest in summer. The winter rise of 0.3°C in mean T_{db} may not be accounted for by rumen fermentation rate, as this is lower in winter, due to reduced food intake. If the fermentation heat increment was important, one would expect a winter decrease i rumen T_{db} and a summer increase. Instead this winter increase can most probably be accounted for by the extremely thick and long winter pelt providing a much lowered fur conductance, as opposed to the summer pelt, for the same amount of the heat production. Thus even with the cold winter air temperatues considered, the winter fur conductance is so low as to cause T_{db} to rise as heat loss is reduced. The T_{db} increase need not be a result of increased metabolism. In fact Segal (1983) reported a 25% reduction in winter metabolic rates for reindeer and Nilssen (1984) studying Svalbard reindeer, observed reductions in the winter resting metabolic rate. Nilssen (1984) suggested the reductions were due to the animal's decreased winter feed intake and not the result of a physiological adaption. The winter rise in mean T_{db}'s may also be to some extent affected by the Svalbard reindeer's very low level of locomotor activity in winter. Cuyler (1984) found that the same two reindeer studied spent 65% of their time resting i winter. Since the present study has shown mean T_{db} was highest while resting, this lack of winter movement may be of importance for thermoregulation and contribute to the high winter T_{db} mean.

In contrast to this study's 0.3°C winter increase in mean T_{db}, work by Segal (1983) and Segal and Ignatov (1974) reported a 0.3°C winter reduction in T_{db} for *R. t. tarandus* (Table 1). This difference may have been caused by experimental methods or may be the result of different strategies for thermoregulation being employed by these two subspecies of reindeer. It is difficult to describe a strategy for the reindeer used in Segal (1983) and Segal and Ignatov's (1974) studies without more information. However from observation, the winter strategy of Svalbard reindeer seems to include a thick insultative pelt, little activity and much rest in curled round ball posture (65% of the time). The resting posture by reducing overall conductance, enables the animal to maintain T_{db} without the expence of extra work or metabolism.

Aknowledgements

This study was financed by the Norwegian MAB project on Svalbard and conducted through the Norwegian Polar Research Institute.

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Woodland caribou and forestry in Northern Ontario, Canada.

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Abstract: Expansion of logging in remote Ontario boreal forest requires mitigation of effects on woodland caribou. Three examples of caribou-forestry interaction are reviewed. In two, caribou were apparently displaced from peripheral portions of their winter range by logging. In the third, caribou disappeared when exposed to: logging in a central third of their winter range; increased deer density, and; a probable increase in predation. In all cases there is no evidence of human harvest. The literature plus experience in Ontario suggest the following mitigative techniques: protection of winter concentration areas, significant calving areas and traditional migration routes from logging; directing timber harvest to forest stands of least value to caribou; restricting disturbance to one large clearcut in a peripheral portion of range rather than dispersing it over a large portion as several small clearcuts; modified site preparation and regeneration, and; restricted road access. Research is required on the effect of forestry on caribou with and without mitigation, and on causes for effects observed.

Key words: caribou, decline, forestry, mitigation.

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Rangifer, Special Issue No. 1, 1986: 87 - 93

Introduction

Woodland caribou (*Rangifer tarandus caribou*) inhabiting boreal forest usually form groups of less than 50 that move ut to 100 km between seasonal ranges. Gregarious in autumn, winter and early spring, they are essentially solitary in late spring and summer (Simkin, 1965; Shoesmith and Storey, 1977; Fuller and Keith, 1981; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984).

The Ontario distribution of woodland caribou has steadily receded since European settlement (deVos and Peterson, 1951). It is still receding (Fig. 1). Population density is low, 0.014 to 0.021/km^2 (Simkin, 1965; Hamilton, 1979). Two hypotheses have emerged as reasons for caribou declines. One states caribou populations are limited by seasonal range quality and availability (Klein, 1968; Geist, 1978). Logging, land clearing, fire and human disturbance force caribou onto unsuitable range. The second states populations are regulated by hunting and predators and are little affected by disturbance (Bergerud, 1974a; Bergerud *et al.*, 1984).

Recent expansion of logging into remote boreal forest of northern Ontario requires mitigation of effects on caribou. Our objectives are: (1) review habitat requirements of woodland caribou in boreal forest; (2) summarize the forest management context; (3) summarize forestry-caribou interactions in Ontario; (4) recommend mitigative techniques, and; (5) identify research needs.

Habitat requirements in boreal forest

Studies of woodland caribou in boreal forest show that: use of mature and overmature pine (*Pinus* sp.) and spruce (*Picea* sp.) forest is high; use of deciduous forest is low, and; open muskegs, lakes and islands are preferred for foraging, bedding, escape and calving (Simkin, 1965; Euler *et al.*, 1976; Shoesmith and Storey, 1977; Fuller and Keith, 1981; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984). While

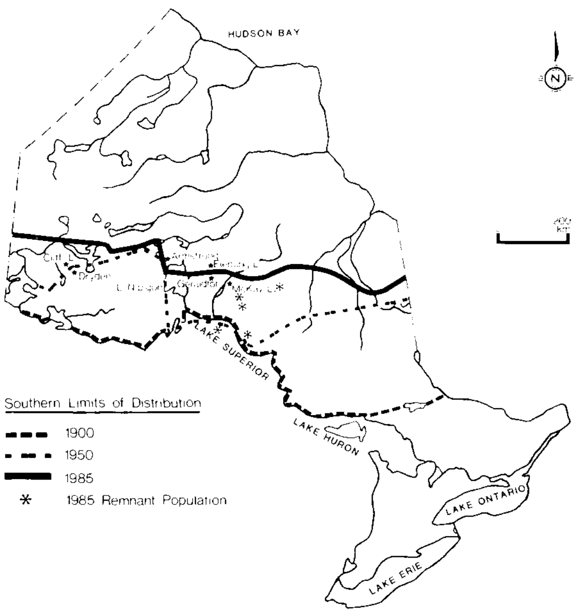

Fig. 1. Distribution of woodland caribou in Ontario from 1900 to 1950 (deVos and Peterson, 1951), to 1985 (unpublished data, OMNR).

caribou can use a variety of habitat types, they nevertheless exhibit strong seasonal preferences governed by forage availability, predators and snow conditions.

In spring and summer, caribou feed on forbs, deciduous leaves, lichens, fungi, grasses and sedges (Simkin, 1965; Bergerud, 1972). Where these are widely abundant, caribou use a greater diversity of habitats in spring and summer than in winter (Fuller and Keith, 1981; Darby and Pruitt, 1984). Spring dispersal of cows and calves plus use of open muskegs, lakes and islands may be anti-predator strategies (Simkin, 1965; Shoesmith and Storey, 1977; Fuller and Keith, 1981). Similarly, caribou may use shorelines, open muskegs and exposed ridges for relief from insects (Shoesmith and Storey, 1977; Edmonds and Bloomfield, 1984).

In autumn and winter caribou feed on arboreal and terrestrial lichens, sedges and bog ericoids; woody browse is not a dietary staple (Simkin, 1965; Bergerud, 1972; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984). During early winter, caribou feed in muskegs until snow restricts activity, then crater on coniferous uplands where snow is less deep, or feed on arboreal lichens. Frozen lakes and creeks are used for travel, escape, resting and drinking slush water (Stardom, 1977; Fuller and Keith, 1981; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984).

Although it has been argued that lichens are not essential for caribou survival (Bergerud, 1972, Euler *et al.*, 1976), they are a valuable winter food. During winter, caribou metabolic rate and protein requirements are reduced while carbohydrate demands are high. Lichens, although low in protein, are rich in carbohydrates (Russell and Martell, 1984). Nutrients missing in lichens are contained in evergreen shrubs and graminoids consumed (Klein, 1982).

Woodland caribou may use traditional migration routes to move between summer and winter range (Stardom, 1977; Edmonds and Bloomfield, 1984), but fidelity to such routes is not strict. Stardom (1977) reported the Sasaginnigak herd in eastern Manitoba followed the same migration route in only 3 of 4 years. In other areas caribou did not show cohesive and unidirectional movements (Shoesmith and Storey, 1977; Fuller and Keith, 1981). Individual or herd movements may be as great as 84 km (Edmonds and Bloomfield, 1984), but distances of 10 — 40 km are more common (Stardom, 1977; Fuller and Keith, 1981). Some caribou use the same range year round (Fuller and Keith, 1981; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984).

Forest management context

Forestry in northern Ontario is directed to mature and overmature conifer for paper production. Clearcuts of 50 to several thousand hectares are common, selective cutting is rare, and cuts are modified only for site protection and other resource values. Post-logging treatment may involve scarification, prescribed burning, natural or artificial seeding, or planting. Forestry activities are governed by forest management agreements (FMA's) between the companies and the Ontario Ministry of Natural Resources (OMNR). Timber management plans, renewable every 5 years, provide direction for 20 years, and operational details for the next 5 years.

Mitigation of effects on woodland caribou must be achieved within the FMA framework. The options for special designation of caribou habitat are limited: (1) exclusion; (2) withdrawal, and; (3) deferment. Exclusions, minimal in size and number, are lands where rights to timber resources are permanently alienated before the FMA is signed. Withdrawals are lands where such rights are alienated after signing. All FMA's stipulate a maximum amount of withdrawal, generally 5% of the annual allowable cut by species group per annum. Deferments are areas where cutting is delayed, usually for 10 years maximum, with no limit on amount deferred.

Areas of Concern are areas of value to other users identified at both the 20 and 5 year planning levels. Examination of the concerns may result in normal on modified forestry operations, or reserves. However, the mechanism for implemention must be withdrawal or deferment. For example, shelter patches and travel corridors are usually deferments. If required for more than 10 years they must be withdrawn or depleted from the productive forest inventory, and equivalent timber elsewhere must be provided to the company. In most cases cut size is only modified through use of shelter patches and travel corridors. Other changes must occur through persuasive negotiation.

Clearcut logging alters caribou habitat in more ways than simple reversion to an early successional stage unfavourable to slow-growing lichens. Stand conversion from coniferous to deciduous species may occur, especially where poplar (*Populus* spp.) are common. This is due to rapid vegetarional reproduction of deciduous trees and shrubs. Lichens, fungi and some ericoids are replaced by vasculars. Woody browse proliferates, benefiting moose (*Alces alces*) in winter, but not caribou.

Forestry and caribou case histories

Since 1960 there have been several cases in northern Ontario where small groups of caribou (10 to 40) disappeared or were displaced when logging occurred in their range. Usually, documentation and data relating to these cases are poor or non-existent, for example at McKay Lake near Geraldton (Fig. 1). However, in three cases there are sufficient data to provide insight to the problem.

Fleming Lake, Geraldton District

For many years woodland caribou were known to winter near Fleming Lake north of Geraldton (Fig. 1). Twenty-one caribou were observed in December, 1981; other caribou were likely present but not observed (Mark Sobchuk, OMNR, Fort Frances, pers. comm.). Forest composition of the winter range (170 km^2 was 61% mature and overmature conifer (80 yrs or older), 11% immature conifer, 9% deciduous forest, 7% mixed forest, 8% muskeg and open land, and 4% water.

From 1980 to 1983, 1130 ha of mature and overmature conifer were cut in a southern 7% of the winter range; 630 ha were clearcut, and 500 ha were modified cut leaving rows of uncut blocks 5 ha in size, spaced 200 m apart. The modified clearcut was intended to protect sandy soils from erosion, improve regeneration success and secondarily mitigate the effects of cutting on caribou (M. Sobchuk, pers. comm.).

Nine aerial transect surveys (1.3 h each) were flown to monitor caribou distribution after cutting; one per month during December, January and February of 1981 — 82, 1982 — 83 and 1983 — 84. Results showed that caribou did not occupy any of the cuts. Instead, they were found in adjacent mature and overmature jack pine (*Pinus banksiana*) north of the cuts where terrestrial lichens were abundant. Some caribou tracks were observed along the northern boundary of the cuts, but none were observed within them. No caribou or caribou sign have been observed in the disturbed area to date (M. Sobchuk, pers. comm.).

No data are available on caribou reproductive or mortality rates. There is no evidence of human harvest of caribou in this winter range despite frequent patrols by Conservation Officers. Moose density (0.12·km^{-2})did not increase after cutting, and white-tailed deer are not present. Wolf density is low but unquantified. However, wolf predation of caribou is not likely to have increased after cutting, because moose density did not increase.

Armstrong, Nipigon District

Since 1975 approximately 100 caribou have summered on islands in lake Nipigon and wintered on the mainland near Armstrong, 10 to 50 km away (Fig. 1). The winter range (180 km^2) is comprised of 35% mature and overmature conifer, 26% immature conifer, 11% deciduous forest, 17% mixed forest, 7% muskeg and open land, and 4% water. Most caribou activity in winter occurs on mature and immature jack pine-spruce-lichen uplands. The community of Armstrong (population 500), a road and the Armstrong airport are located on northwestern and northern boundaries of the winter range respectively.

From 1974 to 1985, several contiguous clearcuts totalling 1140 ha were made in mature and overmature conifer in a western 6% of the winter range. Caribou have not used the cutovers since they were cleared, but continue to use adjacent uncut winter range (Blake Beange, OMNR, Nipigon, Pers. comm.). This was observed: on an aerial transect survey in 1983 and 1985 to monitor caribou winter distribution; on stratified random aerial quadrat surveys for moose in January 1976, 1979 and 1984, and; during casual observations of caribou and caribou tracks by OMNR staff. Local residents frequently view caribou and caribou tracks near the Armstrong airport adjacent to uncut winter range, but not in the cutovers.

No data are available on caribou reproduction or mortality rates. There is no evidence of human harvest of caribou despite frequent patrols by Conservation Officers. Moose density immediately west of the winter range was $0.16 \cdot km^{-2}$ in 1976 and $0.24 \cdot km^{-2}$ in 1979. To the southwest it was $0.36 \cdot km^{-2}$ in 1979. White-tailed deer are not present in the area. Wolves are present but no information is available on their density. Caribou numbers seem unaffected by increased moose density west of the winter range, so increased wolf predation of caribou is not implicated.

Cliff Lake, Dryden District

Brousseau (1978) reported caribou disappeared from the Cliff Lake area northwest of Dryden (Fig. 1) after logging occurred in their winter range. Caribou had been known to exist there for many years. Six aerial transect surveys in winter 1966 — 67 showed the number of caribou exceeded 36. Brousseau (1978) described how the distribution and number of caribou subsequently receded as cutting occurred from 1968 to 1978. Four aerial transect surveys in March, 1978, showed there were only about 12 caribou left, wintering on uncut rocky jack pine ridges. Annual pellet group surveys showed caribou density declined from $0.86 \pm 0.35 \cdot km^{-2}$ ($P<0.05$, $n=318$ plots) in 1972 to zero in 1978 ($n=320$ plots). Cutting in the area has continued to date. No caribou have been seen in Dryden district since 1978 (W. May, OMNR, Dryden, pers. comm.).

Before cutting, the winter range of 270 km^2 (OMNR unpublished data; Brousseau, 1978) was 39% mature and overmature conifer, 15% immature conifer, 9% deciduous forest, 11% mixed forest, 9% muskeg and open land, and 17% water. By 1978, 15% was clearcuts 60 to 1600 ha in size, scattered among lakes in central and eastern portions (33%) of the winter range. A road bisected the winter range, and large cuts and a road surrounded its eastern and northern margins.

Brousseau (1978) suggested the decline or possible emigration of caribou was due to logging. He speculated the reasons may have been direct, through habitat destruction and disturbance, or indirect through increased wolf (*Canis lupus*) predation and illegal hunting. However, it appears other factors were involved. The density of white-tailed deer (*Odocoileus virginianus*) was high from the 1960's to approximately 1975 (W. May, pers. comm.). No data on deer density are available for the Cliff Lake area, but deer density in a wintering area 50 km south was $8.6 \pm 2.3 \cdot km^{-2}$ in 1964. Moose density in the Cliff Lake area ($0.18 \pm 0.07 \cdot km^{-2}$, $P<0.10$) did not increase during the period of caribou decline. There is no information on wolf density, but wolf-killed deer were commonly seen on the lakes. A high density of wolves may have increased predation rates on caribou. The meningeal worm, *Parelaphostrongylus tenuis*, may have been a mortality factor (Anderson, 1971) since deer densities were high for at least 5 years before the caribou started to decline. No evidence of human harvest of caribou was observed during patrols by Conservation Officers from 1972 to 1977, (Carl Hansson, OMNR, Dryden, pers. comm.), even though Brousseau (1978) mentioned the possibility.

Discussion

Concensus in the literature has not been achieved on the reasons for caribou displacement or decline, but it appears that both the habitat-disturbance and predation-hunting hypotheses may be operative. In a few cases, disease may also be involved.

Forage and range condition can limit *Rangifer* population size, and affect distribution (Klein, 1968). Caribou mobility and low reproductive potential are adaptations to avoid population crashes (Bergerud, 1978). Deep snow can limit food availability (Stardom, 1977; Darby and Pruitt, 1984), enhancing the value of such adaptations. The low density of woodland caribou in boreal forest (Simkin, 1965; Hamilton, 1979; Fuller and Keith, 1981) is a reflection of the low productivity of that environment. Populations of 50 caribou or less are very sensitive to slight changes in productivity or mortality (Bergerud, 1978).

Displacement to less suitable range may result in carrying capacity being exceeded, or lower herd productivity. Reimers *et al.* (83) showed that calf and adult reindeer on heavily grazed range in Norway had significantly lower body size than reindeer on good range. Also, pregnancy in female calves occurred frequently on good range but not on poor range.

Cutting of most mature conifer in an area may leave caribou no option but emigration. In Alberta, caribou did not feed in clearcuts larger than 2 ha and were known to cross a larger cut only once in four years (Edmonds and Bloomfield, 1984). Studies by Klein (1971), Calef (1974) and Cameron *et al.* (1979) suggest that abandonment of range may result gradually from the cumulative effect of adverse stimuli. Cows and calves are particularly sensitive to disturbance following parturition (Bergerud, 1974b).

In contrast to the habitat-disturbance hypothesis, Bergerud *et al.* (1984) argued that increased hunting and predation cause caribou declines. They examined eight caribou herds exposed to industrial activities or transportation corridors and found no evidence that disturbance or habitat alteration affected productivity. Instead, they found evidence that increased road access resulted in greater hunting mortality of caribou, and increased moose density resulted in greater wolf predation on caribou. Roads may also facilitate travel of wolves into a caribou area. Hunting of caribou has been prohibited in Ontario since 1929 except for subsistence hunting by native people. Natives harvest 2.4 to 3.6% of the caribou population per year (Simkin, 1965; Gray, 1978).

The three case histories in Ontario are pertinent. At Fleming Lake and Armstrong it appears logging caused displacement of caribou from peripheral portions of their range, yet range abandonment did not result and caribou numbers did not decline. At Cliff Lake the disappearance of caribou probably resulted from a combination of habitat destruction and predation, and possibly parelaphostrongylosis.

While the above information provides a starting point for understanding the effects of logging on caribou, speculation still surrounds the postulated cause and effect relationships. What conclusions then, can be drawn to help develop mitigative techniques? Firstly, caribou may not disappear if a relatively small peripheral portion of range is cut, especially if predation and human harvest are low, and deer are non-existent. Secondly, caribou are likely to disappear if widespread cutting occurs and moose or deer densities (*i.e.* predation or parelaphostrongylosis) are high.

In order for mitigative techniques to be practical they must be economically feasible and compatible with terms of the FMA's. Hence, selective or partial cutting are not viable options. Patch or strip cuts are acceptable only if used in Areas of Concern. Unfortunately, withdrawal and deferment limits, while reasonable for moose, may be unreasonable for caribou. Caribou should not be restricted to isolated areas of mature forest. Wildlife managers must strive to provide adequate habitat for caribou and argue for periods of deferment longer than 10 years.

The efficacy of mitigative techniques recommended below is not known. Research is needed on the effect of forestry on caribou with and without mitigation, and on the causes for any effects observed. The present forest management planning system allows for integrated resource management and implementation of such mitigative techniques.

Mitigative Techniques

1. Do not permit logging of winter concentration areas, significant calving areas or traditional migration routes. Maintain a 2 km and 1 km no-cut buffer around winter concentration areas and significant calving areas respectively. Do not log within one km of traditional migration routes. Avoid road access adjacent to or across such routes between April 1 and mid-May. The size of these buffers, while arbitrary, is our best estimate based on current information.
2. Direct timber harvest to forest stands of least value to caribou, such as black spruce (*Picea mariana*) uplands having a ground cover of feather moss (*Dicranum* sp., *Pleurozium schreberi*), or dense black spruce muskegs with an understory of labrador tea (*Ledum groenlandicum*).
3. Log summer range in winter and *vice - versa.*

4. Allow logging of peripheral portions of caribou winter range if caribou winter use of the periphery is infrequent, or if lichen biomass is low.
5. Restrict cutting to one large clearcut (130 to 500 ha) on the periphery of «caribou range» rather than disperse the same amount of cutting as numerous small clearcuts (less than 130 ha) over a large portion of range.
6. Control road access with signs or gates and scarify roads as soon as practical.
7. Lightly scarify cutovers and leave slash on site to increase humidity and encourage lichen regeneration (Eriksson, 1975). Burning is not recommended because it destroys lichens and stimulates growth of vascular plants (Eriksson, 1975).
8. Implement predator control if wolf predation rates on caribou increase. This is likely to occur if moose or deer densities increase following cutting.
9. Discourage moose and deer populations from increasing in or adjacent to caribou range. Application of herbicides to cutovers may do this while encouraging conifer regeneration.

Acknowledgements

We would like to thank the following personnel of the OMNR for their assistance: Evan Armstrong, Blake Beange, Deb Cornell, Greg Deyne, Gord Eason, Bob Gerrard, Ed Iwachewski, Ted Lucking, John McNicol, Dave Payne, Bruce Sandilands, Sylvio St. Jules, Barry Snider, Ansus Stasus, Mark Sobchuk, Bill Wachsmuth and Randy Wepruk. Pilot Art Colfer skillfully guided us over remote forest and through thunderstorms to inspect areas of caribou habitat.

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Effects of a road system on caribou distribution during calving

J. R. Dau[1] **and R. D. Cameron**[2]

Abstract: In winter 1981 - 82, a 29-km road system was built in a high-use caribou (*Rangifer tarandus granti*) calving area near Milne Point, Alaska. Aerial surveys of this area were conducted annually during the calving period for 4 years before and 4 years after road construction. Effects of the road system on the distribution of caribou were investigated by comparing survey data obtained during these two periods. The 41 400-ha study area was partitioned into 40 quadrats; after construction (1982 - 85), significantly fewer caribou were observed within quadrats encompassing the present road system than before construction (1978 - 81). The area within 6 km of the road system was stratified into six 1-km intervals, and differences in the distribution of caribou among those strata were examined using linear regression analysis. After construction, the density of maternal females was positively correlated with distance, whereas no such relationship was apparent before construction. Density of nonmaternal adults was unrelated to distance during both periods. The results suggest that a local displacement of maternal caribou has occurred in response to roads and associated human activity.

Key words: caribou, calving, roads, disturbance.

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Rangifer, Special Issue No. 1, 1986: 95 - 101

Introduction

The Central Arctic Herd (CAH) is a distinct subpopulation of ca. 13 000 caribou (*Rangifer tarandus granti*) (as of 1983; W. Smith, unpublished data) that ranges the Arctic Slope of Alaska between the Canning and Colville Rivers. Seasonal movements are principally north-south between wintering areas in the Brooks Range and calving grounds/summer range on the Arctic Coastal Plain (Cameron and Whitten, 1979).

In winter 1981 - 82, CONOCO, Inc. built 29 km of gravel road as the initial phase of petroleum development within the Milne Point Production Unit (Fig. 1). This complex is approximately centered on one of two known CAH calving concentration areas (Whitten and Cameron, 1985). In winter 1984 - 85, a single pipeline 35 cm in diameter and approximately 1.8 m above ground was erected adjacent to the Milne Point Road, and a 300-person housing facility was constructed. Human activity and traffic levels near Milne Point were low in June 1983 and 1984 (<10 vehicles per day; 1 active drill rig), moderate in 1982 (10 - 100 vehicles per day; 2 active drill rigs), and high in 1985 (>200 vehicles per day; 3 active drill rigs).

The objective of this study was to determine the effects of roads and associated activity on the local distribution of caribou, especially maternal females, in this high-use calving area. We compared the distribution of caribou within this region during the four years before construction of the road system (1978 - 81) with that during the four years after construction (1982 - 85).

Methods

The study area is ca. 45 km northwest of Prudhoe Bay, lying north of the West Sak Road between the Oliktok Road and Kuparuk River

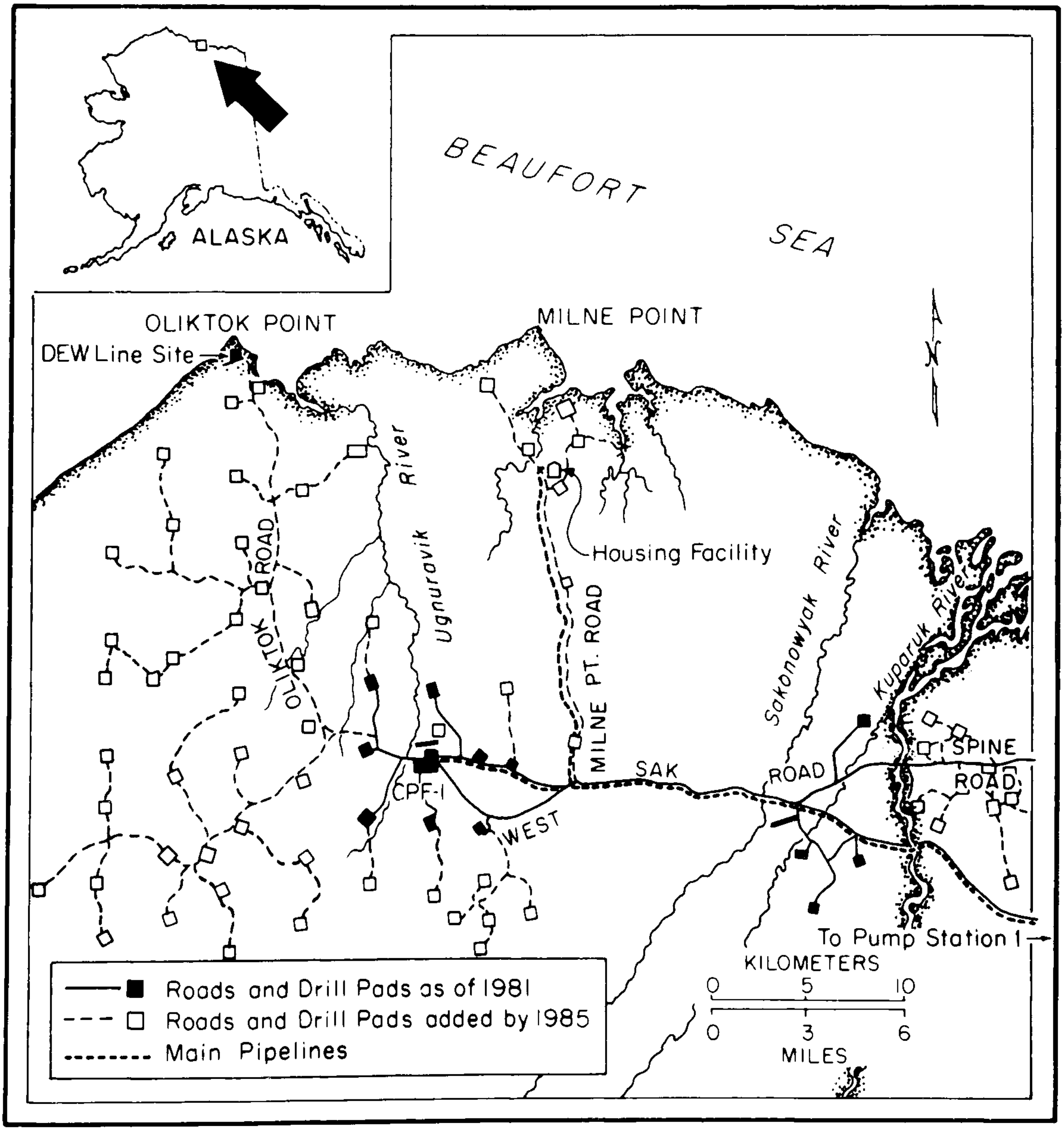

Fig. 1. The Milne Point study area and surrounding region, with roads and gravel pads as of 1981 and 1985.

(Fig. 1). Terrain ranges from sea level to 25 m elevation. Vegetation is typical of the Arctic Coastal Plain (Wahrhaftig, 1965) and similar to that described for the Prudhoe Bay region (Neiland and Hok, 1975; Webber and Walker, 1975).

Aerial surveys of the study area (Whitten and Cameron, 1985; Cameron *et al.*, 1985) were conducted annually between 10 and 14 June 1978 - 85, within a few days after the majority of CAH calving had occurred. North-south strip transects spaced at 3.2 km were flown by helicopter, and observers searched within 1.6 km of the transect center line. For each group of caribou observed, we recorded map location, group size, and sex/age composition.

The study area was partitioned into 40 quadrats of 1036 ha each (Fig. 2). Median percentages of caribou observed within the seven quadrats that include the present road system (i.e., «road quadrats») were compared between the pre- and postconstruction periods using the

Mann-Whitney test; the Z test statistic is reported when ranks were tied (Conover, 1980).

The area within 6 km of the present roads was then stratified into six 1-km distance intervals, excluding portions of strata that were closer to the West Sak Road (Fig. 1), and the data were examined to determine whether the assumptions for linear regression analysis were satisfied (Neter and Wasserman, 1974). Square root transformations eliminated the correlations between means and variances of caribou density within strata. Linear regressions describing caribou density as a function of distance from roads were fit using the full and reduced model approach (Neter and Wasserman, 1974) to examine differences within and between the two four-year periods. Linear models for 1978 - 81 and 1982 - 85 were fit simultaneously and compared through analysis of variance (ANOVA).

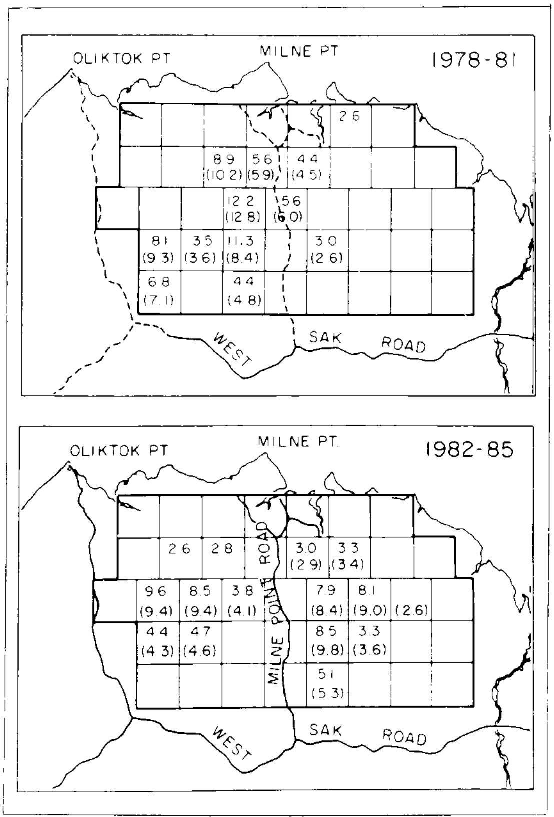

Fig. 2. Distribution of 1036-ha quadrats in the study area (see Fig. 1) preferred by caribou (calves, in parentheses) during calving, 1978 - 81 and 1982 - 85. The occurrence of caribou is expressed as a percentage of the total observed in all 40 quadrats; only those percentages exceeding 2.5% (the percentage of the total area for each quadrat) are shown.

During the surveys, we did not distinguish between maternal and nonmaternal females. Therefore, to describe the distribution of maternal females, the above analyses based on total number of caribou were repeated using number of calves (i.e., neonates). In addition, stratification and ANOVA were used to compare the responses of maternal groups (i.e., ≥25% calves) and nonmaternal groups (i.e., <25% calves) to roads. It should be noted that the latter is an *a posteriori* analysis, and the results should not be granted the same level of objectivity as other results presented here.

All statistical operations were performed using a Compaq Deskpro computer system and SPSS/PC statistical software (Norusis, 1984). Alpha levels (P-values) ≤0.05 were considered statistically significant.

Results

Fewer caribou were near the present road system after construction than before construction. The median percentage of caribou in the seven road quadrats was significantly different between 1978 - 81 and 1982 - 85 (8.5 vs. 2.0%, T = 26.0, P = 0.03). Before construction, 17% of all caribou observed in the study area (465 of 2806) were within these seven quadrats, compared with only 2% (90 of 5424) after construction.

Differences between periods for calves were not clear. Even though the median percentage of calves in the road quadrats was higher during 1978 - 81 (10.5%) than during 1982 - 85 (0.0%), the difference was not statistically significant (z = -1.69, P = 0.09). However, the disparity between pre- and postconstruction periods in the percentage of all calves observed in the seven quadrats was greater than that for all caribou. Before construction, 17% of all calves observed (190 of 1150) were within these quadrats, compared with <1% (6 of 2339) after road construction.

Linear relationships between caribou density and distance from roads were significantly different between 1978 - 81 and 1982 - 85 for all caribou, and for calves (Table 1). The annual variability in these relationships within each four-year period was not significant for all caribou, but was nearly significant for calves ($P = 0.053$). The latter may have resulted from yearly differences in levels of human activity in the study area after 1981. Nevertheless, differences in these relationships were greater between periods than among years within periods (Table 1).

During 1978 - 81, there was no detectable linear relationship between the density of either total number of caribou or number of calves, and distance from roads. In 1982 - 85, however, both density parameters were correlated with distance (Fig. 3). This further suggests that the between-period difference in the relationship between calf density and distance (see above) was real and not attributable to within-period variation.

The similar results obtained for total number of all caribou and number of calves (Fig. 3) indicate that the distribution of maternal caribou was not appreciably different from the distribution of all caribou. This is not surprising considering that most adult ($\geq$2 years) caribou in the study area during June were maternal females (minimum mean = 69%; SD = 15).

The relationships between number of maternal groups per km^2 and distance from roads differed significantly between 1978 - 81 and 1982 - 85, a difference that cannot be attributed to within-period variability (Table 2). No such difference was found for nonmaternal groups, either between or within the pre- and postconstruction periods. Furthermore, there was no linear correlation between the number of maternal or nonmaternal groups per km^2 and distance during 1978 - 81; nor was there any correlation for nonmaternal groups during 1982 - 85. In 1982 - 85, however, the number of maternal groups per

Table 1. Analysis of variance examination of the relationships between numbers of all caribou, and calves, per km^2, and distance from roads, Milne Point, Alaska, June 1978 - 85.

Density parameter	Model[a]	Source of variability	Sums of squares	df	Mean square	F	P	Entering F value	P
All caribou		Total	25.26	47					
	Basic[b]	Regression	3.43	1	3.43	7.23	0.01	7.23	0.01
		Error	21.83	46	0.47				
	Reduced[c]	Regression	8.84	3	2.95	7.89	<0.01	7.24	<0.01
		Error	16.42	44	0.37				
	Full[d]	Regression	15.69	15	1.05	3.50	<0.01	1.91	0.07
		Error	9.56	32	0.30				
	Test[e]	Periods	8.84	3	2.95	5.15	0.02		
		Years/Periods	6.86	12	0.57				
Calves		Total	14.63	47					
	Basic[b]	Regression	2.07	1	2.07	7.58	<0.01	7.58	<0.01
		Error	12.56	46	0.27				
	Reduced[c]	Regression	5.38	3	1.79	8.51	<0.01	7.85	<0.01
		Error	9.26	44	0.21				
	Full[d]	Regression	9.40	15	0.63	3.83	<0.01	2.05	0.05
		Error	5.24	32	0.16				
	Test[e]	Periods	5.38	3	1.79	5.35	0.02		
		Years/Periods	4.02	12	0.34				

[a] Each model tests simple linear relationship(s), where the dependent variable is the square root of caribou density (numbers/km^2) and the independent variable is distance from the road site (km).

[b] Fits a linear model with data pooled across all years; H_0: the eight relationships are not significantly different. The Entering F value tests for the significance of this model beyond the significance of the Basic model.

[c] Fits a separate linear model for each period; H_0: the two relationships are not significantly different. The Entering F value tests for the significance of this model beyond the significance of the Basic model.

[d] Fits a separate linear model for each year within each period; H_0: the four relationships are not significantly different. The Entering F value tests for the significance of this model beyond the significance of the Reduced model.

[e] Tests H_0: the variation in linear models between periods is not significantly greater than the variation in linear models among years within each period.

km^2 was highly correlated with distance from roads (Fig. 4).

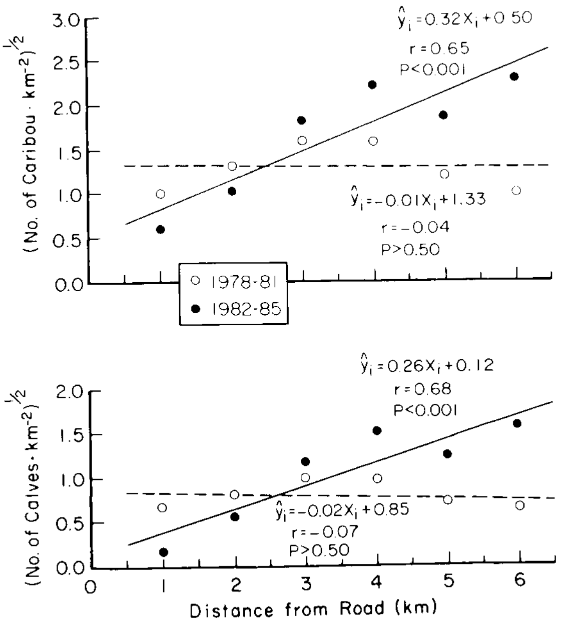

Fig. 3. The relationships between caribou density and distance from roads for all caribou, and calves (i.e., neonates), during June 1978 — 81 and 1982 - 85, Milne Point, Alaska. Data points shown are strata means for each 4-year period; however, linear models were fit using data for individual years.

Discussion

Results of the quadrat analysis for calves are probably misleading. The absence of a statistically significant difference between 1978 - 81 and 1982 - 85 in the median percentage of calves in the seven road quadrats may be attributable to the small sample size (n = 8), tied ranks, and the large effect on ranks of the slightly greater percentage of calves observed during 1985 (1%) vs. 1980 (0%).

Linear regression analyses clearly show significant differences between 1978 - 81 and 1982 - 85 in the relationships between caribou density and distance from roads, differences that are not artifacts of annual variability. Apparently, displacement of maternal females from areas near the Milne Point road system account for this change.

Extrapolating these local effects to a regional level requires some speculation. The logical implication is that an extensive, dense network of roads will result in widespread, partial displacement of maternal caribou from calving

Table 2. Analysis of variance examination of the relationships between numbers of maternal and nonmaternal groups per km^2 and distance from roads, Milne Point, Alaska, June 1978-85.

Density parameter	Model[a]	Source of variability	Sums of squares	df	Mean square	F	P	Entering F value	P
Maternal groups		Total	0.875	47					
	Basic[b]	Regression	0.144	1	0.144	9.09	<0.01	9.09	<0.01
		Error	0.730	46	0.016				
	Reduced[c]	Regression	0.363	3	0.121	10.40	<0.01	9.39	<0.01
		Error	0.512	44	0.012				
	Full[d]	Regression	0.507	15	1.050	2.94	<0.01	1.04	0.44
		Error	0.368	32	0.012				
	Test[e]	Periods	0.363	3	0.121	10.10	<0.01		
		Years/Periods	0.144	12	0.012				
Nonmaternal groups		Total	0.742	47					
	Basic[b]	Regression	0.026	1	0.026	1.66	0.20	1.66	0.20
		Error	0.716	46	0.016				
	Reduced[c]	Regression	0.111	3	0.037	2.58	0.07	2.97	0.06
		Error	0.631	44	0.014				
	Full[d]	Regression	0.273	15	0.018	1.24	0.29	0.92	0.54
		Error	0.469	32	0.015				
	Test[e]	Periods	0.111	3	0.037	2.74	0.10		
		Years/Periods	0.162	12	0.013				

[a-e] See footnotes to Table 1.

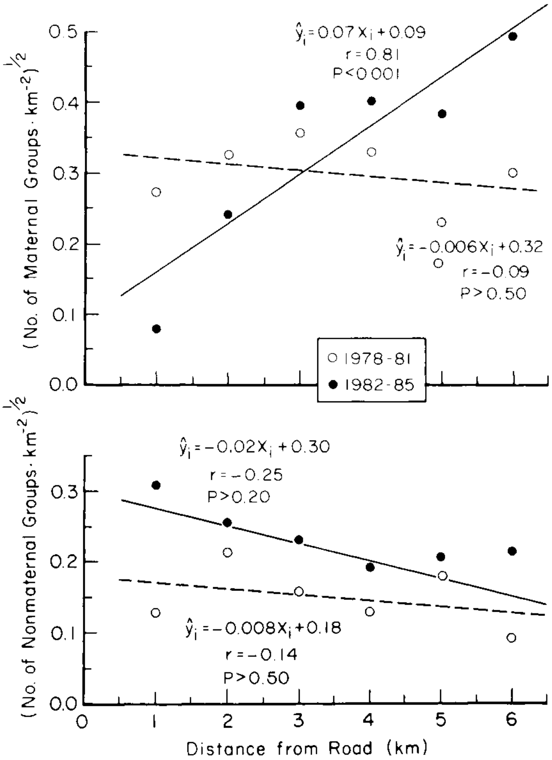

Fig. 4. The relationships between the number of maternal groups (i.e., ≥25% calves) and nonmaternal groups (i.e., <25% calves) per km^2, and distance from roads during June 1978 - 81 and 1982 - 85, Milne Point, Alaska. Data points shown are strata means for each 4-year period; however, linear models were fit using data for individual years.

grounds unless they begin to tolerate these structures and associated activities (Cowan, 1974). Unfortunately, there is no evidence for habituation by maternal caribou. On the contrary, numbers of CAH females calving within the Prudhoe Bay oil field have remained consistently low (Whitten and Cameron, 1985, unpublished data), despite nearly a decade of exposure to manmade structures.

The fidelity that most caribou herds show to calving grounds suggests that these areas may be more important than other seasonal ranges which are used less predictably (Skoog, 1968). Bergerud (1974) stated: «The basic question is.... why the same areas, limited in extent, are used year after year as calving sites.» Valkenburg et al. (in press) discuss some of the factors that could influence the affinity of caribou to calving areas.

The CAH has continued to grow despite the loss of calving habitat. However, this apparent inconsistency does not preclude the possibility that traditional calving areas confer an advantage to caribou. Thus far, displacement of CAH maternal females has been relatively minor, and the low density of this herd on its calving grounds has allowed use of suitable alternative areas (Whitten and Cameron, 1985).

To our knowledge, this study is the first to systematically and quantitatively address the effects of development within a high-use calving area. If petroleum development continues to expand across the central Arctic Coastal Plain, we should have more opportunities to evaluate the importance of calving areas to the CAH. Other seasonal ranges have been only slightly affected by man, losses to predation are thought to be low, and the annual human harvest is small. The absence of these confounding factors provides a unique opportunity to evaluate the consequences of habitat loss to the productivity of a barren-ground caribou herd.

Acknowledgements

Funding was provided by grants from CONOCO, Inc., Continental Pipeline Co., ARCO Alaska, Inc., Exxon Co., U.S.A., and Sohio Petroleum Co. Additional support was obtained from Federal Aid in Wildlife Restoration, and from the Division of Habitat, Alaska Department of Fish and Game. The senior author's travel to the Fourth International Reindeer/Caribou Symposium was provided in part by a grant from the Jack R. Luick Memorial Travel Fund. W. T. Smith and K. R. Whitten were instrumental in the collection of much of the aerial survey data; additional assistance was provided by P. Bente, R. R. Rice, R. G. McAllister, D. Masiak, and R. M. Stearns. We thank W. L. Regelin, W. T. Smith, S. R. Peterson, D. R. Klein, S. G. Fancy, and M. C. S. Kingsley for critically reviewing the manuscript. We are particularly grateful to D. J. Reed for statistical assistance.

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Empirical and theoretical considerations toward a model for caribou socioecology

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Abstract: The Delta and Yanert caribou *(Rangifer tarandus granti)* herds apparently maintained discrete calving areas from 1979 through 1983 (as determined by radio telemetry studies), even though substantial intermixing occurred during other seasons. Also, the Delta herd apparently used a single traditional calving area from the 1950's through 1983, based on results of aerial surveys and 1979-83 telemetry studies. Calving distribution in 1984 changed dramatically; 5 of 25 radio-collared Delta herd cows ≥3 years old and 5 of 24 radio-collared Delta herd cows <3 years old were located in the calving area of the Yanert herd, 72 km west-southwest of the traditional Delta herd calving area. Use of traditional, separate calving areas resumed for the two herds in 1985. One implication of these data is that the current definition of a caribou herd may not always apply. A second implication is that current models of caribou socioecology, based largely on the concepts of traditional use of calving grounds, herd identity/fidelity, and dispersal, inadequately predict or explain all empirical observations. An evolving model of optimal and dynamic use of space can help refine current models of caribou socioecology.

Key words: calving, caribou, conceptual model, dispersal, herd identity, socioecology.

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Rangifer, Special Issue No. 1, 1986: 103 - 109

Introduction

We believe the topic of caribou *(Rangifer tarandus)* socioecology necessitates combining empirical and theoretical science. The purpose of this paper is three-fold: (1) we present sociological data from the Delta (DCH) and Yanert caribou herds (YCH), (2) we cite examples to show that the DCH and YCH data are not sole exceptions to working conceptual models of caribou socioecology, and (3) we discuss theoretical considerations for a more complete model of caribou socioecology.

A conceptual model of caribou socioecology has never been concisely articulated and tested. Indeed, existing models are only in the minds of caribou workers. We believe that most of these models encompass little more than the following concepts: (1) *caribou herds* and (2) *traditional calving grounds* (Skoog, 1968; Thomas *et al.*, 1968), (3) *dispersal* (Skoog, 1968), and (4) *basic caribou social structure* described by Lent (1965) as a «temporary tenuous association(s) of individuals» and by Bergerud (1974*a*) as «open social units.» In contrast, Parker (1972) and Miller (1974) viewed the basic social structure as consisting of persistent nonrandom associations of adult caribou resulting from social attachment.

Consolidating the above concepts into models has resulted in existing models being mostly descriptive and focused primarily on the larger patterns of caribou socioecology. The focus on larger patterns is symptomatic of an emerging discipline (Austad and Howard, 1984). We believe it is now time to redirect the focus on caribou socioecology to include the full range of empirical observations and to expand conceptual models to include explanations of the mechanisms and functions involved in caribou socioecology. We discuss a framework of mechanisms and functions (Bergerud, 1974*a*), which has been available but not widely incorporated into conceptual models, to help explain exceptions to the larger patterns of caribou socioecology.

By monitoring movement of radio-collared caribou in the range of Alaska's DCH from 1979 through 1985, we empirically tested the concepts of herd identity, traditional calving grounds, and dispersal. These concepts have been intertwined for decades. Skoog (1968) and Thomas *et al.* (1968) conceptualized herds based on calving grounds. Skoog (1968) defined «a herd of caribou» as any group which establishes a calving area distinct from that of any other group and uses the area repeatedly over a period of years, with slight modification when deep snow persists. He elaborated that mixing between herds at other seasons may occur occasionally, but this mixing is not considered contradictory to his herd definition. Further, he believed that the herds invariably separate and return to ancestral calving grounds each spring, even though gains or losses in animal numbers may have occurred. Skoog's herd definition applies throughout this paper.

Gunn and Miller (1986) reviewed the concept of traditional calving grounds, so we do not attempt an explicit definition of «traditional» calving grounds here. For this paper, we define traditional or ancestral calving grounds only by what the terms imply.

We consider dispersal in the context of emigration/immigration as used by Skoog (1968). More specifically, for this discussion we define dispersal as any movement by a parturient female that results in (1) her calving outside the distributional range of the herd whose calving area she nsed in the preceding year, and/or (2) her calving on any traditional calving ground other than that of the herd used in the preceding year.

In recent years the need for enlightened and more intensive management of caribou (Bergerud, 1974*b*, 1980; Klein and White, 1978; Miller, 1982) and an increasing need to predict impacts of disturbance and development on caribou and their habitats (Martell and Russell, 1985) have generated a critical reevaluation of current concepts of caribou socioecology.

Methods

Radio-collaring caribou

Between 1979 and 1985, the DCH contained 4000 to 8000 caribou and the YCH contained 500 to 1000, and the herds occupied adjacent or overlapping ranges (Fig. 1). Pertinent information on the history and ranges of both herds is summarized or referenced in Davis and Valkenburg (1985).

From 1979 through 1984, we captured and radio-collared 63 female caribou from the DCH and YCH (60 of these 63 provided data for this paper).

Relocating radio-collared caribou

Radio-collared caribou were relocated from fixed-wing aircraft (Bellanca Scout and Piper Super Cub) equipped with two Yagi antennas. In most years one or more relocation flights were made each month. All radio collars were monitored audibly during each flight and an attempt was made to determine the general location of each signal that was heard. We attempted to visually relocate all collared caribou on each flight during the first several years when fewer than 30 caribou were collared and in subsequent years when logistics permitted. On flights when logistical complications precluded visual relocation of all collared caribou, those individuals which were not recently located were given first priority. Some collared caribou were sighted from the ground during June and July 1979 by Alaska Department of Fish and Game personnel conducting sheep (*Ovis dalli dalli*) studies and caribou composition counts. For each sighting, we attempted to record group size, location, presence or absence of a calf, and group composition. We received some reports from the public, including hunters, on the locations of collared caribou that were observed or shot.

Calving

Annually from 1979 through 1984, calving distribution was monitored in the ranges of the DCH and YCH using fixed-wing aircraft to relocate radio-collared females and to conduct ocular reconnaissance. Geographic separation of calving grounds of the two herds was assessed.

Methods used to monitor calving distribution in 1984 are of particular interest because of the unexpected results. Fixed-wing aircraft were used to relocate radio-collared caribou on 10, 14, 16, 18, and 26 May 1984; a 2-person ground crew classified caribou on the traditional «core» calving area on 20 - 23 May 1984; and a helicopter was used on 26 May 1984 for a composition count in the upper Wood River area (Fig. 1).

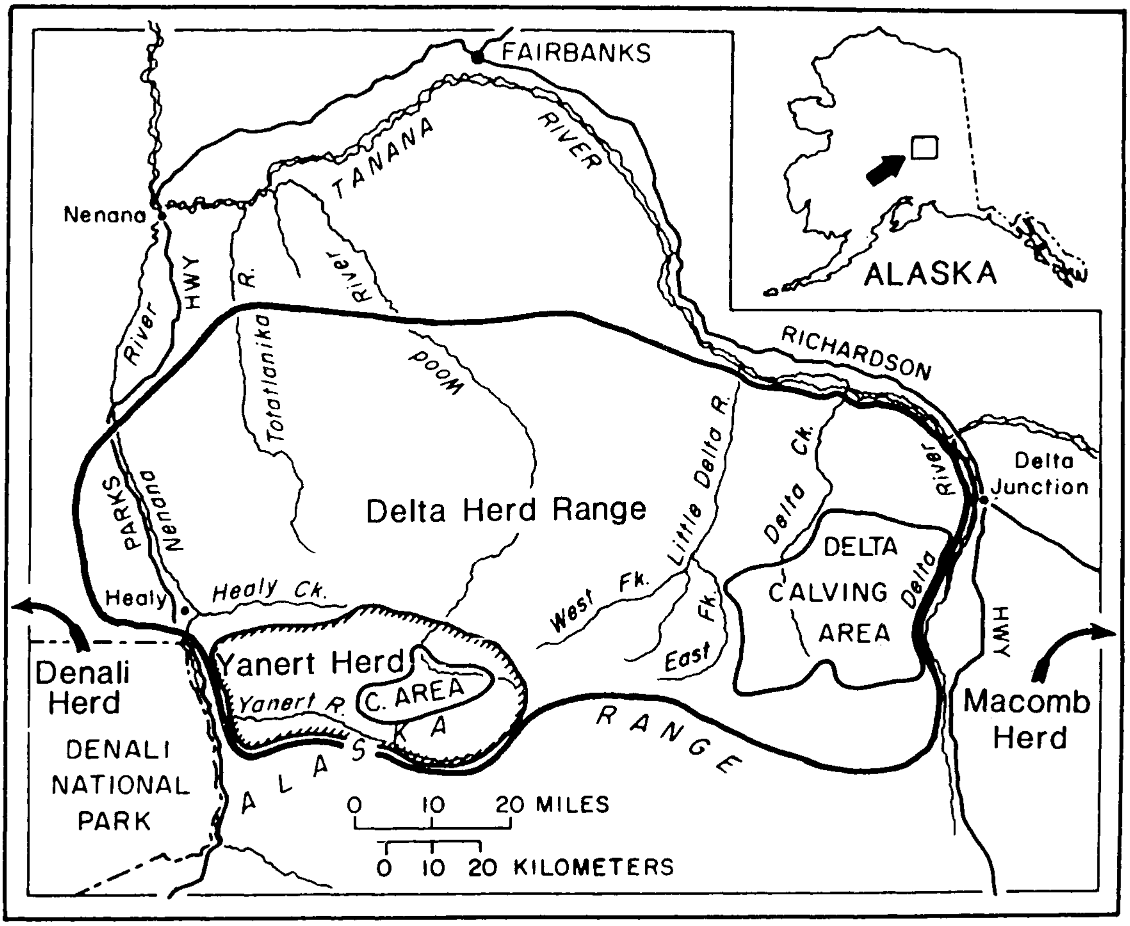

Fig. 1. Study area and distribution and calving areas of the Delta and Yanert Caribou herds.

Herd identities and fidelity

Discreteness of the DCH and the YCH, and the spatial relationships to one another and to neighboring Nelchina, Macomb, Fortymile, and Denali herds, were determined by monitoring movements and calving distribution of caribou that were radio-collared within the range of the DCH or YCH.

Results

Calving distribution

Based on results of aerial surveys and 1979-83 telemetry studies, the DCH apparently used a single calving area (i.e., one contiguous geographic area separated from the 1980-85 Yanert calving area) from the 1950's through 1983 (Fig. 1). The surveys prior to 1970 were not intensive and may not have located all calving females; however, the surveys did demonstrate annual use of the traditional DCH calving area. The DCH and YCH maintained discrete calving areas from 1979 through 1983, as determined by radiotelemetry, but significant intermixing occurred during other seasons (Davis and Valkenburg, 1985).

Numbers of radio-collared females that used the Delta and Yanert calving areas from 1979 through 1985 are listed in Table 1. Calving distribution in 1984 was of particular interest because 20% (10/49) of the radio-collared DCH females calved and/or were distributed during calving with YCH females in the Yanert calving area. Of these 10 DCH females, five were ≥36 months and five were <36 months old. At calving time in 1984, there was a total of 49 radio-collared females in the DCH, including 25 ≥36 months old and 24 <36 months old.

During calving in 1985, all radio-collared females, except one, resumed calving in their respective traditional calving grounds. The single exception (Table 1) was a caribou radio-collared

Table 1. The number of female caribou radio-collared annually from the Delta and Yanert herds and their calving range location, 1979-85.

	Delta herd[a]			Yanert herd[b]		
Year	Number radio-collared	Delta calving range	Yanert calving range	Number radio-collared	Delta calving range	Yanert calving range
1979	11	11	0	0	-	-
1980	0	11	0	0	-	-
1981	10	18	0	8[c]	0	7
1982	11	28	0	0	0	7
1983	12	39	0	0	1	6
1984	11	38	10	0	1	6
1985	0	44	0	0	1	7

[a] All radio-collared females were collared in the range of the Delta Caribou herd and assumed to be DCH members.

[b] All radio-collared females were collared in the range of the Yanert Caribou herd and assumed to be YCH members.

[c] A human recording error of radio frequencies caused one of the eight caribou collared in 1981 to not be located until 1985.

in April 1981 on the YCH's winter range. She calved in 1981 and 1982 on the Yanert calving ground, but calved on the Delta Herd's calving ground in 1983, 1984, and 1985.

Dispersal/herd identity

From 1979 through 1985, only one of 60 radio-collared females «permanently» switched between the DCH and YCH calving grounds, suggesting a 98% (59/60) fidelity of females to their calving ground. However, in 1984, 21% (10/43) of the radio-collared DCH females calved in the YCH's calving ground. The «dispersal» of DCH females in 1984 was apparently only a 1-year phenomenon because all 10 DCH cows returned to the Delta calving ground in 1985.

Even considering the relative lack of calving ground fidelity in 1984, overall fidelity to respective calving grounds has been high. Based on «calving-ground-years» for caribou $\geq$24 months old, the observed fidelity rate during this study has been 96% (206/214).

Discussion

Our observations of radio-collared Delta and Yanert caribou are partially consistent with conventional definitions and concepts of herds, traditional calving grounds, and dispersal. However, several of our observations indicate the need to expand and refine concepts and definitions to adequately describe and predict phenomena related to herd identity and fidelity to calving areas.

For example, we believe that the existing model(s) of caribou socioecology inadequately predicted: (1) the 1-year «abandonment», in 1984, of the traditional DCH calving ground by 20% (10/49) of the radio-collared DCH females, and (2) the permanent abandonment of the YCH calving ground by the one female. Even if we were to concede that the existing model(s) implies predictions to account for the observations, the existing model(s) certainly do not include credible triggering and functional mechanisms to explain the observations. Rather, the present model(s) labels our observations as exceptions or anomalies.

However, our observations may not be exceptions. They may be infrequent events that are typical for sizable «associations» of caribou observed for a protracted period. Radio-telemetry has provided the first opportunity to test the conventional socioecology model(s) for caribou, and results are just now becoming available. Already, the studies have revealed many «exceptions» or «anomalies». Gauthier (1984) documented temporary egress from the Burwash herd study area by 3 of 26 radio-collared caribou in 1982. In addition, monitoring radio-collared caribou helped determine that approximately 16-19% (62-72/387) of the adults and subadults in the 1981 rutting population did not calve in the two traditional calving areas for the Burwash herd in spring 1982 (i.e., dispersal).

Similarly, monitoring radio-collared caribou helped to document the dispersal of several hundred caribou from traditional range of the Big River Herd in Alaska, and subsequent calving in nontraditional calving areas (Pegau 1985). More questions than answers have accrued regarding herd identity and traditional calving areas for caribou radio-collared on the Arctic Coastal Plain of Alaska between the calving grounds of the Western Arctic (see Davis (1980) for herd locations) and Teshekpuk herds (Davis and Valkenburg, unpublished data). Radio-telemetry has also aided in documenting frequent shifts in calving distribution in the Fortymile (Valkenburg and Davis, 1986) and Denali herds (Troyer, 1981). And telemetry has helped show that sharing a common calving ground is an inappropriate criterion for defining herds in some situations involving woodland caribou (*R. t. caribou*) (Edmonds and Bloomfield, 1984; R. Farnell, pers. comm., Yukon Wildlife Branch).

One implication of these «exceptions» or «anomalies» is that conventional concepts of traditional calving grounds, herd fidelity, and dispersal (i.e., caribou socioecology) are incomplete. We believe that current concepts must be expanded, refined, and/or revised to better explain dispersal to adjacent calving areas and exceptions to caribou calving in a «traditional» manner.

Currently, there is major debate over the complex subject of caribou socioecology. The debate focuses on three issues: (1) the basis for defining caribou herds, (2) Bergerud's (1974*a*) working hypothesis that caribou optimally and dynamically use space (including short-term shifts in calving distribution) vs. the concept of long-term selection for calving grounds (includes optimal foraging theory), and (3) the theoretical mechanisms contributing to dispersal and/or maintenance of herd discreteness (Haber and Walters, 1980).

Bergerud (1974*a*:582) introduced the concept of optimal and dynamic use of space in a discussion as follows: «However, this temporal-space optimum will soon be altered and it will be more advantageous to be elsewhere.» In discussing caribou socioecology, Bergerud (1974*a*) discussed many of the terms and concepts we believe integral to any model that satisfactorily depicts caribou socioecology.

Bergerud (1974*a*) discussed the role of facultative and obligate behavior in the phylogeny and ontogeny of caribou, and suggested that our understanding of caribou movement and aggregating behavior would be greatly enhanced if we knew how herds return to specific locations. He offered three hypotheses, which may not be mutually exclusive, to explain this phenomenon: (1) that the ability of animals to «home» to a specific area involves learning and tradition; (2) that animals are funneled by topographical features and recognize the calving grounds based on phylogenic imprinting; and (3) that animals have an orientation direction which often results in the animal reaching the same general area. Social facilitation is continually interactive with all three possibilities. Anticipatory adaptation was also discussed by Bergerud (1974*a*), but site affinity was not (albeit site affinity overlaps with learning and tradition). Herd definition was lacking in Bergerud's discussion.

Social facilitation (and/or contagious behavior) seems inescapably involved in the movement and distribution behavior of caribou. We envision a constant tug-of-war in the caribou's mind between yielding to learned/traditional movement and yielding to «group pressure» to do otherwise when the traditions differ among interacting individuals.

Studies of diverse species have shown that bimorphism or polymorphism is common in populations. The literature on invertebrates is replete with studies of morphism (e.g., Iwanaga *et al.*, 1985; Borowsky, 1985) and recent publications, regarding bi- or polymorphism, are common for birds (e.g., Ratti, 1985), fish (e.g., Jurss *et al.*, 1985), and there is increasing cognizance of bi- or polymorphism contributing to variation in large mammal populations. For example, Bunnell and Harestad (1983) concluded that observed movement patterns of black-tailed deer *(Odocoileus hemionus columbianus)* suggested the existence of two phenotypes--«nondispersers» and «dispersers.» They stated further that, «...competition for mates is an important force governing the proportions of «dispersers» to «nondispersers.»

Given that bi- or polymorphism is common in many species and can frequently account for observed variation within populations, it does not seem improbable that morphism in caribou could account for some observed behavioral differences. Edmonds and Bloomfield (1984) recently described two different annual movement strategies for woodland caribou in Alberta. Might the two strategies stem from behavioral bimorphism? Similarly, the calving behavior that we observed in the DCH and YCH caribou, behavior which did not conform to the conventional model(s) of caribou socioecology, may be partly explainable by behavioral morphism.

To conclude, we believe that confusion has resulted from lack of standardized terminology and definitions regarding caribou socioecology. Advances in the field of socioecology have not been timely synthesized by caribou workers and have not been incorporated into the conventional model(s) of caribou socioecology. We believe the conventional model(s) of caribou socioecology is incomplete and warrants modification.

Incorporating Bergerud's (1974*a*, 1985; Bergerud *et al.*, 1984) evolving model of «optimal and dynamic use of space» into other existing models would contribute toward developing a satisfactory model. Further synthesis of the literature on the socioecology of other species will identify components required for a valid model of caribou socioecology. Implications of the following concepts will undoubtedly contribute to the evolving model: (1) intraspecific variation in social systems (Lott, 1984); (2) evolutionarily stable strategy (Maynard-Smith and Price, 1973, cited in Austad and Howard, 1984); and (3) alternative reproductive behaviors (Austad and Howard, 1984).

Acknowledgements

This study was funded by Federal Aid in Wildlife Restoration Projects W-21 and W-22. E. Crain, S. DuBois, L. Jennings, P. Karczmarczyk, T. McCall, L. McManus, C. Nuckols, W. Regelin, and D. Simpson helped in one or more aspects of field work. Visiting scientists, A. T. Bergerud and H. Butler, provided refreshing stimulation, obtained calving-related data in 1984, and directed us to pertinent literature. R. Cameron and K. Whitten critiqued the manuscript, and suggestions by them and reviewers D. Gauthier and R. Farnell improved the manuscript.

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Some herding, record keeping and treatment methods used in Alaskan reindeer herds

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Abstract: Approximately 20000 reindeer (*Rangifer tarandus*) in Alaska are gathered once or twice yearly to facilitate identification, serologic sampling, treatment and antler removal. Various air and land craft are used to bring the animals into a corral system from which they can be herded into a padded, pneumatically operated, squeeze apparatus. Ear tags are applied or read if already in place and ears are notched. A portable, computerized rapid data retrieval system is used to record reproductive success, vaccination and treatment status and other miscellaneous information. Ivermectin is being administered in the early winter months to treat reindeer in many herds for warbles, nasal bots and internal parasites. A killed, homologous *Brucella suis* type 4 vaccine is being used in two large (3500) herds. Efforts are being made to incorporate other innovative methods to improve herding and corralling methods.

Key words: reindeer, *Rangifer tarandus*, restraint, computer, brucellosis vaccine, ivermectin, stress, gathering, corralling.

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Rangifer, Special Issue No. 1, 1986: 111 - 113

Introduction

Reindeer are raised in Alaska as semi-domestic animals and are owned by private native individuals or by native corporations. They represent an unique agricultural endeavor with management demands not experienced by other livestock industries. Herds vary in size from 200 to nearly 10000 animals and are free-roaming on vast tundra ranges. They are raised for meat production and by-products such as antlers and hides. A biologic and socioeconomic review of Alaska's reindeer industry is available (Stern *et al.*, 1980).

Reindeer herders in Alaska gather their animals once or twice yearly to harvest antlers, blood test, vaccinate and identify individuals. Reindeer are gathered in the winter with the use of snowmobiles. In the summer, walkers, horses, dogs, three and four wheel all-terrain-vehicles, snowmobiles and helicopters are used to gather reindeer. Groups of animals are herded along wing fences and into corral systems capable of handling a few hundred to two thousand reindeer. These corrals are located in remote areas usually without road access, electrical power or communications. It is necessary to spend a minimum amount of time handling each individual reindeer because of the large numbers of animals waiting with no food and little if any water. An average of 30 to 60 seconds is spent working on each animal.

Several new reindeer husbandry and disease control methods have been or are presently being developed for use by reindeer herders. This report describes some of these techniques now being used or tested under field conditions.

Reindeer handling aids

Traditionally, reindeer have been herded into a large circular corral from which small groups of from 20 to 50 are placed in «pockets» which lead to a V-shaped chute system. The end of the chute has «windows» cut into it which allows handlers to restrain individual reindeer by holding their head and antlers. This system is effective but requires considerable manpower, allows movement, and adds to the stress of the reindeer which are not accustomed to physical restraint.

A deer squeeze chute developed in New Zealand (MAK Deer Crush, Contract Engineering, P. O. Box 1348, Invercargill, New Zealand) has proved very effective in restraining individual animals with a minimum of personnel and stress. This unit consists of a V-shaped chute approximately 2 m long with thick padded sides. One of these padded sides is hinged at the floor and moves against an animal with the aid of a pneumatically powered ram system. The animal is held firmly and moves very little. (Fig. 1) The head is available at the front of the chute for blood sample collection, ear notching and tagging plus antler removal. The entire chute is mounted on an automatically zeroing scale which allows weighing an animal in 1 or 2 seconds. The scale read-out is digital and can be connected directly to a computerized data management system. A portable air compressor powered by a gasoline engine drives the air ram system for the squeeze chute. This same compressor is used to power hand-held antler cutter. Antlers are harvested in velvet. The rapid cutting action of the pneumatic cutters decreases the time the animal has to be restrained. The cutters are modified pruners which were originally designed to cut tree limbs.

Data management system

Reindeer research projects and general herd management decisions have pointed to the need for the development of a data handling system which could be taken to the corral site, allowing immediate retrieval and updating of an individual animal's records. A Kaypro 10 computer with hard disk drive, Questa data saver with battery back-up and portable generator were selected to serve as hardware for the data management system (Kokjer, K. J.; Ray-Landis, K. A.; Dieterich, R. A., unpublished data, 1985). Software consists of eight major programs in a menu driven system using dBASE II as the data base system. Age, sex, reproductive success, castration, treatments, vaccinations, blood test results, miscellaneous comment codes and body weight information can be gathered for each individual reindeer as it passes through the chute system. Approximately 15 to 20 seconds are needed to display an individual's record and enter new data. Procedures, such as vaccination, which are being carried out on all animals can be pre-programmed for automatic entry.

A separate analysis program allows researches and herd owners to ask complex questions pertaining to both research and management. For example, one might ask: How many 4-year-old females, weighing more than 80 kg, have been blood test positive for brucellosis for the past 2 years and produced offspring? The program can provide both a numerical answer and a print-out of the animals' identification number. A report program is also available which totals the numbers of reindeer in herds by age and sex. The program produces totals for the entire herd plus totals for only those animals seen at the last gathering. It also produces a total count for each of the miscellaneous comment codes such as abscesses, warbles, and broken antlers.

Parasite and disease control

Approval has been obtained from the United States Food and Drug Administration for the use of ivermectin in reindeer. This approval was obtained after safety, efficacy and residue studies were completed. Reindeer are not to be slaughtered within 56 days of treatment. Ivermectin is highly effective in controlling reindeer warbles, nasal bots, lungworms and gastrointestinal helminths of reindeer. Treatment is normally carried out from October through January. Levamisole is administered in some herds during the summer months to control intestinal parasites.

Brucellosis in Alaskan reindeer is caused by *Brucella suis* type 4 infection (Dieterich, 1981). Swollen joints, enlarged testicles, abscesses and, motst importantly, abortion are the results of the infection. The incidence of brucellosis has been increasing in Alaskan herds at an alarming rate over the past few years. An experimental killed, homologous vaccine with adjuvant is now being used in extensive field tests after laboratory testing of its use in reindeer confirmed its ability to prevent *Brucella* abortion. Approximately 3500 reindeer have been vaccinated and will be examined for clinical signs, reproductive success and serologic response as compared to non-vaccinated controls. Widespread vaccination will begin in the near future (Dieterich, 1985).

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Fig. 1. Graphic depiction of reindeer in squeeze chute with data being relayed to computer operator.

Calving of the experimental reindeer herd in Kaamanen during 1970 - 85

Eija Eloranta[1] and **Mauri Nieminen**[1]

Abstract: Calving and calf production were studied in an experimental reindeer (*Rangifer tarandus* L.) herd in Inari, Kaamanen (69°10'N) in northern Finland. Most of the calving took place between May 10 and 29; 50% of the calves were born up to 22.5. and 90% up to 29.5. The percentage of calves (calves/hinds preceeding year) was on average 79.2%. The newborn sex ratio was 1:1. There was a large range (1.8 to 8.5 kg) in the birth-weight of newborn calves; male calves weighed about 0.3 kg more than female. The total loss of calves during summer and autumn was about 34.5% (range 6.3 to 100.0%). During the calving period 111 calves (12.2%) died. They were usually younger than one day, and on average weighed 1.3 kg less at birth than calves who lived until autumn. The hinds of calves dying very early were usually young and calving for the first time. The autumn-weight of hinds correlated significantly (r=0.49) with the birth-weight of their calves. Over-5-year-old and over 80 kg hinds bore the heaviest calves (mean weight 6.3 kg) and the survival of these calves was very good. The first hinds to calve in the spring (calving up to 22.5.) are 5-year-old and older, which are also the heaviest and produce the most vital calves.

Key words: reindeer, calving, birth-weight, age, mortality.

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Rangifer, Special Issue No. 1, 1986: 115 - 121

Introduction

Seasonality and predation are the two main factors invoked to explain the birth synchrony in *Ungulates.* Births are timed to minimize environmental or energetic stress on mother or offspring and the optimal slot, in very seasonal climates, is narrow. Births are also synchronised to reduce predation on the vulnerable newborns either by satiating or confusing predators (Bergerud, 1974; Dauphiné and McClure, 1974).

As a result of high adaptation to seasonal variations reindeer and caribou (*Rangifer tarandus* spp.) undergo seasonal physiological changes with the highest metabolic demands in the spring and early summer. Calves are born, and must be nursed at the same time as the hinds are recovering from the rigors of winter. Although lactation begins before all the snow has melted and hinds are very lean, the milk of reindeer is outstandingly rich in protein and fat and the energy content is high (Arman, 1979).

The reproduction of reindeer and caribou has been extensively studied including the timing of reproduction (Bergerud, 1975; Holthe, 1975), reproduction data of reindeer and caribou (McEwan and Whitehead 1972), reproductive physiology (Dott and Utsi, 1973; Roine, 1974; Parker, 1981; Roine *et al.*, 1982), calving and related social behaviour (Lent, 1966; Espmark, 1980), maternal effects upon calving (Lenvik and Bo, 1983; Skogland, 1984) and mortality rates (Pruitt, 1961; Rognmo *et al.*, 1983). The objective of the present study was to obtain information on calving and calf production of Finnish reindeer.

Material and methods

The study was carried out in the area of Kaamanen reindeer research station (pasture area about 70 km^2) in Inari (69°10'N). In this area the reindeer were freely grazing most of the year excluding the calving period when the females were kept in the calving area (about 8 ha). In winter and during the calving period the animals were offered a supplement containing lichens, molasses and pelleted concentrates. In the study area the 6-month-long winter usually begins in Mid-October. The snow depth is as its greatest in early May (70 - 80 cm) and snow melts usually by the end of May. During the calving period in May-June minimal temperature varies daily between -6°C and +8°C and maximal temperature between +3°C and +18°C.

Altogether 2210 semi-domestic reindeer (*R. t. tarandus* L.) (1132 females, 165 males and 913 calves) were studied. During the calving period newborn calves were caught by hand after the calf had been licked dry by the mother. The calf was weighed with a steelyard to the nearest 0.1 kg. Then the calf was ear-marked with numbered ear-tags and sexed. Also the color of newborns, date of their birth and information on their mother were recorded. Mortality among the calves during the calving period was also recorded. The calving area was examined daily and carcasses found were collected and examined. The calving percentage was estimated according to the number of calves born and the number of hinds the preceeding autumn. All the reindeer including calves were weighed annually (1970 - 84) during the slaughtering period at the turn of November - December and 1985 in addition to this just prior to calving in April using a spring balance to the nearest 0.5 kg. The mortality of calves during summer and autumn was estimated according to the number of calves present during the weighing. The statistical analyses were performed using BMDP-program packets. The significances of the differences between the group mean values were calculated by t-test.

Results

During 1970 - 84 there were altogether 1297 adult reindeer in the Kaamanen reindeer herd. The sex-ratio (female:male) was on an average 11:1. There were annually about 75 females (range 22-132) and 11 males (range 2-25). The average age of 3-year-old and older females was 5.3 years (range 3.0 - 14.0 years, n= 929) and the mean weight of these animals was 70.8 ± 0.3 kg ($\bar{x}$ ± S.E.) (range 50.0 - 106.0 kg, n= 712). Three-year-old and older males were younger, the mean age being 4.1 years (range 3.0 - 8.0 years, n= 88). The mean weight of these males was 95.0±1.7 kg (range 60.0 - 133.0 kg, n= 75). The mean weight of pregnant adult hinds was 71.7±0.3 kg (n= 583), which was significantly greater ($P < 0.001$) than that of barren animals (67.0±0.6 kg, n= 133). The young pregnant hinds weighed on an average 59.6±0.8 kg (n= 96), significantly more ($P < 0.001$) than barren animals of the same age (51.7±0.3 kg, n= 87).

The calving percentage of hinds in this study was on average 79.2% (range 64.3 - 93.4%). Only 44.5% of those hinds weighing under 60 kg had a calf. Of heavier hinds (weighing 60 - 80 kg) 82.2% had a calf and almost every hind weighing over 80 kg produced a calf (94.7%) (Table 1). A highly significant linear regression was obtained between the birth-weight of calves and the weight of pregnant females just prior to calving ($r= 0.58$, $P < 0.001$, n= 70) and also between the birth-weight of calves and the weight of pregnant females in preceeding autumn ($r= 0.49$, $P < 0.001$, n= 619) (Fig. 1).

The body weight of hinds increased clearly up to the age of 5 years. After that it kept quite constant increasing slightly until it started falling after the hinds reached the age of 12 - 13 years. The hinds got pregnant for the first time usually

Table 1. Percentage calving, calf weights at birth, and calf autumn weights in relation to maternal weight in the preceeding autumn in the Kaamanen reindeer herd during 1975-84 (numbers in parentheses)

Weight of hinds (kg)	Calving percent	Birth-weight of calves (kg)	Autumn-weight of calves (kg)
≤50	12.2	4.2 ± 0.58 (4)	37.0 ± 0.0 (2)
51-60	53.9	4.5 ± 0.10 (63)	37.0 ± 0.92 (41)
61-70	80.5	5.0 ± 0.05 (263)	38.7 ± 0.51 (151)
71-80	84.4	5.5 ± 0.06 (218)	42.1 ± 0.52 (143)
81-90	93.4	6.1 ± 0.11 (56)	45.1 ± 1.01 (42)
≥90	100.0	6.6 ± 0.23 (15)	52.3 ± 1.91 (13)

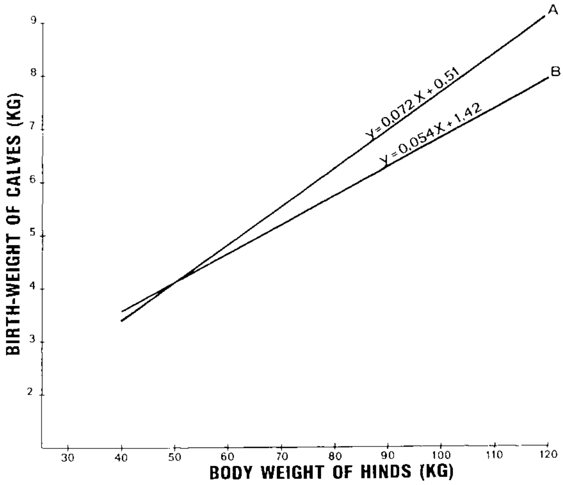

Fig. 1. Mean calf birth-weights in relation to maternal weights just prior to calving (A) and in preceeding autumn (B). The lines were obtained by polynomial regression analyses and are described respectively by the following equations: y= 0.072x + 0.51, r= 0.58, n= 70 and y= 0.054x + 1.42, r= 0.49, n= 619, where y is the weight of calves and x is the weight of hinds.

at the age of 2.5 years. The calving percentage among under 3-year-old hinds was only 38.0%. The 3-4-year-old hinds calved most successfully (calving percentage 87.9%). Although the heaviest hinds which are expected to be also the oldest ones gave birth to the heaviest calves (Table 1), the calf percentage started to decrease with age among middle-aged and older hinds being only 65.7% among over 10-years-old hinds and 41.7 after the hinds reached the age of 12 years. Hinds produced vital calves up to the 9th pregnancy during which the mean age of these hinds was 10.5 ± 0.2 years (n= 15) (Fig. 2).

During 1970 - 84 the calving period began usually on the 10th of May. The first half of calves were born up to May 22nd and 90% up to May the 29th. The beginning and the end of calving period varied greatly annually (27.4. - 15.5. and 22.5. - 5.6., respectively). The peak of calving varied yearly between May the 15th and 25th. The duration of calving time from the first birth until the main calving was on an average 19 days (range 9 - 32 days).

During 1970-84 together 913 calves were born (including stillbirths). The mean birth-weight of calves was 5.1 ± 0.04 kg (range 1.8 - 8.5 kg, n= 823). There was no annual variation in the birth-weight of newborn calves except the year 1973 which was a bad year and the 2 recent years (1983-84) when the birth weights have been significantly (P < 0.001) greater compared to the earlier years. Of the 913 calves born 49.2% (n= 448) were males and 46.9% (n= 427) were females. In addition to this 4.2% (n= 38) of calves could not be sexed. The sex-ratio (female:male) at birth was 1:1. The birth-weight of male calves was on an average 5.3 ± 0.1 kg (n= 423) and it was significantly greater (P < 0.001) than the birth-weight of female calves (5.0 ± 0.1 kg, n= 397). Calves of 3-year-old and older hinds weighed (5.2 ± 0.04 kg, n= 729) significantly more (P < 0.001) than the calves of young hinds (4.3 ± 0.1 kg, n= 90).

The mean age of hinds calving before the peak of calving was 5.6 ± 0.1 years (n= 344), being significantly higher than that of hinds calving

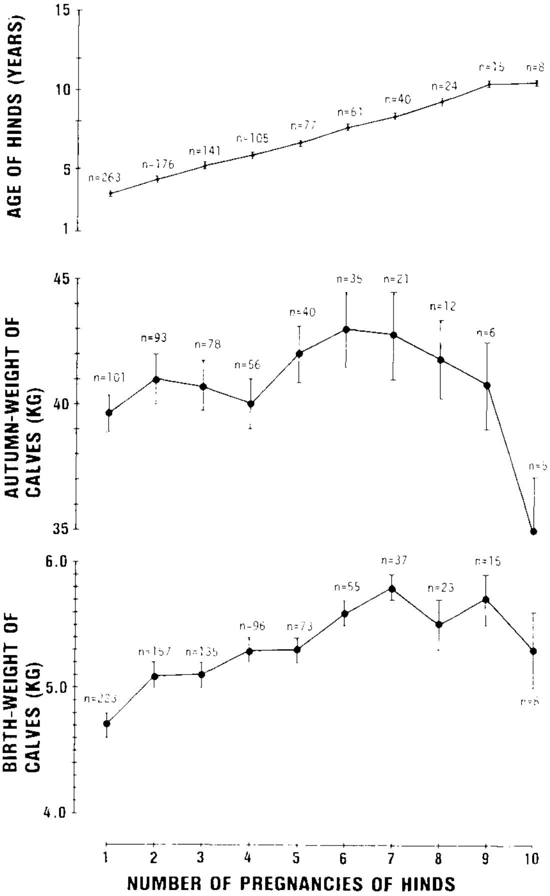

Fig. 2. Changes in calf birth- and autumn-weights as well as maternal age (x̄ ± S.E.) with respect to the number of pregnancies of the mothers.

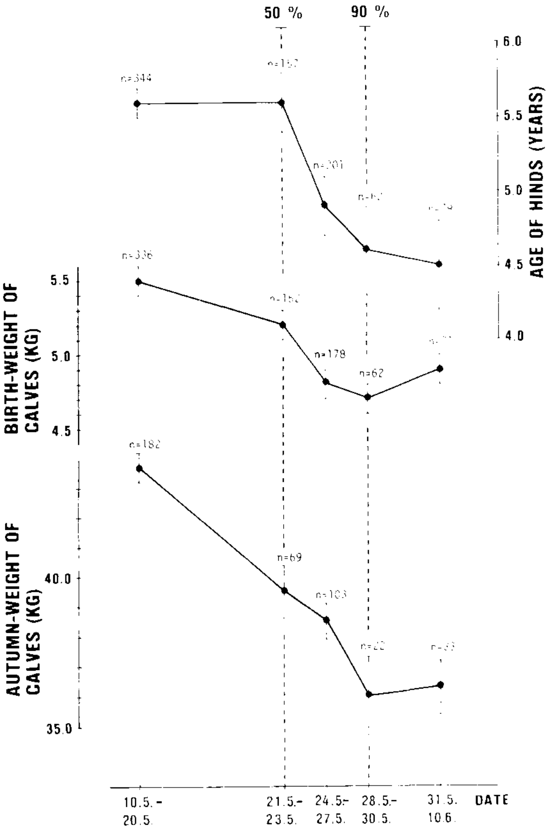

Fig. 3. Birth-weight, autumn-weight and age ($\bar{x}$ ± S.E.) of calved females in relation to timing of births. Peak calving (50% calves born) was 22 May and mean calving (90% calves born) 29 May. The lines are described according to groups; calves born before peak calving, during peak calving, after peak calving but before the main calving, during the main calving and calves born after the main calving.

after the peak (4.9 ± 0.2 years, n= 201) (Fig. 3). The mean age and weight of hinds which calved before the peak of calving time (5.6 ± 0.1 years, n= 344 and 72.7 ± 0.6 kg, n= 256, respectively) were higher than those of hinds which calved after the peak. Those hinds that calved during the main calving time were significantly ($P < 0.001$) younger (4.6 ± 0.3 years, n= 62) and lighter (67.4 ± 1.1 kg, n= 47) than the first mentioned.

The birth-weight of calves was related to the timing of births. The first calves that were born before the peak of calving were significantly heavier ($P < 0.001$) weighing 5.5 ± 0.1 kg (n= 336) than those who were born later. These calves were also the heaviest ones in autumn (Figs 3 and 4). The calves that were born in the beginning of the calving period were about 7.5 kg heavier in autumn than those born at the end. The difference of 0.6 kg (10.9%) increased during the summer and autumn months to 7.5 kg (16.9%).

Of those 913 calves born, 34.5% died before the slaughtering period. Male calves were slightly more likely to succumb (47.5%) than female calves (41.4%). 35.4% of dead calves died during the calving period in May - June, the rest (64.6%)of the calves died until the slaughtering period in November - December. During the calving period the mortality of male calves was on an average 11.6%, being almost double compared to that of female calves (6.8%). After the calving period the mortality ratio was on the contrary 23.7% for females and 21.7% for males.

The birth-weight of calves that died during the first 6 months was significantly lower ($P < 0.001$) compared to those that survived (4.6 ± 0.1 kg, n= 276 and 5.4 ± 0.04 kg, n= 487, respectively). The greatest number of calves that died during the calving period (67.2%) died during their first day of life. These calves were also the smallest ones (birth-weight 3.6 ± 0.2 kg, n= 45) and their birth-weight was almost 2 kg lower than that of surviving ones. Calves that died after the calving period were heavier at birth (4.9 ± 0.1 kg, n= 195) than those dying during the calving period (4.1 ± 0.1 kg, n= 81) but, however, lighter than the surviving ones. The smallest calf that survived during 1970-84 weighed 2.7 kg at birth.

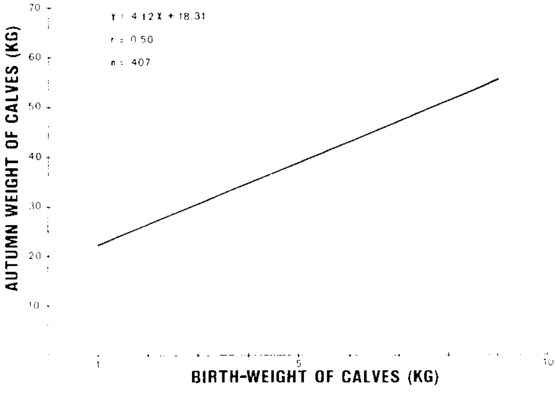

Fig. 4. The relationship between birth-weight and autumn-weight of calves. The line was obtained by linear regression analyses and is described by the following equation: $y= 4.2x + 18.31$, $r= 0.50$, $n= 407$, where y is the birth-weight and x is the autumn-weight of calves.

The principal causes of calf mortality during 1970-84 were stillbirths (17.1%), poor condition (20.7%), abandonment followed by starvation (11.7%), predation (10.8%) (red fox, *Vulpes vulpes* and golden eagle, *Aquila chrysaetos*), due to disease (8.0%) and accident (7.2%). Young hinds had more stillbirths (18.8%) than the 3-year-old and older hinds (3.8%). The mortality rate among the calves from young hinds was almost 10% higher than that of older ones. The largest number of calves of young hinds died just after parturition (45.8%) while the mortality of calves of full-grown hinds occurred mainly after the calving period (68.8%).

Discussion

By the turn of Mid-October over 90% of the hinds have ovulated and the conception rate in Finland is over 60% (Roine, 1974). Gestation takes 208 - 227 days depending on ambient conditions (McEwan and Whitehead, 1972; Dott and Utsi, 1973). Calving in reindeer and caribou usually commences in late April and reaches its peak in Mid-May (Espmark, 1971). In caribou populations calves are born during an effective 2-week period (Lent, 1966). Reindeer calves have been indicated to be born in even briefer periods (Holthe, 1975). In the present study calving from the first birth up to the date when 90% of calves were born took on an average 19 days. The timing of births is due to genetics as well as nutrition. The study by Espmark (1980) supports the theory of parturition delay in undernourished hinds. In reindeer populations the location of the herd home range area also has its effect upon the timing of the calving period. In Norway the peak of calving varied in different populations between May the 6th and the 29th (Holthe, 1975). On the other hand it has been found that when the level of nutrition was lower than usual before the normal time of estrus, the time for the onset of estrus was slightly delayed in white-tailed deer (*Odocoileus virginianus*) (Verme, 1965).

The pregnancy rate of reindeer and caribou in good conditions is known to be very high, in places over 90% (Parker, 1981; Mossing and Rydberg, 1982). The conception rate of Finnish reindeer is on an average 64.5% but the corresponding calving percent is 60%. The present findings about the calving percentage of hinds (on an average 79.4%) differ slightly from earlier Finnish observations. Less than half of those hinds weighing under 60 kg produced a calf but almost every hind weighing over 90 kg was pregnant also gave birth. Because age and weight correlate, it is expected that the heaviest hinds are also the oldest ones (Hamilton and Blaxter, 1980). However, the most successful in calving were the 3-8 years old hinds while the productivity of younger and older hinds was clearly decreased. The present observations about the reproductive ability of hinds and the influence of age and weight to it agree with earlier studies (Clutton-Brock *et al.*, 1982; Skogland, 1984).

Genetic factors, maternal age and weight as well as nutrition are found to be of importance for calf birth-weight, growth and survival (Bergerud, 1975; Albon *et al.*, 1980; Rognmo *et al.*, 1983). The birth-weight of newborn reindeer calves in Finland is about 5-6 kg (Timisjärvi *et al.*, 1984). In Sweden and Canada the corresponding figures are 6.5 - 7.0 kg and male calves are usually about 0.5 kg heavier. The birth-weight of newborn calves was on an average 5.1 kg, which is somewhat lower than is reported in Sweden (Espmark, 1971) and in Canada (Nowosad, 1975) but is however in agreement with earlier Finnish observations.

The birth-weight of calves has been found to correlate with maternal weight just prior to calving (Espmark, 1980; Rognmo *et al.*, 1983). In the present study the birth-weight correlated with maternal weight just prior to calving but also almost as precisely with maternal weight in the previous autumn. The smallest hinds in autumn produced the smallest calves in the spring. The hinds calved for the first time at the age of 3 years and produced vital calves up to the age of 10.5 years. After 10.5 years was reached the birth-weight of calves started to decrease and survival rate dropped (see Fig. 2). This is in agreement with the observations in wild reindeer populations in South-Norway where the weight of fetuses correlated with maternal age as long as the body condition of hinds did not deteriorate with age (Skogland, 1984). Maternal age and calf weight are also found to correlate among Norwegian semi-domestic reindeer (Lenvik and Bø, 1983).

Although the pregnancy rate of reindeer and caribou is known to be high, the net production is highly reduced being 40 - 60% in reindeer (Nowosad, 1975; Rehbinder, 1975) and 30 - 50%

in caribou (Bergerud, 1971; Parker, 1972). Mortality during the first few days of life is assumed to be as high as 20% (Pruitt 1961). The total loss in the period from late pregnancy to the end of lactation can be 55% in wild reindeer (Skogland, 1984). The net productivity of the present study herd was on an average annually 65.5%. The calf percentage dropped until the end of the calving period 12.2% and 22.3% more during the remaining 5 months.

The calves that died were significantly smaller than those surviving and the smaller the calf was at birth the more probably it died. Also in wild ungulates a significantly higher mortality has been found among the smallest neonates (Verme, 1977). The birth-weight of the smallest calf to survive was 2.7 kg, which is somewhat lower than is reported to be the critical birth-weight of neonatal survival among wild reindeer in Norway (Skogland, 1984).

Acknowledgements

We would like to thank Dr Peter C. Lent, Bureau of Land Management (602), Department of Interior, Washington, D.C. 20240 USA and Dr M. Kingsley for useful comments on the draft of this paper.

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Predicting energy expenditures for activities of caribou from heart rates

Steve G. Fancy and **Robert G. White**[1]

Abstract: Highly significant ($P<0.001$) linear relationships between oxygen comsumption (VO_2) and heart rate (HR) were found for six caribou (*Rangifer tarandus granti*) at several times during the year. The standard error of the estimate for predicting VO_2 from HR was within 10% of the mean VO_2 for 9 of 13 caribou/season combinations. Energy expenditures by caribou while feeding on grain at a trough, grazing, browsing and walking within a large enclosure were 12%, 17%, 18% and 46% higher than the cost of standing. HR's recorded during a given activity decreased sharply during September and October, and reached a minimum in January. An abrupt increase in HR's of female caribou occurred 3 weeks prior to parturition. Heart rate telemetry can be used to determine the relative energy expenditures of free-ranging caribou with reasonable accuracy.

Key words: caribou, oxygen consumption, heart rate, metabolic rate, *Rangifer tarandus*, energetics

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Rangifer, Special Issue No. 1, 1986: 123 - 130

Introduction

Measurements of energy expenditures by large animals are frequently made using closely-confined animals encumbered by equipment that restricts their behavior. Development of the CO_2 entry rate technique (Young *et al.*, 1969) and the doubly labeled water method (Lifson *et al.*, 1955) provided the methodology for estimating energy expenditures by free-ranging animals, but these methods are complex and expensive. Heart rate is common used to estimate energy costs by humans because it is easily measured and the measurements do not interfere with the subject's normal acitivites (Bradfield *et al.*, 1969; Acheson *et al.*, 1980). Some investigators working with ruminants have found poor agreement between heart rate and energy expenditure; the relationship is known to be affected by individual differences, season, time since the last feeding, type of activity, ambient temperature, excitement or stress, and other factors (Webster, 1967; Brockway and McEwan, 1969; Johnson and Gessaman, 1973; Holter *et al.*, 1975, 1976; Robbins *et al.*, 1979). However, other researchers, by controlling some of these factors, established relationships which predicted energy expenditure within 10% for individually-calibrated animals (Yamamoto *et al.*, 1979; Pauls *et al.*, 1981; Renecker and Hudson, 1983; Nilssen *et al.*, 1984; Richards and Lawrence, 1984; Fancy and White, 1985a). We investigated the heart rate/energy expenditure relationship for six caribou (*Rangifer tarandus granti*) throughout the annual cycle and used heart rate to estimate energy expenditures for activities as the caribou ranged within a large enclosure. Energy expenditures of caribou while cratering in snow are reported elsewhere (Fancy and White, 1985a).

Methods

Hand-raised caribou were kept within a 19-ha enclosure at the University of Alaska Large Animal Research Station in Fairbanks, Alaska, where they had *ad libitum* access to natural forage and a commercial livestock ration (Quality Texture, Fisher Mills, Seattle, WA). At the time of the experiments, the caribou were 16 - 35 months of age and weighed between 85 and 123 kg. A heart rate transmitter (J. Stuart Enterprises, Grass Valley, CA; see Follmann *et al.* (1982) for transmitter design) was implanted subcutaneously on either side of each caribou adjacent and approximately parallel to the sixth rib. The pulsed signals were received by a Telonics (Mesa, AZ) TR-2 receiver and were either plotted on a chart recorder or counted directly.

The relationship between O_2 consumption (VO_2, $l \cdot min^{-1}$) and heart rate (HR, $beats \cdot min^{-1}$) was determined for each caribou at several times during the annual cycle using an open-circuit respirometry system (Fancy, 1986). VO_2 and HR were measured concurrently once the caribou reached a steady state of O_2 consumption (i.e., when the rate of O_2 consumption was relatively constant) while walking or standing on a treadmill, or while standing in a respiration chamber. Caribou were taken directly from the enclosure prior to measurements.

Data from trials on the same caribou conducted within a 4 - 5 week period were combined to develop regression equations predicting VO_2 from HR for that season. These equations were then used to estimate VO_2 from HR of each caribou at the same time of year as

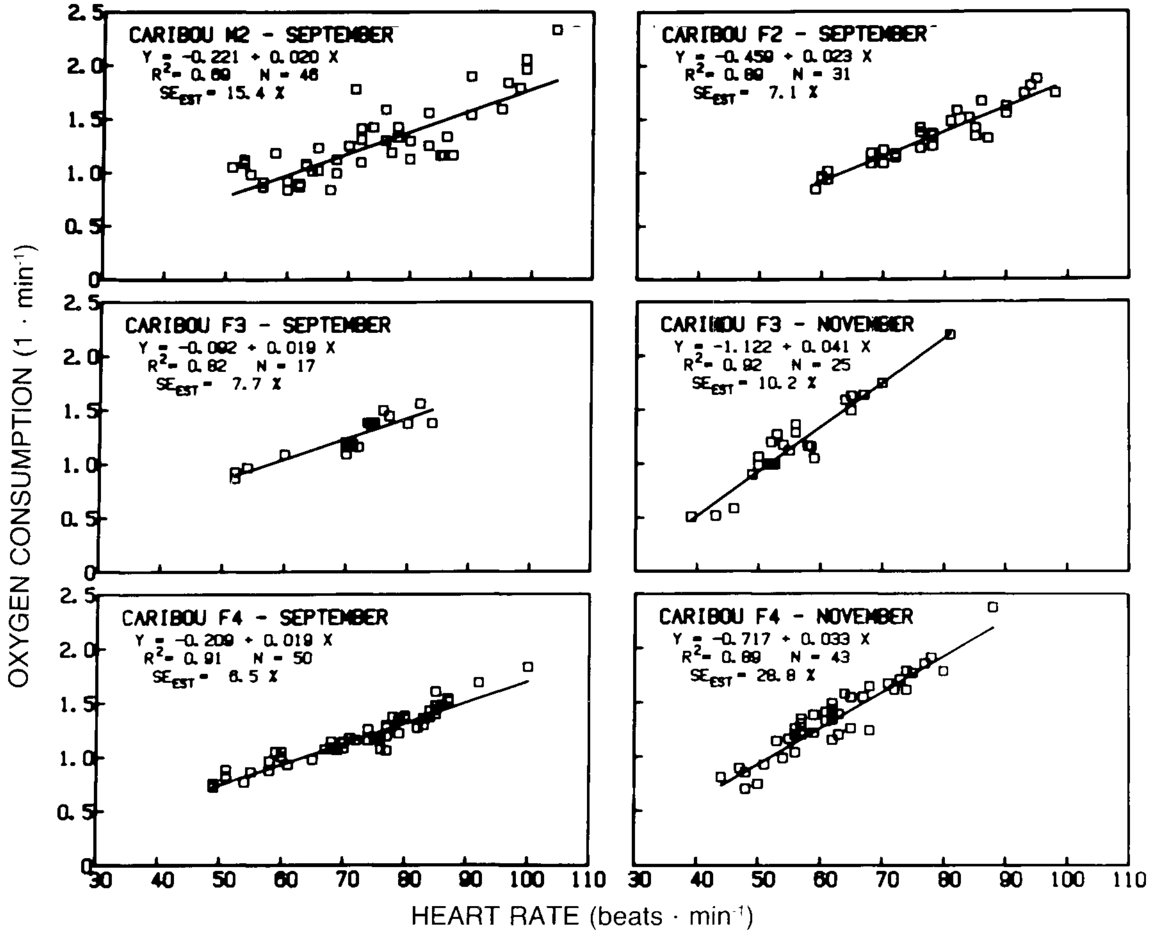

Fig. 1. Regressions of O_2 consumption on heart rate for caribou in late summer (September) and early winter (November). Data were collected while the caribou were standing or walking. The standard error of the estimate is for a new observation at the mean HR, expressed as a percentage of the mean O_2 consumption.

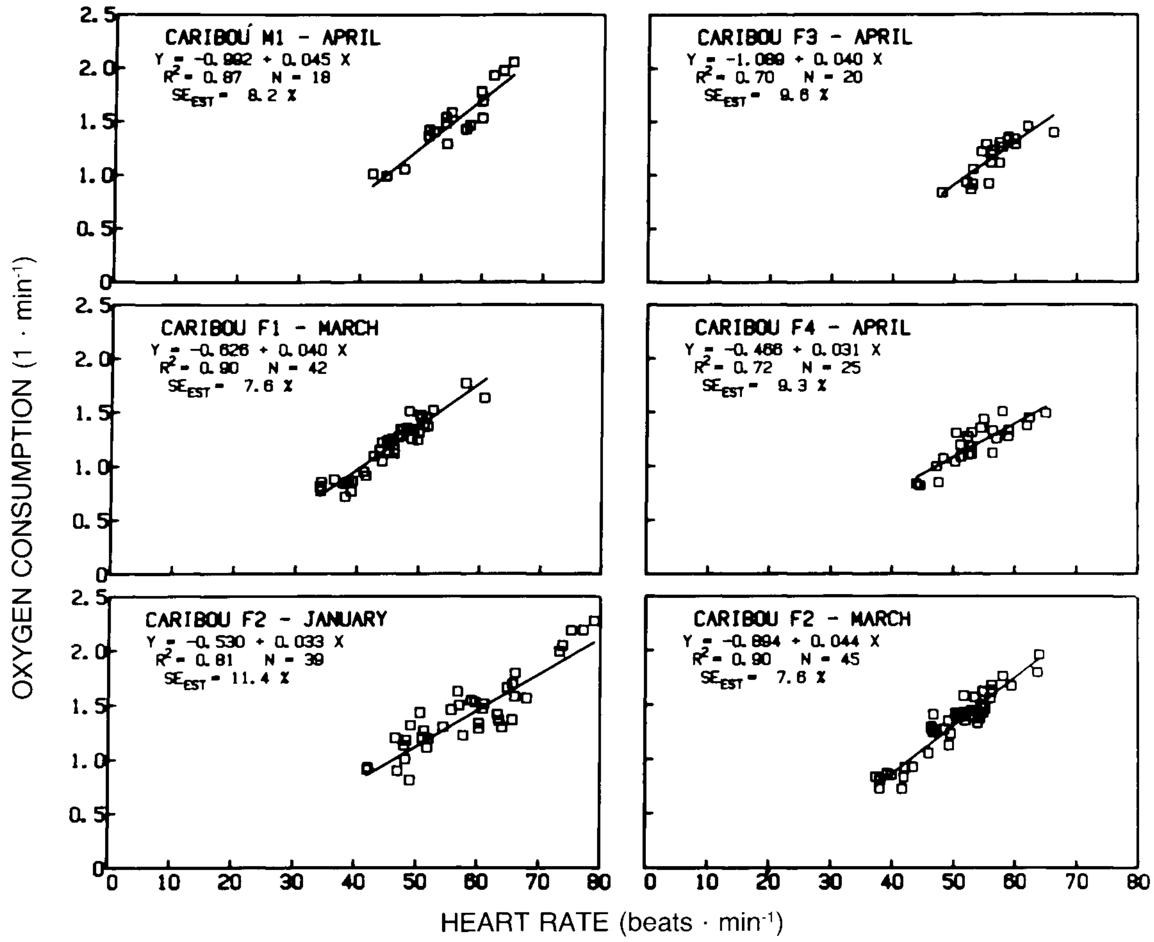

Fig. 2. Regressions of O_2 consumption on heart rate for caribou in winter.

they ranged within the 19-ha enclosure. Energy costs of individual activities of caribou in the enclosure were expressed as a multiple of the predicted energy cost of standing, thereby adjusting for seasonal differences in metabolic rates, time of day and other factors. An energy equivalent of 20.6 kJ·l O_2^{-1} (Brody, 1945) was used to convert VO_2 to energy expenditure. This value was based on a respiratory quotient of 0.90 determined from air samples taken from caribou while in the enclosure.

Eight activity categories were recognized: lying with head on the ground, lying with the head up but not ruminating, lying and ruminating, standing quietly, feeding on grain at a trough, grazing (without walking), browsing, and walking. Mean HR's were calculated from 30 sec counts taken continuously while the caribou was engaged in each activity. Statistical comparisons between regression lines were made by analysis of covariance (Zar, 1973; Neter and Wasserman, 1974). The standard error of the estimate for predicting VO_2 from one additional measurement of HR (at the mean HR) was calculated according to Zar (1973) as:

$$SE_{est} = \sqrt{S_{y \cdot x}^2 \cdot (1+1/n)}. \qquad (1),$$

where n is the sample size and $S_{y \cdot x}^2$ is the residual mean square.

Results

Highly significant (P<0.001) linear relationships between VO_2 and HR were found for all six caribou (Figs. 1 - 3). In 4 of the 13 cases, correlation coefficients increased about 1% when exponential equations were used, but these small improvements did not justify the transformations. Significant differences were found between the slopes of the regression lines (O_2 pulse, l O_2·beat⁻¹) between seasons for individual caribou, and among caribou within a season (Table 1). For example, the O_2 pulses of four

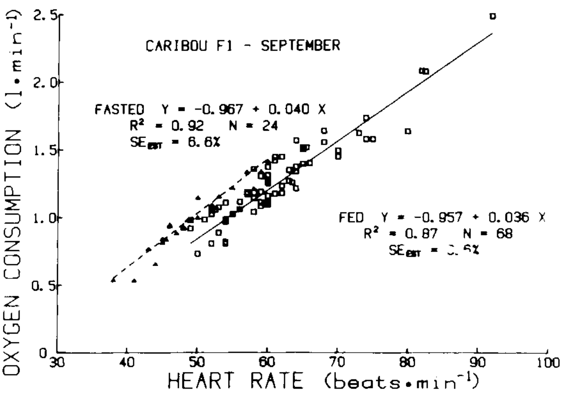

Fig. 3. Regressions of O_2 consumption on heart rate for caribou F1 in September when fed and following a 15 h fast. Measurements were made as the caribou stood or walked on a treadmill.

females averaged 69% higher in late winter (March - April) than in late summer (September). Four of the five caribou had the same O_2 pulse in late summer, but the elevations of the regression lines were significantly different (Table 1). The high O_2 pulse of caribou F1 in summer may be a result of pooling data collected throughout the month of September when HR's were decreasing rapidly (Fig. 4).

Significant differences were also found between the VO_2/HR relationships calculated for the same individual during a season. Although the O_2 pulses of caribou F3 and F4 in November were the same as those calculated 6 months later, the elevations of the two regression lines calculated for caribou F4 were significantly different (Table 1). In contrast, the O_2 pulse of caribou F2 in March was significantly greater than that calculated 3 months earlier. Some of these differences can be attributed to differences in the time since feeding, as fasting increases the elevation of the regression and lowers the range of HR's observed for the same activities (Fig. 3).

Heart rates of caribou decreased sharply during September and October, and reached a minimum in January (Fig. 4). Mean HR's of all female caribou increased by approximately 15 beats·min^{-1} during the 3 weeks preceeding parturition, then decreased sharply within 3 days following parturition (Fig. 4). The calves of caribou F1 and F2 died within 3 days of birth; therefore, these females lactated for only a few days.

The lowest energy expenditures occurred when the caribou were lying with their heads on the ground (Table 2). The expenditure of feeding at a trough was 12% higher than that while

Table 1. Summary of analyses of covariance comparing regression lines relating VO_2 to heart rates of caribou.

Comparison	No. of lines	Degrees of freedom	F-values Lines[1]	Slopes[2]	Elevations
Among individual caribou during summer	5	4, 202	65.2†	17.7†	63.8†
Among individuals during summer, excluding F1	4	3, 136	3.2*	0.8	3.4*
Among individuals during winter	8	7, 241	60.8†	3.4†	66.1†
Summer vs. Winter, Caribou F1	2	1, 106	128.3†	1.2	255.4†
Summer vs. Winter, Caribou F2	2	1, 72	222.3†	60.1†	384.6†
Summer vs. Winter, Caribou F3	2	1, 33	18.6†	11.2†	25.9†
Summer vs. Winter, Caribou F4	2	1, 71	103.5†	11.6†	195.4†
January vs. March, Caribou F2	2	1, 80	26.1†	8.4§	43.8†
November vs. April, Caribou F3	2	1, 41	0.8		
November vs. April, Caribou F4	2	1, 64	8.0†	0.2	15.8†
Fed vs. Fasted, Caribou F1	2	1, 88	10.7†	0.5	21.0†

[1] Test for equality among regressions (Neter and Wasserman, 1974:160)

[2] Test for equality of slopes and elevations among regressions (Zar, 1973).

* $p<0.05$.

§ $p<0.01$.

† $p<0.001$.

Table 2. Energy costs of activities relative to the cost of standing, as estimated from heart rates of caribou[1].

Caribou	Month	Body-weight, kg	Standing cost kJ/kg·h	Ratio[2] LHD	LHU	LR	FT	GRZ	BRW	WAK
F1	September	100	11.14	0.87	1.02	1.00	1.00		1.32	
F2	September	105	11.38	0.93	0.95	1.07				
F2	September	105	9.76	0.72			1.22	1.22	1.14	
F1	November	103	11.64				1.16	1.16		
F1	December	102	10.97		0.96	0.93	1.03	1.06		1.45
F2	December	120	9.02	0.78		0.89	1.04			
F1	January	102	7.09				1.17			1.68
F2	January	120	7.08				1.02	1.18		1.41
F2	January	120	7.02	0.77		0.86	1.03			1.36
F2	January	120	7.64	0.83	0.88	0.88	1.12	1.13		
F1	March	104	10.12	0.84	0.92	0.88	1.03	1.23		1.33
F1	March	104	10.83	0.62	0.95	0.99	1.14	1.17	1.23	1.47
F2	March	120	7.36	0.89		0.91	1.19	1.25		1.60
M1	April	111	7.92	0.71	0.85	0.91	1.15	1.10		1.49
M1	April	111	9.52	0.77	0.91			1.10		
F2	April	122	8.19	0.85		0.97	1.00			
F3	April	95	7.67	0.83		0.90	1.37	1.46		
F4	April	108	8.72	0.89		0.97				
F4	April	108	9.61		0.91	0.94	1.20	1.25		
F4	April	108	11.18	0.86	0.93	0.87	1.06	1.11	1.16	
Mean ratios				0.80	0.91	0.92	1.12	1.17	1.18	1.46
Standard errors				0.02	0.01	0.02	0.02	0.04	0.03	0.04

[1] Estimates are bases on regressions developed for each caribou at the same time of year as its application.
[2] Activity codes are: LHD=lying with the head down; LHU=lying with the head up; LR=lying and ruminating; FT=feeding at a trough; GRZ=grazing without walking; BRW=browsing; WAK=walking

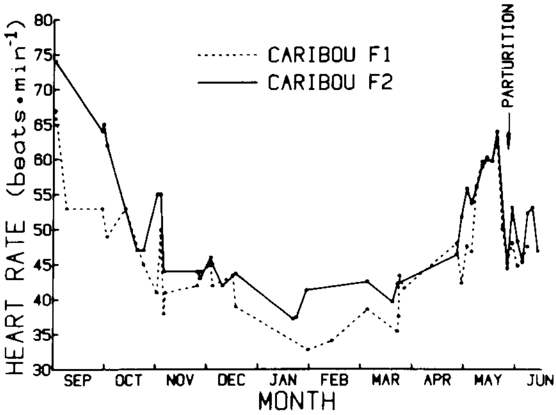

Fig. 4. Seasonal trends in heart rates of two female caribou feeding on grain at a trough.

standing. The highest energy expenditures involved locomotion; the energy cost of walking was 46% above the cost of standing (Table 2).

Discussion

The physiological components involved in the relationships between VO_2 and HR can be expressed by the following equation (Morhardt and Morhardt, 1971):

VO_2 ($l \cdot min^{-1}$) = $HR \cdot SV \cdot (A\text{-}V)O_2$ diff (2),

where HR is in $beats \cdot min^{-1}$, SV is the stroke volume ($l\ blood \cdot beat^{-1}$), and (A-V) O_2 diff is the difference between the O_2 concentrations of arterial and venous blood ($l\ O_2 \cdot l\ blood^{-1}$). Equation 2 can be rearranged to show that the volume of O_2 consumed per beat, or O_2 pulse, is equal to the product of SV and (A-V) O_2 diff. If the O_2 pulse is constant, or varies systematically over a range of HR, errors in the prediction of VO_2 from HR will be small. This was the case in summer, when only slight increases in O_2 pulse with HR were observed for four of five caribou (Fig. 5); this indicated that variations in O_2 requirements within the range of HR's observed were met primarily by changes in HR. Changes in stroke volume and (or) the arteriovenous O_2 differences were more pronounced in winter (Fig. 5). Because of seasonal differences in O_2 pulse, regression equations based on pooled data collected in summer and winter, such as those presented by Pauls *et al.* (1981), may be misleading.

Nilssen *et al.* (1984) measured VO_2 and HR of Norwegian reindeer (*R. t. tarandus*) and Svalbard reindeer (*R. t. platyrhynchus*) standing or running on a treadmill. The regression equations given by Nilssen *et al.* (1984) were recalculated for comparison with our results by assuming mean body weights of 89.1 and 76.0 kg for Norwegian and Svalbard reindeer, respectively (K. Nilssen, pers. comm.). The slopes of the regression lines for Norwegian reindeer ($0.033\ l\ O_2 \cdot beat^{-1}$) and Svalbard reindeer ($0.030\ l\ O_2 \cdot beat^{-1}$) in summer were within the range of those calculated for caribou (Figs. 1 - 3), but the intercepts calculated for Norwegian and Svalbard reindeer were lower than those for caribou. Conseqnently, the same HR would be associated with a lower VO_2 for reindeer when compared to caribou. The slope of the winter equation for Norwegian reindeer ($0.035\ l\ O_2 \cdot beat^{-1}$) was also within the range of those calculated for caribou, but the slope for Svalbard reindeer ($0.025\ l\ O_2 \cdot beat^{-1}$) was lower. Some of the differences noted above may be explained by the higher treadmill speeds used by Nilssen *et al.* (1984). Results of studies with humans (Rusher, 1965; Davies, 1968) and small mammals (Morhardt and Morhardt, 1971) indicate that as HR approaches a maximum, further increases in VO_2 are associated with only small changes in HR.

Pauls *et al.* (1981) and Renecker and Hudson (1983) used HR to predict energy costs of activites for wapiti (*Cervus elaphus*) and moose (*Alces alces*), respectively. The relationships between metabolic rates and HR they presented were curvilinear, probably because they included data for lying as well as active animals. Studies with dogs and humans have found that the mean O_2 pulse of inactive subjects is lower than that for the same individuals during exercise (Warnold and Avidsson Lenner, 1977), and that abrupt decreases in stroke volume can occur as a subject changes from a lying to standing position (Wang *et al.*, 1960; Rushmer, 1965). These findings suggest that when relationships between VO_2 and HR are developed using only standing and active animals, as in this study, they will give unreliable estimates of lying costs. Indeed, the predicted 8.7% increase for caribou in the cost of standing relative to the cost of lying and ruminating, is only half of that determined from 22 paired VO_2 measurements of caribou lying and standing in a respiration chamber (16%; Fancy, 1986), and is much lower than the incremental cost of standing reported for other wild ruminants (Fancy and White, 1985b). Consequently, the costs of lying were overestimated and the values in Table 2 should not be used to calculate energy budgets.

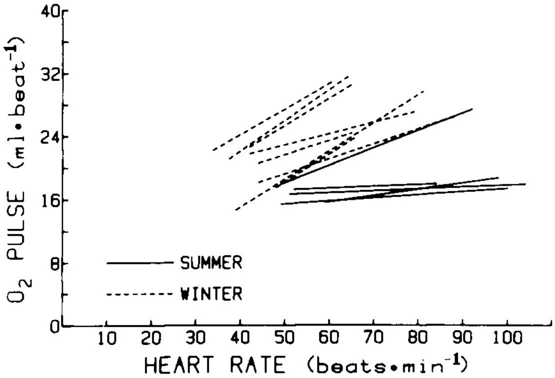

Fig. 5. Regressions of O_2 pulse on heart rate in summer and winter; values were calculated from data presented in Figures 1 - 3.

Because ruminants spend a large portion of the day grazing and browsing, the costs of these activities are a major component of daily energy budgets. The estimated 17% increase in the energy cost of grazing above standing for caribou (Table 2) agrees closely with the mean difference of 16% between VO_2 of caribou standing and feeding in a respiration chamber or headstall (n=4; Fancy, 1986). Movements of the neck and mouth apparently account for most of the incremental cost, as VO_2 returned to standing values within 30 sec after the end of the feeding bour. The reported incremental costs of grazing by wapiti (6.0%; Pauls *et al.*, 1981) and moose (4.6%; Renecker and Hudson, 1983) are lower than those for caribou, possibly because standing costs for those two species are higher than those for caribou (Fancy and White, 1985b). The mean energy cost of browsing costs for moose and wapiti were also similar (2 - 4% higher) to grazing costs (Pauls *et al.*, 1981; Renecker and Hudson, 1983).

The energy cost of walking, above that required for standing, increases linearly with walking speed for caribou and most other species (Fancy and White, 1985b). The energy cost of walking predicted from HR's of caribou M1, F1 and F2 was 46% higher than the standing metabolic rate. From VO_2 measurements for these three caribou while walking on a treadmill (n=407), we determined that the metabolic rate of these caribou would be 46% above the standing rate when they walked at 3.4 km·h^{-1}. We did not measure walking speeds of caribou in the enclosure, but the energetically-optimal walking speed (Fancy and White, 1985b) for caribou is approximately 3.5 km·h^{-1}, and a mean walking speed of 3.4 km·h^{-1} during HR measurements appears reasonable.

The close relationships between VO_2 and HR suggest that HR telemetry could be extremely useful in describing the energetics of wild caribou, particularly in summer when variations in O_2 requirements are met primarily by changes in HR. The pulsed signals can be received several kilometers from the transmitter; therefore, it would be possible to monitor HR's without influencing the behaviour of the caribou. Reasonably accurate predictions of VO_2 from HR could be made using an equation combining data from several caribou. For example, the standard error of the estimate calculated from the combined summer data for caribou M2, F2, F3 and F4 ($Y=-0.242+0.020\,X$; $r^2=0.79$; n=144) is within 10.6% of mean VO_2. Changes in stroke volume and O_2 extraction from the blood are of greater importance in winter than in summer for meeting varying O_2 requirements. Because these components differ substantially between individuals in winter (Fig. 5) it is unlikely that a general regression equation for accurately estimating activity costs from HR in winter could be developed.

Acknowledgements

This research was supported by a Graduate Fellowship in Resource Problems to S. G. Fancy from the University of Alaska, and by the Institute of Arctic Biology. S. G. Fancy's travel to Whitehorse was supported in part by a grant from the Jack R. Luick Memorial Travel Fund. We gratefully acknowledge Drs. R. D. Cameron, F. C. Dean, C. C. Gates, D. R. Klein, E. C. Murphy, D. L. Thomas and an anonymous reviewer for their comments on an earlier draft of the manuscript.

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Comparison of caribou physical characteristics from Yukon and neighboring caribou herds.

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Abstract: Data on seven external body measurements of caribou from six woodland and two barren-ground caribou herds from Yukon, Alaska, Alberta and British Columbia were compared. Comparisons between females in the fall and winter and mature males in the fall revealed that (1) barren-ground Porcupine caribou were consistently smaller than caribou from other herds, (2) British Columbia and Alberta caribou tended to be larger than Yukon caribou, or the Alaskan caribou studied, (3) central Yukon caribou were intermediate in body size, (4) no difference was found between Yukon «mountain» and «woodland» type caribou in body size, and (5) the barren-ground Fortymile caribou were more similar in physical characteristics to Yukon woodland or mountain caribou than to those of the barren-ground Porcupine herd. These data support Banfield's (1961) view of a gradient of decreasing physical size from the northern British Columbia — Alberta herds through the Yukon mountain or woodland herds to the northern barren-ground herds.

Key words: caribou, body measurement, barren-ground caribou, mountain and woodland caribou, taxonomy

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Rangifer, Special Issue No. 1, 1986: 131 - 135

Introduction

Banfield (1961) identified two subspecies of caribou (*Rangifer tarandus*) in Yukon, the «woodland» or «mountain» caribou (*R. t. caribou*) in the south, and the barren-ground caribou (*R. t. groenlandicus*) (also referred to in the literature as *R. t. granti*) in the north. He further suggested that caribou of the central and northern Yukon mountains were integrades between the larger northern British Columbia (B.C.) and southern Yukon caribou and the smaller barren-ground caribou. The size of external body parts of caribou should therefore show a declining gradation from southern (Alberta — B.C.) herds through to northern barren-ground herds (Fortymile, Porcupine), with southern and central Yukon herds intermediate to those two extremes.

Little information has been presented subsequent to Banfield's work to either support or reject his view of intergradation. The advent of more efficient capture techniques and access to previously remote areas has allowed the collection of more detailed information on the distribution and physical characteristics of Yukon and neighboring caribou herds to test Banfield's intergradation hypothesis (Alaska Department of Fish and Game, unpublished data; Farnell, 1982; Farnell and Russell, 1984; Gauthier and Theberge, 1985; Larsen, 1980; Yukon Wildlife and Fisheries Branch, unpublished data). We report data on body measurements of caribou gathered from four Yukon *R. t. caribou* herds and one *R. t. groenlandicus* herd as well as data from two *R. t. caribou* herds in western Alberta and B.C. and one *R. t. groenlandicus* herd in Alaska.

Study area and methods

The names and location of herds were taken as given from the researchers reporting on them (Fig. 1). For data on the Fortymile, Porcupine and Carcross herds we have relied on the generosity of researchers from those areas. The Fortymile and Porcupine herds are classified as *R. t. groenlandicus* following Youngman (1975). The remaining herds are considered *R. t. caribou*. We have divided *R. t. caribou* herds into «woodland» or «mountain» types on the basis of winter range use, with «mountain» type herds using boreal forest ranges (Bergerud, 1978; Edmonds and Bloomfield, 1984; Farnell, 1982; Farnell and Russell, 1984; Gauthier, 1984; Hatler, 1983; Larsen, 1980). Based on this criterion, the Western Alberta, Carcross and Finlayson herds are classed as «woodland» demes, the Burwash and Wernecke herds as «mountain» demes, and the Spatsizi herd as an intergrade.

Age, sex and seasonal differences are often reflected in body measurements, and we therefore classified data according to those categories. We grouped seasons into summer, fall, winter and spring, but have sufficient data to report only on mature females in the fall and winter and mature males in the fall. We defined «mature» as an animal of reproductive age ($>=2$ years of age for females and $>=3$ to 4 years of age for males).

Seven measurements were recorded for animals live-captured among the herds (Table 1) but not all data were collected in the same manner nor were all standard body measurements collected consistently from all herds. For most herds, data were collected for only selected age and sex groups (Figs. 2 and 3). Table 1 shows the sample sizes for each herd according to season, age and sex. We recognise that sample sizes for each herd when classed by the given categories are relatively small, and that the use of external physical characteristics in distinguishing among subspecies is potentially biased by the effect of environmental factors (for example, nutritional regimes) on body size. We urge that the results be treated as preliminary and therefore with caution. Descriptive statistics were calculated for each variable according to herd, season, age and sex, and were tested for differences using analysis of variance and the studentized maximum modulus test (Sokal and Rohlf, 1981).

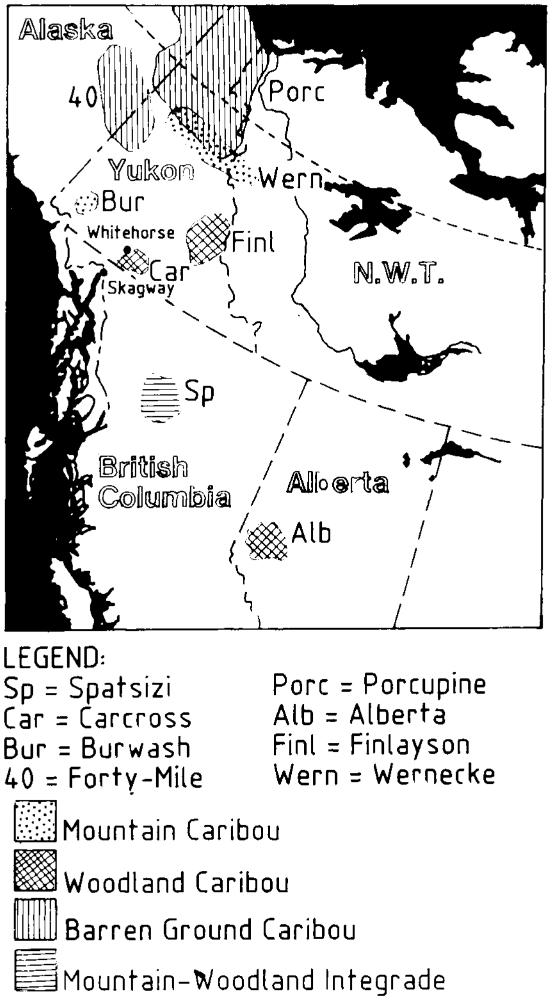

Fig. 1. Locations and designations of caribou herds used for comparisons of body size characteristics.

Results and discussion

Five major features are evident (Table 1; Figs. 2, 3). First, Porcupine caribou (*R. t. groenlandicus*), which comprise the northernmost herd, are consistently smaller in external physical measurements than any of the other herds measured. Second, the southernmost herds (Western Alberta, Spatsizi), tend to be larger in most physical measurements than Yukon caribou. Third, Yukon *R. t. caribou* of the central and northern mountains tend to be intermediate in size between the larger caribou of the southern herds and the smaller northern barren-ground caribou. This result supports Banfield's (1961) view that the caribou of the central and northern Yukon mountains are intergrades between the

Table 1. Summary statistics of caribou body size characteristics according to season, sex and herd.

Season	Sex	Herd	Heart girth (cm)			Total length (cm)			Hind foot length (cm)			Shoulder height (cm)			Chest height (cm)			Min. neck circumference (cm)			Weight (kg)		
			N	Mn[1]	SE[2]	N	Mn	SE	N	Mn	SE	N	Mn	SE	N	Mn	SE	N	Mn	SE	N	Mn	SE
Fall	Female	Porcupine	9	119.3	2.81	9	177	4.37	10	53.28	0.58	9	104.4	1.44	9	59.00	1.14	0			10	88.9	3.34
		Carcross	16	127.4	1.23	15	208.5	2.02	11	55.56	1.00	6	119	1.59	6	69.83	2.63	0			15	132.3	2.78
		Burwash	24	122.7	1.13	25	204.6	4.49	11	56.27	0.30	12	115	0.69	12	80.00	1.21	19	52.47	1.76	21	116.9	3.87
		Spatsizi	10	133.5	1.72	10	203.5	2.65	10	58.60	1.02	10	117.8	1.84	0			10	58.20	1.49	1	154	
		Fortymile	19	121.1	0.92	20	196.4	1.38	20	57.95	0.48	2	112	3.00	0			17	51.18	0.81	6	110.7	3.54
Winter	Female	Wernecke	8	122.8	1.81	8	203	2.66	2	48.00	5.00	0			0			7	50.57	1.31	5	110.8	5.29
		Finlayson	23	133.6	1.78	22	216.6	3.65	23	57.71	0.53	15	115.9	2.17	21	67.48	1.82	0			0		
		West Alberta	10	134.8	3.04	10	222.9	2.56	0			10	130.4	1.36	0			0			0		
Fall	Male	Porcupine	10	128.6	1.55	13	194.9	2.29	13	57.75	0.62	11	112.1	1.46	11	63.45	0.94,	0			13	125.5	3.54
		Carcross	4	159	3.70	4	246.8	6.16	3	62.23	0.72	2	127	0.00	2	70.00	4.00	0			4	206.5	5.56
		Burwash	8	135.5	4.31	8	214.1	9.00	0			0			0			5	70.40	5.54	8	176.8	12.33
		Fortymile	5	136.4	3.67	5	215.6	5.09	6	64.50	0.56	0			0			5	62.80	1.66	0		

1. Mn=Mean 2. SE=Standard Error

southern *R. t. caribou* and northern *R. t. groenlandicus*. Fourth, when comparisons were made between «mountain» and «woodland» types at relatively the same latitude, no consistent differences were found. Fifth, Fortymile caribou, classed as *R. t. groenlandicus*, appear more similar to *R. t. caribou*, particularly the Burwash animals, than they do to the other barren-ground herd (Porcupine) with which they were compared. This degree of physical difference between the Fortymile and Porcupine herds is unexpected given reports of migration and intermingling of large numbers of animals had taken place between the herds as suggested by Skoog (1968). In spring 1957 an estimate of 30000 animals of the Fortymile herd migrated northward with the Porcupine herd, and in spring 1964 a large portion of the Fortymile herd once again moved north with Porcupine caribou. Such large-scale intermingling should preclude findings of significant differences on physical characteristics between the two herds. However, more recent radio telemetry work indicates that intermingling between the herds commences post-rut (Whitten and Cameron, 1982). While the two herds may share winter ranges in some years, individuals of each herd tend to return to their respective calving grounds (Farnell and Russell, 1984).

Regarding the close relationship between Fortymile and Burwash caribou, during the 1880's and 1890's, the majority of an apparently much larger Fortymile herd ranged farther east and southeast than during later periods and extended as far as the Whitehorse-Skagway area (Skoog, 1968). A large movement of caribou occurred again in 1924 along the summit of the coast range above Skagway and were observed near Whitehorse, at a time when east-central Alaska herds were thought to be at peak numbers (Murie, 1935). In 1936 Fortymile caribou apparently migrated southeast and wintered near Kluane Lake (Rand, 1945). It may be that caribou of southwest Yukon are remnant herds of a once much larger Fortymile herd migrating through southwest Yukon. The available data suggest that Fortymile herd caribou are more closely related in body size characteristics to the Burwash and Carcross caribou than to the Porcupine animals.

Whether the differences in body measurements among herds are phenotypic or genotypic in origin will require more detailed comparisons

Physical Measurement	Mature Females–Fall					Mature Females–Winter			Mature Males–Fall			
	South ──► North					South ──► North			South ──► North			
Heart Girth	1 Sp	2 Car	3 Bur	4 40	5 Porc	1 Alb	2 Finl	3 Wern	1 Car	3 Bur	2 40	4 Porc
Total Body Length	3 Sp	1 Car	2 Bur	4 40	5 Porc	1 Alb	2 Finl	3 Wern	1 Car	3 Bur	2 40	4 Porc
Hind Foot Length	1 Sp	4 Car	3 Bur	2 40	5 Porc		1 Finl	2 Wern	2 Car		1 40	3 Porc
Shoulder Height	2 Sp	1 Car	3 Bur	4 40	5 Porc	1 Alb	2 Finl		1 Car			2 Porc
Chest Height		2 Car	1 Bur		3 Porc				1 Car			2 Porc
Minimum Neck Circumference	1 Sp		2 Bur	3 40						1 Bur	2 40	
Weight	1 Sp	2 Car	3 Bur	4 40	5 Porc				1 Car	2 Bur		3 Porc

Fig. 2. Ranking of caribou herds according to sex and season for each physical measurement. Legend: Sp=Spatsizi, Car=Carcross, Bur=Burwash, 40=Fortymile, Porc=Porcupine, Alb=Alberta, Finl=Finlayson, Wern=Wernecke.

1. Numbers above the herd names indicate the rank order for each variable from largest (1) to smallest (5).
2. If herds are not joined by a line, they are statistically different at P=0.05. In a few instances, no lines are present indicating insufficient data to test for significance. Dotted lines are used in a few instances to join herds which are not statistically different.

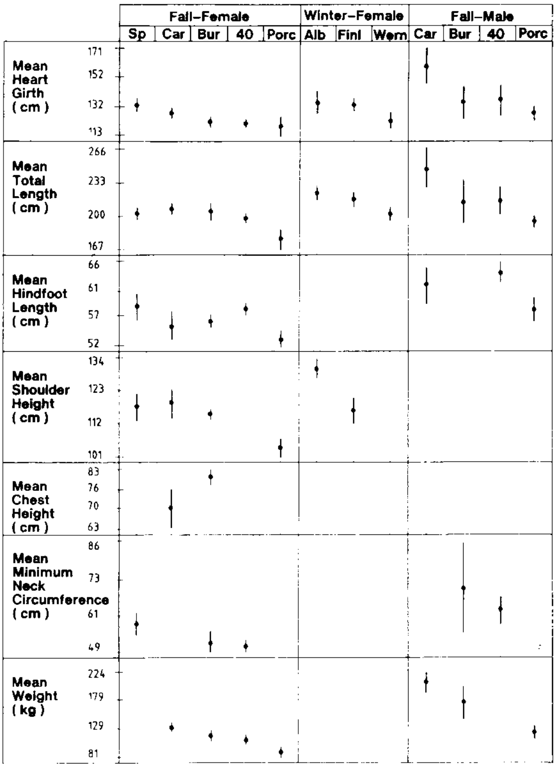

Fig. 3. Chart of summary statistics of caribou body size characteristics.

using techniques which assess genetic relatedness. The time is long past due for an extensive taxonomic study of herds within the zone of intergradation.

Acknowledgements

We wish to express our gratitude to T. H. Manning, W. Regelin, A. W. F. Banfield, M. Hoefs, D. Hatler and J. Davis for helpful comments on an earlier draft. We also thank D. Larsen (Carcross herd), M. Hoefs and B. Horejsi (Porcupine herd), and J. Davis (Fortymile herd) for providing us with data on caribou measurements from their respective herds. J. McDonald assisted in compiling data and initial drafts of figures, and T. Rodgers prepared final figures.

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Wolf predation in the Burwash caribou herd, southwest Yukon

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Abstract: The role of wolf predation as a proximate mortality factor influencing caribou herd growth was assessed in the Burwash herd (400 animals) in the southwest Yukon between 1980 - 1982. Ten to 14 wolves in two packs preyed primarily on caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) with disproportionate consumption of caribou (relative to available biomass) in the rut and winter periods. Wolf predation was responsible for 72% of total annual mortality in 1980 - 1981 and 46% in 1981 - 1982. Losses due to human harvest varied between 7 to 13%. Additional limited data on climatic factors and winter forage indicated forage-climate were not major proximate mortality factors in 1980 - 1981, but that early-calving climate may have been a factor in increased calf mortality in 1982.

Key words: wolves, caribou, predation, forage-climate

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Rangifer, Special Issue No. 1, 1986: 137 - 144

Introduction

There is general agreement among researchers that the population growth of many mainland caribou (*Rangifer tarandus*) herds is primarily limited by low recruitment to breeding age due to mortality (Bergerud, 1980; Kelsall and Klein, 1979). Wolf predation has been identified as an important source of mortality in a number of caribou studies (Davis, *et al.*, 1980; Kuyt, 1972; Miller and Broughton, 1974) with some researchers arguing that predation alone can limit population growth (Bergerud, 1980). However, numerous researchers have pointed out the potential complexity of interactions of predation-forage-climate, among other factors, which can confound interpretation of the identity and degree of factors primarily responsible for changes in numbers (Connolly, 1981; Keith, 1974).

The study of a caribou (*R. t. caribou*) herd in southwest Yukon known as the Burwash herd examined the likely contribution of wolf predation as a proximate mortality factor in the limitation of herd growth. We reasoned that the likelihood that predation was a major proximate mortality factor would be strong if changes in herd numbers were not related to natality, ingress or egress and human harvest. Earlier reports on the abundance (Gauthier and Theberge, 1985) and distribution (Gauthier *et al.*, 1985) of the Burwash herd provided data on these factors. In addition, studies of wolf food habits should show that the number of caribou eaten was significant in relation to caribou productivity. The significance of predation as a limiting factor depends upon the likelihood that the prey population is not at or near a range carrying capacity. If it were, any decrease in predation would theoretically be compensated for by increased starvation (Theberge and Gauthier, 1985). In this paper we report data on wolf food habits and the general contribution of some key range components.

Study area

The study area was located on the northeastern flank of the St. Elias Mountains (Fig. 1). It included a 160 km^2 western subregion of rolling tundra plateau between 1200 and 2000 m known as the Burwash Uplands, a 60 km^2 eastern subregion of largely tundra plateaux between 1100 and 1900 m known as the Brooks Arm plateau, and a central forested lowland subregion of 1450 km^2 (the Shakwak Trench) bisecting the two upland plateaux subregions. The remaining areas of the Burwash and Brooks Arm subregions consist of mountain peaks rising to 2350 m and ridges and river valleys covered by boreal forest generally below 1220 m.

The study area lies on the rain shadow of the St. Elias Mountains and is characterized by a dry cold-continental climate. Major vegetation cover types include boreal forest (largely *Picea glauca*, *Populus balsamifera* and *Populus tremuloides*), mainly below 1220 m, and subalpine and alpine habitat (principally *Salix* spp., *Betula* spp., and sedges and grasses) above 1220 m.

Three other species of ungulates inhabit the region: Dall's sheep (*Ovis dalli*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*). Large predatory mammals are wolves (*Canis lupus*), grizzly (*Ursus arctos*) and black bears (*Ursus americanus*), coyotes (*Canis latrans*), fox (*Vulpes vulpes*), wolverine (*Gulo gulo*), and lynx (*Lynx lynx*).

Gauthier and Theberge (1985) reported demographic data on the Burwash herd. All evidence indicated stable or slowly increasing numbers from the fall of 1978 until winter 1982 when a decline in numbers was attributed to movement of short duration (1-month) from the study area. Ingress did not appear to be a significant factor influencing herd size. Since there was no evidence of variations in productivity among years and movements from the study area were accounted for in changes in numbers, the results suggested that mortality factors were important in limiting growth of the herd over time.

Methods

Wolf predation

Information on wolf numbers, sex and age composition were collected from aerial and ground observations of wolves, telemetric monitoring data of radio-collared wolves and information provided by local trappers and residents. Three wolves were equipped with radio collars: two by aerial capture from a helicopter with CapChur equipment using M99 and rompun, and a third by live- trapping using modified Victor No. 4 leg-hold traps. Aerial radio relocations of the collared wolves were made on 137 separate occasions, with an additional 43 sightings of uncollared wolves.

To assess wolf food habits, a total of 388 wolf scats were collected from September 1978 to June 1982 on transects and at one wolf denning site (during the spring of 1980 and 1981) within the area of wolf distribution. Techniques of aging, laboratory cleansing of scats and the method of sample selection of hairs have been described in Gauthier (1984). Caribou and moose calf hair could be distinguished from adult-subadult-yearling hair only for the calving season (15 May - 30 June), the only season for which caribou and moose were separated into age classes. Identification keys for calf versus older-aged caribou hair were developed from calf hair taken from Burwash animals during the calving period and older-aged caribou during the summer. The proportion of prey hair in scats for the calving (May - June), rut (September - October) and winter (November - April) periods was used to predict the number of prey animals consumed by wolves in each of those seasons.

Floyd *et al.* (1978) proposed a regression method to estimate the amount of prey biomass consumed by wolves based on knowledge of individual prey weights. We derived seasonal estimates of weight for caribou from live-capture data and for moose from literature sources (see Gauthier, 1984 for complete description). These weight data were used in the regression method to estimate the biomass of each prey type consumed by wolves seasonally (for example, scat analysis showed that adult caribou accounted for approximately 70 kg of prey consumed by wolves in calving 1980, or 17% of total prey biomass). Numbers of caribou and moose (Gauthier, 1984; Gauthier and Theberge, 1985) derived from censuses were converted to biomass values and compared to estimated biomass values derived from scat data (representing amount of prey consumed by wolves). Contingency table analysis was used to assess whether the prey biomass ratio of caribou:moose derived from scat analysis was significantly different from the

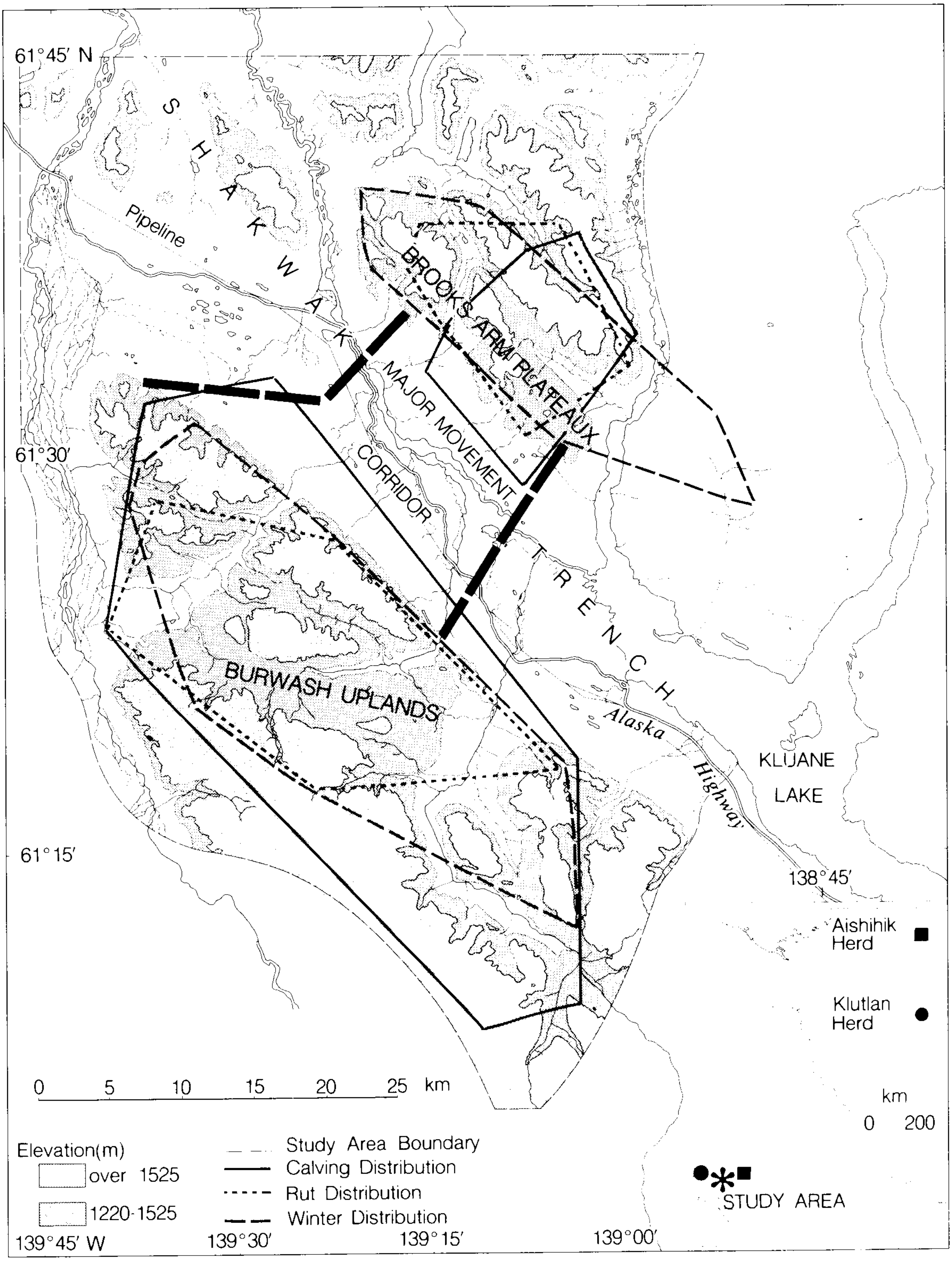

Fig. 1. Burwash caribou herd study area.

total prey biomass ratio for each of the three seasons.

Based on the number of wolves in the region, wolf seasonal food requirements were calculated; approximately 2.0 kg of food per day for adult wolves and 2.5 to 3.8 kg of food per day for wolf pups (Mech, 1970; Haber, 1977). For example, in the 123 day calving/post-calving period of 1980, we estimated approximately 2500 kg of food would be required by the 10 adult wolves in the region. We recognize that wolves may not meet their requirements and these figures are therefore relatively crude estimates. Each of the seasonal estimates was apportioned to prey type based on the estimated proportion of that prey type derived from scat analyses (for example, wolf scat analyses showed that adult caribou accounted for 17% of prey biomass consumed in the 1980 calving period or 425 kg of the 2500 kg estimated wolf food requirement). Each estimate of prey species biomass was divided by the estimated individual prey weight to give the number of prey consumed (for example, the estimate of 425 kg of adult caribou consumed in calving 1980 was divided by an estimated weight value of 84 kg to give five adult caribou consumed by wolves in calving 1980). In all of the foregoing calculations, estimates of scavenging activity and the amount of carcasses consumed were included. Complete details of methods and calculations are given in Gauthier (1984).

Forage and climate

Vegetative cover types were classified through Landsat satellite image analysis (Gauthier, 1984). The number of caribou observed in each habitat type was compared with the area size of each habitat type for each of the three seasons.

Caribou food habits were assessed through analyses of fecal pellet samples, a recognized technique for ungulates (Sparks and Malechek, 1968). Twenty-nine samples of pellets were collected: 4 during calving, 5 during rut and 20 during winter. The microhistological analytical techniques used were the same as those described by Hansen *et al.* (1982), using 100 samples or readings of plant fragments per pellet group. Seasonal differences in the proportion of five vegetation classes present in caribou feces were assessed by contingency table analyses.

Based on analyses of food habits, emphasis was placed on assessing lichen biomass. One 100 m straight-line transect was sampled in each of six sedge-grass-lichen communities using a 25 x 25 cm square at 32 randomly selected points along each transect from which to collect lichen samples. Samples were sorted and identified in the laboratory, oven-dried and weighed. Total lichen biomass estimates per transect were correlated (using Pearson's product-moment correlation test) with the cumulative total number of caribou observed in each transect area on all winter aerial surveys.

Possible effects of weather were assessed from climatic information: total snowfall and precipitation from 1967 to June 1982 (monthly records of Atmospheric Environment Service); snow thickness and hardness were recorded on transects (rammsonde penetrometer; Skogland, 1978) with 10 sample points per transect, conducted during the winters of 1979 - 1980 (n=73) and 1980 - 1981 (n=87) in caribou feeding areas, caribou movement pathways and areas of no caribou activity, as determined from aerial and ground surveys. Insufficient data were collected in the winter of 1978 - 1979 to allow analysis and the ground study ended in December 1981. Daily minimum temperatures and mean windspeeds (during daylight hours) were recorded in upland tundra and mountainous locations during the calving periods of 1979, 1980 and 1981.

Results and discussion

Ten to 14 wolves in two packs occupied the herd's range. The Burwash pack occupied non-caribou range in the Shakwak Trench and caribou range in the eastern section of the Burwash Uplands. Pack numbers varied between a low of 5 wolves (adult-subadults) from 1978 to 1980 to a high of 9 wolves (5 adult-subadults, 4 pups) in 1981 when the pack denned. Based on telemetry information, this pack had not denned in 1980 nor did it den again in 1982. The 1981 den site was located within caribou calving range and wolf pack movements during calving 1981 corresponded to primary calving areas within and surrounding the Burwash Uplands. The fate of the pups between May 1981 and May 1982 was unknown and we assumed a maximum of 5 adults and 4 pups for that period. An additional group of 5 wolves of unknown sex occupied caribou range in the Brooks Arm subregion. It is unknown if the pack denned during the study although no pups were observed in that subregion. The estimated densities during 1979 and 1980 were 1 wolf/297 km^2 and 1 wolf/212 km^2 in 1981. Since the survival status of the pups past August 1981 was unknown, we estimated 10 to 14 wolves (1 wolf/212 to 297 km^2) in the study area between September 1981 and June 1982.

Wolf fecal analysis revealed the average number of prey per scat was 1.7. The biomass method of estimation showed that ungulates comprised two-thirds of food items for wolves over the study period, with small mammals comprising the remainder (Table 1). No significant difference in the proportion of ungulates and small mammals was found among seasons (P=0.646). Caribou were the dominant ungulate prey item followed by moose, and hares were the dominant small mammal prey item. Results suggest that wolves were eating caribou and moose in proportion to their available biomass during the calving period and were disproportionately eating caribou during the rut and winter periods (Table 2).

We estimate that wolves consumed 66 caribou from calving 1980 through winter 1981, 47% during calving, 21% during rut and 32% during winter (Table 3). From calving 1981 through winter 1982, wolves consumed between 80 to 111 caribou, approximately one-half during calving and one-quarter of the total for the year during each of the rut and winter periods. Thirty to 50 caribou were consumed by wolves in calving 1982. The total annual mortality rate for adult

Table 1. Percentages of individual prey species biomass found in wolf scats according to season.

Prey species	Calving	Rut	Winter	All seasons
Caribou[1]	30	55	40	35
Moose[2]	36	6	25	30
Hare	20	22	27	21
Ground squirrel	8	11	6	8
Other small mammal spp.	6	6	2	6

[1] comprised of 17% adults/subadults and 13% calves.
[2] comprised of 29% adults/subadults and 7% calves.

Table 2. Comparison of the proportion of prey biomass from wolf scats with total prey biomass derived from censuses.

Season and prey species	Scat estimate[1] (%)	Total ungulate biomass (%)	Probability
Calving			
Caribou	35	40	ns[2]
Moose	42	60	
Rut			
Caribou	66	34	s[3]
Moose	8	66	
Winter			
Caribou	43	30	s
Moose	28	70	

[1] Small mammals (hares, cricetids, microtines) comprise remaining percentages in each season.
[2] ns=not significantly different, P=0.05.
[3] s=significantly different, P=0.05.

Table 3. Summary of sources of losses in caribou numbers, Burwash herd, 1980 - 1982.

	1980-1981	1981-1982
Difference between number of caribou in calving period and the number by next calving period (excluding new calves).	92	286
Estimated gain due to ingress	negligible	negligible
Estimated loss due to egress	negligible	85
Subtotal (mortality losses)	92	201
Estimated loss due to wolf predation	66	95
(% of total mortality)	(72%)	(47%)
Estimated loss due to human harvest	12	14
(% of total mortality)	(13%)	(7%)
Other sources of mortality	14	92
(% of total mortality)	(15%)	(46%)
Percentage of total annual calf mortality between the calving and rut periods.	58%	53%
Percentage of calf mortality between the calving and rut periods due to wolf predation.	22%	23%

and subadult caribou varied from 6 - 7% (1980 - 1981) to 8 - 9% (1981 - 1982) and for calves from 58% (1980 - 1981) to 69% (1981 - 1982) (Gauthier and Theberge, 1985).

A decrease in the proportion of caribou mortality between 1980 - 1981 and 1981 - 1982 as a result of wolf predation (72% to 47%) was not due to a decrease in wolf consumption rates (6 caribou/wolf in 1980 - 1981 versus approximately 8 caribou/wolf in 1981 - 1982). Other mortality factors assumed importance in 1981 - 1982. Our data indicate that increases in caribou losses over the previous year occurred in the winter and early calving periods of 1982.

The rate of wolf predation on caribou neonates was relatively low. In 1980 and 1982, 58% and 53%, respectively, of total annual calf mortality occurred between the calving and rut periods. Wolf predation accounted for 22% and 23%, respectively, of that seasonal mortality. These data suggest that wolf predation was an important mortality factor on caribou, not through its effect on neonates, but principally on older-aged animals during the rut and winter periods.

Caribou food habits, forage availability, and weather

We observed a shift in caribou distribution from shrub habitats in calving to sedge-grass-lichen units in the rut and winter, indicating that caribou food habits would also show a shift. Shrub species (principally *Salix* spp.) were the dominant food item in caribou diet over all seasons (46%) followed by lichen species (33%). This pattern was repeated seasonally. Shrubs were the dominant forage item during calving (81%), rut (47%) and winter (39%), while lichens were secondary in each of the three seasons at 12%, 25% and 39%, respectively. Lichen proportion differed significantly among seasons ($P>0.014$), doubling from calving to rut and tripling from calving to winter.

Caribou occupied predominantly sedge-grass-lichen (42%) and shrub (26%) environments over all seasons, i.e. mainly alpine and subalpine habitats. Tests of nonsignificant interactions in contingency table analysis showed that the major difference between the calving and the rut/winter periods was the decrease in occupancy of shrub habitat (from 37% to 26%) and increase in sedge-grass-lichen habitat (from 32% to 43%). Comparisons of the ratio of the number of caribou observed in each landform category to the amount of area in each category showed that caribou distribution was proportional to the amount of area of life-form classes during calving periods but disproportionate in the rut and winter periods when caribou had shifted to sedge-grass-lichen habitats. We suspected that winter sightings of caribou in sedge-grass-lichen environments were probably a function of their use of those habitats to obtain terrestrial lichens and possible prostrate shrubs. This observation was enhanced by the results of the food habits analyses that showed a predominance of lichen and shrubs in winter feces.

We examined only the availability of lichens as partial indicator of the forage available to wintering caribou. Lichens were relatively abundant in the sedge-grass community, one of nine communities described by Gauthier (1984), averaging 189 kg/ha based on six transects. Lichen biomass values and numbers of wintering caribou were significantly correlated ($P<0.01$).

The portion of the major home range of the Burwash herd classified as sedge-grass community from Landsat analysis was 542 km^2 and the total estimated lichen biomass for this community was 10 234 350 kg (Gauthier, 1984). Assuming caribou of the Burwash herd consumed the highest lichen biomass reported (5 kg/caribou/day; Hanson *et al.*, 1975), and that the herd size was 402 animals (the largest number estimated from winter censuses), the herd would require 2010 kg/day of lichen or 331 650 kg over the winter period (165 days), or 3% of the estimated total biomass in sedge-grass-lichen communities. We have no information on the relationship between annual growth and lichen biomass in the study area, the extent of loss of lichen biomass through scraping and trampling by animals, or the long-term ability of the range to support animals. Given these deficiencies and our crude estimate of total available biomass, we can only infer that the large difference between the dryweight lichen intake required for the herd and that estimated as existing in the main community type within which they forage suggests little absolute shortage of lichen to affect the nutritional status of animals.

Lichen availability to caribou was not likely influenced by snow conditions. Burwash caribou do not have to contend with large snowfalls. The average yearly total snowfall as measured at a snow station in forested habitat (area of greatest snow accumulation) in the Burwash area from 1967 to 1978 was 127.7 cm. In the first 3 years of this study, total snowfalls were less than the average, ranging from 70 to 83 cm. In 1981 - 1982, total snowfall of 135 cm exceeded the long-term average, however, no significant difference in snowfall levels among years was found ($F=1.80$; $P=0.149$). Snow depth averaged 28.3 cm in 1979 - 1980 and 18.0 cm in 1980 - 1981, while snow hardness values averaged 10.1 kg and 8.3 kg, respectively. Average snow thickness and rammsonde hardness values were well below many reported levels (for example, LaPerriere and Lent, 1977; Stardom, 1975).

Neonate mortality rates in the Burwash herd were 40% in the first 3½ weeks of calving in 1980, 13% in the first 2½ weeks in 1981 and 49% in the first 2½ weeks in 1982 (Gauthier and Theberge, 1985). No differences in mean minimum temperatures, total precipitation rates or mean windspeeds were found between the calving periods of 1980 and 1981 (Gauthier, 1984), suggesting that variations in neonate mortality rates between the 2 years were not related to microclimatic conditions. However, for 1982, Downes (1984) reported periods of cold, wet weather in the Burwash Uplands region during the calving period. An explanation for the high neonate mortality in 1982 may have been short but severe periods of low temperatures and wet conditions. We note that, regardless of year, the influence of climatic conditions as indirect factors influencing susceptibility of calves to more proximate mortality factors is unknown.

With range and weather implicated in caribou mortality to the minor degree discussed, other factors must have been proximal causes of the non-wolf related mortality (15% of total mortality in 1980 - 1981 and 46% in 1981 - 1982). We noted that human harvest amounted to 13% and 7% of total mortality in the 2 years. As well, we documented predation by grizzly bears through incidental observations. Grizzly bears have been shown to be important mortality agents in wolf-ungulate systems, principally through their effect on neonates (Ballard and Larsen, 1985). The neonatal caribou losses documented in this study which could not be accounted for by wolf predation, may have been at least partially a result of predation by other predators.

Conclusion

Wolf predation was numerically the largest proximal cause of mortality in the Burwash herd. Its significance relative to other causes of mortality may be variable as shown in 1982 when it appeared that weather or other predators may have been an important cause of calf loss. We view our analysis of range carrying capacity as only partial, for reasons discussed. As well, the degree of compensation that may exist among the three main predatory species (wolf, bear and man) is not known. Therefore, while our data document an important role for wolf predation on the herd further work is necessary to assess its limiting effect.

Acknowledgements

We wish to express our gratitude to A. T. Bergerud and D. E. Russell for helpful comments on an earlier draft. This work was funded by the Yukon Wildlife Branch, Foothills Pipelines (South Yukon) Ltd., the National Sciences and Engineering Research Council, and the University of Waterloo. We express our gratitude for field and laboratory assistance to D. Larsen, R. Coshan, C. Wedeles, D. Whitehouse, M. Fitzsimmons, K. Brown, L. Martin and R. Bondy.

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Fertility and twinning in Canadian reindeer

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Abstract: This study was carried out from 1976 to 1981 on the Mackenzie Delta reindeer herd with the co-operation of the owners, Canadian Reindeer Ltd., Tuktoyaktuk, Northwest Territories. The reproductive organs of 4050 female reindeer (*Rangifer tarandus*) were collected at slaughter. The pregnancy rates averaged 99.5% of the females examined. In the years 1978 and 1981, 24.7% (713) of the animals were carrying twins, as compared to a twinning rate of 0.4% observed for the intervening years. Nineteen animals were not pregnant. Of these, 14 were emaciated with no gross pathology of the reproductive tract. Five females had either a mummified fetus or uterine adhesions preventing a viable pregnancy. Estimated fawn survival rates from birth to June varied from 51.7 to 95.7%. Fawn survival from June to yearlings of June the next year varied from 51 to 86.4% as determined by count at roundup. Increment averaged 15.8% per year after a slaughter of 13.4% of the herd yearly.

Key words: reindeer, pregnancy rates, twinning, Canada, fawn survival, recruitment, Arctic.

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Rangifer, Special Issue No. 1, 1986: 145 - 150

Introduction

Domestic reindeer, transplanted to Alaska in 1891, came from two Asian stocks, a large form presumably from forest reindeer stock and a small form presumably from a tundra subspecies (Banfield, 1961). A herd of some 3000 reindeer was purchased in Alaska in 1929 by the government of Canada and, after an epic journey of 63 months, was delivered to the Mackenzie Delta region in 1935 (Scotter, 1978). The larger form, which calved in April, was selected for introduction to Canada (Porsild, 1954).

The following is a report of my evaluation of reproductive rates, occurrence of twinning, and fawn survival in the Mackenzie Delta herd from 1976 to 1981, based on examination of female reproductive tracts obtained from reindeer slaughtered either in November or in February — March of each year and annual records of sex and age composition of the herd obtained during June roundups.

Study herd

The reindeer are managed on an open herding basis on the winter range; that is, the herd is kept in a certain region selected by the owner, but no attempt is made to keep the herd as one group. The summer range is the Tuktoyaktuk Peninsula where no herding is required except for periodic surveillance by aircraft. As the herd migrates southward down the peninsula in the fall, it is met by the herders and guided to the grazing area selected for that winter. The herd is kept under surveillance by aircraft and snowmobile to prevent straying and to check for wolves. During the winter the herders use snowmobiles to bring straying animals back to the vicinity of the main herd.

The major slaughter is conducted between 18 February and 5 March in order to utilize the ice road to ship the meat to southern markets. Occasionally there has been a small inspected slaughter in November, mostly for northern markets. The slaughter site is moved each year to an area where there is enough forage to sustain 1500 to 2000 reindeer for two weeks. About 1500 reindeer are separated from the main herd and brought to the slaughter area. Selected animals are slaughtered, that herd is moved away and another group is brought in. Nutrition is at its lowest ebb and fawning time is near, so the slaughter period is also the most critical time of year for the reindeer. Therefore, an attempt is made to utilize a sub-unit of the herd for only 2 days to minimize the stress.

After slaughter the whole herd is guided towards the fawning area, so as to arrive by fawning time. Fawning takes place in an area protected by hills from the cold spring winds. The first fawn will be born 30 March to 2 April and fawning will be general 10 days later. Most of the fawns are born by the middle of May although an occasional fawn may arrive as late as the middle of August. Most of the fawns born late probably do not survive the following winter.

Immediately after fawning the herd begins to migrate towards the Tuktoyaktuk Peninsula for summer range. The migration is led by older females who fawned early or lost their fawns, with the majority of the bulls following 1 or 2 days later. The remainder of the herd is strung out for 100 km with the females with late born fawns and the yearlings bringing up the rear. The leaders reach the tip of the peninsula about 20 June, with the last ones arriving 2 weeks later. The reindeer have to summer on the Arctic coast for minerals and possibly also to avoid insect harassment, which they do by standing in the water or lying on sandy beaches.

Materials and methods

Examination of reproductive tracts

Between 1976 and 1981, 5700 reindeer were examined at slaughter under the auspices of the Food Production and Inspection Branch, Agriculture Canada. Most of the slaughter was done in the month of February each year, although some small slaughters were done in November.

The female reproductive organs were placed to one side by the butcher during evisceration so they could be counted and examined at the end of the day's kill. Data recorded included (1) the number of pregnancies, (2) the number of fetuses per pregnancy (3) stage of gestation, and (4) gross reproductive pathology.

Since 1976 the herd has been rounded up beginning about 18 June each year by helicopter and corralled under supervision of Agriculture Canada. In 1976 and 1977 the roundups were incomplete, but from 1978 to 1981 for all practical purposes the complete reindeer herd was corralled.

The spring roundup is conducted to cut the velvet antlers from the bulls and females for export. All the animals were run through a chute, the fawns are tagged with color coded tags for the year of birth, females to be slaughtered the following winter are marked with ear ribbons and bulls which are surplus or inferior for breeding purposes are castrated.

The yearling females with fawns at the spring roundup were counted in with the mature females for the years under review. The percentage of yearling females producing fawns each year (bred as fawns) was not determined.

The numbers of major segments of the herd were recorded so the number of yearling bulls and yearling females without fawns allowed an estimate of survival to 1 year of life of previous year's fawns.

Results

Between 1976 and 1981, 5700 reindeer were examined at slaughter, mostly in February of each year. All but 19 of the 4050 2-year-old and over female reindeer examined at slaughter from 1976 to 1981 were pregnant with viable fetuses (99.5%). Five of the 19 females exhibited gross reproductive pathology: three had uterine adhesions and two each a mummified fetus. The

Table 1. Annual reproductive rates of female reindeer obtained at slaughter (Feb.-Mar.), Mackenzie Delta herd, NWT, Canada.

		2+-yr-old females sampled		
Year	N	% pregnant	% single fetus	% twin fetuses
1977	357	99.2	99.2	0.8
1978	932	99.6	73.8	26.2
1979	481	99.4	99.6	0.4
1980	231	98.7	99.6	0.4
1981	2042	99.7	76.9	23.1

Table 2. Proportions of females and fawns in the annual June roundup of Mackenzie Delta herd reindeer, NWT, Canada.

	Herd	females[b]		%	Fawns/ 100 females	
Year	sample[a]	1+yr	2+yr	Fawns	1+yr	2+yr
1977	5205	45.0	36.9	35.3	78.5	95.7
1978	8245	47.7	37.2	35.0	73.4	94.1
1979	9855	43.2	32.4	24.2	56.2	72.0
1980	12745	46.5	38.5	24.3	52.4	63.2
1981	10879	41.9	34.8	21.5	51.3	61.8

[a] All reindeer corralled.

[b] The category 1+-yr females includes all females 1-yr or older; and the category 2+-yr females includes all females 2-yr and older, plus yearling females with calves (excludes only yearling females without calves).

remaining 14 were not pregnant but showed no gross reproductive pathology (emaciation, either from old age or injury, probably had led to an anestrous condition during the rut). The annual rate of pregnancy (with a viable fetus or fetuses) averaged 99.5% (±0.4% S.D.).

Only seven 2+-year-old females were examined at slaughter in 1976: all were pregnant, each with a single fetus. Relatively large samples of 2+-year-old females were slaughtered from 1977 to 1981. Over the whole study period 17.8% of the mature females slaughtered were pregnant with twins. In 1978 26.2% and in 1981, 23.1% of the females at slaughter were carrying twins (Table 1). In the other 3 years under review the average twinning rate was 0.56% per year.

From 1977 to 1981 the fawns aged about 2 months made up 21.5 to 35.4% of the herd with an average of 26.7% (Table 2). The number of fawns per 100 females ranged from 51.3 to 78.5% averaging 64.9%. Since the yearling females with fawns are counted as adults, all the female yearlings have been included in the female counts (Table 2), for comparative purposes. Females comprised from 41.9 to 57.7% of the herd sample, averaging 44.7%. The yearling females without fawns comprised from 16.9 to 23.4% of the female population with an average of 19.3% (Table 3). Fawn survival to 1-year of age averaged 64.7% (Table 4). There has been an average slaughter of 13.4% of the herd yearly from 1977 to 1981 and increment has still averaged 15.8% per year. The size predicted for the total herd in 1980, calculated from these

Table 3. Reindeer production and survival to the 2nd month of life, Mackenzie Delta herd, NWT, Canada.

	No. females producing[a]			Fawns	% early
Year	Singles	Twins	Fawns born	alive mid June	fawn survival
1977	1889	15	1919	1836	95.7
1978	2253	800	3853	2884	74.9
1979	3286	13	3312	2389	72.2
1980	4824	19	4862	3102	63.8
1981	2903	872	4647	2338	50.3

[a] Calculated from reproductive rates given in Table 1.

Table 4. Reindeer fawn survival from birth to the 2nd June of life, (13-14 months), Mackenzie Delta herd, NWT, Canada.

Year	Herd sample (less fawns)	Number of yearlings	% yearling recruitment	% fawns[a]	% fawns surviving to 1-yr[b]
1977				36.9	
1978	5361	1238	23.1	46.7	67.4
1979	7466	1721	23.1	33.6	59.67
1980	9643	2064	21.4	38.1	86.4
1981	8541	1582	18.5	42.7	51.0

[a] Percentage fawns equals estimated number of fawns born (Table 3) as proportion of herd sample (Table 2).

[b] Calculated by dividing the number of yearlings by the number of live fawns from the preceding year.

Table 5. Herd numbers calculated from increment 15.8% yearly.

Year	Calculated Herd	Actual Count
1974		5000
1975	5795	
1976	6716	
1977	7784	5205
1978	9022	8245
1979	10457	9855
1980	12120	12745
1981	14047[a]	10879
1982	12598	
1983	14588	

[a] Reduced by all large slaughter and a heavy neo-natal and fawn loss.

numbers, was at variance with the actual count at round up by —5% (Table 5). In 1981 the herd numbered 22.6% below the calculated number (Table 5) because of a large female slaughter. As well there was the lowest fawn survival in both the new born fawns and the coming yearlings of all the years under study (Table 3).

Discussion

The pregnancy rates observed in this reindeer herd (Table 1) seem to be higher than those reported in other *Rangifer tarandus* populations in the world (McEwan, 1963; Michurin, 1967; Kelsall, 1968; Dauphine, 1976). The rates reported here were based on counts of pregnancies at slaughter, mainly in females over 6 years old. These rates may have been slightly higher than the rates for the population as a whole, since the majority of does in the herd are under 4 years of age and are, therefore, least likely to be pregnant. However, the error appears to be slight, since in 1977 the birth of 1920 fawns was predicted on the basis of projected observed pregnancy rates at slaughter, and the actual count in June was 1863 (Table 3) for an error or a fawn loss from all causes of 4.3%. In Alaska fawn crops from 50 to 60% of the adult does are usual, but under ideal conditions fawns crops may reach 85 to 95% (Palmer, 1934). A fawn crop of 51.3% in the worst year (1981) (Table 2) is not below normal for other populations.

There was no way to determine how many of the females with fawns were just a year old. In Alaska, up to 5% of yearling females have been observed with fawns (Hadwen, 1942). Many of the yearlings with fawns appear to have fawned later than the main herd judging by the size and apparent age of the fawns in June. Yearling females have been observed fawning as late as 21 June.

The fawns of yearlings are weaker at birth and the young mothers do not have as much milk as the mature females, thus increasing the fawn loss from yearlings. However this loss is partly balanced by the more careful tending of a fawn by a yearling cow than by an old cow (Hadwen, 1942). When herding by helicopter the young females will drop behind with the fawn when it is exhausted, whereas the old females will leave the fawn to rejoin the herd.

Twinning has been reported in reindeer and caribou by Palmer (1934) and Nowosad (1973); for captive barren-ground caribou (*R. t. groenlandicus*) by McEwan (1971); and free-ranging woodland caribou (*R. t. caribou*) by Shoesmith (1976).

Twinning varied markedly from nearly no production of twins in 3-yr (mean = 0.5% ± 0.23% S.D.) to about 25% of the pregnancies in 2-yr (mean=24.7%±2.19% S.D.).

The high percentage of females observed with twin fetuses at slaughter in 1978 and 1981 has never been reported before in any *Rangifer tarandus* populations. Forty percent of barren-ground caribou in the wild produce two ova at one cycle, but no evidence of advanced development of a second embryo has ever been found (McEwan, 1963). If dual ovulation also occurs commonly in reindeer, then a trigger mechanism could be postulated which operates on occasion to allow the development of the second embryo.

Variable factors during the period of study included weather and antler removal. Climatological data for the Tuktoyaktuk area show that precipitation was slightly higher than normal in late June and early July, 1977 and again in 1980. This increased precipitation may have produced more forage earlier in the season by drawing the frost sooner and thus increased body condition to stimulate multiple ovulation and implantation. In caribou, full recovery of fat deposits during the summer is critical to reproduction, growth, and winter survival (Dauphine, 1976). The velvet antlers were removed from the reindeer herd for the first time in 1977. When a high rate of twin fetuses was found at slaughter in the following spring, the possibility of a casual relationship between antler removal and twinning was considered. However, twin pregnancies occurred at what appears to be the usual rate in the next 2 years, despite the annual antler harvest, and increased in frequency again in 1981. The only effect antler removal may have on twinning is the stimulation caused by roundup which promotes early shedding of the winter coat, which in turn may enhance early fattening.

Neo-natal mortality (between March 1 and June 30) estimated from pregnancy rates, (fawns dropped before April 1) due to abortion, lack of milk, abandonment, stillbirths, (fawns born after April 1 that are dead or so weak they are unable to move) weak fawns, and inclement weather (Table 3) varied from 4.3% in 1977 to 49.7% in 1981. In 1981 the snow depth at the end of April was 66 cm as compared to 55 cm in 1980, when mortality was 36.8%. In the other years under study the snow depth was 15 to 33 cm, with fawn loss varying directly. In 1978 there were many females with twins at the roundup, and the snow depth at the end of April was 23 cm, whereas in 1981 only two females were seen with twins.

Predation is not a major factor in fawn mortality as the herd is under constant supervision after the first heavy snowfall in the fall until the end of May. The stress of herding, prolonged food deprivation, and hazing during the slaughter period is probably one of the major causes of fawn mortality, affecting both pregnant females and coming yearlings. In 1981 the slaughter was terminated early because of excessive fat vascularization from the rapid loss of body condition. After the harassment had been almost continous for 3 weeks, subsequent fawn losses were heavy from March until the middle of May. That year the herders reported many abortions and stillborn fawns. The fawns surviving at roundup were smaller than normal with very little antler growth. The females with the most fat reserves appeared to have the best rate of fawn survival. Whether the early fawns were aborted or the gestation time was prolonged could not be determined. A high plane of fat reserves and good nutrition decreases gestation time (Krog, 1980).

Since 1981 the slaughter procedure has been changed so that the animals to be slaughtered are corralled and the rest of the herd is not harassed all day. This reduces the stress on all the animals and helps prevent the loss of critical body fat reserves in the fawns and females.

Fawn mortality until the end of June seems to be directly related to the snow depth at the end of April and the amount of harassment at slaughter. Fawn losses from stress of handling start in March and continue, whereas losses from weather occur only at birth or shortly after. Twins most years are a disadvantage because of poor survival rates if conditions are not ideal, and thus they cause an increased net fawn loss.

The percentage of fawns surviving to one year of age (Table 4) is inaccurate to the extent that yearling females with fawns are counted as adults. Also small groups of just yearlings at roundup are not brought in for count because they have no antler of commercial value. The actual number of yearlings is, therefore, greater than the value given in Table 4.

The survival of fawns from June to yearlings would be greatly enhanced if coralling and slaughter procedures were modified. Too many fawns are separated from the females during the corralling and handling procedure for too long with some never getting back together. The fate of these fawns is unknown.

Fat reserves in February are excellent on the older females while the fat reserves on the fawns and young females are only moderate to poor, especially if they are badly infested with warbles. Therefore the fawns and young females will withstand very little food deprivation or harassment without serious consequences.

This initial investigation raises many questions:

(1) do range conditions govern rates of fertility in these reindeer;

2) is twinning related to the age of the breeding females (I suspect it is); and

(3) do they really have a different and usually greater genetic potential for growth than North American caribou.

Acknowledgements

The author wishes to thank Drs. G. W. Scotter and D. C. Thomas, Canadian Wildlife Service, for encouragement to proceed with the preparation of this paper. Many thanks are extended to Betty Ann Stanton for typing and manuscript preparation. The help of Dr. Barbara Kingscote for manuscript suggestions and review is gratefully acknowledged.

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Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou

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Abstract: Evidence for the fidelity of female barren-ground caribou (*Rangifer tarandus* spp.) of each herd to specific calving grounds is convincing. Involvement of learned behaviour in the annual return of those cows to the same calving grounds implies such actions are a form of «traditional» behaviour. Even wide variations in population size have not yet knowingly led to marked changes in size or location of calving grounds or prolonged abandonment of established ones. Rarely is the adoption of new calving grounds reported and emigration to another herd's calving ground or interchange between calving grounds has not yet been unequivocally documented. The calving experience of individual caribou and environmental pressures may modify the cow's use patterns of her calving grounds. The current definition of herds based on traditional calving grounds may require modification, if increasing caribou numbers result in changes in traditions. However, current data do not contradict either the fidelity to traditional calving grounds or the concept of herd identity based on that fidelity.

Key words: barren-ground caribou, calving grounds, learned behaviour, management, Northwest Territories

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Rangifer, Special Issue No. 1, 1986: 151 - 158

Introduction

The annual use of specific areas for calving by barren-ground caribou (*Rangifer tarandus groenlandicus* and *R. t. granti*) was known to local hunters for many years, but not by biologists until the 1940s (Lent, 1964; Skoog, 1968; Thomas, 1969). Consequently, quantitative data on the use of calving areas only spans some 45 years, at most. However, qualitative documentation of calving over longer periods is possible for some areas from historic and prehistoric records. Evidence for the use of specific areas for calving by barren-ground caribou cows of one herd is convincing. For example, the calving grounds of the Beverly, Kaminuriak and Bathurst herds in the Northwest Territories (NWT), Canada, have been surveyed 54 times between 1957 and 1985 and calving cows were annually observed, (although densities varied between years). The return of individual cows to the same calving grounds has been documented mostly in Alaska from the radio-collaring of caribou (e.g., Cameron *et al.*, 1986).

Bergerud (1974) suggested that annual fluctations in the numbers of caribou on a calving area would contravene the idea of a discrete homing population. Wide differences between annual counts supposedly, however, resulted from sampling errors and difficulties rather than movements between populations (Bergerud, 1971). Annual differences in numbers of caribou counted on barren-ground caribou calving grounds are also attributable to changes in the numbers of barren cows, juveniles and yearlings accompanying the parturient cows, or environmental conditions such as deep late-lying snow delaying the return of the caribou, and or survey bias.

Investigating the annual return of individual parturient cows to the same calving ground has only been feasible since the use of radio-telemetry. In the Central Arctic herd (Alaska), about 90% of the radio-collared cows were annually relocated on the summer ranges (Cameron *et al.*, 1986). However, the fate of the other 10% was inexplicable, because mortality of the missing radio-collared cows or failure of the radio transmitters could not be ruled out (Cameron *et al.*, 1986). Timing of the surveys did not always verify exact use of the traditional calving grounds. However, no known instance of a radio-collared cow being located on other herds calving grounds was determined dispite overlap of other herds on the Central Arctic herd's wintering ranges.

Lent (1964) and Skoog (1968) were among the first to emphasize that annual use of calving grounds was one of the most consistent behavioural characteristics of caribou and called the use «traditional». The use of the term «traditional» has continued but the concept and implications of traditional behaviour have been little discussed. Questions about the fidelity of caribou cows to their calving grounds and the nature of traditional calving grounds have been raised in regard to human activities on those areas (e.g., Cameron, 1983; Bergerud *et al.*, 1984; Gunn, 1985). Likewise, the recent large increases in the numbers of caribou estimated in the Kaminuriak herd (Gates, 1985; Heard and Calef, 1986) and the Bathurst herd (D. C. Heard, pers. comm.) have raised questions about the fidelity of caribou cows of each herd to traditional calving grounds. Our paper reviews the reported changes in the use of traditional calving grounds by various herds and relates those changes to traditional behaviour. We advance definitions of an annual calving ground and traditional calving grounds and discuss the implications of those definitions for caribou management.

Definitions of an annual calving ground and traditional calving grounds

Annual calving ground

The «annual calving ground» of a herd is restricted in time to 1-year and is the land area occupied by the majority of parturient caribou from that herd. The «annual calving ground» should not be referred to directly as a *traditional annual calving ground* because of its restriction to a single year. That is, it is not *traditional* in itself as it occurred only in 1-year but it is an *annual calving ground* within the area of the *traditional calving grounds.*

Traditional calving grounds

The «traditional calving grounds» of a herd is the overall (known) land area where at least the majority of the parturient caribou of that herd come annually to calve. It includes all of those known locations where caribou of that herd have calved, including areas occupied during years when environmental stress (poor travelling conditions) apparently prevented parturient cows from reaching more central sections of their *traditional calving grounds*, (because we reason that it was their *traditional behaviour* that enforced their movements to that point in time and space).

Majority

Technically the majority only requires 51% but to be practical as a basis for defining a specific caribou herd it would require between 80% and 90% of the parturient caribou in a herd maintain their affinity for their specific *traditional calving grounds.*

Wilson (1975:168) called tradition the «...ultimate refinement in environmental tracking» and he described tradition as a specific form of behaviour passed between generations by learning. Wilson (1975) characterized traditional behaviour as that which can be altered or initiated by one successful individual; can quickly spread through a population in less than a generation; is cumulative and is precise in application often to specific localities. The key feature is, however, that it is a learned behaviour which then allows a relatively rapid and flexible response to environmental changes. Bergerud (1974) described several lines of evidence to support the role of learning in the annual return of caribou cows to calving grounds. Wilson's (1975) definition of traditional is similar to the everyday usage of the term: e.g., Webster (1980) defines tradition as «...The handing down of information, beliefs and customs by word of mouth or by example from one generation to another without written instruction». The synonym for traditionalist (meaning strongly favouring retention of existing order) is «conservative» and «conventional» is the synonym for traditional (Roget's Thesaurus, 1980).

The connotation of conservative may have sometimes lulled us into thinking that caribou calving grounds are permanent fixtures in the annual use of time and space. The evidence is, however, that, while cows of each herd exhibit long-term fidelity for a specific calving area, locational changes have occurred in the areas traditionally used by calving caribou cows.

Variations in the use of caribou calving grounds

Overlapping shifts in calving ground location

The boundaries of calving grounds of many barren-ground caribou herds are delineated during aerial surveys to count caribou. Annual variations in the areas delineated (e.g., Davis *et al.*, 1978b; Fleck and Gunn, 1982) may result from shifts in the distribution of calving cows or may result from different criteria used (which are rarely reported) between years to determine the boundary. Timing of the survey relative to the peak of calving can significantly change the area delineated as the calving area.

There is sometimes a directional trend among years in the location of the calving grounds even though there is general overlap in the boundaries of calving grounds. For example, that of the Beverly herd has shifted to the northeast between 1957 and 1982 (Fleck and Gunn, 1982) onto areas used for early postcalving. There are no obvious environmental factors that account for that directional shift. Changes in the distribution or density of denning wolves (*Canis lupus*) during and after wolf control in the 1950s and 1960s may, however, have been the environmental change to which the Beverly calving cows responded.

Temporary abrupt changes in calving ground location

Environmental changes on travel routes to the calving grounds, or on the calving ground itself, can cause some or all cows to calve on an area with little or no overlap of the area used in the preceding year. For example, deep or wet snow occasionally slows the migration of cows, and calving may occur before reaching the usual calving area. Deep snow delayed the Beverly herd in 1979, and cows calved up to 200 km south of the usual calving grounds (Fleck and Gunn, 1982).

The Delta herd (Alaska) has used the same mostly *Eriophorum* spp. tussock covered calving area since late 1950s. In 1981, however, about half the cows calved in areas up to 40 km west of the traditional area. Davis *et al.* (1982) speculated that the shift may have occurred because part of the herd foraged on the traditional calving area during April and May when it was snow free and may have diminished the quantity or quality of forage, though now they believe that explanation to be improbable (J. L. Davis, per. comm.). In 1982, the Delta calving ground was still snow-covered in late May; and 90 — 95% of the cows calved on a snow free area 16 km northwest of the traditional area (Davis and Valkenburg, 1983).

Distinction between temporary or permanent abandonment of traditional calving grounds is partially dependent upon the time period implied or stated. The Fortymile herd between 1977 and 1983, annually calved in areas not contiguous to the area used in the 1960s and early 1970s. However, in 1984 calving occurred contiguous to the calving area that was «abandoned» in the early 1970s (Valkenburg and Davis, 1986).

Permanent abandonment of traditional calving grounds

In the NWT, a small proportion of cows of the Bluenose herd calved on the Cape Bathurst area in 1974, 1975 and 1976 (Hawley *et al.*, 1978). Counts of calving cows dropped from 4500 in 1974 to almost zero in 1978 and 1979 (Brackett *et al.*, 1979), and cows have apparently not calved there since. Other examples of permanent abandonment of calving grounds include only situations where the habitat has become unusable. The George River herd used two major and one minor calving grounds in the 1970s (I. Juniper, pers. comm.). Between 1975 and 1979, the Lac Champdone calving ground was progressively abandoned after severe natural flooding in 1975, and the numbers of caribou using the other main calving ground (Ford River) increased during that period.

Formation of new calving grounds and emigration to or interchange between calving grounds

Creation of a new calving ground (i. e., a discontinuous distribution of calving cows from all previously used areas) has been rarely documented, but if the initial colonization of a new calving ground involved only a few individuals, it likely would go unnoticed during aerial surveys. The Mulchatna and Big River herds in Alaska are examples of caribou herds apparently using new areas for calving (Patten, 1985; Pegau, 1985).

Skoog (1968) hypothesized that a caribou herd increased in number to a «threshold» density which caused erratic movements and ultimately lead to emigration. Davs *et al.* (1978a) pointed out that Skoog's hypothesis requires a triggering mechanism such as a correlation between densities of caribou on the calving ground and population size. Their data from the Western Arctic herd suggest, however, that there is no relationship between population size and use of the calving grounds, nor was there evidence for the formation of new calving areas or abandonment of the traditional calving grounds as the herd changes in size. Similarly, the traditional calving grounds used by the Bathurst and Kaminuriak herds have not apparently shifted despite large changes in population size. Davis *et al.* (1978b), noted, however, that «drawing lines around the calving area is a subjective and somewhat arbitrary process». Thus, the apparent absence of any correlation between population size and density on the calving grounds is not conclusive.

The Big River (375 caribou in 1984) and Mulchatna (33 000 in 1984) herds are both increasing in size and occupying new ranges (Patten, 1985; Pegau, 1985). In 1983, both herds used new summer ranges and some cows returned to calve there the following year (Patten, 1985; Pegau, 1985) although other cows in the herd continued to use their traditional calving grounds.

Emigrations, possibly from herds in the Northeast Keewatin to the Kaminuriak herd's calving ground has been suggested on the basis of the increase in numbers of caribou estimated on Kaminuriak calving grounds, which exceeded the intrinsic rate of increase (Gates, 1985; Heard and Calef, 1986). Likewise emigration of caribou to the Bathurst herd has been advanced to explain the apparent doubling in the number of caribou estimated to be in the Bathurst herd from 1982 to 1984 (D. C. Heard, pers. comm.). However, change in survey techniques, inadequate definition of annual calving grounds and annual variations of the dispersal of calving cows are also plausible explanations, especially, in the absence of supporting evidence for immigration. Large numbers of breeding cows moving from one traditional calving grounds to another traditional calving grounds have not been previously documented which is not to say that it is not possible. However, such an unusual event should not be accepted without supporting evidence.

Possible emigration of calving caribou from the calving grounds of one herd to the known calving grounds of another herd may have occurred between the Delta and Yanert herds. The Yanert herd was only recognized as a discrete herd in 1980 (from radio-collaring of caribou) on what used to be considered as part of the annual range of the Delta herd (Davis and Valkenburg, 1985a). In 1984, 10 of 25 radio-collared Delta cows calved on the Yanert herd's calving area, but in 1985 those cows returned to the traditional Delta calving grounds (Davis *et al.*, 1986). The area of overlap for calving was used by yearlings and subadult females of the Delta herd in previous years which may be partly the explanation for the limited calving and movement of other cows into this area (the upper Wood River area) during or shortly after calving in 1984. There is, then, no compelling evidence to distinguish between the temporary expansion of a new calving ground by the Delta herd or temporary emigration to the Yanert herd's calving ground. There is also the question of whether the two herds are in fact separate herds, as overlap in distribution occurs during the rut (J. L. Davis, pers. comm.).

Human activities and abandonment of traditional calving areas

Strength of the caribou's affinity to, and potential abandonment of, traditional calving grounds in the face of human activities has been central to debates about those activities on calving grounds (e.g., Cameron, 1983; Bergerud *et al.*, 1984; Gunn, 1985). The concerns over human activities potentially causing abandonment of calving grounds are twofold. Besides the possible direct effects (Cameron, 1983; Gunn, 1985), there is also the untested assumption that if the activities were sufficiently severe to cause the cows to abandon the calving grounds, the enforced use of a new calving grounds could be deleterious. The key factor would be the availability of suitable calving habitat. Strong affinity to an area could mean that caribou will tolerate more human activities, through local redistribution of cows and calves, before abandoning the area. The density of cows and calves is low in the vicinity of pipelines and roads on the Central Arctic herd's calving grounds (Whitten and Cameron, 1985), but the area has not been abandoned.

The initial responses of the caribou to human activities on their calving grounds were not documented in the 1950s for the Delta herd whose calving grounds are on a military training area (Davis and Valkenburg, 1985b), nor early 1970s for the Central Arctic herd. But evidently, some cows habituated to the aircraft (Delta herd) or adopted avoidance behaviour (Central Arctic herd) and those adaptions would have spread quickly in a small population (Bergerud, 1974) and both herds then had only or less than a few thousand caribou.

Management implications of traditional behaviour and traditional calving areas

Traditional calving areas are not discrete physical entities and are not readily recoghized by physiographic or vegetation characteristics (Bergerud, 1974; Fleck and Gunn, 1982). It is the caribou cow's traditional behaviour that characterizes use of those areas (e.g., Fleck and Gunn, 1982). Recognition of the role of traditional behaviour emphasizes that the use of a specific area is not permanent. New traditions can be learned even through the new experience of only a few dominant members of the population.

Bergerud (1974) has stressed the optimal and dynamic use of space by caribou and the emphasized that the use could change with time. Bergerud (1974) suggested that social facilitation was a contributing factor to that dynamlc use of space. We believe that traditional behaviour is also a likely mechanism in imparting both stability and the potential for change if the caribou's environment changes. The source of a change could result as individuals in a population do not necessarily all follow identical foraging or reproductive strategies (e.g., Smith, 1983). Not only do some individuals follow different strategies, but there is individual variation in the consistency and demonstration of behaviours within a strategy. This individual variation as a factor in population ecology often seems overlooked — possibly because of our reliance on statistical procedures that smooth over individual variation or merge it with sampling error. The presence of a few individuals in a population that, for example, do not gregariously calve, may rapidly increase that behaviour in the population if, for example, the level or type of predation changes. Bergerud (1971) reported that calving in the Avalon herd became dispersed and less synchronized in time as lynx (*Felis lynx*) predation increased. However, direct evidence is lacking that the experience of individual caribou on the calving grounds can modify their subsequent use of the area. Likewise, there are virtually no published data on the variation of affinity among individuals to their calving grounds.

The current concept of herd identities is based on the fidelity to calving grounds (Skoog, 1968). Some workers have recently questioned the fidelity to the calving grounds and thus herd identity (e.g., D. R. Carruthers, 1983. The Central Arctic herd myth. unpublished paper read at 1st North American Caribou Workshop, Whitehorse, Yukon Territory. 36 p.). Two points have to be considered in evaluating the concept for basing a herd's identity on fidelity to its calving grounds. Firstly, that the original designation of the calving grounds included all the previously used areas. Core (principal), secondary and satellite calving grounds are terms used but require definition as well as inclusion in the boundaries of the traditional calving area. Cows can rapidly move considerable distances even when with calves only a few days old. Thus, care must be taken in categorizing areas as calving grounds based on sightings of cow — calf pairs in mid to late June (i.e., calving grounds must be delineated during the peak of calving). Secondly, that although patterns of caribou migration change and calving may be in «unexpected places» (Davis *et al.*, 1978b), the presence of some calving cows in an area for 1 or 2 years is not necessarily evidence for the existence of a separate herd. Additional supporting evidence would be needed as the cows may return to their original calving grounds (e.g., Delta and Fortymile herds).

Predation is part of the environment of a caribou calving ground. Predation is, however, especially prone to variation because predator numbers vary in response to many factors including harvest or control by humans. If the level of predation changes over a period of years the caribou may also respond by a change in behaviour, including gradually shifting their distribution. Bergerud (1974) emphasized the influence of predators on the density and distribution of where caribou cows calved. The gradual change (partial overlap between years) in calving distribution of the Fortymile herd may reflect changes in the numbers of wolves on those calving grounds or in the type of wolf hunting such as wolves supporting cubs or non-breeding wolves (P. Valkenburg, pers. comm.). Bergerud (1971, 1974) reported a change in the behaviour of breeding cows in the Avalon herd as the introduced lynx increased predation of newborn calves.

The examples of abrupt (discontinuous) changes in calving distribution in the absence of drastic habitat changes such as flooding are from herds increasing in size and expanding their range distribution. The occupation of new calving grounds has occurred on previously used summer ranges (i.e., familiar area sensu Baker, 1978). What or how environmental change leads to the behavioural change is unknown but, speculatively, in an expanding population (which had a high proportion of younger animals) there may be a higher proportion of caribou with a tendency toward pioneering or explorative behaviour. Explorative behaviour and or a threshold density response may explain a change in traditional behaviour. Possibly, the higher proportion of younger animals in an expanding population could mean that the affinity to an area is not so strongly developed as in older animals who have strengthened the affinity through repetition. The expansion in areas of winter and summer range use by herds increasing in number of individuals may indicate that explorative behaviour increases with population size.

The status of caribou herds in 1984 was determined from aerial surveys for 16 of the 23 herds in Alaska: 10 herds were increasing and 6 were stable in number (Seward, 1985). Similarly, in the NWT, most herds that are surveyed are increasing in number and those and other herds are expanding their distribution (Williams and Heard, 1986). Caribou learning to use new ranges can overlap with other herds or occupy unused ranges, though so far the overlap of ranges has not lead to documented examples of herd interchange on calving grounds.

Previously, when caribou numbers were increasing or decreasing, the inability to positively recognize and track movements of individual caribou meant that assertions of immigration and emigration were largely based on circumstantial evidence. Hence, discussions as to whether some shifts in caribou distribution are density-dependent were inconclusive. Increasing use of radio-telemetry with its capability to repeatedly locate individually identifiable caribou will increase the probability of correlating changes in population size with distributional changes. Current radio-telemetry data have reinforced the validity of the concept of traditional behaviour in maintaining the fidelity of caribou cows to specific calving grounds (e.g., Cameron *et al.*, 1986). Radio-telemetry data have, however, identified an apparent exception to that fidelity (Davis *et al.*, 1986). Time has been too short to interpretate whether the movement of some Delta cows to the Yanert herd's calving grounds in 1984 was temporary and reflected individual variation, or was a change in traditional behaviour. The example of the Delta herd does indicate that before individual shifts are designated as emigration or herd interchange, some criteria (hypothesis testing) will be required. For example, how many radio-collared caribou (what proportion of the population of breeding cows) will constitute a change or individual variation and for how many years — a generation?

The dependence of caribou management on the herd concept which is currently based on the practical convenience of ascribing herd identity by use of a traditional calving grounds may require refinement. The dependence of the herd concept on a behavioural pattern whose definition includes the potential of change implies identification of herds may also be subject to change. The use of morphometrics, genetics and radio-telemetry (to identify isolation of breeding populations — distribution during the rut) would likely result in more biological and stringent definitions of herds.

The implications for managers of traditional behaviour resulting in fidelity to calving grounds is that (1) the use of calving grounds although relatively stable, is flexible in space and time, (2) the experience of individuals on the calving grounds can modify their subsequent use of the area, and (3) individual variation in the use of a calving ground may be expected. The most recent radio-telemetry data (e.g., Cameron *et al.*, 1986; Davis *et al.*, 1986) emphasize that some individual variation in the degree of fidelity may occur by insignificant numbers of females. Management decisions will be required to identify when the level of individual variation becomes a population-level change and over what time period. The evidence to date still suggests that, in the absence of major habitat changes such as flooding, long-term abandonment of calving grounds is rare, and fidelity to calving grounds is still the rule rather than the exception. The general increase in caribou numbers in Alaska and in Canada will lead to situations to test the relationshop between use of traditional calving grounds and herd size. As our knowledge of caribou increases, our concepts and definitions, which are only working models, may require flexibility and modification.

To date, however, only insignificant levels of change have been measured, none that would demand or justify a change in the criteria used for defining a caribou herd.

Acknowledgements

We thank J. L. Davis and P. Valkenburg, Alaska Department Fish and Game, who helped us by providing data and reviewing an earlier draft. We also thank G. D. Hobson, Director, Polar Continental Shelf Project, Energy, Mines and Resources Canada, for his continued support of our caribou research.

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Population dynamics of the Kaminuriak caribou herd, 1968 - 1985

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Abstract: The Kaminuraik caribou herd apparently declined from about 120 000 animals in 1950 to 63 000 in 1968. Beginning in 1968 documentation of herd trend was based on the estimate of the number of breeding (pregnant and post-partum) females on the calving ground during the birth peak. It appeared as if we understood the basic population processes responsible for the decline when we correctly predicted a drop from 14 800 breeding females in 1977 to 13 000 in 1980. However a three-fold increase, to 41 000 breeding females in 1982, and continued growth thereafter, was unanticipated. Most of that increase must have resulted from an immigration of cows to the herd's traditional calving ground around Kaminuriak Lake, although increased birth rates, and increased survival rates also contributed to herd growth. Immigrant cows probably came from the northeastern mainland of the NWT.

Key words: caribou (*Rangifer tarandus*), Kaminuriak herd, N.W.T., numbers, composition, hunting, predation

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Rangifer, Special Issue No. 1, 1986: 159 - 166

Introduction

The Kaminuriak caribou herd (KCH) is the easternmost of the four great herds of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) inhabiting Canada's Northwest Territories (NWT) (see Williams and Heard 1986). The KCH's traditional range encompasses the southern Keewatin District NWT, northern Manitoba and northeastern Saskatchewan and the herd calves near Kaminuriak Lake, NWT (Parker, 1972; Simmons *et al.*, 1979; Heard, 1983a).

Size of the KCH was estimated to be 120 000 in 1950 (Banfield, 1954), 149 000 in 1955 (Loughrey unpublished data) and 63 000 in 1968 (Parker, 1972). This paper describes changes in herd size, sex ratio, age composition, hunting pressure and wolf abundance between 1968 and 1985.

Methods

Four methods have been used to estimate size of the KCH since 1968 (Heard, 1985): 1) range-wide transect strip samples, 2) calving ground transect strip samples, 3) aerial photographic strip samples of calving grounds and 4) aerial photography of post-calving aggregations. The range-wide transect strip survey was conducted in March and April 1977 by Thompson and Fischer (1979). Transect strip surveys of the calving ground where caribou were counted visually were conducted in 1974 (Hawkins and Howard, unpublished data), 1976 (Calef and Hawkins, 1981), 1977 (Heard, 1981), 1980 (Heard, unpublished), 1983 (Gates, Heard and Kearney, unpublished) and 1985 (Heard and Stenhouse, unpublished). Photographic surveys of the calving ground were carried out in 1983 and 1985 and post-calving aggregations were photographed in July 1983. The senior author participated in all surveys after 1974 except the 1977 winter survey by Thompson and Fischer (1979) and the 1982 calving ground survey by Gates (1985). Extrapolation of total herd size from calving ground estimates followed the method described by Heard (1985). All population estimates refer only to those animals 1-year-old and older and breeding females refers to pregnant and post-partum cows on the calving ground.

Herd composition was estimated in November 1979 and 1981, annually in April from 1979 through 1985 and on the calving ground each year a survey was conducted except for 1974 and 1976. Only calves (caribou less than 1-year-old) were distinguished from other caribou in November 1979 and in April 1980 and 1981 but during all other composition surveys the sex of all caribou over 1-year-old was also recorded. Observers recorded the presence or absence of distended udders on all females seen during calving ground composition counts. Classification was done primaily from the ground with the aid of a spotting scope but some samples also included observations made from fixed-wing aircraft (Nov 1979, Apr 1980, Apr 1981) and helicopters (Jun 1985).

The reporting year for hunter kill began in the summer, usually 1 July. In the NWT, kill estimates were based on annual interviews with each hunter from 1968/69 through 1975/76. In 1975/76 monthly interviews began in Eskimo Point and by 1979/80 they were carried out in all settlements (Gamble, 1984; Gates, 1985). Data were incomplete from 1976/77 through 1978/79. In Manitoba, the estimated kill was based on best guesses made by government biologists until 1976 when in each community a resident was hired to interview hunters when they returned from the field (Kearny, pers. comm.).

Results and discussion

Numbers

Between 1968 and 1980 the number of breeding females on the calving ground near Kaminuriak Lake declined from 22 000 in 1968 (Parker, 1972) to 13 000 in 1980 (Table 1). The 1982 estimate was more than three times higher than in 1980 and the 1983 and 1985 visual surveys confirmed that there had been a big increase and indicated that herd size was probably growing.

If visual calving ground surveys accurately indicated herd trend, as we believe they did, then all breeding females must have been included in the census zone each year and the variation in sightability among surveys must have been low relative to the actual change in numbers. We did extensive reconnaissance, that covered at least the areas used for calving in previous years, to ensure that the census zone was large enough to include almost all breeding females. For example, in 1980 we flew 11.3 h (1800 km) within a 25 000 km^2 area to define a census zone only 50 kmx50 km. In most years tracks in the snow helped to locate animals but there was always a possibility that some breeding females were missed.

Calving ground photography in 1983 and 1985 yielded estimates of 71 000 and 97 000 breeding females respectively (Table 1). The corresponding visual estimates were 31 000 and 50 000. Surveys of other calving grounds also indicated that density estimates based on photographic counts were about twice as high as those obtained visually (Heard, unpublished data). Thus the variation in sightability was probably low, at least relative to the increase in numbers between 1980 and 1982.

The four estimates not based on calving ground surveys were consistent with the calving ground data; showing a decline between 1968 and 1977 and an increase between 1977 and 1983 (Table 1).

Composition

The age ratio of the herd changed drastically with the 1979 cohort. The proportion of calves in the fall of 1979 and spring of 1980 were twice as high as earlier estimates and calf percentages remained high thereafter (Table 2). Problems with sampling to determine composition existed because age and sex classes were segregated, especially in the spring, but the magnitude of the change and the consistency of the results among seasons and from year to year suggest that there was a real increase in the proportion of calves. High calf proportions in the fall of 1979 and 1981 corresponded to high calf percentages the following springs and April calf percentages were positively correlated with the number of 12-month-old caribou on the calving ground ($r=0.66$, $n=5$). The abundance of yearlings on the calving ground was especially noticeable in 1980 when the calving ground estimate increased

Table 1. Kaminuriak caribou herd population estimates 1968 to 1985

	Calving ground estimate			Total herd size		
Year	Total	(±SE)	Breeding females		Comments	Source
1968	27 000	(± 4 500)	22 000	63 000		1
1968				51 000	Jan-Apr surveys	1
1968				40 000	post-calving photo	1
1974	23 000	(± 3 600)		54 000		2
1976	18 900	(± 2 800)		44 000		3
1977				31 000	March-April survey	4
1977	16 500	(± 1 940)	14 800	44 000		5
1980	20 000	(± 1 260)	13 000	39 000		
1982	54 000	(± 7 200)	41 000	180 000		6
1983	42 000	(± 3 600)	31 000	120 000		
1983	98 000	(±17 200)	71 000	230 000	calving ground photo*	
1983				126 000	post-calving photo	
1985	76 000	(± 5 700)	50 000	200 000		
1985	142 000	(±17 400)	97 000	320 000	calving ground photo**	

1. Parker (1972).
2. Hawkins and Howard (unpublished data).
3. Calef and Hawkins (1981).
4. Thompson and Fischer (1979).
5. Heard (1981).
6. Gates (1985).

* the standard error of 230 000 was about 50 000 based on estimates of the variances of the variables involved in the extrapolation.

** the standard error of 320 000 was about 60 000 based on estimates of the variances of the variables involved in the extrapolation.

because of the presence of large numbers of 1-year-olds, even though the number of breeding females declined.

The increase in the proportion of calves in the herd was probably due to both higher birth rates and higher calf survival. In the late 1960s Dauphine (1976) found only 2% of yearlings and 82% of older females were pregnant. Birth rates were higher in the 1980s. Collections by Gates (1985) between 1981 and 1983 indicated that 8 of 9 yearlings and all 140 older females were pregnant. Blood progesterone levels (Rehbinder *et al.*, 1981) indicated that all 25 cows live-captured in April and May 1985 were pregnant (Heard, unpublished data). Calf survival rates must have gone up because the increase in the proportion of calves in the herd was too large to be solely the result of increased pregnancy rates. The change in calf:cow ratios from the fall of 1981 to the spring of 1982 indicated that overwinter calf mortality was 40% and within the range found by Parker (1972; 50% in 1967/68 and 30% in 1968/69) but that estimate may not be representative because of the exceptionally high calf:cow ratio in the fall of 1981.

The increase in both birth and survival rates may be related to reduced wolf densities (see below). Calf survival has been shown to be related to wolf densities in other caribou herds (Bergerud, 1983). Bergerud (pers. comm.) suggested caribou may forage more efficiently when the risk of predation is reduced. Calef (unpublished data) observed wolves stampeding large post-calving aggregations for considerable distances near Kaminuriak Lake in 1976.

Increased foraging efficiency could result in superior body condition and therefore increased birth (and survival) rates.

Mortality from hunting

Of the 4700 people living on the KCH's range in 1983, 3500 in the NWT and 1200 in Manitoba, about 85% were native. (annual report of the Beverly and Kaminuriak Caribou Management Board 1983/84). Both Indian and Inuit populations were growing rapidly, with the annual finite rate of increase for Inuit estimated at 3.2% (Hamelin, 1979).

Caribou hunting by natives occurred throughout the year without restriction on age, sex or numbers shot. Hunting by non-natives was insignificant. The recorded kill increased between 1968/69 and 1984/85 (1968/69 - 2200, 1969/70 - 2700, 1970/71 - 2700, 1971/72 - 2900, 1972/73 - 3900, 1973/74 - 3100, 1974/75 - 3100, 1975/76 - 5200, 1976/77 to 1978/79 - no data collected from one or more communities, 1979/80 - 5300, 1980/81 - 4400, 1981/82 - 10 400, 1982/83 - 6300, 1983/84 - 5600 and 1984/85 - 5800) but part of that increase was probably the result of more accurate data collection. Prior to 1975/76 the kill was probably underestimated because hunters were asked to remember their entire year's kill. Monthly interviews should result in a higher and more accurate estimate of kill, but prior to 1981/82 the proportion of hunters contacted was sometimes quite low and no extrapolation for missing data was attempted (Gates, 1985). Large differences in the number of caribou shot between successive years (eg., 1981/82 vs. 1982/83) was a result of caribou wintering closer to villages in some years and therefore being more accessible to hunters. Regardless of winter distribution caribou were always accessible to some communities. There was no reason to believe that the kill from 1976/77 to 1978/79 was either exceptionally high or unusually low.

Table 2. Sex and age composition of the Kaminuriak caribou herd, 1966 — 1985

	% in sample						
Date	Cows[1]	Bulls[2]	Calves	Sample size	Calves/ 100 cows	Estimate of % calves in the herd[3]	Source
11/66			12	300			4
2/67			9	813			4
9-11/67			17	2 183			4
3-4/68			10	3 270			4
9/68			14	3 073			4
3/69			11	967			4
4/79	76	10	14	1 966	19	9	5
9/79			29	7 115			6
4/80			28	499			5
4/81			23	6 438			6
11/81	40	33	28	7 097	70	28	6
4/82	62	10	28	8 503	44	20	6
4/83	64	17	19	8 388	30	14	6
4/84	68	6	26	15 619	40	18	7
4/85	59	12	30	8 819	50	21	7

1. females over 1-year-old.
2. males over 1-year-old.
3. assumes that bulls were underrepresented in the spring samples and that there were 83 bulls/100 cows in the herd as determined in 11/81.
4. Parker (1972).
5. Kearney (pers. comm.).
6. Gates (1985).
7. Mulders (pers. comm.).

Calves comprised between 3 and 13% of the animals shot and males made up between 53% and 58% of the kill of caribou over one year old (Gates, 1985; Gamble, 1984). We assumed wounding losses accounted for an additional source of mortality equal to 25% of the reported kill.

Distribution changes

The amount of range used by the KCH during the year varied with population size. winter herd movements south into the Manitoba forests shrank from about 500 km in the 1950s (Banfield, 1954) to 300 km in the 1960s (Parker, 1972). By the mid-1970s most of the herd was wintering on the tundra and only small numbers crossed the Manitoba border short distances (Simmons *et al.*, 1979; Thompson and Fischer, 1979). The decline in the amount of range used was considered further evidence of declining numbers (Simmons *et al.*, 1979). In the winters of 1982/83 and 1984/85 the trend reversed as caribou moved over 100 km into Manitoba; into areas and in numbers not seen for 10 years (S. Kearney, pers. comm.). We predicted that caribou would continue to expand their distribution into Manitoba as numbers increased and they did. In the fall of 1985 large numbers of caribou moved 300 km into Manitoba and by January 1986 their distribution was similar to that Parker (1972) observed in the late 1960s (Kearney, pers. comm.).

In spite of major changes in winter distribution, observations during spring migration indicated that cows continued to migrate to the traditional calving ground at Kaminuriak Lake (Simmons *et al.*, 1979; Thompson and Fischer, 1979; Gates, pers. comm.). No calving was observed elsewhere on the range. Tag return locations between 1959 and 1973 did not indicate any significant interchange among herds (Heard, 1983a) but the absence of marked animals precluded any documentation of herd immigration or emigration after 1973. Many Inuit in Baker Lake believed that emigration was the cause of the herd's decline.

Relative wolf abundance

The number of wolves observed per hour of flying during all caribou related studies indicated that wolf densities declined between the late 1960s and 1985. Between 1966 and 1968, when caribou wintered in the forest, Parker (1973) observed 1400 wolves per 1000 flying hours in winter (Nov — Apr) and 250/1000 h in summer (May — Oct). During June and July 1971 Miller and Broughton (1974) saw 103/1000 h (n=311 h) and summer observations from 1978 through 1983 averaged only 15/1000 h (n=549 h). Between one and two hundered hours were flown during winter caribou work on the tundra from 1978 — 1984 but no wolves were seen. Over the same period Kearney (pers. comm.) saw an average of 123/1000 winter flying hours (n=154 h) in the forest. Kearney's observations suggested that wolf densities in the forest were higher than on the tundra (where most of the caribou were) but much lower than Parker found in the same forests in the late 1960s.

The frequency of wolf sightings on the calving ground did not decline over time. An average of 2.8 wolves were seen per calving ground survey (SE=0.60, n=8, 1971 — 1985); about 56/1000 h. However, wolves killed 35% of 52 neonates found dead on the calving ground in 1971 (Miller and Broughton, 1974) but only 3% of 31 calves found dead in 1985 (Heard, unpublished data).

Wolves were more common on adjacent caribou ranges. Wolf observations on the Beverly herd range averaged 134/1000 h (n=410 h, 1978 — 1983) in summer, 1027/1000 h (n=136 h, 1981 — 1984) in winter and an average of 27 wolves were seen per calving ground survey (SE=10.5, n=6); about 540/1000 h. Wolves accounted for 68% of 225 neonatal calf deaths on the Beverly calving ground (Miller, Gunn and Broughton, unpublished data). Seventy-nine wolves/1000 h (n=120 h) were seen on the Northeastern Mainland range in a May 1983 survey (see Williams and Heard, 1986 for range location).

The number of wolf pelts sold to fur buyers in the Keewatin, an index of the number shot, averaged about 90/yr from 1965/66 to 1971/72, 250/yr from 1972/73 to 1977/78 and 75/yr from 1978/79 to 1983/84. Few wolves were shot or trapped in northern Manitoba. The increase in kill in the mid 1970s was probably the result of the increase in pelt value, the increased use of snowmobiles and higher wolf densities. Pelt value rose from $80 in 1970, to $130 in 1977 and to $200 in 1980 (Heard, 1983b). Most wolves were shot after being tracked by hunters on snowmobiles. Snowmobiles were first introduced in the Keewatin in 1963 and by 1970 most hunters owned one (Bowden, pers. comm.). A widespread wolf poisoning program was terminated in 1963 and wolf numbers probably recovered quickly (Heard, 1983b) ie. between 1963 and 1970. The low kill after 1977/78 suggests (as did the sighting frequencies) that wolf numbers declined during the 1970s. The kill was low even though pelt prices were at an all time high, caribou wintered close to Keewatin communities and the introduction of faster snowmobiles made wolf hunting an exciting and desirable sport. Hunting may have contributed to the wolf decline but it is also possible that the kill was largely a reflection of wolf abundance that was determined by other factors.

Another factor contributing to the decline in wolf numbers may have been the caribou's change in winter range use. We suggest the following mechanism for that relationship (see also Bergerud, 1983). The wolves associated with caribou on the tundra are migratory non-breeders recruited primarily from forest-resident productive wolves. The numerical response of forest-resident wolves is dependent on per-capita caribou densities. Reduced caribou densities in the forest result not only in fewer wolves in the forest but also in reduced recruitment to the migratory wolf population on the tundra. This scenario suggests that wolf numbers will increase over the entire KCH range as more caribou winter in the forest.

Population dynamics

The discussion of the Kaminuriak herd's population dynamics falls into two periods. In the late 1960s birth rates and calf survival were low and wolves were abundant. After 1980 birth rates and calf survival were high and wolves were rare. Between 1968 and 1980 the herd was small and declining. After 1980 the herd was large and increasing.

The conclusion of a Canadian Wildlife Service study in 1969 was that the KCH was stable (Parker, 1972; Miller, 1974; Walters *et al.*, 1975). However as we have shown in this paper, the herd declined. We suggest that the decline was not predicted by Parker because he underestimated natural mortality of adults (at 4.8%/yr). He assumed that wolves accounted for all natural mortality. In our opinion it was unlikely that all caribou dying of other causes were consumed by wolves. Bergerud (1983) showed that natural mortality of adult caribou in herds subjected to wolf predation was correlated with calf survival. Natural mortality of adults based on Bergerud's regression was 10%/yr and the best fit to the data (1968 — 1980) was 7.2%/yr.

The decline was not predicted by either Miller (1974) or Walters *et al.* (1975) apparently because they asumed calf survival was at least 40% (60% mortality) even though Parker's field data showed that it was only 22% (78% mortality). Miller's (1974) analysis demonstrated that survival to age 3 yr must have been at least 41% for stability. Walters' *et al.* (1975) computer simulation model indicated that 60% calf mortality produced a stable population. Their simulation of 75% mortality resulted in a decline that turned out to accurately describe herd trend from 1968 to 1980.

Before the June 1980 survey we modelled herd dynamics using 7.2% natural adult mortality, 75% calf mortality and an average hunter kill from 1977 to 1980 of 4000/yr and predicted that we would find 12 000 breeding females on the calving ground. The survey results indicated 13 000; the close agreement between the data and our prediction led us to believe we understood the basic population processes. Between 1968 and 1980 the KCH declined because the combined effects of hunting and natural mortality exceeded recruitment and we assumed that the decline would continue.

With the dramatic increase in numbers between 1980 and 1982 it was clear that herd population dynamics had changed. There is little doubt that internal herd growth, through recruitment and survival increases, was at least partially responsible for that increase. But the increase was so large that immigration must have contributed to herd growth. Using assumptions that maximized herd growth (eg. 100% pregnancy among 1-year-old and older caribou, 95% survival of all age classes including calves) we calculated that at least 15 000 cows must have immigrated after calving in 1980 in order to have 41 000 breeding females by 1982. If we assumed that the 1980 estimate was underestimated by 50% because of sightability bias (based on aerial photography of other calving grounds and other years) (Heard, unpublished data), we calculated that at least 13 000 immigrants would have been required to end up with 71 000 breeding females in 1983.

Both the Beverly and the Bathurst herds have also increased since 1980 (Williams and Heard, 1986) so substantial emigration from those herds was unlikely. Immigrants probably came from the northeastern mainland of the NWT where unexpected fluctuations in calving densities have occurred in the past and where there were enough caribou to provide the required number of immigrants (Calef and Heard, 1980; Heard *et al.*, 1986). Population estimates in 3 areas of the northeastern mainland (Melville Peninsula and north and south of Wager Bay) have varied by an order of magnitude between years. Emigration from the northeastern mainland was also implicated when the number of breeding females on the adjacent Bathurst herd's calving ground doubled from 72 000 in 1982 to 137 000 in 1984 (Heard, unpublished data).

Because there were no marked animals in any herd and the timing of surveys was not appropriate to document declines on the northeastern mainland coincident with the increases elsewhere, we considered explanations that did not involve immigration. If the 1980 estimate was too low (even after correction for sightability bias) and if we assumed that recruitment increased in the mid to late 1970s, the internal herd growth alone could explain the increase in numbers from 1977 to 1982. When we reviewed the 1980 survey data we could find no reason to reject the results. There were no unusual procedural problems during the field work and, as discussed above, reconnaissance was so extensive that it was unlikely significant numbers of cows calved outside of the census zone. If we rejected the 1982 estimate as being too high, immigration would still have been necessary to explain the 1983 and 1985 estimates.

Skoog (1968), Bergerud (1980, 1983) and Haber and Walters (1980) argued that periodic dispersal has been an important factor in caribou population dynamics. Haber and Walters (1980) suggested that competition for food causes caribou to disperse from herds that have obtained high densities (about 2 caribou/km^2). Herds receiving immigrants increase because the immediate reduction in the predator-prey ratio allows the herds to escape the controlling effects of wolf predation. The herd increases until competition for food again causes dispersel. In Bergerud's model, caribou disperse if they reach 2/km^2 but such high densities rarely occur 1. because wolf predation can halt herd increase before densities get that high or 2. because caribou expand their range to limit their own densities.

We have too few data to comment on the causal mechanism of dispersal but so far our data on the effects of immigration appear to fit Bergerud's second hypothesis. The decline in herd size from 1950 to 1980 resulted in a reduction in the amount of range used. With the abandonment of the forested portion of their winter range in the mid 1970s caribou made less contact with wolves and wolf numbers declined. Immigration provided a further decrease in the predator prey ratio, calf survival increased, caribou numbers increased and the herd began expanding its range.

In the fall of 1984 one of us (DH) began radio-collaring caribou in the KCH and on the northeastern mainland. We recognize that those marked animals cannot prove that immigration occurred between 1980 and 1982. But if we find significant interchange between calving grounds we would be more confident that immigration accounted for the increase in the Kaminuriak herd between 1980 and 1982 and we will be in a better position to test competing hypotheses of population control in caribou.

Acknowledgements

We thank the following people for their assistance in data collection and/or their comments on drafts of this paper; Tom Bergerud, Ed Bowden, Jim Davis, Cormack Gates, Steve Kearney, Kevin Lloyd, Frank Miller, Robert Mulders, Polar Continental Shelf Project, Paul Roy, Gordon Stenhouse, Doug Stewart, Peter Suwaksiork, and Mark Williams.

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Inuit harvesting levels of caribou in the Kitikmeot Region, Northwest Territories, Canada, 1982 — 1984

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Abstract: Information on the native harvest of caribou (*Rangifer tarandus* spp.) has been systematically collected in the Kitikmeot (Central Arctic) Region of the Northwest Territories since October 1982 through a cooperative effort between the Kitikmeot Hunters and Trappers Association and the Department of Renewable Resources. During the first 2 years of the study about 640 active hunters in 7 communities, or 20% of the Inuit population, were included. Local fieldworkers contacted an average of 80% of all hunters each month. The estimated regional harvest between October 1982 and September 1984 was 18 827±260 (SE) caribou. In the reported harvest (n=12 969), bulls dominated (54%) followed by cows (32%) and juveniles (<15 months old; 14%). The successful hunters harvested on the average 3.5 caribou/hunter/month. When extrapolated over the total Inuit population in the Region, the estimated caribou harvest was equivalent to an annual harvest of 3.1 caribou/person. This harvest level was relatively consistent between communities and years.

Key words: Canada, caribou, harvest, hunting, Inuit, Northwest Territories, *Rangifer*

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Rangifer, Special Issue No. 1, 1986: 167 - 172

Introduction

The importance of documenting native harvesting is becoming increasingly apparent both to wildlife managers and users throughout the North. Reliable harvest data are essential not only for responsible wildlife management but also for documenting the economic and cultural importance of wildlife to northern communities. In the Northwest Territories, the latter has become particularly relevant in view of native land claims negotiations, impending industrial developments, and ongoing land use planning.

While information on native wildlife harvests in northern Canada has been collected over the last 40 years, the records are only of limited value due to incomplete, or sporadic, coverage in space and time, lack of systematic sampling techniques and inconsistent, or unknown, reporting rates. The basis and limitations of these data series have been discussed by Kelsall (1968), Berger (1977), Smith and Taylor (1977) and Usher *et al.* (1985). A system to formalize the collection of native harvest data was first used by the James Bay and Northern Quebec Native Harvesting Research Committee (JBNQNHRC, 1982). The system was based on a cooperative approach with extensive local involvement by native residents who were hired in each community to conduct periodic field interviews of hunters.

In the Northwest Territories, comprehensive harvest surveys based on the James Bay model were intiated in the Baffin Region in 1980 (Donaldson, 1984) and in the Keewatin Region in 1981 (Gamble, 1984). A review of the methodologies used in these studies was recently completed by Usher *et al.* (1985). In late 1982, the Kitikmeot Hunters and Trappers Association passed a resolution in favour of a long-term harvest study to be initiated in the Kitikmeot (Central Arctic) Region. The survey was to be done in cooperation with the Department of Renewable Resources with the aim to establish present community harvest levels of a variety of wildlife species important to the Inuit population in the Region. Caribou (*Rangifer tarandus groenlandicus* and *R. t. pearyi*) is, by far, the most important source of red meat in the Kitikmeot Region and reported here are harvesting levels of caribou based on data collected during the first 2 years of the study (October 1982 - September 1984).

Methods

Study design

Community visits were made to explain the purpose of the harvest study and, in consultation with the local Hunters and Trappers Association, to hire a native fieldworker in each of the seven communities of the Region (Fig. 1). The fieldworkers were encouraged through a bonus pay system to collect harvest information by personally interviewing as many active hunters as possible each month. Most interviews were conducted in the native language (Inuktitut) using translated data forms. A «hunter» was defined as a holder of a General Hunting Licence (GHL) who hunted at least once a year. Lists of GHL holders from government records were updated by the fieldworkers to define the hunter population for each community. The definition of an active hunter included native residents 18 years of age or older and was, with few exceptions, restricted to males. Female GHL holders were not considered to take an active part in the harvesting of caribou and were, therefore, not contacted by the fieldworkers. To maintain the anonymity of respondents, hunters were assigned numbers and the master list was then kept by the local fieldworker. The only other person with access to the list was the project biologist, for purposes of data verification.

A hunter status form was used to determine the proportion of all hunters contacted (sample population) and whether or not a hunter had successfully hunted that month. A hunter who was away from the community for a whole month, as a result of travelling, rotational wage

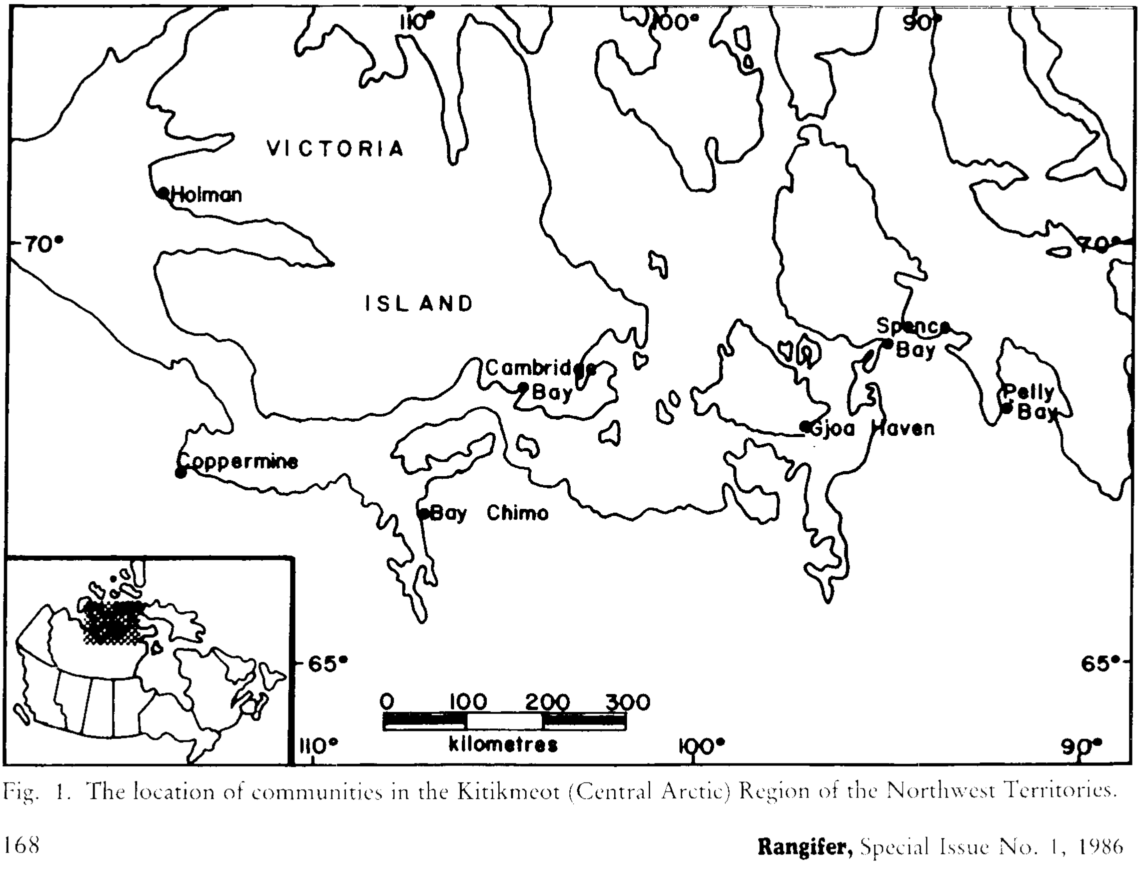

Fig. 1. The location of communities in the Kitikmeot (Central Arctic) Region of the Northwest Territories.

employment, etc., was not included in the hunter population for that month. Successful hunters were asked to report their harvest for several species including caribou, muskox (*Ovibos moschatus*), wolves (*Canis lupus*), marine mammals, waterfowl and fish. For caribou, information included numbers taken, age and sex (bull, cow, and calf), and location of harvest. Harvest kill was defined as the number of caribou actually retrieved and brought back to the community. It did not include crippling loss or any caribou cached and not retrieved. To aid hunter recall and facilitate data collection, calendars where individuals could record their own harvest were translated into local dialects and given to all hunters.

Data analysis

A method of proportional projection (JBNQNHRC, 1982; Donaldson, 1984) was used to estimate community harvest by month from the reported harvest, the sample size, and the number of hunters in the population. The respondents were treated as a random sample assuming the non-respondents were not different from the sampled population and the sample was large enough to contain a representative selection of the hunter population.

However, hunters were not selected strictly at random by the fieldworker but, rather, fortuitously depending on the availability of individual hunters in the community each month. To evaluate potential sampling biases and determine the nature of non-respondents, several verification tests of the data were made (Graf, 1984). Based on 1983 data from each of three communities (Cambridge Bay, Spence Bay, and Pelly Bay), the mean reported kill rate for each hunter was plotted to illustrate the distribution of hunters and their contribution to the total community harvest. From each hunter's record, the frequency of non-response was tabulated and compared with mean kill rate for the months when the hunter had been contacted.

Using proportional projection and the notations of Cochran (1963), the estimated harvest for month i in community j ($\hat{Y}_{ij}$) is calculated by:

$$\hat{Y}_{ij} = N_{ij} \Sigma y / n_{ij}$$

where N_{ij} = number of hunters in the Inuit population in month i, community j;
Σy = harvest reported by those contacted;
n_{ij} = number of hunters contacted in month i, community j.

The variance for the estimated harvest, Var ($\hat{Y}_{ij}$), is calculated as:

$$\mathrm{Var}(\hat{Y}_{ij}) = N_{ij}^2 (1 - f)\, s^2/n_{ij}$$

where 1 - f = finite population correction factor and
$f = n_{ij}/N_{ij}$ (Cochran, 1963);
s^2 = sample variance

Since each month is treated as a separate stratum, the estimated annual harvest for at particular community is the sum of estimates from each month ($\Sigma \hat{Y}_i$). The standard error of that estimate, SE($\hat{Y}_j$) is calculated from the sum of each month's variance, *viz.*

$$SE(\hat{Y}_j) = \sqrt{\Sigma \mathrm{Var}(\hat{Y}_i)}$$

Similarly, the estimated annual harvest for the entire region is based on the sum of estimates from all communities with their associated variances.

To analyze differences in harvesting levels between years, data were divided into two 1-year periods: October 1982 - September 1983 («1983») and October 1983 - September 1984 («1984»). In two communities, Bay Chimo and Coppermine, collection of harvest data did not start until January 1983. To allow for comparisons of annual regional harvest totals and per capita harvesting levels between communities, it was necessary to extrapolate harvests for those missing time periods by applying the proportion of the annual harvest (in %) that was respresented by the similar period during the following year when data were collected. An individual hunter «harvest rate» was calculated as the number of caribou taken per successful hunter per month. Per capita harvesting levels were calculated by dividing the estimated annual harvest of caribou by the total population size (number of caribou/person/year) and by the total number of hunters in the population (number of caribou/hunter/year).

Results

During 1983 and 1984, the size of the hunter population averaged 640 hunters (Table 1) which represented 20% of the Inuit population in the Kitikmeot Region. During 159 monthly sampling periods including 10 912 individual hunter contacts, the mean response rate was 80% (Table 1). Sample sizes varied depending on season and the energy of individual fieldworkers. The lowest response rates occurred in early summer

(June—July) when many families moved out into summer camps and could not be reached by the fieldworker. As the study progressed, mean response rates increased from 74% in 1983 to 86% in 1984 (Table 1).

Distribution plots, based on 1983 data and used to evaluate potential sampling biases, showed that individual hunter harvest rates approximated a normal distribution. This suggests that average hunters were responsible for most of the caribou harvest and not the very active hunters who may be more easily missed by the fieldworker. Apparently, missed hunters were not exceptional as there was no relationship between individual hunter harvest rate and the frequency of contact. Given the high response rates (74 - 86%) and that few individual hunters were missed more than 3 months of the year, the assumption of a representative («random») sample for the purposes of data analysis seems reasonable.

The total reported harvest for the 1983 and 1984 periods were 12 969 caribou (Table 1) and the corresponding estimate was 18 827±260 caribou. While the reported regional harvest was similar between years (Table 1), hunter response rates were higher in 1984 resulting in less inference and a lower ($P<0.05$) estimated harvest. Community harvest levels were lower throughout the Region in 1984. The largest proportion of the estimated harvest in both years was taken by hunters from Coppermine (23%), Cambridge Bay (20%), and Gjoa Haven (20%). Of the total reported harvest, 83% occurred between early and late winter (October to April). The successful hunters took, on the average, 3.5 caribou per hunter per month and this harvest rate was similar between years for most communities (Table 1).

When the annual caribou harvest is compared with Inuit population size for each community, the overall regional harvest was equivalent to 3.1 caribou per person per year (Table 2). The higher levels of harvesting by hunters in Bay Chimo is consistent with the dependancy on caribou as part of the traditional lifestyle maintained in that

Table 1. Community harvesting levels (means ± SE) of caribou in the Kitikmeot Region, NWT.

Community	Year	Hunter population[a]	Sample size (%)[b]	Reported harvest	Estimated harvest	Harvest rate[c]
Bay Chimo	1983	24±1	94±4	338	479±14[d]	3.8±1
	1984	27±2	99±0	295	298±3	3.2±0
Cambridge Bay	1983	132±3	77±6	1897	2351±59	4.3±0
	1984	127±1	94±1	1352	1445±24	3.7±0
Coppermine	1983	127±3	47±4	723	2279±117[d]	3.5±0
	1984	156±4	76±7	1437	2027±69	3.8±0
Gjoa Haven	1983	104±1	55±5	1097	2098±126	4.8±1
	1984	103±2	79±7	1035	1551±111	4.5±1
Holman	1983	58±1	72±7	723	1177±102	5.0±1
	1984	55±2	85±2	852	1072±38	3.6±1
Pelly Bay	1983	50±0	87±4	627	765±24	2.3±0
	1984	49±1	81±5	492	691±29	2.4±0
Spence Bay	1983	127±1	86±5	1050	1390±37	2.2±0
	1984	135±3	88±4	1051	1183±22	2.4±0
ALL	1983	622±4	74±7	6455	10 539±213	3.7±0
	1984	652±7	86±5	6514	8288±149	3.4±0
ALL	Combined	640±5	80±9	12 969	18 827±260	3.5±0

[a] The number of hunters determined monthly (N) between Oct. 1982 — Sept. 1984.

[b] The number of hunters contacted (n) expressed as a proportion of the hunter population.

[c] The number of caribou taken per successful hunter per month.

[d] Includes proportional estimates for periods with missing data (see Methods).

Table 2. Per capita harvesting levels (means ± SE) of caribou in the Kitikmeot Region, NWT.

Community	Year	Population (Inuit)[a]	Estimated harvest (±SE)	No. caribou/ person/year	No. caribou/ hunter/year
Bay Chimo	1983	81	479±14	5.9	19.8
	1984	82	298±3	3.6	11.0
Cambridge Bay	1983	706	2351±59	3.3	17.8
	1984	714	1445±24	2.0	11.4
Coppermine	1983	810	2279±117	2.6	16.9
	1984	815	2027±69	2.5	13.0
Gjoa Haven	1983	563	2098±126	3.7	20.2
	1984	615	1551±111	2.5	15.1
Holman	1983	308	1177±102	3.8	20.3
	1984	325	1072±38	3.3	19.5
Pelly Bay	1983	263	765±24	2.9	15.3
	1984	261	691±29	2.7	14.1
Spence Bay	1983	415	1390±37	3.3	10.9
	1984	413	1183±22	2.9	8.8
ALL	1983	3146	10 539±213	3.6±0	17.3±1
	1984	3225	8288±149	2.8±0	13.3±1
ALL	Combined	6371	18 827±260	3.1±0	15.3±1

[a] Based on GNWT Bureau of Statistics (1984) and Statistics Canada (1982).

community. About one-third of the residents in that community were reported to be active hunters by the fieldworker. While the per capita harvesting levels in the Region were similar between years and communities, the number of caribou harvested annually per hunter was more variable ($\bar{x}=15.3$; Table 2).

Of the total reported harvest (12 969; Table 1), 54% were bulls, 32% cows, and 14% «calves». Since some «calves» were reported taken in summer, this category includes yearlings up to 15 months old and is more appropriately called «juveniles». Differences in the sex/age distribution of the harvest were apparent between communities. The largest proportion of bulls were taken by hunters in Bay Chimo (74%) and Pelly Bay (72%). Cows dominated the harvest in Coppermine (46%) while the largest proportion of juveniles were taken by hunters in Holman (23%).

Discussion

The proportion of active hunters (20%) to total Inuit population size in the Kitikmeot Region is similar to the range of 19—21% reported for the Baffin Region (Donaldson, 1984). To maintain accurate lists of active hunters in each community, periodic updating of the lists were necessary as hunters and their families moved between communities and new GHL holders were added. The mean response rate (80%) compares favourably with the Baffin study (72% in 1981, 79% in 1982; Donaldson, 1984). Since the harvest of caribou is spread over a large number of hunters and months, high hunter response rates will help to ensure that a representative, or unbiased, sample is obtained. In the James Bay study, Steiger (1981) confirmed that a large fortuitous sample of hunters (>60%) yielded an unbiased estimate of total harvest using the proportional projection method. In the Kitikmeot Region, the unsampled hunter population does not appear atypical or likely to influence community harvest levels. The lower response rates in early summer do not significantly affect caribou harvest estimates as over 80% of the harvest is taken during fall, winter and spring.

Biases arising when hunters forget, or deliberately misrepresent their harvest (strategic response bias), have the potential to affect the reliability of survey data. I do not believe hunter recall was a serious problem due to the frequency of interviews (monthly), the use of calendars and the fact that hunters have little problem remembering their harvest of larger species, such as caribou. Strategic response bias, or misrepresentation of the harvest, cannot be eliminated by technical methods as it depends on how the respondents perceive the survey and how they believe its results may affect their interests (Usher *et al.*, 1985). Short of demanding proof of kill, there is little that can be done to verify the accuracy of the reported caribou harvest. Through the establishment of trust and the acceptance of the need for reliable harvest data among hunters, fieldworkers and researchers, the effects of response bias should be reduced. Since this harvest study was cooperative and personal interviews were made by fieldworkers familiar with the local hunters, there was little reason, or opportunity, for misrepresenting the actual harvest. Underreporting, for fear of enforced controls, was not likely a factor for caribou as subsistence use has never been regulated in the Kitikmeot Region.

The per capita harvesting levels of caribou in the Kitikmeot Region ($\bar{x}=3.1$ caribou/person/year) were surprisingly consistent between communities and years despite local differences in caribou distribution and availability. When compared with other regions, the harvest levels remain reasonably consistent. Based on harvest data presented by Gamble (1984) from the Keewatin Region, I calculated the annual harvest in 1981/82 and 1982/83 to represent 3.2 and 2.8 caribou per person, respectively. Similar figures from the Baffin Region, based on data by Donaldson (1984), are somewhat lower (1.8 caribou/person/year in 1981 and 2.4 caribou/person/year in 1982). The greater dependancy on marine mammals in the Baffin Region will likely contribute to the apparently lower per capita harvest of caribou there. The estimate that Inuit annually need 5 to 7 caribou per person, stated in the Federal Court of Canada in 1979 (Miller, 1983), seems high in view of the harvest data now available. I believe present harvesting levels are sufficiently similar between communities, regions, and years, to suggest that Inuit in the Northwest Territories now require between 2 to 4 caribou per person on an annual basis.

Acknowledgements

I thank the fieldworkers and hunters of the Kitikmeot Region for their cooperation and support in collecting the harvest data. A. Gunn supplied raw data from May to September 1984 and is continuing the harvest study. T. C. Meredith and D. L. Stewart critically reviewed the manuscript and provided helpful comments.

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Rutting behaviour in an enclosured group of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.)

Ilpo Kojola[1]

Abstract: The rutting behaviour of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.) was studied 1981 - 83 in a 15 ha enclosure located in Kivijärvi, Central Finland (63° N). The group consisted of two old stags, 6 - 9 hinds and their calves and yearlings. The main sections of the study were social structure, social signals, time budget and daily activity. In early September the aggressiveness of the stags towards females concentrated on those individuals which had last dominated them. Adult females were more aggressive to young females than to each other. The proposed aggressiveness of the hinds towards yearlings may be explained by the lower predictability of the hierarchial status of the young animals. The main character of observable social signals seemed to be similar to those described in earlier studies concerning the genus *Rangifer*. Stags often made snapping-like movements with their mouths during agonistic behaviour. Low-stretch displays and investigation of the urine of the females concentrated on the estrous hind during the day preceeding the pre-copulatory period (which commenced when the hind did not yet avoid the stag). The stag always sniffed at the vulva of the female after copulation. The harem stag did not stop grazing during the peak of the rut. Differences in the time budget between the dominant and subdominant stag as between estrous and anestrous hinds were clear. Mating occurred most often during the 3 hours after sundown. In the dark the old stags often sparred and their activity towards females seemed to be weaker than in the daylight hours. During the peak rut the stags were observed to spar only while the females were resting.

Key words: wild forest reindeer, rut, social behaviour, time budget, daily activity.

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Rangifer, Special Issue No. 1, 1986: 173 - 179

Introduction

The wild forest reindeer (*R. t. fennicus* Lönnb.) is at present classified as a subspecies of genus *Rangifer* (Siivonen, 1975, Nieminen, 1980), and its present numbers and distribution 8000 individuals in Soviet Karelia (Danilov and Markovsky, 1983), about 600 individuals in eastern Finland (Pulliainen, 1983) and about 50 individuals as an introduced population, in Central Finland (Kojola *et al.*, 1985).

The aim of this presentation is to describe the rutting behaviour of wild forest reindeer and, in some respects to compare the behaviour with other *Rangifer* subspecies and other ungulates.

Thomson (1980) has found differences in the rutting behaviour between reindeer and caribou as has Skogland (1981) between Norwegian wild reindeer (*Rangifer tarandus tarandus* L.) and Svalbard reindeer (*R. t. platyrhynchus* Vrolik). Previously Montonen (1974) and Helle (1982) have presented some observations of the behaviour of wild forest reindeer. The main section of this study are social structure, social signals, time budget and daily activity.

Adult reindeer observed in this study were transported from eastern Finland to Central Finland (distance about 300 km) into an enclosure prior to subsequent introduction. The enclosurement period offered a chance to observe the details of the rutting behaviour in a small group of this reindeer.

Study area and methods

The wild forest reindeer were observed in 1981 - 83 in a 15 ha enclosure (Fig. 1) located in Kivijärvi, Central Finland (63°N, 24’E). The constantly enclosured group consisted of two adult stags, 6 - 9 females and their calves and yearlings. The reindeer were daily fed with lichens (*Cladonia* spp.), molasses and fresh hay. The natural vegetation was quite abudant on the bog and fen areas, but in the forests the coverage of the undervegetation was only 20 - 30% of its original.

The early observation period was initiated on the first day of September and finished at the beginning of November. This period was divided into seven periods each lasting 10 days. The field examination took 368 hours altogether (302 h in 1981, 110 h in 1982 and 44 h in 1983), usually lasting 2 - 3 hours at a time (scale from 10 minutes to 24 hours). A spot light was used in the dark.

The behaviour displays, individual distances and the activity of the animals (at intervals of 60 sec in the males and 5 min in the females) were recorded on tape or directly into a notebook using abbreviations. The distribution of observations between different subgroups or individuals was tested using the chi-square test.

Results

Timing of the rut

The dates of the off-rubbing of the antler velvet deviated at most one day in the same individual in successive years (stag 1: 31 Aug. 30 Aug. and 30 Aug.; stag 2: 9 Sept., 9 Sept. and 8 Sept.; hind 1: 15 Sept. (1981) and 16 Sept. (1982); hind 4: 25 Sept. (1981) and 25 Sept. (1982); hind 10: 17 Sept. (1981) and 16 Sept. (1982). On average yearling males (n=5) rubbed the velvet off on the 10th of September (S.D.=1.5). In the year 1981 6 females removed the velvet on the average on the 21st of September (S.D. =4.2) and the mean interval from the velvet removal to their first estrous took 15.5 days (S.D.=3.9).

In the year 1981 seven of nine adult females had their first heat during 1 - 10 October (defined to be «the peak of the rut»). In 1982 I could determine the timing of two heats (both on the 2nd Oct.) and in 1983 none. The calving dates in 1982 - 84 were nearly the same from year to year (Kojola, unpublished data).

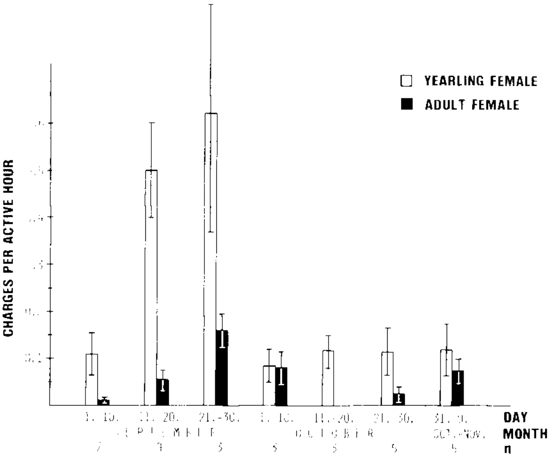

Fig. 1. The charges of the hinds towards the yearling females and towards each other at the feeding site (means with S.E.)

Social structure and agonistic behaviour

The hinds rested more often as a single group during 21 September - 10 October than between 1 - 20 September or between 11 - 30 October. The average lying distances between hinds seemed to be smaller from 21 September to 10 October (11.5 ± 0.65 m) (x ± SE), n=575) than during 1 - 20 September (16.2 ± 0.92 m, n=237) or during 11 - 30 October (22.2 ± 1.16 m, n=290). Average lying distance between the estrous hind and the dominant stag was 3.7 ± 0.72 m (n=15), while the corresponding value between the stag and anestrous hinds during the peak rut was 11.2 ± 0.86 m (n=88). Yearling males followed the harem while the subdominant old stag moved individually. Stag 2 rose over stag 1 on the 6th (1982) and 4th (1983) October.

During the pre-rut (see Espmark, 1964) the agonistic behaviour of the stags concentrated on those females that had last dominated them (two females dominated both stags in early September). One of five yearling males rose over the hinds and this occurred in late October. During every autumn one yearling male was found towards which the dominant stag behaved more aggressively than towards the subdominant old stag or other yearling males.

Charging, chasing and snorting characterized the agonistic behaviour of the stags. They also often made small, rapid snapping - like movements with their mouth during agonistic behaviour. First symptoms of herding (see

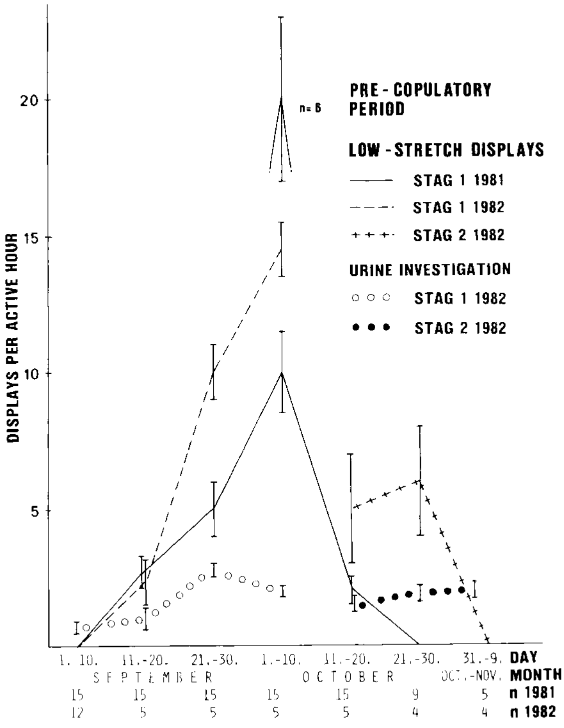

Fig. 2. Frequency of the low-stretch displays and investigating of the urine by the dominant stags (means with S. E.; urine investigation was not recorded in 1981).

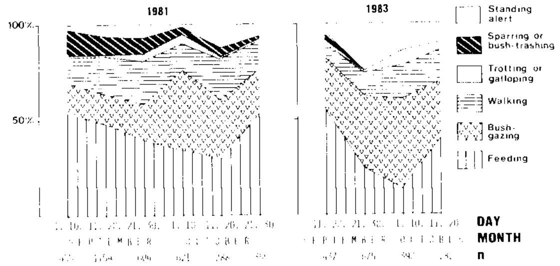

Fig. 3. Activity budget of the harem stag on his feet in 1981 (two subordinated males) and in 1983 (five subordinated males).

Bergerud, 1974) were observed at the beginning of the period 21 - 30 Sept. The harem stag herded the hinds most intensively during 1 - 10 October. During this period only single, mated females were observed for longer times (several tens of minutes or so, 5 obs.) outside the harem. When the subdominant stag tried to herd them they vigorously ran towards the harem. The hinds charged young males more often than young females (P<0.001, n=82), young females more often than calves (P<0.001, n=34). Aggressiveness of the hinds towards young females and towards each other seemed to be most intensive in late September (Fig. 1). The hinds seemed to behave more aggressively towards young males after the peak rut than before it.

Behaviour observed in both sexes

The bush-trashing was most frequent during 21 - 30 September in both sexes. The females usually thrashed those trees and bushes the stags had earlier rubbed bare. The reindeer frequently interrupted the bush-trashing for licking and sniffing at the tree.

«Yawning» was here defined as a wide mouth-open display lasting 2 - 3 secs (distinguished from slight mouth openings which were seen while the animals were stretching after getting up, from more rapid displays which occasionally stopped feeding on the molasses and from the flehmen display (see Schneider, 1930; Fraser, 1968) which frequently followed olfactory stimulus. Yawning display was preceeded by antler contacts in 67% (n=39) of males (with tree or another reindeer) and 56% (n=12) in females (with tree). The lying animals usually yawned after licking their hooves.

During 11 - 30 September the hinds were observed to be grazing in five and lying in seven cases while the old stags sparred with each other. During 1 - 10 October these stags were seen to spar with each other only while the females were lying (n=5). When the hinds become active, the dominant stag began to threaten the subdominant. The sparring was most often (P<0.001, n=29) commenced upon the initiative of the dominant stag.

The sparring was very frequent among yearling males. Yearling females sparred with calves, yearling males or with each other. Adult females were observed to spar in eight cases with their calves, twice with a yearling male, but never with each other or with a yearling female.

Male rutting behaviour

The low-stretch displays (see e.g. Walther, 1974) were most frequent during 1 - 10 October even if the pre-copulatory periods (see chapter «Mating behaviour») are ignored (Fig. 2). Displaying activity was less frequent after the peak rut in 1981 than in 1982, when the dominance relationships between the stags

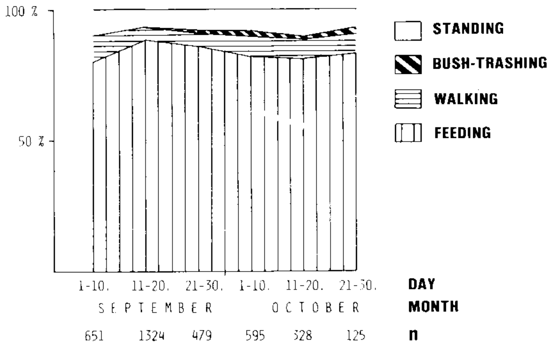

Fig. 4. Activity budget of anestrous hinds on their feet.

changed during the peak of the rut. The low-stretch displays and investigation of the urine concentrated ($P<0.001$, n=32 and 30) during the day before the pre-copulatory period of the estrous female. During 11 - 15 October the harem stags made advances more frequently ($P<0.001$, 1981: stag 1, n=43; 1982: stag 2, n=27) to the unmated than mated females. Yearling males (43% of observations, n=28) and male calves (46%) were most active in mounting on anestrous females. A subordinate male (male calf) was once seen to mount the estrous female. Other females did not mount the estrous hind. The urine investigation was followed by the flehmen response, which usually lasted 20 - 30 sec at a time. Yearling males, male calves and hinds showed the flehmen occasionally.

The dominant stag hunched during 21 - 30 September more frequently ($x^2=18.7$, $P<0.001$, n=55) after other activity had been directed towards males than towards females. During 1 - 10 October this kind of difference was not observed ($x^2=0$, n=55). Complete erections (penis fully extended and horizontal) followed antler contact with another reindeer in 72% observations (n=18). During sparring the penis of males was often semi-erect.

Mating behaviour

The pre-copulatory period prior to mating was defined to commence when the estrous female did not yet avoid the displaying stag. That period took, on average, 74 ± 7.3 min (6 estrous females). During the pre-copulatory period the stag made 4.5 ± 1.09 (n=6) mounting efforts on the hind. Mean duration of the mating was 8.4 ± 1.2 sec (n=7). The stag always sniffed at the vulva of the hind immediately after mating.

Time budget and daily activity

The same stag used a considerably smaller proportion of the time resource for grazing in 1983 than in 1981 (Fig. 3). The were four yearling males inside the enclosure in 1983 and one in 1981. The dominant stag grazed 5 - 15% and subdominant 45 - 55% during the peak of the rut. The hinds used 80 - 88% of the time for grazing while on their feet (Fig. 4). During estrous the proportion of time the hind spent feeding tended to decline and the proportion of time she spent in bush-trashing or inactive standing tended to increase (Fig. 5).

During 24-hour observation periods (18 - 19 Sept., 15 - 16 Oct. in 1981 and 10 - 11 Sept. in 1982) long resting periods took place during the hours before midnight. (Figs. 6 and 7). The proportion of lying tended to differ slightly between the dominant stag and hinds (46.2/49.6 % in 10 - 11 Sept. 1981 (6 females), 42.1/43.2 % in 18 - 19 Sept. 1982 (9 females) and 50.0/61.8 % in 15 - 16 Oct. 1981 (1 female)). In the dark the stags sparred more frequently and the activity towards the hinds was weaker than in the daytime (Table 1). During 1 - 10 October in 1981 five matings (n=7) took place during 3 hours after sundown.

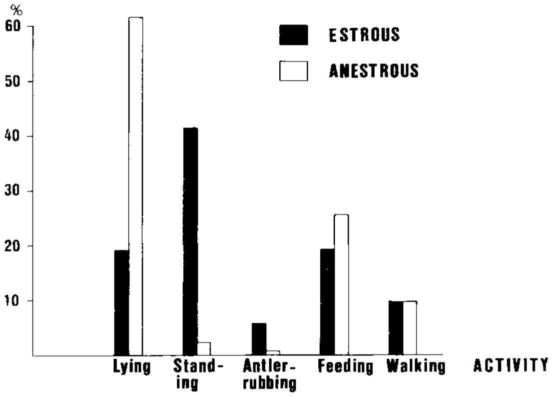

Fig. 5. Comparison of the proportion of time during 5 hours prior to mating by estrous (No. obs. 172) versus anestrous hind (No. obs. 616).

Discussion

The peak of rut of wild forest reindeer takes place in the middle of October (see Helle, 1977). Kojola *et al.* (1985) suppose that the transition of 1 week earlier in the timing of the main estrous season occuring in the enclosure from 1980 to 1981 (concluded from the subsequent calving

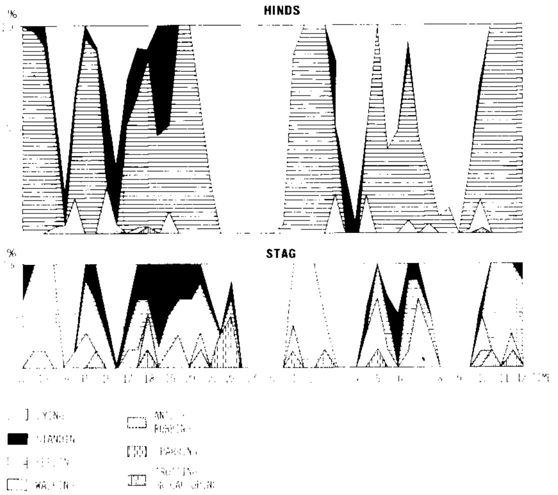

Fig. 6. Activity budget of the harem in 18 - 19 Sept. 1981.

dates) was due to the intensification of the artifical feeding. The amount of fresh hay especially had been increased.

According to Bergerud (1974) the proposed aggressiveness of the stags towards the hinds during the pre-rut confirms the male dominance. My findings on the distribution of aggressiveness at the individual level tend to support this suggestion. The rise in the aggressiveness of the hinds took place at the same time as the final ossification of the antlers and the removal of the antler velvet. The proposed aggressiveness of the hinds towards yearlings in this small group may be explained by the lower predictability of the hierarchial status of the young animals from the point of view of the hinds (see e.g. Lindsay *et al.*, 1976).

The main character of observable social signals for wild forest reindeer seemed to be similar to those described in earlier studies concerning the genus *Rangifer* (see Espmark, 1964; Bergerud, 1974; Thomson, 1977). The prevalence of those communicative signals which Thomson (1980) mentions seems to be similar to Norwegian mountain reindeer (*R. t. tarandus* L.) apart from the excitation jump, which is more common and better developed in wild forest reindeer (see Helle, 1982). Small snapping-like oral movements are common in the aggressive behaviour of females of the semi-domestic reindeer (*R. t. tarandus*) (Kojola *et al.* 1985). I had seen the males of wild forest reindeer of various age classes present it, but never the female.

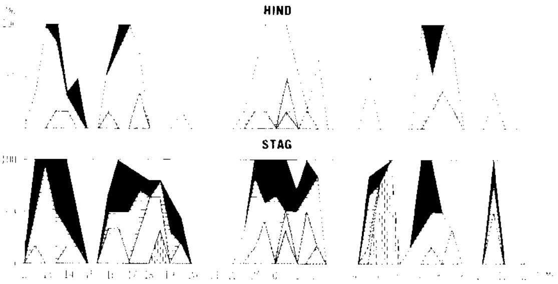

Fig. 7. Activity budget of one unmated hind and the dominant stag in 15 - 16 Oct. 1981.

Table 1. Nocturnal and diurnal activity of dominant stag in sparring and presenting low-stretch displays.

Date	Time	Sparring (min)	Low-stretch display (n)
18 - 19 Sept.	2200 — 0500	30	4
	1000 — 1700	4	32
15 - 16 Oct.	2200 — 0500	59	0
	1000 — 1700	5	15

n Legends to figures

My observations indicate that one evolutive purpose of the odour marking (here urinating) may be threatening (see Espmark, 1964; Geist, 1966). Herding is the most common activity directed towards the females before the hunching (Kojola, unpublished data). During the peak of the rut, which was characterized with the intensive herding the sex-related differences observed in the distribution of the objects of the preceeding activity of the dominant stag, disappeared.

According to Reinhardt (1983) the flehmen may be a male olfactory test of the females' reproductive stage, and helps in the detection of oestrus. In contrast to flehmen, mounting behaviour towards anestrous hinds was more frequent in young males than in the adult stag. This observation makes it unlikely that mounting serves as a demonstration of dominance in reindeer in the way it does it mountain sheep *(Ovis canadensis)* (Geist, 1968); Grant's gazelle *(Gazella grantii)* (Walther, 1965) and American buffalo (*Bison bison*) (Lumia, 1972). In cattle (*Bos indicus*) the low ranking animals had a tencency to mount more often than high ranking ones (Reinhardt, 1983). In contrast to this examination, the other females were seen to mount the estrous female e.g. in cattle (Fraser, 1968), in red deer (*Cervus elaphus*) (Clutton-Brock *et al.*, 1982) and in caribou (Bergerud, 1974).

Espmark (1964) and Thomson (1977) have mentioned that the stags stop grazing during the rut. In the enclosure the well-fed stags of wild forest reindeer did not completely stop grazing even during the estrous of the hinds. The longest grazing periods took place in the dark. The number of subordinate males might have an impact on the time budget of the harem stag. On the other hand the stag may invest more heavily in the rut as it aged (see Leader-Williams, 1979; Clutton-Brock *et al.*, 1982). Estrous caused changes in the time-budget of the female. The observed changes tended to be similar to those in white-tailed deer (*Odocoileus virginianus*) (Ozoga and Verme, 1975) and in red deer (Clutton-Brock *et al.*, 1982).

The semi-domestic reindeer mated most often at sunrise and at sundown (Espmark, 1964). In this examination the wild forest reindeer was most frequently observed to mate from 1 to 2 hours after sundown. The Newfoundland caribou also commonly mates in the afternoons (Bergerud, 1974). Although the reindeer has a polyphasic activity pattern it is essentially a diurnal animal (Erikson *et al.*, 1981). Rutting activity of the stags tended to be weak in the night (see also Espmark, 1964). If the female is more frequently inactive in the dark the concentration of his rutting activity with other daytime activities is obviously relevant for the fitness of the stag.

Acknowledgements

I would like to acknowledge Dr. Matti Helminen for arranging the field working facilities and Dr. A. T. Bergerud, Dr. Y. Espmark and Dr. Mauri Nieminen for their critical reviews of this manuscript.

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Distribution, activity and range use of male caribou in early summer in Northern Yukon, Canada

Arthur M. Martell[1], Wendy Nixon[2] and Donald E. Russell[2]

Abstract: Males of the Porcupine Caribou Herd separated from females from the onset of spring migration until they joined them on the calving grounds in late June or early July, 4 - 6 weeks later. From late May to late June males spent an average of 50% of their time feeding and less than 2% standing and trotting/running. Males spent an average of 29% of their time lying and 19% walking, except in mid-June (40% lying, 6% walking). The average lengths of active and resting periods were 112 minutes and 104 minutes, respectively, from late May to mid-June, but decreased sharply in late June to 78 minutes and 69 minutes, respectively. Tussock meadows were selected in late May and early June, wet sedge meadows were avoided until late June, dwarf shrub heaths were avoided after late May, and alluvial willow thickets were avoided in late May and early June but were selected in mid-June and late June. Caribou fed primarily on lichens and *Vaccinium* in late May, lichens and *Eriophorum* in early June, *Eriophorum* in mid-June and *Salix* in late June.

Key words: *Rangifer,* caribou, activity budget, habitat selection, food habits, Yukon

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Rangifer, Special Issue No. 1, 1986: 181 - 189

Introduction

The Porcupine Caribou Herd (*Rangifer tarandus granti*) calves on the Arctic Coastal Plain of northeastern Alaska and northwestern Yukon, and winters primarily in north-central Yukon and adjacent Alaska. Calving occurs from late May to mid-June with a peak in the first week of June. During calving, and for a variable period before and after calving, males are segregated from females. It has been suggested that this segregation occurs because males follow the northward initiation of growth of forage while pregnant females move quickly to the calving grounds for other reasons, such as predator avoidance (Whitten and Cameron, 1979). Recent proposals for a seaport, quarries and roads in northern Yukon in the area used intensively by males in early summer have focused attention on the need for information on that component of the herd.

Study area

Investigations were conducted in northern Yukon, north of the Porcupine River (Fig. 1). The area can be divided from south to north into three broad ecoregion bands: Old Crow Basin, Northern Mountains and Northern Coastal Plain (Wiken *et al.*, 1981). The Old Crow Basin, which includes the Old Crow Flats and the surrounding pediments, is generally flat or gently undulating terrain covered by boreal forest - tundra transition zone vegetation. The Northern Mountains include the British, Barn and Richardson Mountains with broken, ridged terrain interspersed by river valleys and intermountain basins. Vegetation consists of arctic and alpine tundra communities except for some intrusion of boreal forest along river valleys. The Northern Coastal Plain slopes gently from the mountains to the Beaufort Sea and is covered by arctic tundra vegetation.

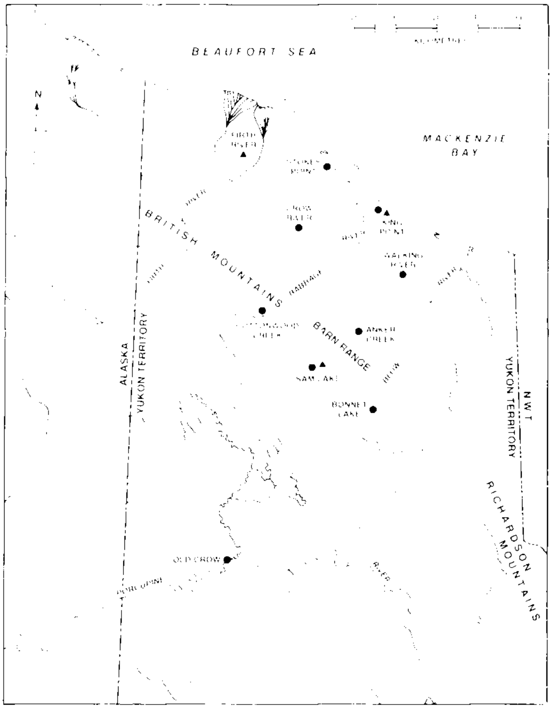

Fig. 1. Map of northern Yukon showing locations of field camps (triangles) and sites for documenting plant phenology (circles).

Three campsites were used for observing caribou in 1983: Sam Lake, 21 May - 12 June; King Point, 13 - 21 June; Firth River, 22 - 30 June (Fig. 1). The Sam Lake camp was at the southern edge of the Barn Mountains and overlooked rolling, tundra-covered pediments. The King Point and Firth River camps both lay on the coastal plain in rolling arctic tundra. Sites for documenting plant phenology (Fig. 1) were established on the Old Crow pediments (Sam Lake, Bonnet Lake), in the intermountain basins (Cottonwood Creek, Anker Creek), on the inner coastal plain (Crow River, Walking River) and at the coast (Stokes Point, King Point).

Methods

Distribution

To follow the movements of caribou, radio transmitters on collars were placed on animals on the winter range. Between 5 and 15 caribou were available for relocation each year (1981 —5; 1982 — 5; 1983 — 15). In 1981 and 1982, four relocation surveys were flown between 3 and 28 June and in 1983 six surveys were flown between 8 May and 1 July. In addition to the locations of radio-collared animals, the locations of all male caribou observed on aerial surveys and reported by other researchers were plotted on maps.

Activity

We observed caribou with 15x - 60x zoom spotting scopes from the three field camps. A band of caribou was defined as a socially interacting group of animals spatially distinct from other bands in the area. Activity data were collected using the instantaneous scan method (Altmann, 1974). We scanned each band at 15-minute intervals and tallied the number of caribou engaged in each of five general activities. The proportion of caribou observed in each activity and the estimated 95% confidence limits were calculated by the ratio estimator method (Cochran, 1977). Because of serial correlations among 15-minute observations of a given band of caribou, but not among different bands, estimated 95% confidence limits were based on a single ratio for each band observed. Differences were considered to be significant if the estimated 95% confidence limits did not overlap.

Phenology

We observed snowmelt and the development of vegetation in eight relatively flat cottongrass (*Eriophorum vaginatum*) tussock meadows (Fig. 1). We estimated the relative stage of development of the flowers of *Eriophorum vaginatum* (flower bud, early flower, full flower, past flower, seed) for 24 tussocks at approximately 5-m intervals along a transect at each site. Along the same transect we also documented the relative stage of development of the leaves of 24 plants of *Salix pulchra, Betula glandulosa* and *Ledum palustre* (leaf bud, leaf unfolding, full leaf).

Habitat selection

We divided the area of observation at each campsite into six distinct habitat types and determined their availability by mapping them on aerial photographs. The habitat types and their approximate classification according to Viereck and Dyrness (1980) were: Tussock Meadow, 2C2c; Wet Sedge Meadow, 2A3a; Dwarf Shrub Heath, 2D2a and 2A4a; Alpine Barren, 2E1b; Alluvial Willow, 3A1a; and Open White Spruce, 1A3d. We also documented the use of late snow patches and sandy beaches at some camps. The areas observed at campsites appeared to be representative of much wider areas based on examination of aerial photographs and observations from aircraft.

Food habits

We collected composite fecal samples at Sam Lake (22 May, 4 - 5 June, 12 June), King Point (15 - 17 June), Firth River (26 - 27 June) and Stokes Point (15 June, 27 June). Each composite sample contained 20 fecal pellets, one from each of 20 different fresh pellet groups. Fecal samples were analyzed (Sparks and Malechek, 1968) at the Composition Analysis Laboratory at Colorado State University, Fort Collins. The relative density of plant fragments was based on 100 fields per sample. All samples were analyzed at the same time by the same technician. The accuracy of fecal analysis is influenced by differential digestion among plant species (Holechek *et al.*, 1982). Therefore, the results represent proportions of discerned fragments in fecal samples rather than actual proportions of the ingested diet.

Data analysis

For the purpose of comparison among data sets, the field season was divided into four periods: late (20 - 31) May, early (1 - 11) June, mid (12 - 20) June and late (21 - 30) June. Statistical procedures follow Siegel (1956) and Sokol and Rohlf (1969).

Results and discussion

Distribution

Male caribou follow the females on spring migration along essentially the same routes leading from the two principal wintering areas, the Ogilvie Mountains of north-central Yukon and the Arctic Village region of northeastern Alaska. Females reach the calving grounds in mid to late May while males fan out into the rolling pediments north and east of the Old Crow Flats and into the wide basins near the headwaters of the Firth River (Fig. 2a). In early June, at the time of calving, males are distributed in a broad crescent south and east of the calving grounds (Fig. 2b). By this time, if not earlier, males from both the Alaskan and Yukon wintering areas are well mixed. Males then move eastward south of the British Mountains and northwestward from the Richardson Mountains and by mid-June large aggregations begin to form in the intermountain basins near the headwaters of the Spring, Trail, Babbage and Running rivers as well as, in some years, on the Firth River (Fig. 2c). By late June males are found moving westward and northwestward towards the coast of the Beaufort Sea near the Alaska-Yukon border (Fig. 2d). At this time, band sizes frequently number in the thousands and smaller bands which have lingered behind move quickly to join the larger concentrations. Most males meet and mix with females and young on the Alaska-Yukon coastal plain by early to mid-July before returning eastward to the Richardson Mountains.

Males, therefore, are essentially segregated from females during May and June. The consistent pattern of distribution and movements among years and the formation of aggregations in mid-June prior to joining females and prior to the insect season suggest a response to food resources combined with a form of social facilitation.

Activity

In late May, at Sam Lake, many females were moving through the area and males occurred in both male-dominated and female-dominated bands. Therefore, observations included both types of bands. After that time, only male-dominated bands were observed. The average size of bands was relatively constant from late May to mid-June but increased significantly in late June (Table 1).

There was no significant difference in the proportion of time spent feeding or trotting/running among observation periods (Table 2). In mid-June the proportion of time spent lying was significantly higher than during other periods and the proportion of time spent walking was significantly lower than during other periods. The proportion of time spent standing was significantly lower in late June than during other periods. The rate of movement (Table 1) mirrored the proportion of time spent walking (Table 2) and was conspicuously low during mid-June.

It is not possible to make precise comparisons of activity budgets among studies because of differences in methods of calculation. In general, for the same season, Roby (1978) found that male

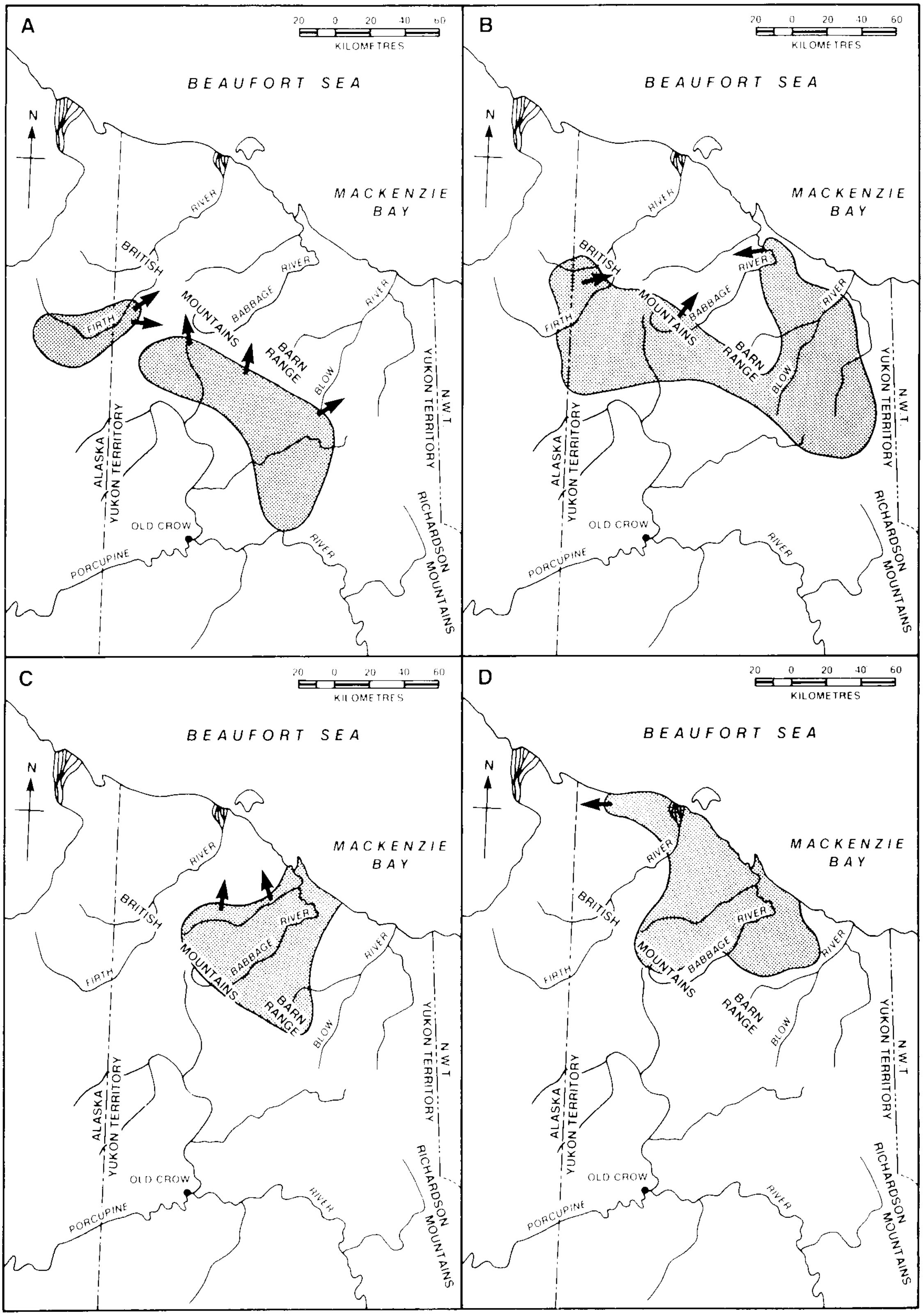

Fig. 2. General distribution (shaded) and direction of movement (arrows) of male caribou in northern Yukon in late May (A), early June (B), mid-June (C), and late June (D).

caribou in north-central Alaska spent less time feeding (39%) and more time lying (47%) than males we observed.

The mean length of both active and resting periods declined significantly from late May to late June (Table 3). The decrease from mid-June to late June was particularly conspicuous. The mean late May to mid-June active period we observed (112 minutes) was shorter than reported for summer for male reindeer (135 minutes) (Segal, 1962), while the mean late May to mid-June resting period (104 minutes) was not significantly different (105 minutes).

Phenology

On 18 - 19 May 1983, the Old Crow pediments were about 80% snow covered while farther north all sites were about 95% snow covered. By 3 June the snow cover had declined to less than 5% on the Old Crow pediments and

Table 1. Size and rate of movement (km/h) of bands of male caribou in northern Yukon in 1983[1].

Period	Size		Rate[2]	
	(n)	x ± SE	(n)	x ± SE
late May	(45)	17.5 ± 1.78^a	(574)	0.35 ± 0.026^a
early June	(55)	24.2 ± 2.90^a	(730)	0.54 ± 0.025^b
mid-June	(65)	19.9 ± 4.47^a	(1088)	0.15 ± 0.007^c
late June	(29)	103.8 ± 21.62^b	(301)	0.74 ± 0.042^d

[1] Band sizes or rates of movement with the same superscript are not significantly different from each other at the P = 0.05 level.

[2] Rate was measured from the estimated distance moved by bands between 15-minute scans.

Table 2. Daily activity budgets (% time ± estimated 95% confidence intervals) for male caribou in northern Yukon in 1983.

Date	Late May	Early June	Mid-June	Late June
Number of observations	619	787	1153	330
Number of bands	45	55	65	29
Number of individuals	8443	14 498	19 554	25 592
Feeding	51.0±4.0	47.6±3.4	52.0±3.0	49.0±2.8
Lying	31.1±6.4	31.9±5.0	40.4±3.3	25.4±4.3
Standing	1.8±1.1	0.9±0.3	0.9±0.2	0.4±0.1
Walking	14.8±4.9	19.1±2.4	6.3±0.9	24.1±5.6
Trotting/running	1.2±1.1	0.5±0.3	0.3±0.3	1.0±0.4

Table 3. Length (minutes) of active and resting periods[1] ($\bar{x}$±SE) for male caribou in northern Yukon in 1983[2]. Sample sizes in parentheses.

	Late May	Early June	Mid-June	Late June
Active period	(7) 118 ± 18.4^a	(10) 111 ± 12.9^{ab}	(29) 110 ± 6.4^{ab}	(5) 78 ± 11.0^b
Bedded period	(23) 103 ± 6.9^a	(34) 98 ± 5.2^a	(46) 109 ± 4.7^a	(12) 69 ± 6.5^b

[1] The length of an active period was calculated as the time between the point when the majority of a group ceased lying until the majority of the same group was again lying. The length of a resting period was calculated in an analogous manner.

[2] Active periods (or bedded periods) with the same superscript are not significantly different from each other at the P = 0.05 level.

the coast but was about 50% (30 - 70%) beetween those sites. By 10 June the intermountain and inner coastal plain sites were about 10% (5 - 20%) snow covered and by 17 June all sites were essentially snow-free.

In general, the development of vegetation was most rapid on the Old Crow pediments (Table 4). In early June, the development of *Eriophorum vaginatum* was more advanced on the coastal plain than at inland sites but by mid-June plant development on the coast was behind that at other sites and remained so. This was probably due to the temperature gradient which develops between the coast, which is strongly influenced by the ice-covered Beaufort Sea, and the thermal basin surrounding the Old Crow Flats (Pearson and Nagy, 1976). In general, plant development on the Old Crow pediments was at least a week in advance of that on the coast.

Habitat selection

Tussock Tundra was weakly selected in late May and early June while Wet Sedge Meadow was strongly avoided until late June (Table 5). Dwarf Shrub Heath began to be avoided weakly after late May and Alluvial Willow shifted from being avoided in late May and early June to being selected in mid-June and late June. Other habitat types were too poorly represented to compare.

Food habits

In late May *Cladonia*-type lichen and *Vaccinium* (likely *V. vitis-idaea*) were the most important components of the fecal sample (Table 6). Those species continued to be important in early June, although *Eriophorum* (likely *E. vaginatum*) was the most important item. *Eriophorum* predominated in the samples in

Table 4. Phenology of vegetation in northern Yukon in 1983. The percentage of plants in each stage of development is presented in sequence. Blank spaces indicate that the plant had not yet begun to develop.

	Date				
	June 3	June 10	June 17	June 24	July 1
Eriophorum vaginatum	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]	B/E/F/P/S[1]
coast	0/33/67/0/0	0/6/92/2/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
coastal plain	0/48/52/0/0	0/0/88/12/0	0/0/0/100/0	0/0/0/0/100	0/0/0/0/100
mountain basins	0/88/12/0/0	0/2/67/31/0	0/0/0/90/10	0/0/0/0/100	0/0/0/0/100
pediments	0/60/40/0/0	0/4/46/50/0	0/0/0/0/100	0/0/0/0/100	0/0/0/0/100
Salix pulchra[3]	B/U/L[2]	B/U/L[2]	B/U/L[2]	B/U/L[2]	B/U/L[2]
coast		100/0/0	0/100/0	0/96/4	0/0/100
pediments	58/42/0	38/62/0	0/10/90	0/0/100	0/0/100
Betula glandulosa			B/U/L[2]	B/U/L[2]	B/U/L[2]
coast			56/27/17	2/54/44	0/0/100
coastal plain			46/50/4	0/0/100	0/0/100
mountain basins			48/38/14	0/0/100	0/0/100
pediments			2/29/69	0/0/100	0/0/100
Ledum palustre					B/E/F/P/S[1]
coast					86/14/0/0/0
coastal plain					80/20/0/0/0
mountain basins					66/34/0/0/0
pediments					0/0/100/0/0

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[1] flower bud/early flower/full flower/past flower/seed.

[2] leaf bud/leaf unfolding/full leaf.

[3] *Salix pulchra* was not sufficiently abundant to tally on the inner coastal plain and intermountain basin sites.

Table 5. Availability (A, % area), utilization (U, % caribou) and selection (S)[1] of habitat types by male caribou in northern Yukon in 1983. Approximate area observed at each campsite in parentheses.

	Sam Lake (29 km^2)					King Point (26 km^2)			Firth River (23 km^2)		
	Late May			Early June		Mid-June			Late June		
Habitat type	A	U	S	U	S	A	U	S	A	U	S
Tussock Meadow	51	60	+0.16	82	+0.24	88	97	+0.05	76	80	+0.02
Wet Sedge Meadow	18	3	—0.69	1	—0.88	10	1	—0.87	19	17	—0.05
Dwarf Shrub Heath	21	18	+0.02	14	—0.20	-	-	-	4	2	—0.20
Alpine Barren	1	1	0.00	1	—0.05	-	-	-	1	<1	—0.83
Alluvial Willow	8	3	—0.36	1	—0.73	<1	1	+0.54	<1	1	+0.90
Open White Spruce	1	-	—1.00	<1	—0.87	-	-	-	-	-	-
Beach	-	-	-	-	-	1	<1	—0.75	-	-	-
Late Snowpatch[1]	-	15	-	-	-	-	<1	-	-	<1	-

[1] Selectivity measured as (U—A)/(U+A). Utilization values were adjusted by removing late snowpatches because their availability could not be measured.

mid-June but declined sharply in late June. *Salix* increased markedly from early June to mid-June and dominated the samples in late June.

There were no marked differences in diet, as reflected in fecal samples, at the two sample sites in late June, but there was a noticeable variation among sites in mid-June. In mid-June the proportion of *Eriophorum* increased from Sam Lake (50%) to King Point (61%) to Stokes Point (91%) while evergreen shrubs declined over the three sites (25%, 3%, 1%, respectively). Also, *Salix* was highest at King Point (32%), lower at Sam Lake (16%) and lowest at Stokes Point (1%). Those variations did not appear to be precisely related to either availability or phenological stage. The phenological stages of

Table 6. Average percentages of discerned plant fragments in fecal samples collected from male caribou in northern Yukon in 1983. Sample sizes in parentheses.

Food Items[1]	Late May (1)	Early June (1)	Mid-June (3)	Late June (2)
Moss	8.6	4.3	2.6	0.1
Lichens	33.9	34.9	3.0	0.3
Cetraria-type	4.5	3.0	0.6	0.2
Cladonia-type	23.4	28.7	1.6	0.2
Stereocaulon	5.2	3.2	0.8	-
Horsetails (*Equisetum*)	-	1.5	0.3	0.1
Graminoids	10.0	36.7	67.3	2.3
Carex	6.8	3.1	1.0	0.7
Eriophorum	3.2	33.6	65.8	1.5
Deciduous shrubs (*Salix*)	-	2.0	16.5	95.8
Evergreen shrubs	47.5	19.9	9.6	0.6
Dryas	1.5	0.7	5.0	0.3
Ledum	5.3	3.7	1.1	-
Vaccinium	40.8	14.7	3.6	0.1
Forbs	-	0.6	-	0.7

[1] *Astragalus, Festuca,* fungi, *Lupinus, Peltigera, Picea, Poa, Saxifraga* and unidentified Ericaceae occurred at average frequencies of less than 1% in some sampling periods.

Eriophorum and *Salix* were more similar between Stokes Point and King Point than to Sam Lake.

Thompson and McCourt (1981) have previously reported on the diet of the Porcupine Caribou Herd based on fecal analysis. They reported that *Eriophorum* (56%) and lichens (37%) were the most important components in fecal samples in late May and that samples were dominated by *Eriophorum* (77%) in early June and by *Salix* (99%) in late June. Although the proportions of lichen in late May and *Salix* in late June are consistent with our findings, the proportions of *Eriophorum* are not; they appear high in relation to expected phenological stage, especially in late May. Duquette (1984) reported on diet of females of the Porcupine Caribou Herd based on fecal samples and found that in late (16 - 26) May samples were dominated by lichens (41%), *Salix* (22%) and evergreen shrubs (16%), with *Eriophorum* making up less than 1%. The high proportion of *Salix* is noticeably different either from that we observed (0%) or from that reported by Thompson and McCourt (1981) (0.1%). In late May, therefore, caribou of the Porcupine Herd apparently feed primarily on lichens but supplement the diet with whatever palatable green matter is available.

Summary and conclusions

In late May male caribou were distributed south of the mountains where snowmelt was more advanced than farther north. Caribou used tussock meadows, dwarf shrub heaths and alpine barrens but avoided low-lying wet sedge meadows and alluvial willow thickets where snowmelt was slower. Diet consisted primarily of lichens and evergreen shrubs which were widely distributed in the habitat types utilized. By early June, as snowmelt progressed south of the mountains and on the eastern coastal plain, males moved northward to those areas. Intermountain basins, where snowmelt was retarded, were avoided. As the season progressed males continued to use, and avoid, essentially the same habitat types but there was less use of dwarf shrub heaths. They continued to feed on lichens but began to use *Eriophorum* as it came into flower. In mid-June, males moved into intermountain basins as snowmelt there progressed. Caribou used tussock meadows and alluvial willow thickets as the diet shifted to *Eriophorum* and *Salix*. At that time, large aggregations of caribou formed in intermountain basins and they spent more time lying, less time walking, and had a lower rate of movement than in other periods. By late June, males began to use the western coastal plain where they used tussock meadows, wet sedge meadows and alluvial willow thickets. *Salix*, which was common in all three habitat types, predominated in the diet. At that time, *Salix* on the coast was at a similar phenological stage to that at inland sites 2 weeks earlier when it was not used as heavily as *Eriophorum*. However, by late June *Eriophorum* was in seed and therefore not as desirable as a food for caribou. In late June average band size increased significantly and rate of movement was greatest as males moved westward towards Alaska. As well, the mean length of active and resting periods decreased by about one-third. This sharp decrease may reflect both the high availability and high digestibility of young willow leaves.

In general, the distribution of male caribou followed the pattern of snowmelt and plant phenology and diet reflected both preference and phenologieal stage. Activity and movements, however, were not related to snowmelt, plant phenology or diet. Rather, they appeared to follow a temporal pattern.

Acknowledgements

We would like to thank the many people who helped with various aspects of the study, in particular L. Hartman and F. Jensen for their assistance with the field work. We are grateful to G. Hobson of the Polar Continental Shelf Project, Canada Department of Energy, Mines and Resources, and to P. Lewis and J. Ostrick of the Western Arctic Scientific Resources Centre, Canada Department of Indian Affairs and Northern Development, for their continued logistic support. The study was conducted while the first two authors were with the Canadian Wildlife Service, Whitehorse, and the third author was with the Department of Renewable Resources, Government of Yukon, Whitehorse.

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Spectralradiometry and caribou range classification

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Abstract: The utility of Landsat in caribou range studies has been limited by problems of heterogeneity in cover type at the scale of pixles and by logistic barriers to ground truthing. Spectralradiometry provides an economical way of collecting ground truth data that are precisely comparable with Landsat data and which could provide a basis for hierarchic key classification rather than classification based on prinicipal components analysis. Spectral curves are presented for six common cover types and it is shown how the information could be used to develop classification criteria. Airborne data which could have provided a direct comparison with Landsat data proved to be too highly variable because of equipment constraints but there do not appear to be any significant barriers to developing the technique.

Key words: caribou, range, Landsat, spectralradiometry, Ungava, Quebec.

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Rangifer, Special Issue No. 1, 1986: 191 - 194

Introduction

There are many reasons for wanting to be able to map accurately the ground cover of caribou range. Among them are questions of range size and distribution, food availability, food preference, and relationship between behaviour and the enviroment. However, the large size and geographic remoteness of caribou range makes detailed mapping through conventional means difficult, expensive and consequently for many regions, unlikely. Satellite imagery has been widely recognized as providing new opportunities (Thie *et al.*, 1974).

While great advances have been made using Landsat data, the problem of formulating consistent, accurate and precise classification algorithms has limited the utility of Landsat for heterogeneous environments and sites for which it is difficult to collect ground-truthing information. Thus for agricultural landscapes where the land use assures homogeneity over field-size blocks, and where land users typically have detailed information available about cover type, growth stage and ground conditions, it is possible to produce very detailed maps from Landsat. However, for wilderness areas, and particularly those areas where there is a high degree of variablity and mixing in the assemblages of dominant species at a scale finer than that of useful management blocks and even finer than pixle size, it has proven very difficult to produce useful maps. These problems are acute in the case of caribou range (Cihlar *et al.*, 1978; Thompson *et al.* 1980; Bråcher and Meredith, 1985) and are compounded by the difficulty of collecting detailed and widespread ground truthing data.

Landsat records the intensity of reflectance from a pixel area as a single value for each of four wave bands (0.5-0.6 um, green; 0.6-0.7 um, red; 0.7-0.8 and 0.8-1.1 um, both infrared). Both of the major methods of deriving classifiers (supervised and unsupervised (Alfoldi, 1978)) presume a fixed and consistent - though rarely defined - correlation between the distribution of pixel intensity values and the nature of the corresponding ground surface type. The final precision is a function of the amount of pre- or post-classification ground truthing and the uniformity of the landscape.

Ground truthing consist of recording physical parameters of study sites within the area covered by the Landsat image. Such characteristics as dominant species, age of community, soil moisture and nutrient status, and elevation and aspect may be recorded. Correlations will then be sought between these data and the digital reflectance data from Landsat. However, because the relationship amongst the range of known parameters and the four-variable Landsat data must be interpretted subjectively by the analyst (and ultimately classes are defined and named subjectively), and because the statistical treatment of the variance of the Landsat data may mask, and itself be made ambiguous by, significant anomalies, there is a kind of «black box», trial-and-error, empiricism in most classification.

Spectralradiometry provides the opportunity for collecting detailed refectance curves or spectral signatures for single species, species assemblages, or physiognomic cover types (*sensu* Hare, 1959). From this information it is possible to determine precisely what radiation is being directed back towards the Landsat sensors. The information should be useful in developing non-statistical classification algorithms and in distinguishing attributes on the ground which can be expected to be detectable and distinguishable by Landsat.

This paper reports on spectralradiometric data collected for several dominant cover types in the region of Schefferville, Quebec and discusses its consistency and its potential utility for Landsat classification.

Methods

Using sites that had been studied in previous range classification work (Bracher and Meredith, 1985) areas were selected which had representative and characteristic cover types. The work began with ground level reconnaissance of pure stands and continued with low level aerial surveys.

A portable spectralradiometer (Li-Cor Model 1800) was used to collect site-specific spectral signatures of known plant species growing in pure stands or of common assemblages of species. Readings were taken under field conditions over a range of from 0.4 um to 1.1 um at .005 um intervals. Species and/or cover type, exposure, sky conditions and height and position of the sensor were noted. Reading were taken from 2 m or less with a handheld sensor or were taken from a sensor mounted on a plane flying as low as 50 m and as high as 200 m above ground.

Date were plotted on graphs (0.3 um intervals) for comparison of subject matter and recording conditions.

Integrals were calculated for the parts of the spectrum conforming to Landsat sensors. Integral values, band ratios, and total reflectance were plotted for comparison. Clearly distinct patterns were sought as a basis for classification algorithms.

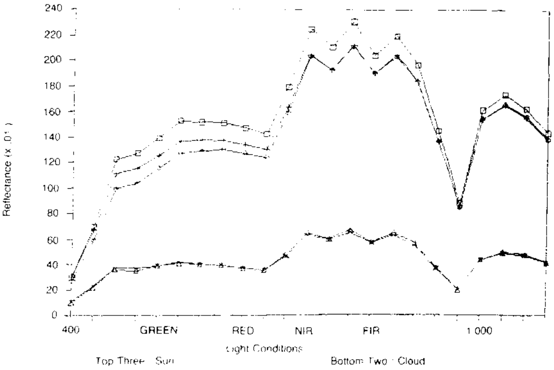

Fig. 1. Spectral curves for five lichen samples in differing light conditions. Top three curves are for full sunlight, bottom two are in open shade.

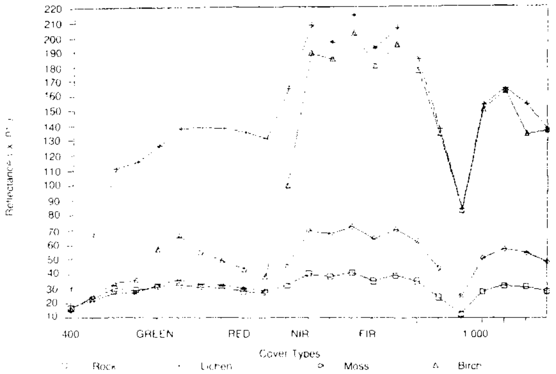

Fig. 2. Average spectral curves for four different cover types. From top to bottom at near infra-red (NIR) they are Lichen, Birch, Moss, Rock. Averages are of three or more samples. All values were recorded under full sunlight.

Results and discussion

Similar cover types show consistent patterns of reflectance although the intensity of reflectance varied with the cloudiness (Fig. 1). It can be seen that readings for three different lichen (*Cladina alpestris*) dominated sites monitored in full sun the refeectance curves are very similar. For the two sites monitored under cloud the patterns of reflectance were similar although values were much lower. It is clear from this that sites visible from Landsat but shaded by cloud will be statistically distinct from fully lighted areas covered by the same species unless pattern of reflectance, rather than net reflectance, is considered. This can be accomplished through the use of ratios rather than absolute values.

Whereas there is uniformity within a single species, there are conspieuous differences in patterns and values (averages) under uniform light conditions between species groups (Fig. 2). Of the four cover types shown it is evident that while in some cases pairs for species are similar over part of the spectrum, no two are identical throughout. However, these date are more complete than is obtainable from Landsat.

Converting these to integrals gives relative values which are comparable to Landsat data for a single pixel (Fig. 3). From these it is possible to sort visually on the basis of differences in reflectance in single bands, the six species that were selected for ground level study.

These same data may be presented as total reflectance (Fig. 4.a.), or to compensate for variation in total reflectance intensity, as proportions for total reflectance (Fig. 4.b.). Each of these presents a distinct quantitative profile of the cover type which may be used by an analyst in the selection of sorting criteria.

If integrals for the four spectral bands are used to calculate the six possible sets of band ratios (Fig. 5), differences are further highlighted. From four variables twelve can be generated and plotted graphically for use by the analyst in attempting to identify optimal classification criteria.

In attempting to distinguish the six selected cover types on the basis of data which is structurally comparable to Landsat data, three parameters appear to be sufficient: ratios of green or red to near IR, ratios of visible to IR, and total reflectance (Fig. 6).

Results for mixed vegetation from airborne readings proved much less distinctive, with very high coefficients of variation for each of the nominal cover types. This was found to be a result of the field-of-view of the sensing

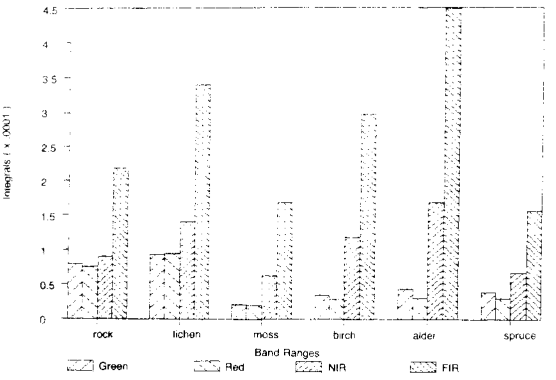

Fig. 3. Integrals for Landsat bands for selected low, pure-stand cover types. Columns within each block are, left to right, green, red, near infra-red, far infra-red. Blocks are, left to right, rock, lichen, moss, birch, alder, spruce.

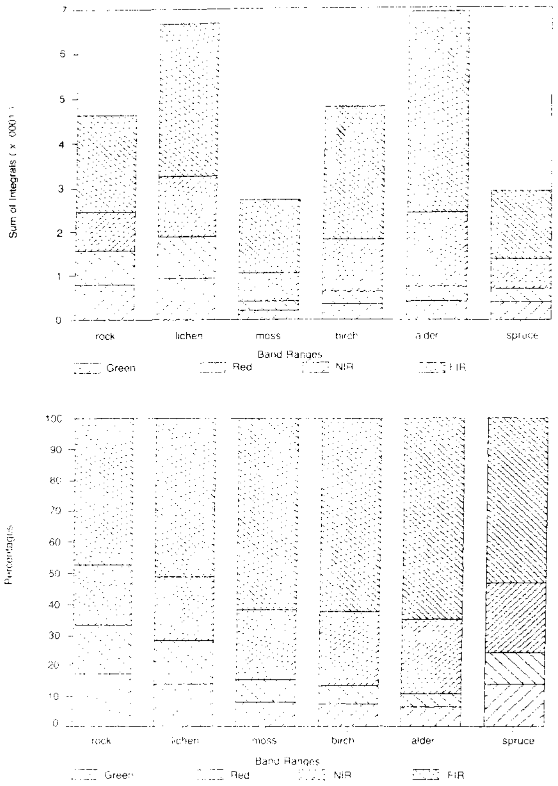

Fig. 4. (a) total reflectance and (b) distribution of reflectance for selected low, pure-stand cover types. Blocks within each column are, bottom to top, green, red, near infra-red, far infra-red. Columns are, left to right, rock, lichen, moss, birch, alder, spruce.

receptor: readings were taken from a larger and more heterogeneous area than had been hoped despite the low elevation of the aircraft. This techincal problem is relatively minor: a range of different field-of-view sensors are presently manufactured for different applications (though none presently is as restricted as this task requires), or an existing sensor could be remounted and recalibrated in such a way that wide-angle light would be blocked. Only funding and access have prevented this being tested. In principle the techniques used for the pure stands will be applicable to recording spectral signatures of mixed species stands. However, until more data are available it is impossible to know if there are clear distinctions or gradual transitions between the spectral signatures of useful physiognomic classes.

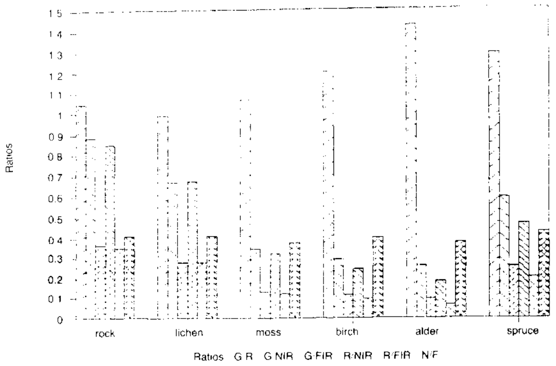

Fig. 5. Band ratios for data in Figure 4. Columns within blocks are, left to right, ratios of: green/red, green/NIR, green/FIR, red/NIR, red/FIR, NIR/FIR. Blocks are left to right, rock, lichen, moss, birch, alder, spruce.

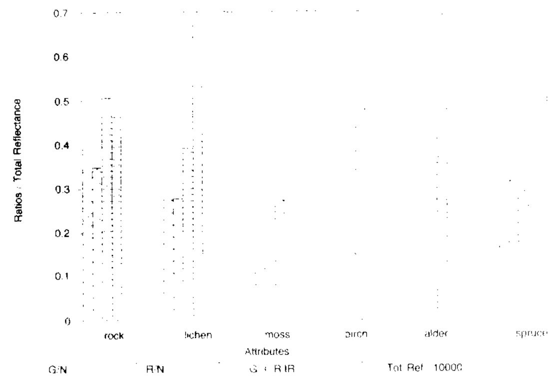

Fig. 6. Selected attributes of reflectance. Columns within blocks are, left to right, green/NIR, red/NIR, green+red/NIR+ FIR, total reflectance.

Conclusion

The ability to record accurately from known sites the same information that is recorded by satellite permits much more freedom to develop a testable rationale for sorting Landsat data into useful classes. A dendritic or hierarchical selection key for the cover types shown in Fig. 6 could be based on three parameters.

Airborne data which provides information at a physiognomic scale directly comparable to that measured by Landsat, will be required before classification and mapping comparisons can be made between structured nonstatistical classification keys and conventional classifiers based on principal components analysis.

If the precise spectral signatures of defined cover types are known, it will be possible to select unambiguously pixles which conform to defined criteria sets. This will not eliminate the problem of heterogeneous pixles, but it will provide tools for the informed assessment of groups of pixels which are unclassified, double classified or patently incorrectly classified by conventional means.

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Asymmetry in antlers of barren-ground caribou, Northwest Territories, Canada

Frank L. Miller [1]

Abstract: Pairs of antlers were obtained from 287 barren-ground caribou (*Rangifer tarandus groenlandicus*) of the Kaminuriak herd in the Northwest Territories, Canada. The morphological dominance of the brow tines by antler pair was determined: 15.7% were enlarged on the left; 14.6% on the right; 14.6% on both sides; and 55.1% on neither side. No evidence for a greater rate of occurrence of left or right dominance of the brow tine was obtained when considered by sex or age class ($P > 0.05$). Antler pairs with both brow and bez tines present varied from 84.4% for males with their 5th to 10th set of antlers; 39.3% for males with their 2nd to 4th set; 21.2% for females with their 5th to 16th set; and 6.3% for females with their 1st to 4th set. Both brow and bez tines were present proportionately more often than expected on antler pairs from males compared to females regardless of age ($P < 0.005$). Both brow and bez tines also were present proportionately more often than expected on antler pairs from males ($P < 0.005$), females ($P < 0.01$), or both sexes combined ($P < 0.01$) with their 5th or later set than compared to when they had their 4th or earlier set.

Key words: barren-ground caribou, antlers, asymmetry, Northwest Territories, Canada.

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Rangifer, Special Issue No. 1, 1986: 195 - 202

Introduction

Pairs of antlers from cervids tend to exhibit bilateral symmetry, with the exception of those from *Rangifer*. Therefore, the consistent lack of bilateral symmetry due to pronounced asymmetry of various opposing tines especially the enlarged brow tine creates interest and speculation about the probable causes and functions of this, seemingly, variant phenomonon in rangiferine antler sets. Particular interest is shown for possible left- or right-sided dominance in asymmetry of rangiferine antler pairs because it could be linked to the more general phenomonon of basically symmetrical organisms occasionally exhibiting functional or morphological one-sided dominance (for related references see: Davis, 1973; Goss, 1980, 1983). To date, however, investigations of the expressions of left- or right-sided dominance in the asymmetry of rangiferine antler pairs have been restricted to the examination of only brow tines (e.g., Banfield, 1954; Skoog, 1968; Davis, 1973; Goss, 1980).

Antler asymmetry in caribou or reindeer (*Rangifer tarandus* spp.) involving the brow tines only has been reported on by Banfield (1954), Skoog (1968), Davis (1973, 1974), and Goss (1980, 1983). All of those researchers but Skoog (1968) concluded that enlarged left brow tines predominated over right ones in *Rangifer*. However, Goss (1980) reached his conclusion by combining his sample with samples from Murie (1935), Banfield (1954), and Davis (1973, 1974).

Motivated by the apparent discrepancies among samples used by Goss (1980), I analyzed the tine configuration of the lower main beam of 287 pairs of antlers from barren-ground caribou (*R. t. groenlandicus*) of one population - the Kaminuriak herd. The following are my findings for the brow tine only analysis and a more detailed combined brow tine and bez tine analysis of those antlers.

Materials and methods

Barren-ground caribou (n = 999) were collected from the Kaminuriak herd, Northwest Territories, Canada, from March 1966 to July 1968 (Miller, 1974b; Dauphine, 1976). The age of each caribou was determined by histological examination of the annulations in the dental cementum of the mandibular teeth (Miller, 1974a, 1974b) and the eruption and wear patterns of the mandibular teeth (Miller, 1972, 1974b).

I obtained 287 pairs of hard antlers (hereafter referred to simply as «antler pairs») from those caribou shot between April and November 1966 (n = 41 pairs), April and December 1967 (n = 181 pairs), and April and July 1968 (n = 65 pairs). The 574 antlers were photographed in lateral view so that the left and right antlers would be facing each other (brow tines directed inwardly), when the left antler is on the left and the right one is on the right (Fig. 1). I placed antler pairs in antler «year» classes: the 1st year class being the set of antlers grown and carried in the 1st year of life; the 2nd year class, those in the 2nd year; *et cetera* to the 16th year. I have followed the classification used by Pocock (1933) for the first two tines of the main beam: (1) first tine equals «brow tine»; and second tine equals «bez tine». Bubenik (1975b:53-55) has, however, argued that the second tine in rangiferine antlers is homologous with the trez tine in *Cervus*.

Brow tine analysis

A branched or palmated brow tine was designated by an upper case letter: (L) left-sided dominance; (R) right-sided dominance; and (LR) both-sided («double» of Goss, 1980) dominance, regardless of relative size differences (Fig. 1). When the brow tine was a simple single-pointed tine («reduced» of Goss, 1980) it was designated by a lower case letter: (l) left; (r) right; and (lr) no dominance on either side, relative size was not considered (Fig. 1). The same procedure applied when one or both of the brow tines were absent (lr). If a single-pointed brow tine had a flattened cross-section it was still considered simple, if it lacked pronounced terminal bottons and the maximum width of the

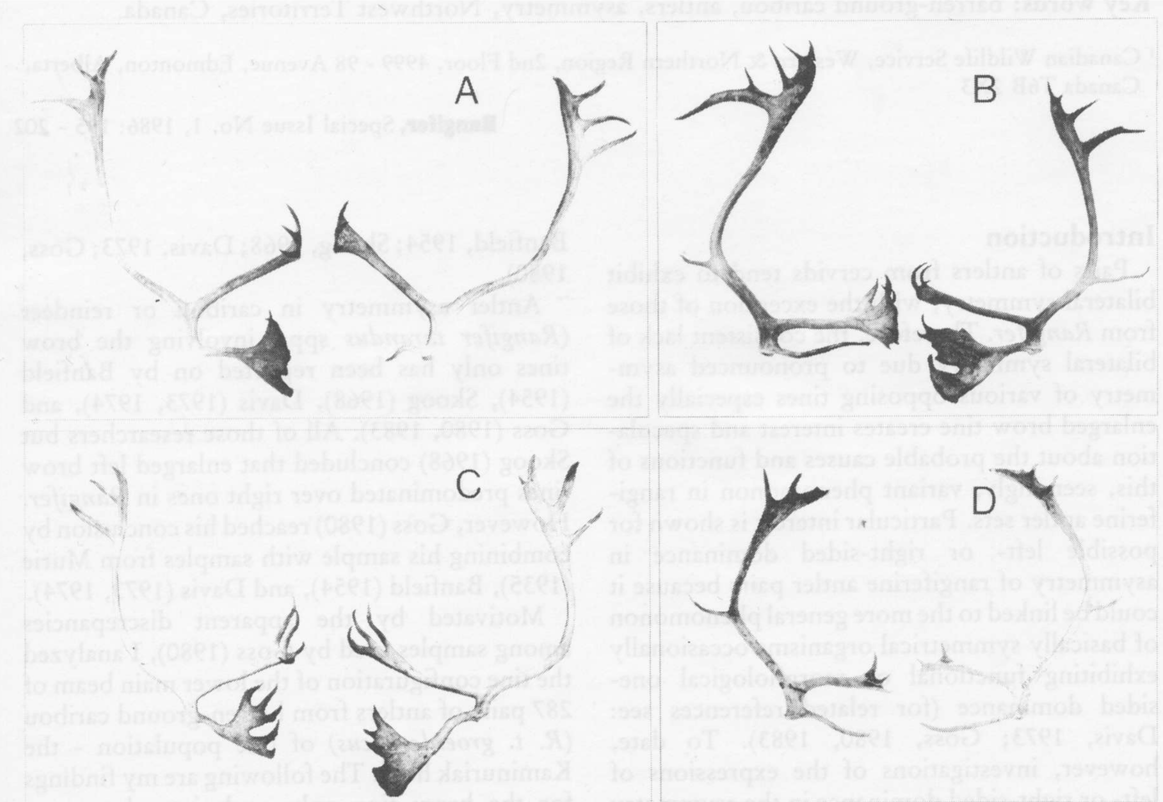

Fig. 1. Illustration of the four types of dominance expressed in the brow tines of rangiferine antler pairs: (A), left sided, (B) right-sided, (C) both sides, and (D) neither side.

flattened surfaces was less than twice the maximum width of the compressed surfaces.

Initially, I recognized a tine as a brow tine from its form, position or origin on the main beam, and generally its orientation to the main beam. However, the form of the tine and its orientation on or to the main beam («descending» of Banfield, 1954) did not appear to be consistent diagnostic characteristics of the brow tine, especially in antlers from females (regardless of age) and from young males. Therefore, when only one tine was present on an antler, it was classed as a brow tine when it originated at the burr on the main beam or within its diameter distance. That is, if a tine was 3 cm in diameter at its origin on the main beam and it originated within 3 cm of the burr, it was classed as a brow tine. If that tine originated beyond 3 cm up that main beam from the burr, it was classed as a bez tine.

Antlers and antler pairs were further classified as: (1) antler pairs with both brow and bez tines present; (2) single antlers with both the brow and the bez tines present; (3) single antlers with the brow tine missing; (4) single antlers with the bez tine missing; (5) antler pairs with no brow or bez tines present; and (6) antler pairs with no tines, just a main beam present, the simplest form being «spikes».

Brow and bez tine analysis

I decided to make a more detailed analysis of the expression of dominance or the complexity of pattern of caribou antler pairs by considering both the brow and the bez tines of each antler in each pair. The analysis was essentially the same as that for only the brow tine but instead of four possible combinations, when only the brow tine was used, there were now 16 possible combinations (L, R. l and r).

Statistical analyses

In all cases the Pearson Chi-square or goodness-of-fit tests were used (with «Yate's correction» where applicable) to statistically evaluate the assumption that each possible expression of dominance (left-sided, right-sided, both sides, or neither side) of the brow tine or the brow and bez tines together had an equal opportunity to occur in the sample of antler pairs. Therefore, all expected proportions tested with the goodness-of-fit test were equal percentages in all cells. The working hypothesis based on Goss' (1980) results was that, «left-sided dominance of the brow tine of caribou antler pairs in the northern hemisphere predominates over right-sided, both sides, or neither side expressions of dominance in the brow tine». The probability $P < 0.05$ was the level of acceptance for significant relationships.

Results

Brow tine only

Brow tines (or their absence) on the 574 antlers of the 287 antler pairs from barren-ground caribou of the Kaminuriak herd exhibited

Table 1. Frequency of occurrence of brow tines or brow and bez tines together (brow/bez) as expressions of dominance in antler pairs from barren-ground caribou, Northwest Territories, 1966-68.

Antler year class[a] by sex	Antlers N	% dominance[b] Left-sided		Right-sided		Both sides		Neither side	
Male									
2nd-4th	61	19.7	(24.5)	18.0	(18.0)	29.5	(37.7)	32.8	(19.8)
5th-10th	45	35.6	(40.0)	37.8	(26.7)	22.2	(33.3)	4.4	
2nd-10th	106	26.4	(31.1)	26.4	(21.7)	26.4	(35.9)	20.8	(11.3)
Female									
1st-4th	63	3.2	(9.5)	3.2	(8.0)	3.2	(11.1)	90.4	(71.4)
5th-16th	118	12.7	(18.6)	10.2	(12.7)	10.2	(28.0)	66.9	(40.7)
1st-16th	181	9.4	(15.4)	7.7	(11.1)	7.7	(22.1)	75.2	(51.4)

[a] Antler year class is based only on age: 1st year class, 5-12 months, 2nd year class, 17-24 months, *et cetera*.

[b] Expressions of dominance: brow tines, left-sided (Lr), right-sided (lR), both sides (LR), and neither side (lr); brow and bez tines together (brow/bez), left-sided (LLrr, LLrR, LLRr, Llrr, lLrr), right-sided (RRll, RRlL, RRLl, Rrll, rRll), both sides (LLRR, LlRr, lLrR, LlrR, lLRr), and neither side (llrr).

Table 2. Percentage distribution of 574 antlers from barren-ground caribou by presence of the brow and bez tines and absence of the brow or the bez tine, Northwest Territories, 1966-68.

Antler year class	Antlers N	% antler pairs with both brow & bez tines present	% single antlers with brow & bez tines present	% antlers with tines absent: Brow absent[a] Left	Brow absent[a] Right	Bez absent[a] Left	Bez absent[a] Right	Brow & bez absent Left	Brow & bez absent Right
Males									
2nd-4th	122	39.3	49.2	4.9	3.3	19.7	21.3	0.8	0.8
5th-10th	90	84.4	92.2	4.4	2.2		1.1		
2nd-10th	212	58.5	67.5	4.7	2.8	11.3	12.7	0.5	0.5
Females									
1st-4th	126	6.3	11.1	19.0	19.0	8.7	6.4	16.7	19.0
5th-16th	236	21.2	30.5	14.8	15.3	7.6	11.0	11.0	9.8
1st-16th	362	16.0	23.7	16.3	16.6	8.0	9.4	13.0	13.0

[a] Best guess, based on criteria in methods section.

left-sided dominance 15.7% of the time; right-sided dominance, 14.6%; both sides dominant, 14.6%; and no dominance on either side, 55.1% (Table 1). No predominance of left-sided over right-sided dominance of the brow tine was found (P >0.05).

Expressions of dominance or the lack thereof by the brow tines on antler pairs from young males (Table 1:2nd-4th sets) varied non-significantly (P >0.05). Among bulls (Table 1:5th-10th sets) expressions of left-sided and right-sided dominance of the brow tine in antler pairs were proportionately overrepresented while dominance on both sides and, more so, no expression of dominance were underrepresented (P <0.01). The frequency of occurrence among left-sided, right-sided, and both sides expressions of dominance in the overall sample, by age, or by sex were not significant (P >0.05). Antler pairs with both brow tines simple or absent (lr) were proportionately overrepresented among females regardless of age (Table 1:P <0.005) and were proportionately underrepresented among bulls (Table 1:P <0.01).

Many of the antlers (43.4%) were lacking a brow or a bez tine, especially on antlers from females (regardless of age) and young males (Table 2). Only 39.9% of all antlers had both the brow tine and the bez tine present (Table 2). The brow tine was apparently missing more often than the bez tine on antlers from mature bulls and females (regardless of age); while on antlers from young males it was the bez tine (Table 2). Both brow and bez tines were missing from 16.8% of all antlers. The brow tine only was missing from 23.5% of the antlers: 12.0%, left side; and 11.5%, right side. The bez tine only was missing from 19.8% of the antlers: 9.2%, left side, and 10.6%, right side.

Only 6.8% (39) of the antlers were spikes (26 individuals) with no tines or palmation of the main beam. All but two of the spike antlers were from females (Table 3). Nine (45.0%) of the 20 antlers from female long yearlings (2nd year class) and two (7.1%) of the 28 antlers from male long yearlings were spikes (P <0.005). Some

Table 3. Percentage distribution of 37 spike antlers from female barren-ground caribou by antler year class, Northwest Territories, 1966-68.

Antler year class	Antlers N	% paired spikes	% additonal spike antlers Left	% additonal spike antlers Right	% total spikes in year class
1st	6	100.0			100.0
2nd	20	30.0		15.0	45.0
3rd	60	13.3		8.3	21.7
4th	40			2.5	2.5
6th	26			3.8	3.8
7th	66	3.0			3.0
8th	30		3.3		3.3
9th	42	2.4			2.4
10th	24	8.3			8.3

females up to the 10th year class carried spike antlers (Table 3), while no males beyond the 2nd year class did. An additional nine of the females (3rd-16th sets) with no brow or bez tines present had relatively small antlers with short terminal tines (bifurcations) or slight palmations of the main beam compared to others in their antler year classes (based on this sample, field workers should note that small size and simplistic form, even spikes, does not necessarialy identify an animal as a long yearling).

I subsequently isolated all those antler pairs with both the brow and the bez tines present, as I was not always confident of my classification of a tine as a brow tine, when only one tine was present on the lower portion of the antler. Consequently the sample was reduced from 287 to 91 antler pairs: 68.1% from males and 31.9% from females. Seventy (76.9%) of these 91 pairs exhibited dominant brow tines: most (54.3%) were contributed by mature bulls (5th-10th sets); then 24.3% by young males (2nd-4th sets); and 21.4% by cows (5th-16th sets). The observed distribution of the expression of dominance of the brow tines in the 91 pairs was: left-sided, 29.6%; right-sided, 26.4%; both sides, 20.9%; and no dominance, 23.1%. There was no significant difference (P >0.05) in the distribution of the 91 pairs by the four possible combinations of the brow tines or among the 70 pairs by side of dominance exhibited by the brow tines.

Brow and bez tine together

In all cases the frequency of occurence of left-sided dominance of the brow and bez tines together are non-significantly (P >0.05) higher than the rate for brow tines only (Table 1.) This condition also was apparently true for the occurence of both sides dominant (Table 1:P >0.05) Thus, those antler pairs exhibiting either right-sided dominance or no expression of dominance for both brow and bez tines together were seemingly lower proportionately (P >0.05) than for the brow tine only (Table 1).

Antler pairs with brow or bez tines that exhibited dominance on both sides or were left-sided dominant were proportionately overrepresented and those that were right-sided dominant or lacked any expression of dominance were underrepresented (P<0.005) in the observed sample of male antler pairs. However, no significant difference (P>0.05) could be found among left-sided, right-sided, and both sides dominance expressions of the brow or bez tines in those antler pairs, nor between left-sided and right-sided dominant sets (P>0.05).

Antler pairs with brow and bez tines that were simple or absent (no expressed dominance) were overrepresented (P<0.005) in the observed sample of female antler pairs. Expressions of left-sided, right-sided, and both sides dominance of the brow and bez tines were all less than expected among female antler pairs (P <0.005). No evidence could be obtained for any significant variation among the occurrences of left-sided, right-sided, and both sides dominance (P >0.05) or between antler pairs expressing left-sided versus right-sided dominance (P >0.05).

Discussion

Only tentative acceptance of the apparent predominance of enlarged (dominant) left brow tines over right ones for the entire species (at least, in the northern hemisphere) is currently warranted on the basis of existing data (Table 4). I could not find a disproportionately high occurrence of left-sided dominant brow tines compared to right-sided dominant ones in my sample; nor was there in the samples from Murie, Skoog, or Goss (Table 4), when treated separately. Only two (Table 4: Banfield and Davis) of the six samples reported in Table 4 demonstrate significantly high occurrences of left-sided dominance over right-sided dominance in the brow tines of antler pairs. Thus, most of the contribution to the Chi-square comes from only 32.4% of the antler pairs with left or right dominant brow tines (Table 4: Banfield and Davis). When the other 67.6% of the antler pairs (Table 4: Murie, Skoog, Goss, and this study) are combined, that overall sample yields a non-significant difference in the rates of occurrence of left or right dominant brow tines in antler pairs. All the caribou in Banfield's (1954) sample were adult bulls and on the basis of what can be gleaned from Davis' (1973) report, it is likely that all of his specimens were also only from adult bulls. As essentially all of the significant difference in the occurrence of left versus right dominant brow tines is contributed by these two samples of adult bulls, it seems an exaggeration of fact to suggest that the trait is necessarily common to all members of the species (in the northern hemisphere). If Banfield (1954) and Davis (1973) actually wanted to investigate this antler growth phenomonon at the species level, one must ask as why they did not examine antler pairs from females and young males as well as those from adult bulls(?). Surely, such material was available to both of them.

I see no objective reason for accepting the sample of 70 antler pairs obtained from reindeer introduced to South Georgia (54°-55°S, Leader-Williams, *in* Goss, 1980) as strong evidence for a predominance of enlarged right brow tines (n = 27) over left ones (n = 19) in the southern hemisphere; and thus, supposedly opposite to *Rangifer* in the northern hemisphere. The supposed disproportionate representation of an expression of dominance in right versus left brow tines (27 vs. 19) is non-significant (P >0.1). Thus, the suggested higher occurrence of right dominance over left dominance in these brow tines likely could be due to chance alone from the small sample size.

If further work is done on this subject, I suggest that standard criteria be used for recognizing the brow tine, when only the brow or the bez tine is present on one or both antlers of a pair. Differing criteria could confound initial findings and subsequent comparative results. Form, orientation to the main beam, or even origin on the main beam may not always be a diagnostic characteristic of the brow tine in *Rangifer*, especially when related to antlers from females or young males. The fixed relationship for the point of origin on the main beam that I used should continue to be used as an objective criterion for designating a tine as the brow tine (see Methods). Also, if a single-pointed brow tine is flattened in cross-section but not broadly palmate, its form should be considered simple (subject to the width restrictions given in the Methods).

I also suggest that each antler pair in future samples be identified by sex and at least approximate age of the donor animal to allow evaluations of antler pairs by sex and age class. Whenever possible antler pairs should be separated by sex and at least two age classes for subsequent evaluation, such as 1-4 years and 4 years or older. Antler pairs from young prime bulls (4-5 yr), prime bulls (6-9 yr), and possible 10 years olds, are undoubtedly the best specimens to describe side of dominance in the brow tines, as prime bulls have the most advanced development in the rangiferine antler, while female antlers apparently represent one of the earliest stage of morphogenesis of antlers in *Rangifer* (Bubenik, 1975a).

The function(s) of the brow tine in *Rangifer* has not been analyzed. Suppositions about feeding animals using them to move snow have no bases in fact. Goss (1980) suggested that future considerations of the function of the brow tine should include, «....the possibility that enlarged brow tines could function in the semiannual migration of reindeer and caribou, or might protect the eyes against wind and snow.» These two possibilities seem most unlikely as (1) essentially all animals that would have been carrying large antlers with markedly enlarged

Table 4. Summary of 1168 pairs of antlers from *Rangifer* in the northern hemisphere showing percentages possessing brow tines observed to be left-sided dominant, right-sided dominant, dominant on both sides, and neither side dominant by six different investigators.

	% dominance of brow tine[b]				
Source[a]	Left-sided (n = 395)	Right-sided (n = 287)	Both sides (n = 125)	Neither side (n = 361)	Subsample total
Murie (1935)	7 (ns)	7 (ns)	11		25
Banfield (1954)	24 (**)	8 (**)	3		35
Skoog (1968)	150 (ns)	132 (ns)	26	193	501
Davis (1973)	123 (***)	66 (***)	22		211
Goss (1980)	46 (ns)	32 (ns)	21	10	109
This study	45 (ns)	42 (ns)	42	158	287

[a] Data from Murie (1935), Banfield (1954), Davis (1973), and Goss (1980) also given in Table 1 of Goss (1980).

[b] Left- versus right-sided dominance of the brow tines in antler pairs: ns = non-significant; ** = $P < 0.01$; and *** = $P < 0.005$.

brow tines would be antlerless (if anything, new antler growth would be beginning) during spring migration; (2) autumn migration includes the time of the rut, and migration is not necessarily consistent or always unidirectional and often actually occurs in multidirectional stages; (3) also, essentially only mature bulls have enlarged brow tines of significant size and such males do not normally lead migrations; (4) essentially all adult males, many young males, and some females would be antlerless during the wintery period when antlers would be needed the most, if enlarged brow tines were for the protection of the eyes against wind and snow; and (5) even during the period of the year when antlers were present about half, at least, of the caribou in a herd would be without the benefit of enlarged brow tines.

Pruitt's (1966) suggestion that brow tines serve to protect the eyes of mature males, when thrashing bushes.during the rut, might have some truth to it. However, it is difficult to accept that such and elaborate appendage would have evolved for that sole function. Reluctance to accept Pruitt's (1966) reasoning is particularly strong, when one considers that all other North American male cervids are equally vigorous bush or tree thrashers without the benefit of any such elaborate protection, and they apparently are not plagued by eye injuries. Bubenik (1975b) disagrees with Pruitt's (1966) interpretation and argues that it is the function of the second tines, and not the enlarged brow tine, to protect the eyes (and also the whole facial region). Bubenik (1975a:448) suggest that the function of the enlarged brow tine is for offensive use and display.

Goss (1980:364) believed that, «Whatever the true function might be, it must be consistent with the fact that brow tines do not develop fully until sexual maturity, that they are present in both males and females, that antlers are shed in winter by males and barren females but in spring by calving mothers, and that one, both, or neither of the brow tines may be enlarged.» The majority of female caribou likely do not even possess antlers with (enlarged) brow tines present; and those that do, have only primitive, small models compared to the advanced, large models of mature bulls (these conditions also apply to many young males). Therefore I do not think that the function, if any, of the morphologically dominant but relatively small brow tine of females or young developing males is necessarily the same as that of the large, morphologically advanced brow tine of mature bulls.

Future investigation of the possible primary function of the enlarged brow tine in *Rangifer* should be restricted to mature bulls or bulls should be considered separately from females. Thus, the major points to be considered seem to be (1) development is delayed until sexual maturity; (2) most all mature and essentially all prime bulls possess at least one enlarged brow tine; (3) the antlers of most mature and essentially all prime bulls are shed in late autumn and not fully regrown again until pre-rut during the following early autumn. This means that the function of the enlarged brow tine of mature bulls is restricted to, at most, about 3 months of the year which coincides with the pre-rut and rutting periods. This seemingly leads to the likelihood that the probable function of the enlarged brow tine in mature bulls is linked to their courtship behaviour.

Acknowledgements

The pairs of antlers were collected by teams of Canadian Wildlife Service (CWS) biologists during a 3-year study of the Kaminuriak caribou herd, Northwest Territories, 1966-68. I thank Dr. H. Butler, Salt Spring Island, B.C.; and Dr. H. Thing, Game Biology Station, Rønde, Denmark, for critically reading an earlier version of the manuscript. S. M. Popowich, CWS, prepared the figure.

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Caribou calf deaths from intraspecific strife — a debatable diagnosis

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Abstract: In our review of the literature we found only one example of an instance when intraspecific strife supposedly led to the deaths of several newborn barren-ground caribou (*Rangifer tarandus groenlandicus*) calves within a short period of time and on a small area. This event took place during calving in June 1958 on the calving ground of the Beverly caribou herd in the Northwest Territories. The lack of other examples of multiple deaths of newborn caribou calves from intraspecific strife and our findings on the same calving ground during a study of calf mortality in June 1981, 1982, and 1983 and a study of cow-calf behaviour in June 1981 and 1982 cause us to question the published explanation. As we rarely saw aggressive behaviour among cows and newborn calves that involved actual physical contact and none that resulted in injury or death and because we found instances of multiple killings of calves by wolves (*Canis lupus*) we suggest that a probable alternative explanation of the 1958 findings is surplus killing by wolves. Most importantly, only direct observation of an event allows separation of a death caused by injuries due to intraspecific strife from a death caused by accidental injuries.

Key words: caribou, calf, mortality, intraspecific strife, Northwest Territories, Canada.

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Rangifer, Special Issue No. 1, 1986: 203 - 209

Introduction

Field observations of behaviour of barren-ground caribou (*Rangifer tarandus groenlandicus* and *R.t. granti*) on calving grounds document few instances of aggressive behaviour involving actual contact (e.g., de Vos, 1960; Pruitt, 1960; Lent, 1966; Kelsall, 1968; Skoog, 1968). For the most part, those observations were unsystematic (excluding Lent, 1966) and none of those studies reported rates of occurrence of aggressive behaviour relative to «active time periods» of the cows or calves involved. The observations of aggressive behaviour emphasized, however, that the likelihood of injury to or death of calves due to intraspecific strife was slight as the aggressive behaviour rarely included physical contact (e.g., Lent, 1966; Kelsall, 1968).

Studies of the causes of mortality of newborn calves (e.g., Lent, 1966; Skoog, 1968; Bergerud, 1971; Miller and Broughton, 1974) have also found only few instances of calf deaths that apparently could have been caused by aggressive behaviour and those few instances were the finding of single carcasses. The exception is de Vos' (1960) report of finding seven dead calves in one locality on the calving ground of the Beverly herd and subsequently ascribing, at least, five of those deaths to injuries caused by intraspecific strife among cows and newborn calves.

Our studies of calf mortality and cow-calf behaviour were not carried out specifically to address the subject of intraspecific strife among caribou cows and calves but it was part of our overall consideration. After completing our studies and reexamining the literature related to intraspecific strife among caribou we came to the conclusion that the single example of multiple deaths of calves supposedly resulting from intraspecific strife (de Vos, 1960) warrants revaluation. Furthermore, our own findings and the limited diagnostic evidence previously presented by de Vos (1960) and Kelsall (1960) led us to speculate that a second alternative explanation is as likely as the original interpretation made by de Vos (1960) or the alternative explanation offered by Kelsall (1960). The following is our evaluation of the evidence for intraspecific strife among barren-ground caribou cows and newborn calves causing injury or death to calves. Our emphasis is on the unlikelihood of such agonistic behaviour leading to deaths of calves, especially multiple deaths at one time and in one place.

Methods

We used standardized all-occurrence sampling (Altman, 1974) to measure the rate of occurrence of head swings, kicks and rushes by caribou during calving and early postcalving. One observer of a pair would continually watch one to four cow-calf pairs for a 10-minute sampling period while the second observer recorded the behaviour on a prepared form (Jingfors *et al.*, 1982; Gunn *et al.*, 1983). The daily observation period was between 1000 and 1700 h: three 10-minute samples of behaviour were taken each hour provided a cow-calf pair was visible.

The causes of calf mortality were determined by field necropsies of calf carcasses found during low-level helicopter searches. All calves were skinned, eviscerated and examined in detail by a veterinarian-pathologist (E. Broughton, CWS) and us for injuries, even when the cause of death (e.g., crushed skull) was immediately obvious.

Results

We watched caribou for 220 h between 2 - 23 June 1981 and obtained 578 10-minute samples which totalled to 6464 active cow-minutes and 4329 active calf-minutes (Jingfors *et al.*, , 1982). We observed 264 aggressive acts with the observed cow and calf as the recipient or aggressor: 67.8% (179) were head swings; 25.4% (67) were rushes and 6.8% (18) were kicks. Usually the aggressive act was a single event but 42 head swings (23.5%) were followed by rushes and two head swings (1.1%) were followed by kicks. During calving (2 - 9 June), observed cows initiated aggressive acts toward their calf or other calves in similar proportions, 35.5% and 37.1% (Table 1). The maternal cow's aggression toward her calf decreased during postcalving (11 - 23 June) as only 2.6% of the maternal cow's aggressive acts were toward her calf compared to 72.7% toward other calves. The level of aggression toward the observed calf by other cows was similar during calving and postcalving (Table 1).

In 1982, we observed caribou for 166.7 h between 3 and 29 June and we obtained 498 continual 10-minute samples which totalled 4754 active cow-minutes and 3201 active calf-minutes (Gunn *et al.*, 1983). The proportion of rushes and head swings of the 201 aggressive acts were similar (45.7% and 44.3%, respectively) and

Table 1. Seasonal variation in the initiator and recipient of aggressive acts among barren-ground caribou, Beverly calving ground, Northwest Territories, 1981 - 82.

			% Recipients			
			Focal pair		Other pairs	
Year	Season	Initiator	cow	calf	cow	calf
1981	calving	focal cow	—	22	17	23
		other cows	12	40	—	—*
	postcalving	focal cow	—	2	19	56
		other cows	12	49	—	—
1982	calving	focal cow	—	4	27	26
		other cows	11	74	—	—
	postcalving	focal cow	—	0	3	22
		other cows	1	17	—	—

* Only aggressive acts involving one or both members of a focal pair are given in this consideration.

only 10.8% were kicks. Most aggressive events were a single act but 17 events were two acts and three were three-act events.

Little aggression by the maternal cow towards her calf was seen during calving (3 - 13 June) as only 7.0% of the maternal cow's aggressive acts were toward her calf compared to 45.6% against other calves (Table 1). The maternal cow was not aggressive towards her calf during postcalving (4 - 29 June) but directed 88.0% of her aggressive acts towards other calves compared to 45.6% during calving (Table 1).

The mean rate of aggressive acts was not significantly different ($P > 0.05$) between 1981 and 1982 when the mean rates were 2.0/100 cow-minutes and 1.72/100 cow-minutes, respectively. In both years, aggressive acts occurred more frequently than expected when group size changed (Table 2).

We observed no apparent injuries to calves during 204 aggressive acts toward calves in 1981 and 146 acts toward calves in 1982. Physical contact was rare and the calves were nimble in avoiding the aggressive behaviour.

Only three (1.0%) of the 287 dead calves found on the Beverly calving ground in June 1981 - 83 exhibited trauma most likely caused by adult caribou. All were found as singles and no absolute distinction could be made as to whether or not the fatal injuries occurred accidentally or were the results of deliberate acts of aggression. In 1981, a 1 - 3 day old female calf apparently was kicked in the right rib cage, causing compression of the thoracic cavity and hemorrhaging in the lungs. Hemorrhages in the mouth were traced from blood clots accumulated throughout the trachea. The second calf in 1981, less than 1-day-old of indiscernible sex, appeared to have been kicked at the base of the skull but the carcass had been extensively scavenged. In 1983, a 1-3-day-old female calf had a ruptured liver, there was extensive hemorrhaging throughout the abdominal cavity in association with the injury. Most likely the calf's death resulted from it being trodden on by an adult caribou. The calf was lying at the edge of a small island just above the snow on the lake where many caribou had left the lake. None of the three calves had other injuries or pathological conditions.

Table 2. Distribution of aggressive acts by caribou cows by changes in group size or composition, Beverly calving ground, Northwest Territories, 1981 - 82.

Year	Rate of aggressive acts	Change in group size or composition	
		Change	No change
1981	above median	62*	20
	below median	262	227*
1982	above median	46*	10
	below median	125	149*

* Significantly greater than expected, $P < 0.005$.

Table 3. Percentage occurrence of utilized carcasses of wolf-killed barren-ground caribou calves found in clumped associations, Beverly calving ground, Northwest Territories, June 1981 - 83.

Size of clumped association	Number of clumped associations	% individuals not fed on by wolves
8	1	100.0
34	1	50.0
5	2	30.0
3	5	26.7
6	1	16.7
2	8	6.0
11	1	0.0
4	1	0.0

We found 154 carcasses of caribou calves that we determined were killed by wolves (*Canis lupus*) in June 1981 - 83. Most of the calves (72.1%) were estimated to have been less than 4 days old at death; 26.6% were estimated to have been between 4 and 7 days old; and 1.3% greater than 7 days old (but less than 2 weeks old). Most (44.1%) of the wolf-killed calves were males; 35.1% were females; and the sex of 20.8% was indiscernible, due to carcass utilization.

One hundred and four (67.5%) of the 154 wolf-killed calves were found in 20 «clumped associations» (within 500 m of each other) of 2 to 34 carcasses each (mean 5.2 ± 7.18 S.D.). In 1981, 1982, and 1983 the locations of the wolf-killed calves that we found (assuming that we did not miss adjacent kills around single finds) suggested that 43.5% (10), 75.4% (52), and 67.7% (42) were in clumped associations. In 1981, 3 calves in one clump were within about 6 to 45 m of each other and the 3 calves in the other clump were within about 60 to 170 m of each other. The two individuals in each of the two clumped pairs in 1981 were about 10 and 30 m apart, respectively. On 17 June 1982, we found 34 carcasses from wolf-killed calves within a 3 km^2 area (Miller *et al.*, 1985). All of the calves had been killed by wolves, all within a short period of time of each other, and all within about the previous 24 hours. In 1982 we found 11 wolf-killed calves together (all within 300 m of each other) on a small island only several hundred metres in size in a large frozen lake. In 1982 the 3 wolf-killed calves in one clump were within about 50 to 200 m of each other. The two individual calves in each of the two clumped pairs in 1982 were within about 100 m of each other. In 1983 within clump distances for the individuals in the clump of eight were about 50 to 500 m; in the clump of six, about 5 to 500 m; and one clump of five, about 100 to 500 m. The individuals in the second clump of five in 1983 were within about 200 to 500 m of each other; those in the clump of four, about 20 to 300 m; those in the two clumps of three, about 50 m and 300 m; and those in the four clumped pairs, about 5, 50, 200, and 200 m.

The number of calf carcasses in each of these 20 clumped associations that were fed on by wolves varied from none to all (Table 3). The most extreme examples of no or little utllization being the killing of eight calves in one area with absolutely no feeding on them by wolves; and the killing of 34 calves with absolutely no use made of 17 by wolves and only minimal feeding on the remaining 17.

Discussion

Our observations of caribou cow-calf behaviour documented a low incidence of aggressive behaviour between cows and calves. Our postmortem findings also suggested that intraspecific aggression rarely, if ever, caused fatal injuries. We could not isolate (if it occurred) accidental injury inflicted by trampling in stampedes from deliberate aggression. The knocking over and trampling of calves during panicky behaviour of caribou groups cannot be termed intraspecific strife as it is accidentally caused by other caribou.

Most all of the limited literature related to aggressive acts by barren-ground caribou cows towards strange caribou calves or less frequently towards their own offspring is descriptive and lacks any objective measure of severity. Observers tend to vary in their subjective evaluations of the severity of aggression by caribou cows toward newborn calves but there is one common thread that prevails - the lack of evidence for such intraspecific strife commonly leading to the deaths of newborn calves.

Maternal cows maintain social stability through the bond with their own calf and by reinforcing the bonds of other cow-calf pairs by the maternal cow reacting agonistically toward strange calves (Lent, 1966). Lent (1966) described that cows threatened calves more frequently than any other aggressive act compared to yearlings which cows were more likely to hook at with their antlers. Pruitt (1960:33) has stated that the «threat pose» is «a true instinctive action» and serves as a «flight releaser» even in newborn calves. Thus, it seems unlikely that fatal encounters between newborn calves and strange cows would be a frequent event, as the calves would perceive the warning that most always precede any aggressive acts. Lent (1966: 744) noted that the frequency of actual striking of calves by cows during agonistic interactions was low, 6%. He observed cows only actually contact calves during foreleg strikes and he doubted that any of the kicks were hard enough to cause serious injury and also the calves are adept at avoiding agonistic acts. Lent (1966: 745) concluded that, «Although under certain conditions calf mortality may result from agonistic interactions, it must be considered relatively rare. Most agonistic activity clearly results in no contact between individuals. Not only is there little contact, there are no long sequences of agonistic behaviour, at least outside of the rutting period.»

Breeding females usually cast their antlers at about the time of calving: some parturient females, within a few days before; and some maternal females, within a few days after (e.g., Lent, 1965; Kelsall, 1968; Skoog, 1968; Espmark, 1971; Bergerud, 1976). Thus, if the social function of antlers in intraspecific roles during calving or early postcalving was a significant one in terms of inflicting injury on calves, one would not expect the timing of antler drop that one sees. Also, that both antlered and antlerless cows make «threat» and «attack» postures (e.g., Pruitt, 1960; Lent, 1966) against calves (and actual contact is seldom made), strongly suggests that the function of such acts is simply to displace the calf rather than to do it any real harm. Thus, these conditions, seemingly,all would greatly reduce the likelihood of antler attacks by cows on calves during, at least, late calving and early postcalving.

Bergerud (1971) found only two calves dead with punctures (supposedly from antlers) and one calf trampled in a sample of 121 dead caribou (*R. t. terraenovae; R. t. caribou* Banfield, 1961) calves in Newfoundland though he did not describe the actual injuries. Skoog (1968: 575) noted that 3 of 16 calves found dead on the Nelchina herd's calving grounds in 1956 apparently had antler punctures and he believed that young calves especially those <5 days old received a great deal of abuse during the calving period, particularly when bands stampeded and calves were stepped on (not intraspecific strife). Skoog (1968: 575) agreed with Lent (1966) that such mortality from intraspecific strife is usually low but suggested that under some situations (not expounded on) could be significant. However, he only mentions six single calves that appeared to have died from antler punctures (apparently not verified by postmortem examination) and four that had been trampled or kicked to death.

Studies of calf mortality using radio-collars to detect and locate dead calves have not documented calf deaths due to intraspecific strife. Sixty-two calf carcasses were examined from a sample of 169 radio-collared newborn calves of the Porcupine herd between 1982 and 1984 (Mauer *et al.*, 1983; Whitten *et al.*, 1984, 1985) and none of the 62 calves had died from injuries following intraspecific strife. Maternal cows had subsequently abandoned 23 of the 169 radio-collared calves but the rejection of the handled calves was observed on only one occasion. That calf was abandoned by the cow after the cow struck it with her forefeet; however, the calf did not have any signs of traumatic injury but died from starvation (Mauer *et al.*, 1982).

Although the views on intraspecific strife among cows and calves at or about the time of calving vary qualitatively, the consensus is that mortality due to aggression under normal conditions will be low at worst and most likely only negligible. Possibly intraspecific strife is most likely to occur during and after some stampedes when temporarily separated calves are approaching strange cows while searching for their maternal cows. Furthermore, the reported observations of intraspecific strife suggest that foreleg kicks are more likely to result in injury rather than punctures from antlers during head threats or swings.

Death of calves in 1958 - as reported by de Vos (1960)

de Vos (1960:256) reported that he had «... surveyed a drumlin on which a calving band estimated at 600 cows had spent about 24 hours during the 2 previous days. On an area of about 25 acres, 7 dead calves were located. All of these, except one had died during the previous 24 hours. When five of these calves were skinned and examined more closely, it was found that all had bruises, two had body punctures, one a broken skull, and another one a broken vertebral column. From all appearances, the punctures were made by antlers, and it seems clear that all these calves died as a result of violence by adult caribou. Their ages varied from 1 day to 1 week. It was possible that these calves became lost in the band, tried to attach themselves to strange females, and were violently attacked. It seemed likely that this cause of mortality was restricted to calves not more than 1 week of age as older calves are able to elude attacking cows.»

Kelsall's (1960) evaluation of de Vos' 1958 findings

Kelsall (1960: 47 - 48) reported the following with regard to the skepticism about de Vos' (1960) interpretation of his findings in 1958, «de Vos's assessment of mortality observed differs from the conclusions of the other field men and for that reason it is worth mentioning... These observations (the ones reported in de Vos (1960:256)) were discussed, shortly after they were made, with de Vos and other of the field men. It seemed that something unusual was involved. While all field men had occasionally noted females striking or butting at strange calves, such instances seemed to be uncommon among calving bands under reasonably normal conditions. In fact, serious intra-band strife seemed to be relatively uncommon at any time. It was supposed that some of the dead calves had died somewhat earlier than de Vos estimated, during periods of adverse weather. With as many as 600 adult caribou on a 25-acre hill, dead or dying calves might easily receive bruises and injuries through trampling. Also, if predators had seriously disturbed so large a herd, the resulting confusion might easily have resulted in injury to young calves, even in fine weather.»

Summary comparative discussion

de Vos' (1960) description of the injuries sustained by the five calves that he skinned and examined more closely in 1958 are comparable to the descriptions of wolf-inflicted injuries that we observed between 1981 and 1983. We found wolf-killed calves with various combinations of injuries some of which could have been simply described as broken skulls, broken vertebral columns, or bruises. Those injuries were not invariably associated with discernible tooth punctures. The injuries briefly described by de Vos (1960) are not diagnostic of the cause of death in themselves especially as antler punctures would not be readily distinguishable from single canine punctures. Also, the absence of tooth punctures does not reliably preclude predation as a cause of death. de Vos' (1960) description of the calves' injuries are as consistent with wolf predation or, as Kelsall (1960) suggested, accidental trampling as with intraspecific strife. The description of the five calves (de Vos, 1960) is indistinguishable from an example of surplus killing by wolves. de Vos' (1960) interpretation cannot be discounted but the reported incidences of injuries caused by aggressive behaviour and observed rates of aggressive behaviour among caribou cows and calves suggests that to find five (or more) calves dying at the same time and place from an unusual cause of death is extremely unlikely. Our identification of an alternative explanation to de Vos' (1960) interpretation and Kelsall's (1960) alternative explanation does highlight the importance of detailed postmortem examinations and their complete reporting. In the absence of diagnostic injuries, only direct observation of an event allows separation of a death caused by injuries due to intraspecific strife from a death caused by accidental injuries.

We think that it is important that a clear distinction be maintained between mortality of newborn calves due to intraspecific strife versus mortality caused by accidental injury. Death from intraspecific strife requires a deliberate lethal act of aggression against the calf while death from accidental injury results from an unpremeditated chance event. Most importantly, if significant mortality to calves routinely occurs due to intraspecific strife among maternal cows and calves, it would indicate a, seemingly, serious flaw or weakness in the evolutionary development of the socialization of caribou. Such a significant fault would warrant detailed documentation before it is accepted as a truism.

Acknowledgements

This study was carried out under the Canada-Northwest Territories Wildlife Research Agreement: support was provided by the Canadian Wildlife Service (CWS); Indian and Northern Affairs Canada; Polar Continental Shelf Project (PCSP), Energy, Mines and Resources Canada; and the Wildlife Management Division (WMD), Department of Renewable Resources, Government of the Northwest Territories. We are especially grateful to G. D. Hobson, Director, PCSP, for his continued support of our caribou studies. We thank the following for their assistance in the studies: E. Broughton, CWS, (1981 - 83); R. Glaholt, WMD, (1981 - 82); K. Jingfors, WMD, (1981 - 82); R. Mulders, WMD, (1981 - 82); J. Adamczewski, WMD, (1981); H. Kiliaan, CWS, (1981); G. Arlooktoo, WMD, (1982); M. Lawson, WMD, (1982); and H. McLeod, WMD, (1982). We thank Dr. P. C. Lent, U.S. Fish and Wildlife Service, and Dr. J. P. Kelsall, Delta, B. C. for critically reading earlier versions of the manuscript.

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Effect of adverse weather on neonatal caribou survival — a review

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Abstract: This paper reviews the relationship between adverse weather and neonatal caribou (*Rangifer tarandus* spp.) survival in North America by examining the available literature and our own findings. The viewpoint that adverse weather on the calving ground can result in major losses of newborn barren-ground caribou (*R. t. groenlandicus*) calves is largely unsupported. Published reports of calf mortality caused by adverse weather are questionable because causes of death were rarely determined by postmortem examinations. Circumstantial evidence associated with the small samples of dead calves does not support published assumptions that the mortality was weather related, or that high losses due to adverse weather are common events. The applicability of results from physiological testing are questionable, because the calves were restrained and the behaviour of unrestrained animals was ignored in the conclusions drawn from the tests. The relationship between adverse weather and calf mortality is more speculation than documentation yet often has been uncritically cited. In our view, healthy newborn barren-ground caribou are well adapted physiologically and behaviourally to cope with all but the most severe adverse weather.

Key words: adverse weather, mortality, newborn barren-ground caribou, Northwest Territories, Canada.

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Rangifer, Special Issue No. 1, 1986: 211 - 217

Introduction

Adverse weather has been indicated as a principal cause of death of newborn caribou (*Rangifer tarandus* spp.) (e.g., Banfield, 1951; Kelsall, 1968; Skoog, 1968; Bergerud, 1978). Most studies of the possible importance of inclement weather as a mortality factor of newborn caribou calves were in Canada (Cottle, 1959; McEwen, 1959, 1960; Kelsall, 1957, 1960, 1968; Lentz and Hart, 1960; Hart *et al.*, 1961; Pruitt, 1961; Bergerud, 1971; Miller and Broughton, 1974). Skoog (1968) put forth additional information on the supposed relationship between adverse weather and calf mortality in Alaska.

We had the opportunity to describe the effect of adverse weather during a study of calf mortality in the Beverly herd of barren-ground caribou (*R. t. groenlandicus*) during each June 1981, 1982, and 1983. In conjunction with our field studies, we intensively reviewed previous descriptions of calf mortality. Under closer examination we found that the validity of weather related mortality has not been well documented, especially the supposed catastrophic effects of inclement weather at or about the time of calving.

In this paper, we review the earlier accounts of mortality of newborn caribou calves supposedly caused by adverse weather, to demonstrate that the relationship is more tenuous than usually realized. Although our own study of caribou calf mortality was not carried out specifically to address this subject, the matter was part of our overall consideration. Therefore, we also present some of our data to further support our contention that the role of adverse weather in caribou calf mortality has been overemphasized.

Earlier field studies of calf mortality and adverse weather

Banfield (1951:36, 1954:44) did not directly study the effects of adverse weather on newborn caribou in Canada although he concluded that «Weather also plays an important role as a mortality factor for the caribou population. The greatest losses are suffered by newborn calves when exceptionally severe weather conditions occur during the calving season». Banfield (1951, 1954:44) seemingly based his conclusion on an observation of a resident of Eskimo Point, Northwest Territories, in June 1947 who estimated, «....an 80 percent calf loss in the Keewatin District herds that season.». the estimate was unsubstantiated by recording sample sizes of dead calves, how the cause of death was determined, or how extrapolations to the calf crops were made.

Kelsall (1957, 1960, 1968) is most frequently cited regarding adverse weather as a major cause of mortality of newborn caribou. Kelsall (1957:37-38) based his original thinking, at least partially, on a sample of six dead calves found after a period of «rough weather» in June 1951 (although he does not describe the cause of death of those calves) and circumstantial evidence about weather conditions at or about calving in 1948 through 1951.

Kelsall (1960:51) seemingly used the sample of six dead calves from June 1951 as a basis for, «....considerable mortality among young calf caribou, which they (field personnel) ascribed, directly or indirectly, to adverse weather.». Kelsall (1960:51) also suggested that finding 30 intact skeletons of young calves in spring 1954 that apparently had died in spring 1953 did not implicate wolves but «...might be correlated with blizzard conditions which had prevailed in 1953 during the height of calving.». We suggest that other causes of death could also just as likely have been implicated as could adverse weather.

Kelsall (1960:45) attributed four of nine calf deaths to adverse weather in June 1957 which is confusing in light of Kelsall and Loughrey's (1958:27) observations during the same calving period of, «Fifteen caribou evidently killed or eaten by wolves were found, including five adults, one yearling, and nine calves». Possibly, the 1958 calf sample was 18: 11 suspect wolf kills; 4 deaths due to adverse weather (exposure or starvation); and 3 unknowns, though postmortem examinations are not reported. If this is correct, it would further reduce the basis for the speculation about the supposed relative importance of adverse weather, at least, when based on direct evidence from samples of dead calves.

Kelsall (1960:56) states, «More than 100 dead calves found appeared to have died during the adverse weather of June 1 to 3 and June 5 to 10. (1958)... At Camp 26, where Wilk, Thomas and Pruitt discovered about 90 dead calves, most of the mortality had occurred during the first ten days of June.». Those 90 carcasses were found until 26 June but, «...most of them were thought to have died during the adverse weather experienced up until June 11.». The causes of death were discussed for 85 of them and only «35 pereent» of rhem (30) were attributed directly to adverse weather (p. 45). It is, however, difficult to determine adquately the «time of death», except when the carcass is relatively fresh and only then, if detailed necropsies were performed — which is never specified. Kelsall (1960:48) mentions the skinning of five carcasses by de Vos but not detailed postmortem examinations.

The field workers determined the cause of death by finding the carcass after periods of inclement weather and not finding any external evidence for each calf's death by other causes. Our study of calf mortality on the Beverly calving ground in June 1981 — 83 and studies on the calving ground of the Porcupine caribou herd in Alaska (Mauer *et al.*, 1983; Whitten *et al.*, 1984, 1985) emphasized the need for detailed necropsies to determine the cause of death. Determination of death from exposure by an external examination of a carcass is impossible. Even after performing a detailed necropsy, the diagnosis of exposure would often still be questionable, as it is made by elimination of other causes.

de Vos (1960) is often cited in relation to adverse weather contributing to deaths of newborn caribou although in fact his only relevant statements were, «In this particular study inclement weather did not appear to affect calf mortality seriously. On June 12, four dead calves were found which appeared to have succumbed during a blizzard three days previously.». de Vos' camp was one of the three camps that Kelsall (1960) used to provide data on the importance of adverse weather in 1958, and in fact de Vos' camp was only about 5 km from the camp where the 85 carcasses were found

(D.C. Thomas, pers. comm.; and map no. 2 of Kelsall, 1960:137).

Also relevant is Pruitt's (1961) findings referred to by Kelsall (1960:48) that suggested that only, «...about 4.5 percent (or possible less) of the fawns (calves) born on this particular hillside...» in June 1958 died during that period of adverse weather. Pruitt's (1961:551) subsequent conclusion has gone unheeded: «It is clear that near-blizzard conditions prevailed during most of the period of observation.» — (yet mortality was very low).

Altman (1962:16) stated that, «It is enigmatic that caribou are born well before the warmest time of the year on the barren grounds, and yet, may be highly susceptible to incliment (sic) weather.». He suggested that one possible explanation was that if caribou were born earlier the influence of adverse weather would be more likely and if born later they would not make sufficient growth to survive the first winter.

Kelsall (1968:236-242) in his final consideration of weather (especially wind chill) in relation to newborn calf mortality reiterated his previous reports and those by Lentz and Hart (1960) and Hart *et al.* (1961). Kelsall (1968) included additional data for June 1959 when no dead calves were obtained. Kelsall's (1968:239) statement that, «Numerous dead calves were found following severe storms in all three of the later years, (1957-59) with losses in 1959 being relatively minor, and those in 1957 quite severe» was based apparently on the samples of four of nine calves in June 1957; 30 of 85 calves in June 1958; and none in June 1959. Also, we think, that Kelsall's circumstantial evidence from weather records and counts of cow-calf ratios obtained in the above studies do not necessarily support the conclusion that mortalities of newborn calves in those years must be attributed directly to adverse weather.

Kelsall (1957:38) speculated that «It seems likely that there is a «chilling point» at which the bodily functions of the caribou calf are greatly impaired. The crucial conditions are probably brought about by various combinations of high winds, low (sic) moisture content, low temperatures (not necessarily below freezing), and continuous or frequent precipitation. There is no shelter on the calving grounds except from winds, which seem to make caribou nervous and keep them on the move for greater distances and longer periods than usual.».

Kelsall (1960:46) also identified two other possible consequences of adverse weather causing calf mortality. He speculated that calves would become separated from their maternal cows during blizzards. Kelsall (1960-46) also referred to calves mired in unseasonable deep snow as one of the examples of adverse weather and a late season indirectly causing calf mortality. Pruitt (1960:30) observed that caribou on the Beverly calving ground in 1958 avoided soft snow areas when travelling during the thaw. He noted that when caribou did attempt to cross deep soft snow areas, «...individuals frequently broke through the snow, went in up to their bellies and had trouble getting out.» (Pruitt, 1960:30). Pruitt (1960:30) also saw a wolf pick up a calf carcass that had become mired in soft snow and died.

Field experiments to document effects of adverse weather on calf mortality

Kelsall's (1957) concerns for severe weather leading to the death of calves led to experiments to describe the influence of adverse weather on metabolic and thermal responses of newborn caribou (Hart *et al.*, 1961; Kelsall, 1968:238-240). Extrapolating Hart *et al.*'s (1961) study to healthy, free-ranging calves is questionable: the experimental calves were (1) captured and flown to holding areas; (2) held in small corrals, without forage, and fed a substitute diet of mainly evaporated milk; (3) tethered by a rope during tests; (4) some were blindfolded to prevent struggling during tests; and (5) tested while in the standing postition. Only four calves were tested and all died apparently of direct results caused by adverse weather. Those four calves were tested during a heavy rain storm on 15 June 1959; two died during and two shortly after the tests. The four untested (control) calves free to find shelter around the camp during the storm all survived, which led Hart *et al.* (1961:855) to recognize the probable importance of behaviour. Additionally, Hart *et al.* (1961) and Cottle (1959:10) when discussing the 1959 wind chill study noted that the effect of the storm during the test period was not detected by subsequent repeated counts of cows with calves. The absence of a decrease in the calf to cow ratio suggested that behaviour of free-ranging calves enables them to cope to some extent with the adverse weather conditions that led to the deaths of the four restrained, test calves.

Other North American studies of calf mortality and adverse weather

McEwen (1959:37) also on the Beverly calving ground in 1959 saw 20 dead calves from the air on 16 June, following an exceptionally severe storm on 15 June with rain and winds of 80 km/h gusting to 121 km/h. He (McEwen, 1959:37) extrapolated the 20 dead calves seen on a 86 km^2 area to 533 dead calves on a supposed calving ground of 2778 km^2 and estimated a 2.6% mortality on 15 June (by assuming 19800 calves present). When he compared this loss to earlier losses McEwen (1959:37) concluded, «Although this is perhaps not a valid comparison, it does indicate that the effect of weather on calf mortality was lower than anticipated.»

In 1960 McEwen (1960:27) concluded that calf survival was high because of favourable weather throughout the calving period, with the exception of one day. He implied that the sighting of seven dead calves on 9 June, a «... slightly higher than daily average.» resulted from inclement weather on 8 June with 9.0 cm of rain and winds averaging 32 km/h.

Bergerud (1971) who worked on woodland caribou in Newfoundland *(R. t. terraenovae; R. t. caribou,* Banfield, 1961), concluded that there was no evidence that calves succumbed from exposure between 1957 and 1967. He reported that of six calving grounds the one with the coldest weather had the second highest 10-yr average rate (15.2%) of calf survival (Bergerud, 1971). However, Bergerud (1971) also pointed out that the maximum daily wind chill values for June in those 11 years were less than those given by Kelsall (1960) and Hart *et al.* (1961) as causing mortality of newborn caribou calves in the NWT. He also suggested, and we concur, that as newborn Newfoundland caribou calves are heavier than barren-ground caribou calves the former might be able to withstand greater exposure to inclement weather (Bergerud, 1971).

Bergerud (1978:86) when discussing North American caribou in general, states that: «Wind chill is the second most common cause of death of newborn calves during inclement weather *(cf.* Kelsall 1968).» «...(and) this cause of mortality can deplete an entire calf crop.». The above unsupported statement is then followed by erroneous citation, «The Kaminuriak herd lost much of its 1962 calf crop from this factor (Miller, 1974).». Miller (1974:65-66), however, had only concluded that, «...we must assume that either the survival of calf crop in 1962 was very low, or the mortality of juveniles and subadults of that cohort was exceedingly high.» In other words, Miller (1974) had not concluded the possible importance of wind chill on calf mortality in 1962. Record snow thicknesses in the winter range (Parker, 1972:Table 5) and extremely poor physical condition of caribou during spring migration in 1962 (J. D. Robertson, pers. comm. in Miller, 1974:66) argue for the causes of calf mortality to have been initiated prior to calving. Bergerud (1980:560) subsequently correctly evaluated the problem of prevailing weather on the Kaminuriak calving ground in June 1962, when he stated that, «We do not know the severity of the weather on the calving grounds, in 1962.».

Bergerud (1974:557) concluded that, «The short calving season for caribou cannot be explained by a mortality due to weather of calves born too early in spring. Calf mortality due to windchill has been reported for the Canadian Arctic (Kelsall, 1968) but not for Alaska or Newfoundland (Lent, 1964; Skoog, 1968; and Bergerud, 1971).».

Skoog (1968:581-587) found no evidence for adverse weather at or about calving time causing significant losses of newborn caribou in Alaska. He accepted, however, reports of adverse weather causing high mortality among newborn calves, and concluded (Skoog, 1968:582-583) «There can be no doubt that severe weather and chilling can result in high mortality among newborn calves during some years.». He referred to turn-of-the century reports of high losses within calf crops of reindeer (Skoog, 1968:581-582) and the later Canadian reports (Banfield, 1954; Kelsall, 1957; Lentz and Hart, 1960). Skoog (1968:587) summarized his discussion about weather by saying, «I doubt, however, that weather conditions other than icing exert much influence over caribou populations, except occasionally when repeated losses of a majority of a calf crop may occur over a period of years. The Nelchina herd experienced no such losses during the period of this study.». Bos (1974:17) watched the difficulty with which newborn calves in the Nelchina herd followed their mothers across remnant snowbanks and speculated, «Should newborn calves have to transverse large areas of deep soft snow, the likelihood of calf mortality would become very real.». Such mortality has not yet been recorded, however.

No subsequent studies of caribou calf mortality in Alaska have to date documented any high losses (and for the most part, not even any insignificant losses) of newborn caribou calves due to adverse weather (e.g., Bos, 1975; Davis and Preston, 1980; Davis *et al.*, 1978, Davis and Valkenberg, 1978; Mauer *et al.*, 1983; Whitten *et al.*, 1984, 1985).

Davis *et al.* (1978) found no calves that had died from exposnre to adverse weather in a study of the Fortymile caribou herd in Alaska. While discussing the possible losses of calves to adverse weather they noted (Davis *et al.*, 1978:60), «Caribou investigators in Alaska have pointed out that conditions on Alaskan calving grounds are generally milder than those in northern Canada.». They further noted (Davis *et al.*, 1978:62) that, «It is interesting to note that the Delta caribou herd (the closest neighboring herd to the Fortymile) realized its highest recent initial calf production and survival during 1976. Department biologists surveyd that area because they were concerned that catastrophic calf loss might result from the low temperatures and heavy snowfall in spring 1976. We also documented highly successful calving in the Western Arctic herd in 1975 and 1976 under weather conditions that were harsher than those that occurred on the Fortymile calving grounds during this study.»»

1981-83 studies of calf mortality on the Beverly calving ground

We studied newborn calf mortality on the calving ground of the Beverly caribou herd during June 1981-83, the same calving ground studied by the Canadian Wildlife Service in the late 1950s. We assigned causes of death to 257 of the 287 calves that we necropsied: only nine (3.5%) calves had died from pneumonia and those cases were not associated with adverse weather.

Weather on the calving grounds during calving and early postcalving in 1981, 1982 and 1983, however, was favorable to calf survival: little precipitation fell; temperatures and winds were seasonally mild and moderate, respectively. The highest recorded wind speeds did not exceed 40 km/h but were accompanied by rain and cool temperatures.

An abrupt warming trend in the second week and the seasonal lack of rain on the calving ground in June 1983 created slush mires by melting deep snow banks along the shores of water bodies. Six dead calves were found on 10, 11, and 13 June which had drowned, died of fatigue, stress or shock while trying to cross these slush mires. Although these conditions for potential entrapment and subsequent death may occur in most years, they are probably rarely as bad as in June 1983. Unlike Kelsall (1960:46), we believe that late season would likely reduce the problem because the snow banks would stay hard packed or refreeze «nightly» during early June; thus, allowing the newborn calves to traverse them without difficulty. By late June, the older calves should be better able to cope with the slushy areas in a late season.

Even with a detailed field necropsy, determination of the primary cause from the proximate cause of death is not always possible, especially in cases initially involving separation of the calf from its maternal cow then death of the calf due to a malnutrition, pneumonia, exposure complex. The cases of calf separation and subsequent mortality (14 cases) were also not associated with the adverse weather.

Discussion

The speculation about the importance of adverse weather at or about the time of calving in causing significant mortality of newborn caribou is based on limited quantitative data and, most importantly, the actual cause of death was not determined by detailed postmortem examinations.

Kelsall (1957, 1960, 1968) has been the author most cited as the source of data on adverse weather and calf mortality. The circumstantial evidence associated with Kelsall's small samples of dead calves does not necessarily support the assumption that the mortality was weather related, or that such high losses due to adverse weather are common events. The limited physiological experiments are questionable, especially the meaningfulness of the threshold values, because restraint or only parts of the animal were used and because behavioural considerations were ignored in drawing conclusions.

It appears from our review of the literature that caribou biologists have no sound factual basis for assuming that adverse weather frequently causes major losses of newborn barren-ground caribou. We are not suggesting that extreme adverse weather at or about the time of calving could not ever be an important cause of neonatal caribou mortality, but we do believe that such large-scale mortality remains to be documented. It seems likely that significantly high mortality among newborn barren-ground caribou probably only occurs when the additive effects of several unfavourable conditions combine: e.g., forage unavailability lowers the nutritional status of pregnant cows to the extent that their offspring are light, weak calves. We suggest that it appears that healthy newborn barren-ground caribou are well adapted physiologically and behaviourally to cope with all but the most extreme severities of adverse weather at or about the time of calving.

We think that Bergerud (1980:560) hit on the crux of the matter regarding the probable importance of adverse weather at or about the time of calving (especially at the peak of calving) when he stated that, «We do not clearly understand the relationships between maternal nutrition, calf size and vigor, and the subsequent ability of the calf to survive severe weather.».

Acknowledgements

The study was carried out under the Canada-Northwest Territories Wildlife Research Agreement. The Canadian Wildlife Service (CWS), Western and Northern Region, Environment Canada and Polar Continental Shelf Project, Energy, Mines and Resources Canada funded this reserach. We are especially grateful to G. D. Hobson, Director, PCSP, for his continued support of our caribou studies. We thank Dr. E. Broughton, Agriculture Canada, for performing necropsies on the dead calves, and Drs. M. W. Barrett, Alberta Environment; J. P. Kelsall, Delta, B. C.; W. O. Pruitt, Jr., University of Manitoba; and D. C. Thomas, CWS; for critically reading earlier versions of the manuscript.

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Bone marrow and kidney fat as indicators of condition in reindeer

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Abstract: Back-fat depth, kidney-fat index (KFI), fat and triglyceride contents in femur and metatarsal marrows were measured from 92 semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) in northern Finland during 1980-84. The age of the reindeer varied from 5 months to 10 years and marrow fat content was estimated by five different methods: standard ether extraction, oven-drying (Neiland, 1970), reagent-dry assay (Verme and Holland, 1973), compression method (Greer, 1968) and visual estimation (Cheatum, 1949). The kidney-fat index (Riney, 1955) was significantly related (r=0.892) to the percent marrow fat in femur and metatarsus. The oven-drying method gave high correlations with results obtained by ether extraction and reagent-dry methods. Oven-drying produced a lower mean dry-weight value than reagent-drying (1.31±0.36%). The amount of compression had a concave relationship with the ether-extractable fat content of femur and metatarsal marrows. The subjectiveness of the visual estimation technique limited its use. Femur marrow fat contents (dry-weight %) in reindeer which died from starvation varied between 2 - 8%. Metatarsal fat contents were slightly higher. Adult males had a mean triglyceride content of 46.8 µmol/g in August in the femur. Adult females had slightly lower values. The amount of triglycerides was significantly related to the ether-extractable fat content of the femur (r=0.914) and metatarsal (r=0.911).

Key words: reindeer, fat, marrow, kidney, condition, Finland

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Rangifer, Special Issue No. 1, 1986: 219 - 226

Introduction

Good condition of reindeer (genus *Rangifer*) in autumn is very important to winter survival and optimal reproduction (e.g. Reimers, 1982; Larsen, 1985). Physical condition, physiological condition, and simply «condition» are, however, ambiguous concepts that frequently refer to the general state of health of animals, apparently inferred from their relative fatness (Anderson, 1981). According to LeResche *et al.* (1974) the nutritional status of individual wild animals can be determined grossly or finely and also acutely or chronically. All body tissues reflect nutritional status to a greater or lesser extent. Some indices are more sensitive than others, and some are also more easily obtained than others. No one index can give all the answers, and therefore, several indices are generaly used.

Storage of fat in the strategy of arctic survival is a general principle of vital importance to the Spitsbergen reindeer (*R. t. platyrhyncus*) (Krog *et al.*, 1976; Reimers *et al.*, 1982). The body condition of animals has been defined usually as levels of fat deposited in different parts of the body. Fat animals are not necessarily in good health, but animals with relatively high levels of fat usually also have adequate levels of other resources within the body. Fat is deposited first in bone marrow, than around the kidney, and finally subcutaneously.

Harris (1945) and Rausch (1950) described the depletion of fat deposits in starving deer. As the deer enter an energy deficient state during winter and spring, fat, protein and mineral reserves are gradually used. Fat reserves are generally utilized sequentially starting with the subcutaneous deposits, followed by the omental and mesenteric, kidney, heart and finally bone marrow fat (Random, 1965; Bear, 1971). As this happens the colour of the marrow changes from white to red and the marrow becomes gelatinous in consistency.

Fat content of bone marrow has long been related to the physiological condition of animals (Jackson, 1928), and several techniques have been used to determine the marrow fat levels in different *Cervidae*-species. Prior to 1970, procedures for determining marrow fat content usually consisted of either crude visual estimates based upon marrow colour and consistency, or extraction procedures which were relatively expensive and also time consuming. Neiland (1970) reported that percent fat in the marrow of barren-ground caribou (*R. t. granti*) was almost identical to percent oven-dry weight. The quick dry-weight method is today most commonly used to determine bone marrow fat content as an indication of the condition of ungulates.

Our purpose was to describe the quantitative relationship between the kidney-fat index and the amount of fat in femur and metatarsal marrows, and then to outline the methods for estimating energy reserves in reindeer. Marrow fat content was estimated by five different methods and comparisons were made.

Material and methods

Femurs and metatarsal bones were collected from the hind legs of 92 dead or killed semi-domesticated reindeer (*R. t. tarandus* L.) in northern Finland during different seasons in 1980-84. Age, sex, date dead/killed, anatomical measurements (back length, tarsal length and chest width, see Nieminen and Helle, 1980), and general condition were recorded for each animal. Reindeer ages were estimated by tooth wear and the pattern of eruption (Miller, 1974). The condition of the reindeer was classified into three groups: good (group I), fair (group II) and poor (group III), according to measurements and organ fats (Suomus *et al.*, 1975).

Back-fat depth was measured and kidney and perirenal fat deposits were removed and weighed to the nearest 0.1 g following Riney (1955). The index for each animal was calculated using the fat from both kidneys in order to minimize variation.

The femurs and metatarsal bones were removed and frozen (—20°C) in polythene bags until determined. Storage period ranged from 1 to 4 months. Samples of marrow for analysis were taken from the central portions of the bones after noting evidence of dehydration. Then samples were visually classified into four different groups (Cheatum, 1949).

A 60 mm section of marrow was removed from mid-way along each bone and marrow fat determinations were done by compression (Greer, 1968), oven-drying (Neiland, 1970), and reagent-drying (Verme and Holland, 1973) methods.

Bone marrow triglyceride content was determined fully enzymatically (Boehringer GmbH, Mannheim). About 5 - 10 g sample of fresh bone marrow was extracted with di-isoprophylether and n-buthanol (6:4). The solvent was washed and evaporated with methanol. The fat residue was then soluted in 6% albumine and determined. All marrow and fat values were placed in age cohorts: calves (5 - 12 months), yearlings (13 - 24 months), and adults (>36 months).

Results

Back-fat was the only deposit to disappear in most reindeer during winter. The trend in mean thickness of back-fat with age and season is shown in Fig. 1 and Table 1. During the first 2 years of life, males and females accumulated little back-fat except in late summer and early autumn. In males 3 years and older, however, substantial accumulations of back-fat were also present in

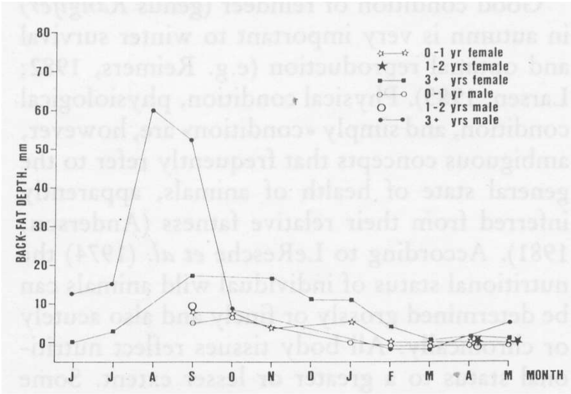

Fig. 1. Seasonal variation in mean back-fat depth in relation to age in male and female reindeer.

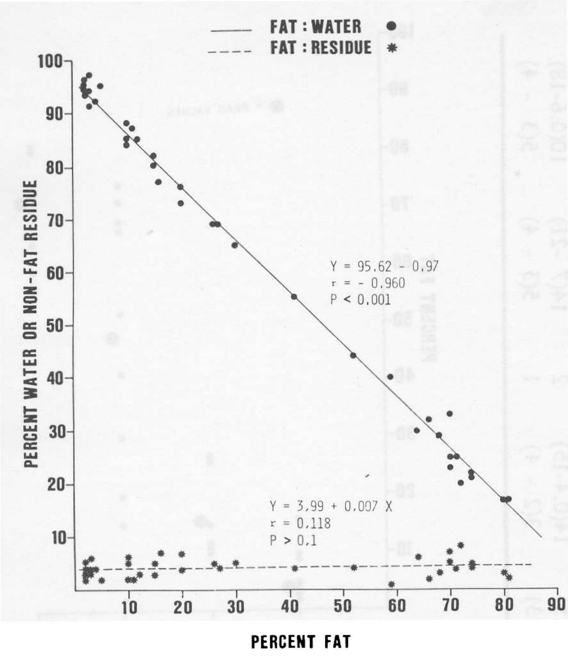

Fig. 2. The relationships between fat and water, and between fat and non-fat residue in reindeer femur marrows. Percent water determined by oven-drying; percent fat determined by ether extraction.

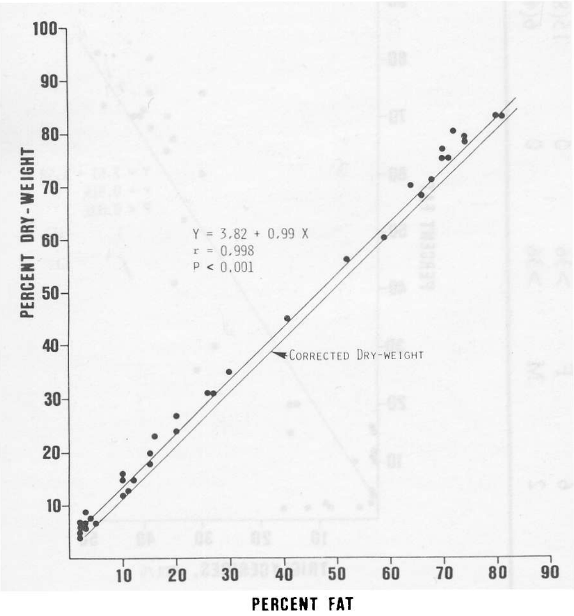

Fig. 3. Comparison of dry-weight, corrected dry-weight, and fat content of reindeer femur marrows. Dry-weight corrections determined from Fig. 2 and calculated according to method by Neiland (1970).

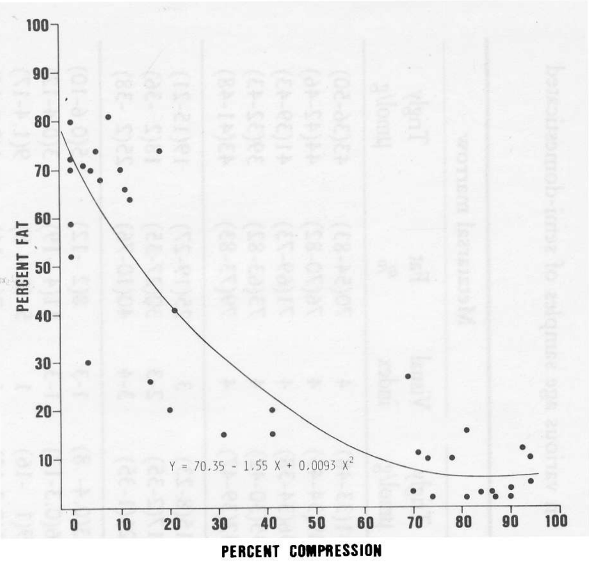

Fig. 4. The relationship between fat content and compression in reindeer femur marrows. Percent fat determined by ether extraction.

spring and summer. Adult males had a mean back-fat thickness of 56.0 mm (range 18.3 - 68.0 mm, n=5) during autumn. In September - November the mean thickness of the back-fat depth in females (17.2 mm) was about one-third that of males. The greatest individual back-fat depth in a female (34.0 mm) was half the largest measurement recorded among adult males.

Kidney-fat was present in all reindeer. The amount of kidney-fat varied with the season in males and females of all ages. A significant increase in the mean kidney-fat index occurred during autumn in the calves and adult males. The female kidney-fat index peaked in late autumn and early winter and gradually declined during winter.

Percentage femur and metatarsal marrow fats had less variation with age and season than other fat deposits. Fat was present in the marrow, especially in the metatarsal marrow of all reindeer regardless of age and season, ranging from 2% to 83%. In adult females marrow fat content had almost the same seasonal variation as did kidney and subcutaneous fat deposits. Values were high in October - January, and gradually declined during late winter and spring.

Ether extraction following oven-drying enabled definition of inversely linear relationships of fat to water in reindeer femur (r=—0.960) and metatarsal marrows (r=—0.999) (Fig. 2). 8 marrows (4 femur, 4 metatarsal) frozen 4 months

Table 1. The condition, back-fat depth (mean and range), kidney-fat index and fat and triglyceride contents in various age samples of semi-domesticated reindeer, F=female, M=male.

							Femur marrow			Metatarsal marrow		
Condition	Group	N	Sex	Age months	Back-fat depth mm	Kidney-fat index	Visual index	Fat %	Trigly µmol/g	Visual index	Fat %	Trigly µmol/g
Good	I	7	F	5-12	6.7(4 - 8)	49(46-52)	3-4	68(52-81)	41(33-48)	4	70(54-83)	43(36-50)
		7	M	5-12	6.0(5 - 7)	54(43-64)	3-4	71(68-74)	39(34-43)	4	76(70-82)	44(42-46)
		2	M	13-24	9.0(6 -12)	68(66-70)	4	70(68-72)	36(34-38)	4	71(69-73)	41(39-43)
		10	F	>36	14(11-18)	48(19-62)	3-4	67(59-74)	35(30-42)	4	73(63-82)	39(32-43)
		10	M	>36	42(15-68)	66(60-71)	3-4	74(70-80)	42(39-47)	4	79(73-83)	43(41-48)
Fair	II	3	F	5-12	5(2-8)	15(8 -21)	3	20(15-26)	15(8-23)	3	25(19-27)	19(15-21)
		5	F	>36	3(2-9)	31(20-50)	2-3	29(20-41)	17(2-35)	2-3	30(27-35)	18(2 -36)
		4	M	>36	4(0-8)	29(15-56)	2-3	36(11-66)	21(1-35)	3-4	40(10-76)	25(2 -38)
Poor	III	12	F	5-12	0	11(8 -14)	1-2	5(2 -10)	3(0.4- 8)	1-3	8(2 -12)	5(0.6-10)
		15	M	5-12	0	4(3 - 5)	1-3	10(2 -16)	6(0.3-12)	1-3	11(4 -19)	3(0.4-12)
		4	F	13-24	0	17(10-24)	1	3(2 - 5)	9(1 -16)	1	5 (2 - 8)	9(1.4-17)
		5	M	13-24	0	4(3 - 5)	1	6(2 -10)	6(0.3-12)	1	7(4 -11)	6(0.4-12)
		6	F	>36	0	15(8 -24)	1-2	10(3 -15)	14(0.4-15)	2	14(7 -21)	10(0.6-18)
		2	M	>36	0	6(4 - 9)	1	2(1 - 3)	3(2 - 4)	1	5(3 - 4)	5(3 - 4)

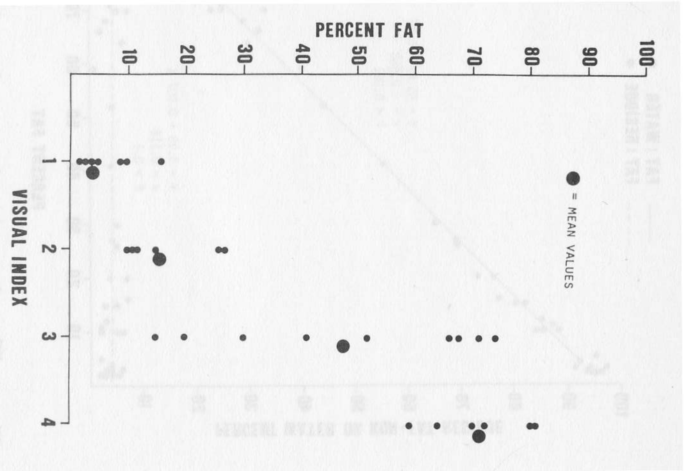

Fig. 5. Comparison of ether extraction and visual assessment method of reindeer femur fat estimation.

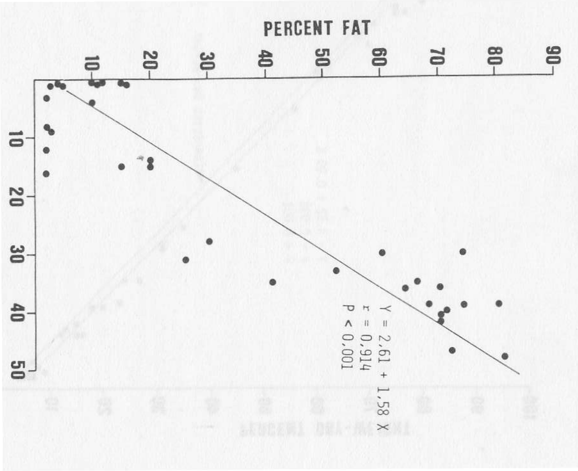

Fig. 6. The relationship between fat content and triglyceride content in reindeer femur marrow. Percent fat determined by ether extraction; triglycerides determined fully enzymatically.

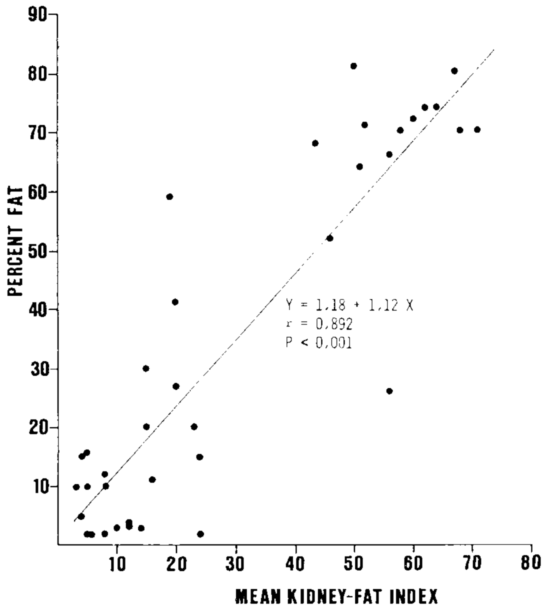

Fig. 7. The relationship between femoral fat content and the kidney-fat index in reindeer. Percent fat determined by ether extraction.

before chemical analysis gave 3±2% higher fat content than a fresh sample. However, the amount of non-fat residue in the marrows would be the prime source of error in dry-weight determinations of marrow fat content. Closer approximation of the fat value using the oven-dry method can be calculated by subtracting a correction factor for the non-fat residue (see Neiland, 1970). Fig. 3 shows the relationships of fat content to dry-weight and corrected dry-weight in the femur. Graphs of residue vs. dry-weight for the oven-dry and reagent-dry methods were very similar. Oven-drying produced, however, a lower mean dry-weight value than reagent-drying (1.3±0.36%). Dry-weight values for the femur and metatarsal marrow samples determined by oven-dry and reagent-dry methods were highly correlated with ether extractable content (r=0.998; r=0.998; r=0.989; r=0.990, respectively).

The comparison of the compression and extraction methods of assessing marrow fats are shown in Fig. 4. The amount of compression had concave relationships with the ether-extractable fat content of femur and metatarsal marrows. The amount of overlap observed between fat values for samples allocated to different visual index grades was also significant. The subjectiveness of this visual estimation technique limited its use (Fig. 5).

The amount of marrow fat triglycerides varied with the season in males and females of all ages. A significant increase in the mean triglyceride values occurred during autumn. Adult males had a mean triglyceride content of 46.8 µmol/g in August and 40.8 µmol/g in September in femur marrow samples. Adult females had slightly lower values (mean 30.4 µmol/g in September). Very low triglyceride values were found during winter and spring in femur and metatarsal marrows. The amount of triglycerides was significantly related to the ether-extractable fat content of the femur (r=0.914, Fig. 6) and metatarsus (r=0.911).

Percentage marrow fat is plotted against kidney-fat index in Fig. 7. Percent marrow fat in femur and metatarsus was significantly correlated with the kidney-fat index (r=0.892 and r=0.887, respectively).

Discussion

Riney (1955) in reference to ruminants stated that «fat can be taken as a direct measure of the condition reflecting the metabolic level or goodness of physiologic adjustment of an animal to its environment». Measurements of fat deposits have been widely used as indices of energy reserves and general nutritional condition in cervids. Growing attention has been also focused on the importance of fat reserves for winter survival of many cervids (see Gasaway and Coady, 1974). Mautz (1978) refers to northern living cervids as semihibernators. According to Franzmann *et al.* (1978) Alaskan moose (*Alces alces*) lost 30% of their body weight from early winter to late spring. It is estimated that 75 - 80% of such a weight loss may be from fat stores, wherein each gram of fat contributes 38.9 kJ (Gasaway and Coady, 1974). The caloric content of body fat in white-tailed deer (*Odocoileus virginianus*) is estimated by Robbins *et al.* (1974) as 9.49 kilocalories (39.7 kJ) per gram.

The ability to store large amount of fat is a common feature among all arctic mammals, and according to Ringberg *et al.* (1980) the Svalbard reindeer are unique in this regard. The calves are born smaller than are other *Rangifer* subspecies. No subcutaneous or perivisceral white fat is found in newborn calves, but during autumn dissectable body fat of Svalbard reindeer makes up 14 - 17% of the total body weight among calves and yearlings and 20 - 22% among the adults (Reimers, 1982). Maximum body fat concentration in the Svalbard reindeer (28.7 - 40.1%, Reimers *et al.*, 1982) is higher than in semi-domesticated reindeer and also higher than reported for other cervid species: less than 20% in white-tailed deer (Robbins *et al.*, 1974) and less than 11% in roe deer (*Capreolus capreolus*) (Weiner, 1973).

In Svalbard reindeer maximum average back-fat depths in males and females do not exceed 83 and 48 mm, respectively (Reimers *et al.*, 1982). The back-fat depths of calves and yearlings are 30.1 - 38.3 mm, which are 5 - 6 times greater than found in Finnish reindeer (Table 1) and also in Kaminuriak caribou (*R. t. groenlandicus*) of the same age (Dauphine, 1976). Upper extreme values on adult males range from 51 - 76 mm on Alaskan reindeer (Palmer, 1934), 75 mm on Swedish reindeer (Jacobi, 1933), 68 mm on Finnish reindeer (Table 1), 40 mm among Kaminuriak caribou (Dauphine, 1976), 71 mm on caribou on Coats Island, N.W.T. (Parker, 1975), 80 mm on wild reindeer in the U.S.S.R. (Shaposnikov, 1955) and 50 mm on wild reindeer in southern Norway (Reimers, 1982). Compared with semi-domestic reindeer wild forest reindeer (*R. t. fennicus*, Lönnb.) in Finland had very little body fat (Nieminen and Helle, 1980).

Fat content of the carcass varies considerably with sex and season in the genus *Rangifer.* Before the rut average back-fat depth in the Svalbard reindeer males is measured at 83 mm, which corresponds to a total dissectable fat weight of 24 kg or 22% of the total body weight (Reimers, 1982). McEwan (1968) reported accumulation of about 20 kg fat in a large male caribou at the end of the summer growth period. According to Spiess (1979), a 110 kg caribou stag killed in late September had about 22 kg (20% of the body weight) fat and 50 kg (55%) meat. This animal provided 198 000 kcal (828 828 kJ) or 66 man-days (3000 kcal/man-day) worth of fat-supplied calories. The femur, tibia, humerus, radius and metabodial bones of a 2-year-old, July-killed male caribou yielded about 520 g of fat from the marrow. An 80 kg female killed in December has a theoretic 10% fat content (8 kg) and 40 kg of meat. This female represents about 34 man-days of food, more than twice what a 90 kg stag killed at the same time represents.

Øritsland (1970) estimated the total body fat as being 15 kg (14.3% of the body weight) in a male Spitsbergen reindeer killed in August. According to Kleiber's (1961) formula m (basal metabolism)=$70W^{0.75}$, this could last for 60 days at basal metabolic level and thermal neutrality. Counting seven months from October through April this would be able to supply about 30% of the basic demand for energy from fat storage during winter (Krog *et al.*, 1976). Compared to pre-rut weights in August adult male body weights were decreased, however, 24% by mid October, the most active rutting period (Reimers, 1982). Franzmann *et al.* (1978) also reported a loss of over 10% for Alaskan moose during the rut, whereas McMillan *et al.* (1980) showed 15 - 20% during the rut of white-tailed deer. By the end of winter, the fat reserves of young reindeer are almost totally depleted (see Table 1), while most surviving adults still have a few kilograms left. According to Krog *et al.* (1976) at the end of March the fat content may be at least 2 kg, of which about 500 g is located around the kidneys.

Bone marrow fat is the last reserve to be mobilized, and its level reflects condition only at the lower end of an overall animal condition (e.g. Riney, 1955; Dauphine, 1976). Thus, the use of marrow fat is dependent upon the initial level of other fat reserves and also the degree and duration of nutritional stress. Bischoff (1954) found that the percentage of femur marrow fat was not well correlated with other fat deposits or femur marrow colour but was strongly correlated with the visual estimate of marrow consistency. Femurs have, however, usually been used for fat content determination in ungulates.

According to Dauphine (1976) the mobilization of deposit fat in caribou of both sexes occur in the sequence back-fat, kidney-fat, abdominal fat, and marrow fat. The exhaustion of the back-fat, and the first use of the marrow fat, coincides with the cessation of the decline on body weight and with a 50% decline in the two visceral fat indices. Ransom (1965) reported that marrow fat in white-tailed deer was mobilized only when kidney-fat had declined to ca. 30% of kidney weight. Cheatum (1949) believed, however, that the health of adult white-tailed deer was not affected until the fat content of the marrow dropped below 25%.

Klein (1968) found no marrow fat in the medullae of long bones from starved reindeer and took that as evidence that all fat was absent from the marrow at the time of death. Femur marrow fat contents (dry-weight %) in reindeer dead from starvation in the present study varied between 2 - 8%. Metatarsal fat contents were slightly higher. Neiland (1970) reported levels as low as 5% in caribou shot in Alaska. The lowest femur marrow fat value recorded from suspected winter kills was 6.1% for Alaskan moose calves and 5.5% for adults (Franzmann and Arneson, 1976).

Cheatum (1949) reported that fat is mobilized from proximal leg bones in deer after other body fat deposits have been exhausted. Bischoff (1954) found, however, no correlation between fat levels in the femur and tibia in mule deer. (*O. hemionus*). In accordance with the present results Peterson *et al.* (1982) reported that fat mobilization was first evident in the limbs of moose in the femur and humerus, then the tibia and metatarsus, and finally the radius and metacarpus.

Many studies indicate that femur marrow could be fat-depleted and the animal dead from malnutrition with the distal bones still containing considerable fat. Cheatum (1949) suggested that fat mobilization might be more advanced in proximal bones because they are closer to the body core and warmer in winter. It seems also reasonable to expect reduced circulation within capillary networks and retarded metabolic processes in colder extremities.

Since its introduction by Riney (1955) the kidney-fat index (KFI) perhaps has been the most widely measure of cervid carcass fat. KFI correlate adequately with percentage of femur marrow fat, carcass density and weight, and depth of rump fat in mule deer (Anderson, 1981). In agreement with present results the measure of kidney-fat is, however, highly variable and consequently requires a large sample. In addition, the KFI — based on one kidney — is not very comparable to indexes using both kidneys. The required number of mature mule deer ranged by season from 88 (winter) to 221 (summer) for males and 114 (winter) to 532 (summer) for females (Anderson *et al.*, 1972). The required number of mature deer (to provide an estimate of depth of back-fat within 10% of the true mean at the 95% confidence level) ranged from 381 (summer) to 2595 (spring) for males and 383 (winter) to 2192 (summer) for females.

The choice of a suitable index of relative fatness may be influenced much by sex, time and manpower available, physical facilities and constraints on collecting procedures. Thus, for female mule deer eviscerated carcass weight may be the best choice, but this may not necessarily be so for males (Anderson, 1981). Both the kidney-fat index and femur and metatarsal marrow fats may be useful in combination for reindeer. When using the bone marrow, caution must be used because in younger animals erythropoiesis may still be occurring in the femur, and the marrow would be red in colour. Present results indicate that the oven-dry method is nearly as convenient as visual and compression methods and as accurate as standard ether extraction.

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Acknowledgements

We thank Dr. A. W. Franzmann and Dr. I. Adamczewski for constructive critisism of the manuscript.

«Pepper's patches» on *Rangifer* pelage

William O. Pruitt, Jr.[1] and **Hubert Pepper**[2,3]

Abstract: We describe and give frequencies of occurrence of a rarely-mentioned pattern of spots in *Rangifer* pelage. We also show that the pattern was well-known to Palaeolithic humans who recorded it in their cave art. We also discuss some of the symbolic possibilities resulting from the recognition by Palaeolithic humans of the biological characteristics of the pattern in *Rangifer.*

Key words: *Rangifer,* caribou, reindeer, pelage, spots, Palaeolithic art.

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Rangifer, Special Issue No. 1, 1986: 227 - 234

Introduction

Virtually all descriptions of coat colour in *Rangifer* fail to mention a series of light-coloured patches or short vertical stripes that occur on the dorso-lateral or lateral surface of the thorax and lumbar regions and as irregular blotches on the upper lateral surface of the rump or hip region (Figs. 1, 2). These are not patches of worn pelage, breaks in the pelage over individual ribs, nor lumps and discoloured fur caused by subcutaneous warble larvae or their scars. These «Pepper's patches» consist of longer, stiffer hairs, sometimes twisted and of a lighter colour than the surrounding fur, from which they are sharply differentiated (Fig. 1a, b). Further studies are proceeding on the histological structure of the skin and hairs.

The earliest printed reference to these patches we can find is a woodcut in Caton (1877: 88) of a young female North American Woodland Caribou (*Rangifer tarandus caribou*). Flerov (1952) mentioned that: «...along the upper part of the trunk a pattern is sometimes developed in the form of 3 - 4 rows of poorly marked light reddish-brown spots, which are lighter in the pelvic region and large, of a diameter twice the length of the eye» (p. 204). Geptner *et al.* (1961 volume 1: 307) stated: «... on the spine there is sometimes a dark stripe. By way of an exception (apparently frequently in Southern Siberia) along the spine there are not rarely outlined and weakly expressed rather large light-coloured spots....» Segal' (1962) mentioned «Inconspicuous... and vertical stripes in body colouring («tiger-like») which is peculiar to most Lappish reindeer (*Rangifer tarandus tarandus)* and is often apparent locally in Karelian domestic reindeer.»

They are shown in a photograph of a caribou museum display (Nowak and Paradiso, 1983: 1223), but are not mentioned by Akaevski (1939), Banfield (1961, 1974), Hall (1982), nor Sokolov and Chernyavaskii (1962).

To our knowledge the patches occur in the following Recent subspecies:

Rangifer tarandus tarandus (dom.) Figs. 1a, b. Because the patterned skins are valued by Saami the frequency in domestic reindeer may be greater than in wild groups. Illustrated in

Huhtanen (1970: 86, 93, 104 - 105) and Alaruikka (1964: 66). The patches are well-known to reindeer herders. The Saami name is «tjoesche» (Swedish Lapp) or «jovje» (Southern Swedish Lapp; John Jonassen, pers. comm).

Rangifer tarandus fennicus - Illustrated in Montonen (1974: 27, 63). From field counts by WP the patches occur in about 20% of the females in this subspecies. Fig 3.

Rangifer tarandus platyrhynchus - C. Cuyler (pers. comm. 1986) recently examined 40 + skins of this subspecies for us and found no Pepper's patches.

Rangifer tarandus terraenovae - Illustrated in Dugmore (1913: plates facing: 2, 12, 50, 106 and 158).

Rangifer tarandus groenlandicus - «Caribou Year» the filmed life-history by WP contains images of 1459 individuals, of which 220 are suitable for detailed visual analysis. Of this number, 5 (2 ♂, 3 ♀) or about 2.3%, exhibit Peppers patches.

David Koamayok of Cambridge Bay, NWT, reported to A. Gunn (pers. comm., 1986) that caribou with Pepper's patches ocur very rarely on Victoria Island. The skins were valued for clothing decoration.

Rangifer tarandus granti - Illustrated in Calef (1981: 56, 63, 111 and 147) but not mentioned in the text. «Caribou Year» also contains images of 79 *granti*, of which 16 are suitable for analysis. Only one (6%) exhibits Pepper's patches.

Rangifer tarandus caribou - See Fig. 4. Illustrated in Caton (1877) (see above). We believe it is significant that a similar woodcut of Barren ground caribou on p. 104 fails to show the patches. No mention is made in Caton's text.

Rangifer tarandus pearyi - occurrence not documented by us.

Discussion

Most known occurrences of Pepper's patches are in females and young. Individuals with the patches exhibit them in successive pelages (John Jonassen, pers. comm.). We suspect the reason the patches are rare among males is that their pelage is markedly modified from the basic pattern because of the importance of rutting behaviour (cf. Fig. 3). The patches appear to be more common in domestic reindeer than in wild caribou and, among caribou, to be more common in forest forms than in tundra forms.

In the *Cervidae* spotting occurs commonly as the spotted pelage in young of several genera and the spotted pelage of adults in, for example, *Cervus nippon* as well as *Axis* and *Dama*. Pelage characteristics of earlier times are usually speculative and rarely subject to proof. So it would be with Pepper's patches but for the fortunate natural history acuity of a relatively restricted population of early *Homo sapiens*, and for their probable cultural attention to them.

Fossil occurrence

These fossil representations of Pepper's patches are from the Upper Palaeolithic of France and Spain, about 19 000 to 10 000 years B.P.

The Abbé Henri Breuil, a prehistorian, noticed the marks when he drew an imaginary scene for his book «Beyond the Bounds of History» (1949: 78). His illustration shows «an artist of the time... finishing the painting of a

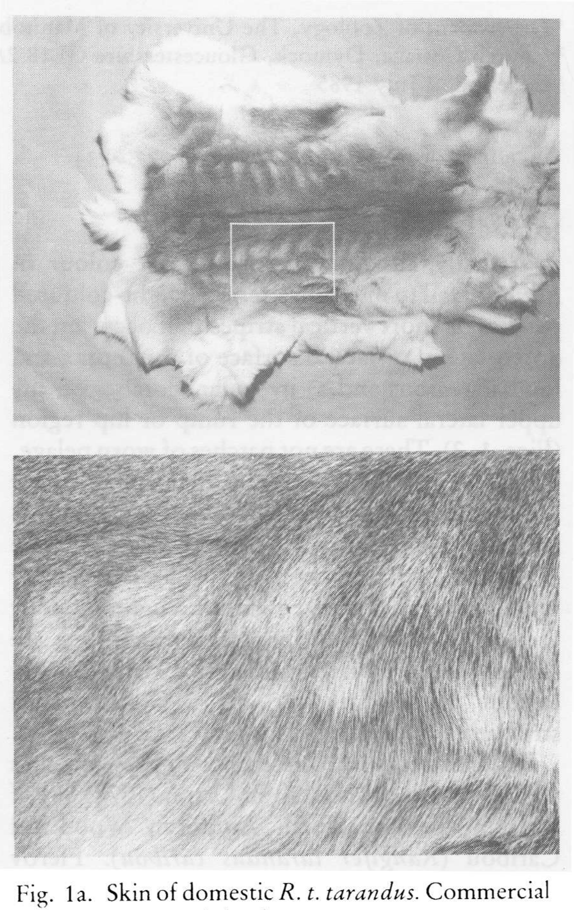


Fig. 1a. Skin of domestic *R. t. tarandus*. Commercial source, Finland.
b. Detail of a.

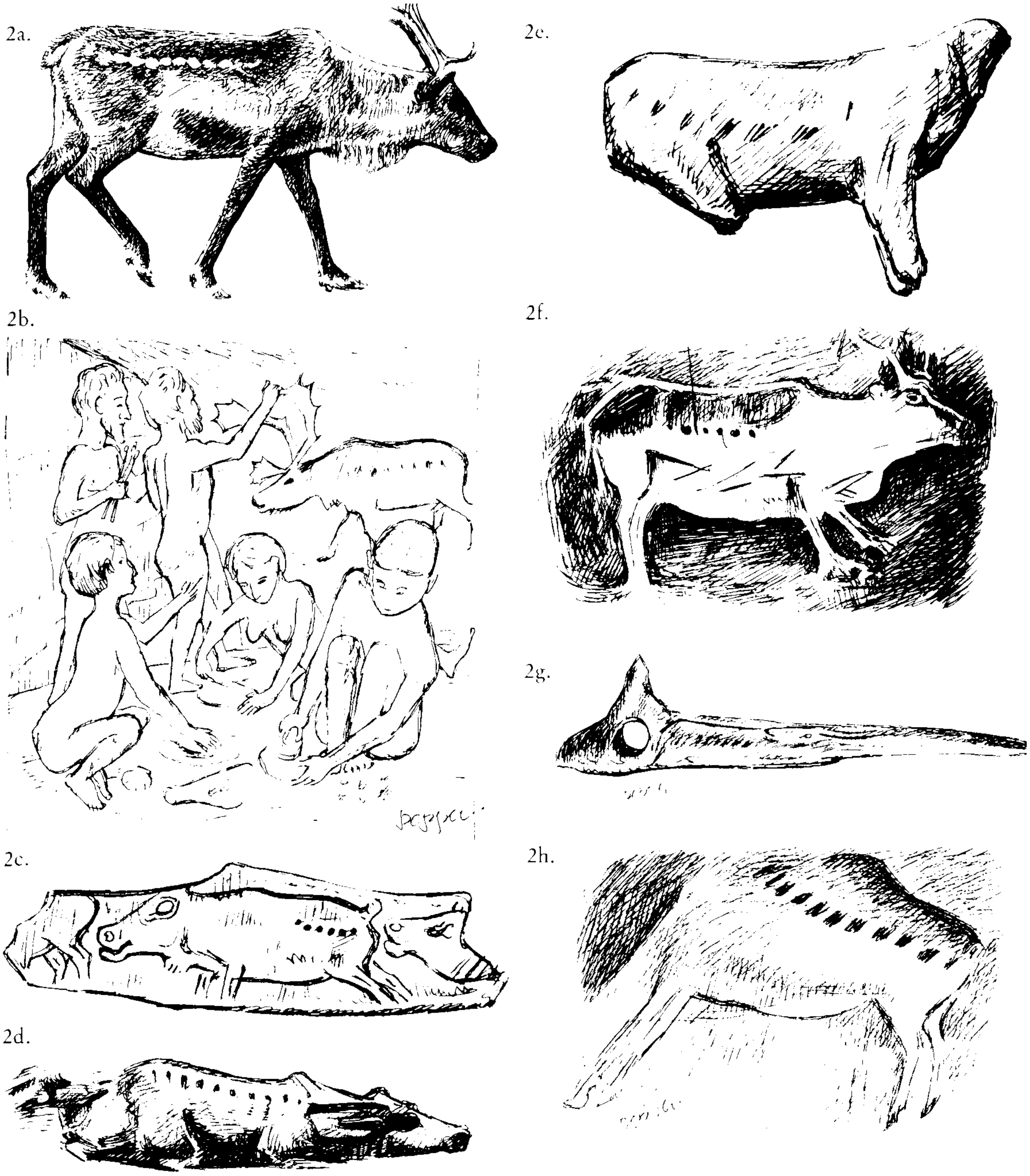


Fig. 2a. *R. t. tarandus.* ♀. Whipsnade Zoo. Sketch by H. P., 1982.
b. «Grinding ochre and painting frescoes on rock». Redrawn by H. P. from Breuil (1949: 78)
c. Reindeer engraved on bone, Massat; Ariège, France. Musée Ste. Germaine, Paris. Sketch by H.P.
d. Reindeer sculptured in ivory; Bruniquel. British Museum, London. Redrawn by H.P. from Graziosi (1960: 34a).
e. Reindeer carved on antler spear-thrower; Arudy. Musée Ste. Germaine, Paris. Redrawn by H.P. from Graziosi (1960: 36c).
f. Rock wall painting; Les Trois Frères, near Montesguion, Arantés, Ariège, France. Redrawn by H.P. from Leroi-Gourhan (1968: 116).
g. Female reindeer on «baton de commandment»; Laugerie Basse. Redrawn by H.P. from Graziosi (1960: 56b)
h. «Spotted Reindeer»; La Mouthe. Redrawn by H.P. from Breuil (1952: 400).

reindeer, executed on a rock wall.» (Fig. 2b). Judging by the large antlers borne by the animal, the Abbé probably intended to show an adult male. He also marked a line of «patches» which, (as his recollection might have suggested), occur on examples of reindeer from La Mouthe (Dordogne: Fig. 2b). The «La Mouthe» drawings by the Abbé figure as interpretations in Fig. 343 and photograph (Fig. 347) in his book «Four Hundred Centuries of Cave Art» (1952) where the reindeer are called «spotted». There is no explanation for the marks in either book.

Sieveking (1976, 1979) mentioned them from both Bruniquel (Tarn-et-Garonne) and Arudy (Pyrénées-Atlantiques) with the comment that «the depiction of the animals' coats is very similar.» She failed to mention the possibility that the pattern might be natural (Fig. 2e). Guthrie (1984) did not mention Pepper's patches in his chapter «Ethological observations from Palaeolithic Art».

In apparent contrast to recent students of Palaeolithic art the actual prehistoric artists knew reindeer well. They were observant enough to select females for patchy coat patterning. An example from Massat (Ariège), (Graziosi 1960: plate 71b) shows a female reindeer with patches (no antlers, no penile tuft shown) in typical urinating posture (in oestrus, perhaps) and an attentive animal (male?) immediately behind (Fig. 2c). The rutting theme is continued in the famous piece from Bruniquel (Tarn-et-Garonne) where a male follows a female, nose to rump, (Graziosi, 1960: plate 34a and b); here the marks are clearly depicted only on the sides of the female. Graziosi has illustrated both sides of the ivory carving with an extra explanation in the form of a drawing by Breuil of one view (1905) as 34b on his plate (Fig. 2d). A relief carved on antler from Mas d'Azil (Ariège) (Graziosi, 1960: plate 56b) might be a female reindeer judging by the weak antler form (Fig. 2g). This may be true also for the animal with patches (Leroi-Gourhan, 1968: Fig. 11; this paper, Fig. 2f). On the other hand, Las Monedas (Santander), a Spanish cave exhibiting reindeer, shows a female without patches (Leroi-Gourhan, 1968: plate 115). Could the patches sometimes have been used by the artists to indicate *femaleness?*

In support of this idea it is worth taking another look at the painted reindeer from the «sanctuary» of Les Trois Frères (Fig. 2f). (Breuil, 1952: Fig. 134). Breuil described 14 reindeer, only one of which is a male, with penile tuft.

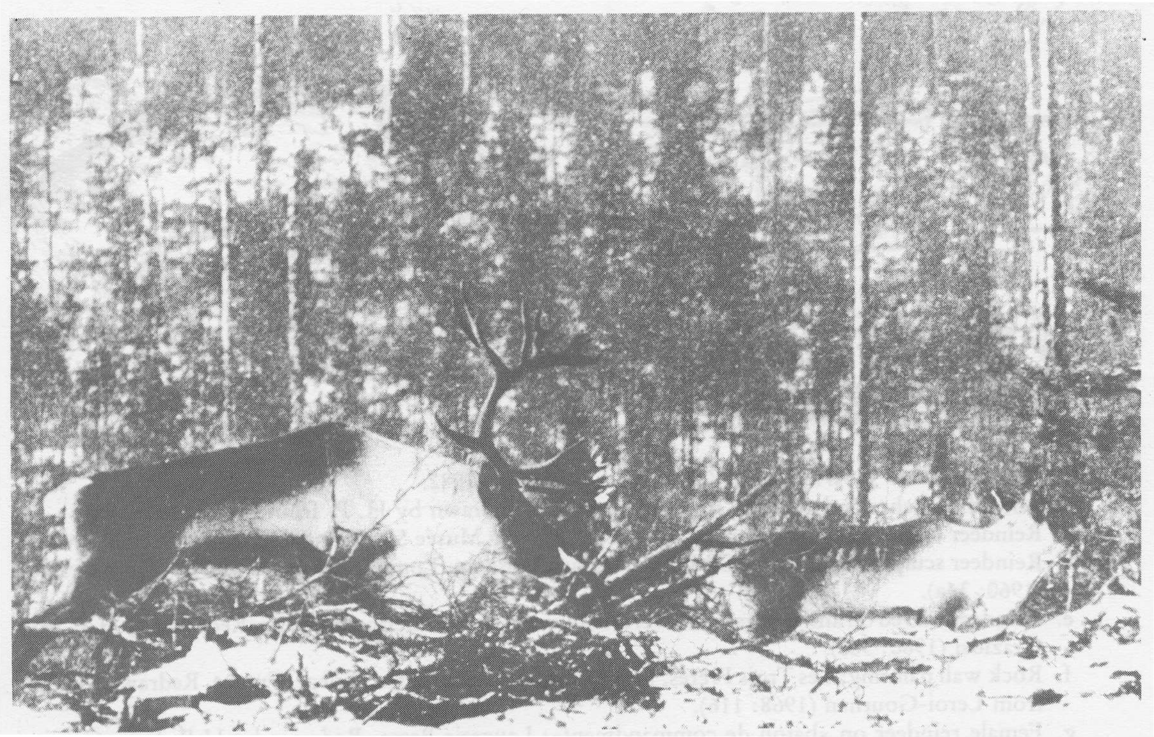


Fig. 3. *R. t. fennicus* ♂and ♀; Finland, Kainuu region, Saksenlampi, 13 October 1973. Note the prominent Pepper's patches on the female. Photo by E. Vannanen.

Fig. 4. *R. t. caribou;* Ontario, 55°N. Lat., 81°15'W. Long, near Cape Henrietta Maria, March 1976. Individuals showing Pepper's patches are outlined. Photo by Fred Johnson.

Breuil (1952: Fig 139) has depicted from the same cave a mythical reindeer/monster as a female which also has patches (Fig. 5a). The monster from Lascaux (the «Unicorn») bears circular (female) patches on its side (Fig. 5b).

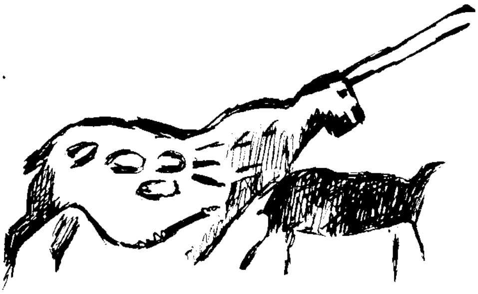
Speculations on cultural symbolism

The relationships of circle or dot/short stroke to animal forms in Palaeolithic artwork do not allow much room for elaborate interpretation. If the possibility of patches representing an atavistic survival is an acceptable natural explanation, they seem to have acquired a new significance for the Upper Palaeolithic artists who deliberately selected this feature for depiction. To see the light golden circles as solar/lunar female symbols might not be mere imagination. As the observer of a living female reindeer with patches finds the attention leads across the flank and rump to the area of the vulva, the eye-catching marks speak of magic, mystery and sex, of light and re-creation to someone looking for a sign.

A symbol is a sermon in shorthand. It is reasonable to find the message of the dots transferred to an animal of another species. At Lascaux, an Aurochs (*Bos primigenius*) bears a row of spots across the upper ribs behind the shoulder. This is closer, perhaps, to the area of the heart and lungs than the vulva (Fig. 5c). The same vulnerable area is also marked in an Aurochs cow from Niaux (Ariège) (Fig. 5d) shown in Breuil (1952: Fig. 161) and at first sight perhaps not comparable with the patches under review. In the case of a cow being closely followed by a bull from Teyjat (Dordogne) (Fig. 5e) a single circle has been placed on the neck of the cow (Leroi-Gourhan: Fig. 486). A circle is usually a feminine symbol, but Leroi-Gourhan pointed out (1968) that a row of dots (circles) may indicate a masculine sign. To see such a masculine row representing the phallus and incorporating in the circles the female sign naturally placed to lead the imagination from

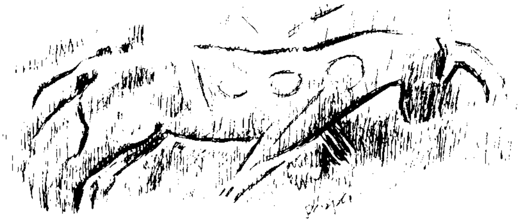
5a.

5b.

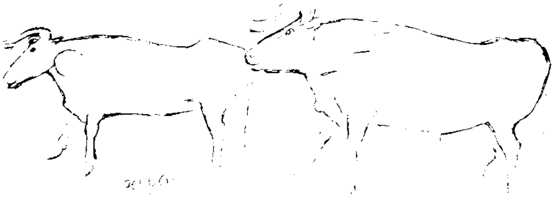


5c.

5d.



5e.



5f.

5g.

Fig. 5a. «Monster/reindeer»; Les Trois Frères. Redrawn by H.P. from Breuil (1952: 129).
b. «Unicorn»; Lascaux. Redrawn by H.P. from Leroi-Gourhan (1968).
c. Spotted aurochs cow (?) bearing a row of spots, and a bull; Lascaux. Redrawn by H.P. from Leroi-Gourhan (1968: 486).
d. Cow aurochs; Niaux. Redrawn by H.P. from Breuil (1952: 161).
e. Cow and bull aurochs; Teyjat. Redrawn by H.P. from Leroi-Gourhan (1968: 486).
f. Cow aurochs; Pech Merle. Redrawn by H.P. from Leroi-Gourhan (1982: 121).
g. Stag (Red Deer) with concentric rings and chevrons; Alaja Hüyük; northern Turkey. Turkish Historical Society. Redrawn by H.P. from Bibby (1962: pl. VIII).

vulva through the bodyline is to understand a purpose fulfilled by noting the marks (patches) on representations of female animals in the artwork. To add emphasis to the theme an example might be taken from the line drawing of an Aurochs cow from the Black Frieze, Pech-Merle (Leroi-Gourhan 1982: Figs. 102 and 121). Here, dots have given way to short, broken lines. Three pairs of lines are used to indicate the anal passage. Below, however, and extending from vulva to chest, are pairs of broken lines which may be seen as phallic (spear) from vulva (wound) to the heart and lungs. In a phrase, in fact - from «life» to «death» (Fig. 5f). In this sectioned cartoon are we to see a mimic of those natural patches, the illuminated line of femaleness which we are discussing in the case of female reindeer?

A post-script to the lateral line of dots might be found in the case of a red deer (*C. elaphus*) (male, self coloured as adult in life) from Alaja Hüyük in Northern Turkey (Bibby 1962: Fig. VIII). Created by «Battle-ax People» of the Russian Steppes over 4000 years BP, the stag, from a standard, bears seven pairs of rings along the body and rump (Fig. 5g). While body decorations of art objects have always been open to many designs and interpretations and the chevrons on the neck may represent an impression of the red deer stag adult mane, is it possible that the circles are a conventional design extending back to delineations of Pepper's patches on Palaeolithic reindeer and here continued as pattern long after the origin, source and purpose in decoration had been forgotten?

Acknowledgements

We are grateful to Dr. Tom Shay for his critical comments during the preparation of this paper. Reviewers Dr. C. R. Harington and Dr. D. Klein offered valuable comments and criticisms. We thank E. Vannanen and Fred Johnson for permission to use their photographs.

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The familiar area hypothesis and movement patterns of wild forest reindeer in Karelia, Northern Europe

E. Pulliainen[1], P. I. Danilov[2], K. Heikura[1], E. Erkinaro[1], S. Sulkava[1] and E. Lindgren[1].

Abstract: The relevance of the familiar area hypothesis to the behaviour of the wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.) was studied in a Fenno-Soviet project by radio and field tracking of these ungulates in Karelia, Northern Europe, in 1978 - 1985. This subpopulation (500 - 600 exx.) has a tradition of overwintering in a restricted area around Lake Lentua (ca. 1000 km^2). The spring migration period is shorter in length than the autumn migration. The migration routes are generally the same in autumn and spring, although exceptions occur, indicating exploratory behaviour. The large winter herds disband into small groups or lone individuals for the summertime, when this subpopulation is spread over a much wider area (ca. 5400 km^2). It is concluded that the observations made support the familiar area hypothesis in all essential points.

Key words: familiar area hypothesis, wild forest reindeer, radio-telemetry.

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Rangifer, Special Issue No. 1, 1986: 235 - 240

Introduction

The long-distance seasonal return migrations of the woodland-tundra transition demes of *Rangifer tarandus* are often easy to detect and follow (review in Kelsall, 1968; Baker, 1978), while the movements of the woodland demes of the species are much more difficult to study. The basic movement behaviour patterns of the woodland demes can be assumed to be similar to those of their woodland-tundra and tundra counterparts, but their potential summer and winter habitats are located so close together that the pattern of their use possesses special interest, especially in the light of the familiar area hypothesis of return migration put forward by Pulliainen (1974), Baker (1978, 1982) and Pulliainen *et al.* (1983). It states that an animal may spend part of its time on one part of its familiar area (suitable during that season) and part of its time in another part of its familiar area suitable during that season. Seasonal return migration system may develop between these two areas. The purpose of the present study is to document the migration patterns of the Kuhmo subpopulation of the wild forest reindeer (*Rangifer tarandus fennicus*) in Karelia, Northern Europe, and see, if they fit the familiar area hypothesis.

Material and methods

A census of the Kuhmo subpopulation was conducted by helicopter in March - early April 1981 - 1985, when the reindeer were in or near their traditional wintering area, Lake Lentua (Pulliainen *et al.*, 1983). The reindeer herds and lone individuals were also followed by walking, skiing or driving with a snowscooter in 1981 - 85, and with the aid of radio-telemetry since 8 April 1983 (230.975 MHz, Ari-Matti Luoma Ky, Oulunsalo, Finland). The reindeer caught (all females) with the aid of a trapping corral constituted a random sample of this subpopulation (500 - 600 individuals together). Conventional methods were used to locate the reindeer.

The mean operating radius of the equipment used was ca. 15 km and attempts were made to keep 10 radio transmitters working at a time. Four field technicians were involved in this task for 5 days a week throughout the year, except that recordings were made every day during the spring migration.

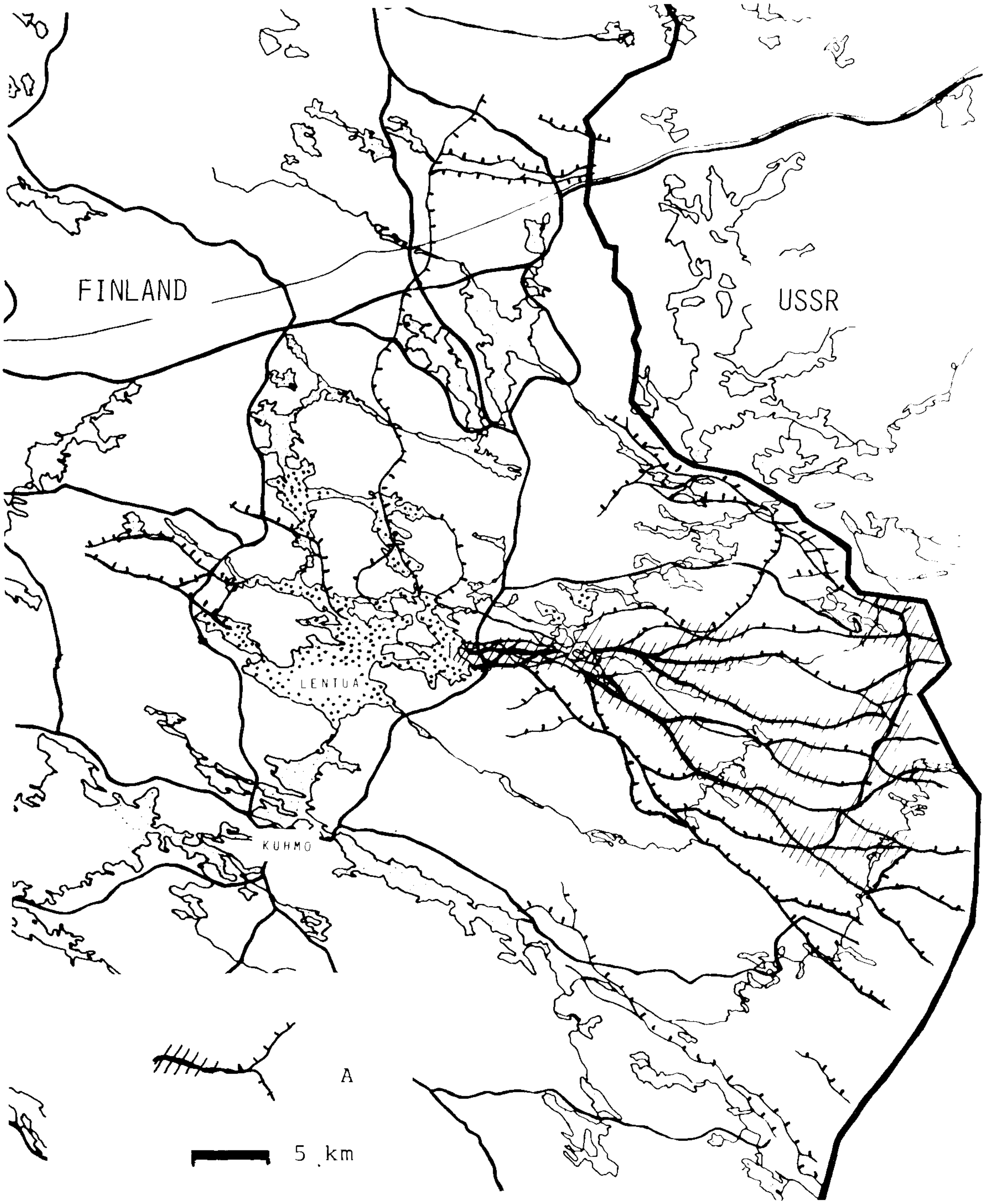

Fig. 1. Principal migration routes (A) of the wild forest reindeer of the Kuhmo subpopulation in eastern Finland in 1981 - 85. The main overwintering area is located around the Lake Lentua (stippled) and the main summer range along the border area between Finland and USSR.

Results

Radio-collared wild forest reindeer used previously documented migration routes during their spring and autumn migrations (Pulliainen *et al.*, 1983) (Fig. 1). Reindeer No. 443 represents a typical case as far as the pattern and timing of its movements are concerned (Fig. 2). However, not all individuals used the same traditional migration routes. Exploratory behaviour does occur, and reindeer No. 442 shows such a behaviour pattern in Fig. 3. The reindeer tend to choose routes along which it is easy to move (e.g., eskers, dry heaths and icy surface of bogs).

The first signs of the commencement of the spring return migration from Lake Lentua, the main overwintering area, are observed at the beginning of April, and the last migratory individuals have left this lake area by the end of the month. The early starters move at a much slower speed than the late ones (Fig. 4). The spring return migration progresses step by step, being characterized by short stops.

In spring 1984, for instance, the first period of return migration lasted about 20 days (2 - 5 April to 24 - 26 April), and this was followed by a short «stop» (30 April to 3 May), after which migration continued. The reindeer appeared in their summer range around 7 May, finally settling in that area in mid-May.

The summer home range may consist of several «parts», but is usually one fairly uniform area, varying in size between 15 and 200 km^2 (mean±S.E. 103±16). The reindeer appear to use the different parts of their summer home range fairly uniformly. The smallest home range (15 km^2) belonged to a wounded animal.

The summer groups vary in both composition and size, the largest recorded being 13 individuals (Fig. 5). As the rut approaches (in mid-September), the groups become larger and movement increases (Fig. 5). Rut was over on 27 October. The autumn return migration commences towards the end of the rut or immediately after it, the first returning reindeer appearing at

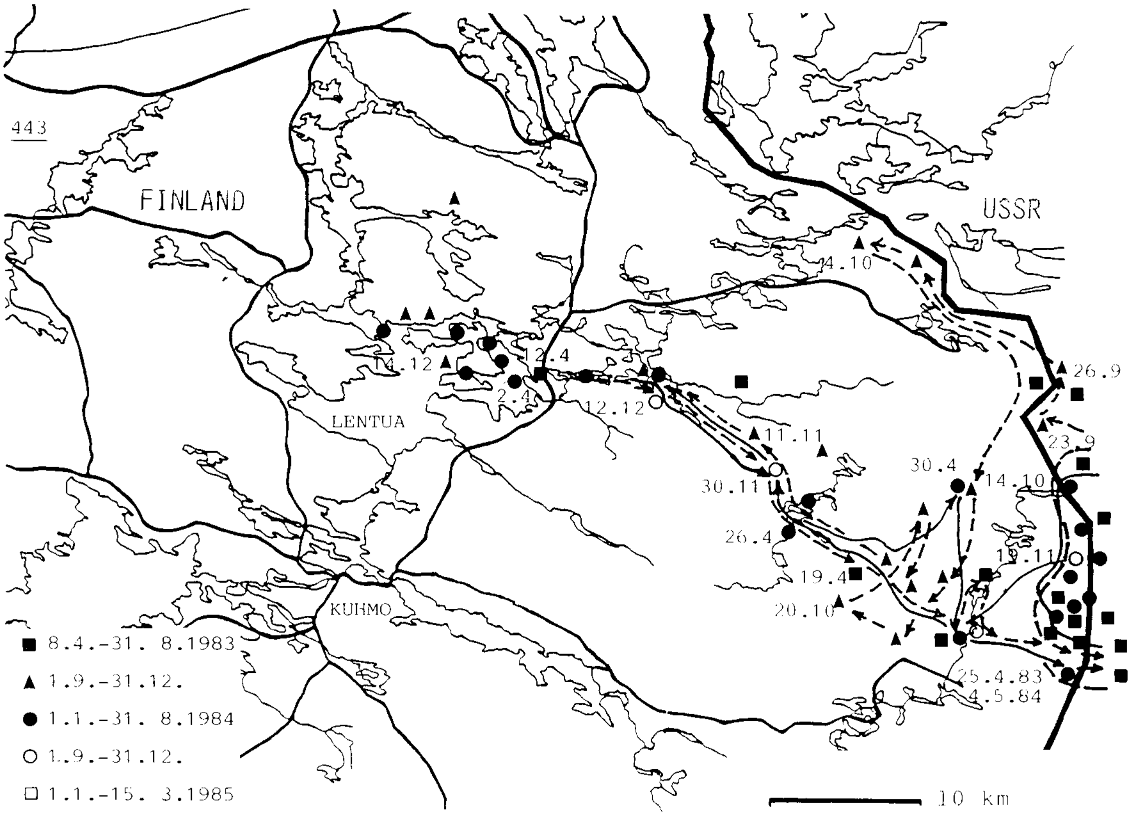

Fig. 2. Movements of wild forest reindeer No. 443 in Kuhmo and the adjacent Soviet territory in April 1983 - March 1985.

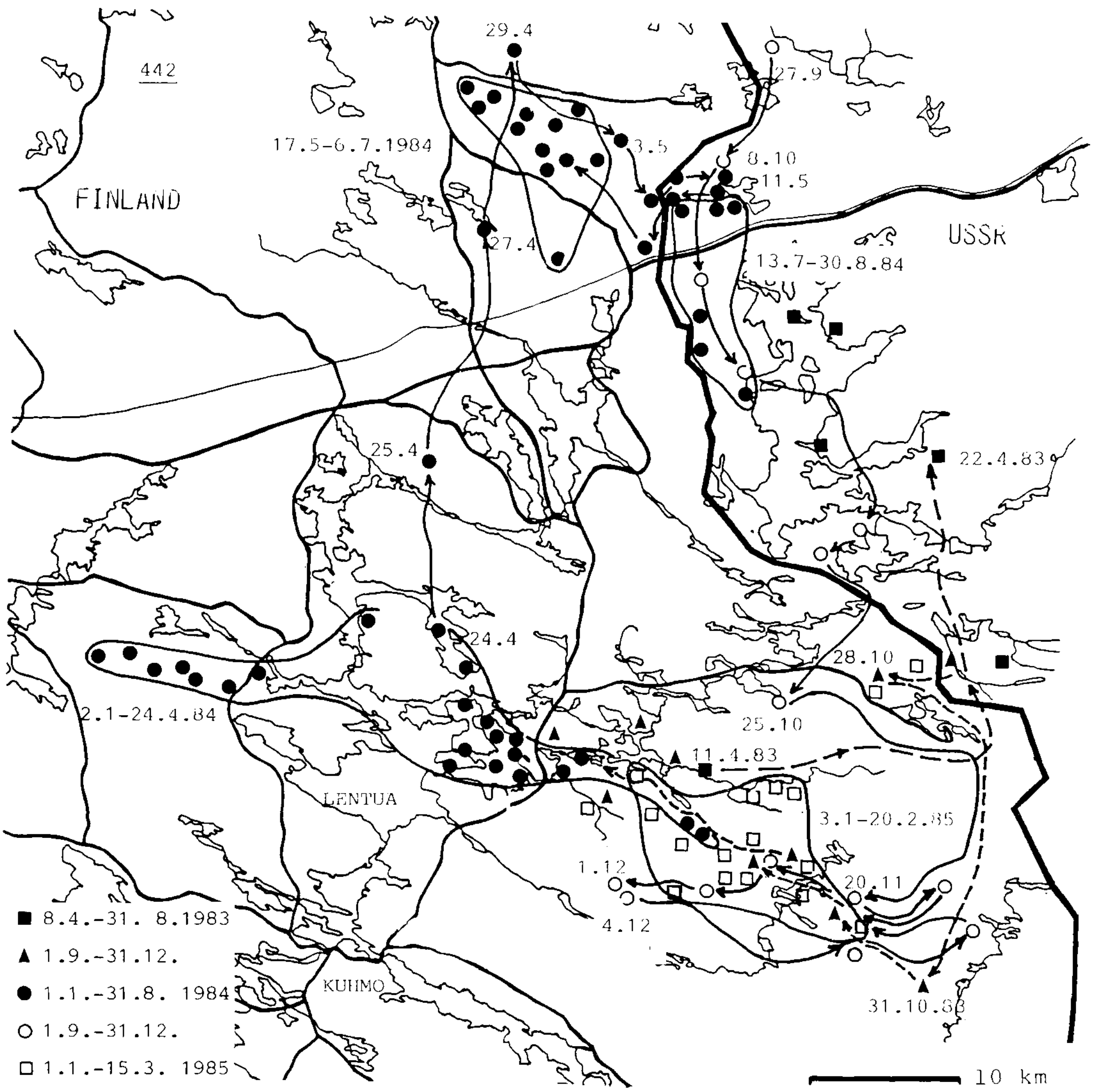

Fig. 3. Movements of wild forest reindeer No. 442 in Kuhmo and the adjacent Soviet territory in April 1983 - March 1985.

Lake Lentua during the second week of December. If the snow conditions are exceptionally favourable (thin layer of soft snow; as in the winter of 1984/85) the majority of the reindeer may not return at all, but stay to feed on the dry heaths of the eskers which otherwise constitute their migration route. On 6 - 7 March 1985, only 17 reindeer were found on the islands and shores of Lake Lentua.

The wild forest reindeer do not stop in one part of their winter range, but are in an almost continuous state of movement within that area. The pastures of this overwintering area are relatively heavily grazed (Lindgren *et al.*, 1983), and it is this that may promote such a continuous pattern of exploratory behaviour. The overall mean size of the winter home ranges is ca. 155 km^2.

The area of the main overwintering range of the forest reindeer (with Lake Lentua in the middle) is ca. 1000 km^2, while the corresponding summer range is much more extensive, ca. 5400 km^2.

A small portion (1 - 2%) of this subpopulation did not migrate at all. It stayed on the islands of Lake Lentua throughout the year. It consisted mainly of bulls and yearlings, a summer group of a bull and a yearling being a typical unit. Some groups consisting of a female with her calf have also been seen on the islands in summer.

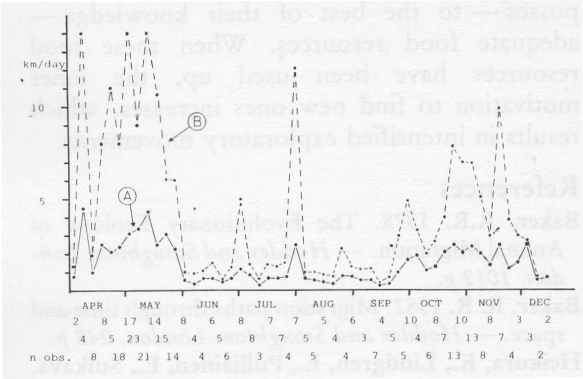

Fig. 4. Mean daily moving speeds (A) of radio-tracked wild forest reindeer in Kuhmo in April - November. The values are calculated as means of distances (on map) between consecutive radiolocations during 5-day periods and they thus represent, in fact, minimum average speed (km/day). B shows the maximum speed recorded during each 5-day period.

Discussion

The familiar area hypothesis of return migration states that an animal that becomes familiar with an area may find that some habitats are more suitable on one part of its range at one time but others thar are more suitable at another time (see also Baker, 1978). In a seasonal environment this means that the animal spends one season in one part of its familiar area and another season in another part. Seasonal return migrations are performed between these parts.

The migratory behaviour patterns of northern ungulates should be dependent on population density and the distance between the winter and summer pastures. When the winter and summer pastures are situated side by side, no real migration occurs, just as the need for migrations disappears when the population density is low (see also Yazan, 1961; Pulliainen, 1974). Once a migration tradition has developed, small portion of the population usually remains resident. In the case of the moose (*Alces alces*), resident individuals may occur in the winter range in summer (Loisa and Pulliainen, 1968). About 1 - 2% of the present Kuhmo subpopulation of the wild forest reindeer remained on the island or shores of Lake Lentua (i.e. in the winter habitats) consuming the food resources there (Sulkava *et al.*, 1983), while the major part of the extensive summer area was empty of reindeer in wintertime (perhaps because the snow was too deep there).

It has been suggested that the migration system of ungulates has a genetic background (Baker, 1982), migrants having a lower migration threshold than residents. A proximate factor here would be the condition of the habitat; i.e. whether or not an animal migrates depends on whether the condition of its habitat exceeds its threshold. Such a system also allows individuals

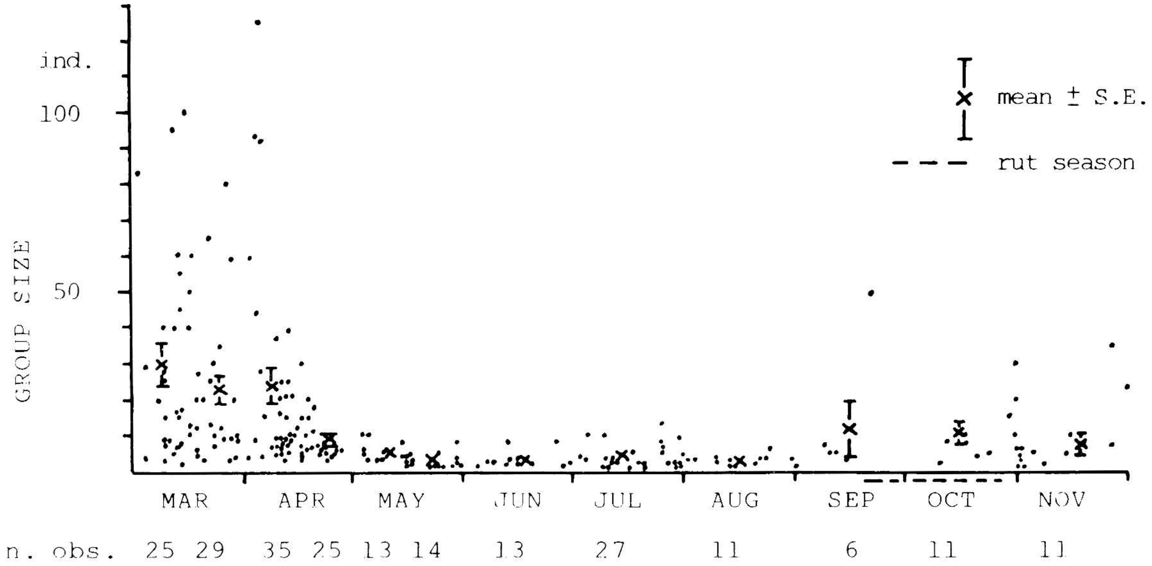

Fig. 5. Sizes of wild forest reindeer groups (individual groups) seen in Kuhmo in March - November 1984. Each spot indicates one sight observation.

to switch between being migrants or residents from one year to another. This phenomenon is well known among birds. The overwintering of waxwings (*Bombycilla garrulus*) in Finland, for instance, depends on the amount of rowan berries (*Sorbus aucuparia*) available. The above explanation can be thought to be valid in the case of the wild forest reindeer as well in the light of the present data.

Baker (1982) has suggested that in general females have a lower migration threshold than males. This statement also seems to be valid in this case, since the bulk of the individuals staying on the islands in Lake Lentua throughout the summer are bulls and yearlings, which may also move together. Only a few non-migratory females with their calves have been observed there so far.

Considering energy alone a resident mode of life would be more advantegous than a migratory one. Especially in the spring, when the wild forest reindeer are not in the best physical condition, speedy migration under variable snow and «water» conditions must consume a great deal of energy. The benefits obtained from migration must nevertheless be obviously greater than the costs incurred. It is likely that the reindeer have a negative nitrogen and mineral balance in wintertime, as is the case with their semi-domesticated relatives living on a lichen-rich diet (Steen, 1968), and must then engage in nitrogen recycling (Valtonen, 1979). A rapid recovery after the long period of lichen consumption during the winter belongs to the system. The wild forest reindeer look for nitrogen and mineral-rich food on the mires in early summer (Montonen, 1974; Pulliainen *et al.*, 1981, and later observations), where the nutrient content of some «key plants» (e.g., *Menyanthes trifoliata*) is remarkably high (Isotalo, 1971). Few nutrient-rich plants are available on the islands, although there is some *Epilobium angustifolium*.

Wild forest reindeer generally follow traditional migration routes (Fig. 2), although some exploratory movements may occur (Fig. 3). As with the moose (Pulliainen, 1974), the calves of the wild forest reindeer follow their mothers at least during their first year of life (Heikura *et al.*, 1983) and thus have the opportunity to learn the traditional migration routes. By moving with their mothers within the familiar area calves are ensured of finding summer and winter areas that posses — to the best of their knowledge — adequate food resources. When these food resources have been used up, the inner motivation to find new ones increases, which results in intensified exploratory movements.

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Management of wild reindeer in Norway

Eigil Reimers[1]

Abstract: Wild reindeer in Norway are found in 26 separate management areas. Predators are virtually absent from all areas and hunting is the most important factor determining population development through alterations of herd size and structure. Average population density (animals/km^2) after hunt was 1.96 in Hardangervidda, 1.18 in North Rondane and between 0.78 and 0.87 in Rondane South, Snøhetta, North Ottadalen and Forelhogna. Body size and female pregnancy rates followed a reverse trend. Average net increase of the herds varied from 42.2±10.0% in Forelhogna to 18.8±8.0% in Rondane North. In areas with animals in prime physical condition a high versus a low average harvest rate of calves resulted in a similar number of animals harvested, but a lower total yield of meat and revenue from hunting licences. At a winter population density of 0.8 - 2.0 animals/km^2 annual harvest (per km^2) of wild reindeer amounts to 0.23 - 0.51 animals, 9 - 18 kg meat and 286 - 850 NKr from sale of hunting licences. There was a significant relationship between body size expressed as carcass weights or mandible length and harvest success.

Key words: density, reproduction, body weight, harvest, population increase.

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Rangifer, Special Issue No. 1, 1986: 241 - 246

Introduction

Wild reindeer in Norway are confined to alpine areas in the southern part of the country. Present population counts indicate some 40 000 wintering animals in 26 hunting areas (Krafft, 1981) which are more or less separated by topographical barriers or by man-made obstacles like railroads, highways and settlement. The areas are generally small and range in size from under 100 km^2 to 8122 km^2. Due to their limited size and fairly dense mountain road system, all areas are easily accessable.

The reindeer hunt takes place between August 20 and September 25 in all areas. Until the 1960's there was no restriction as to sex or age of the animals hunted.

The current management practice is to issue licences for males, females 2+ years, calves and 1+ years of both sexes. The hunting of adult and young males is regulated through body weight limits or number of antler points on some areas. Body weights, pregnancy rates and calf mortality vary among the various reindeer herds (Skogland, 1984, 1985b, 1985c; Reimers, 1983) as do harvest strategies. This paper attempts to evaluate the relationship between animal density, body weight and the harvest of animals and meat as well as revenues on licences from six of the wild reindeer areas in southern Norway.

Material and methods

Aerial total counts of the reindeer herds are usually carried out annually in mid winter, but in Hardangervidda after calving. In this area counts are done every 3 years.

The accuracy of the airial count technique has never been tested in any of the areas.

Up to 1965 harvest statistics included number of licences issued and total number of 1+ year males and females killed. From 1965 calves were hunted and harvest statistics was specified on calves and older animals and total number of males and females. Since 1971 the hunt statistics included yearlings and from 1977 it also specified calves, yearlings and 2 years and older animals of both sexes.

Carcass weight (=dressed weight) is the total body weight minus skin, viscera, head and lower legs. The weights and mandibles from killed animals were obtained from hunters or game wardens during the hunting season. The age of harvested animals was determined from tooth development or annuli in the cementum of the first incisor (Reimes and Nordby, 1968).

Pregnancy rates were measured in animals killed during winter, January through May. Net population increase was defined as the difference between two subsequent population counts plus harvest at percentage of the winter population the first year. When there were 2 (or 3) years between population surveys the calculated net increase value was divided by 2 (or 3). Harvest percentage (harvest as percentage of the winter herd size) estimates net population increase during periods when the populations remain reasonable stable. The highest and lowest values were excluded when calculating average net population increase, harvest percentage and harvest success (animals killed as percentage of licences issued).

As carcass weight variations were small from year to year within each area, weights from the various years were pooled within areas. Table 1 shows the carcass weights used to calculate meat harvest. Calf carcass weights are given as the pooled means of males and females. Carcass weights of 1+ year males or females are calculated from the number of animals harvested in each age class. Prices of hunting licences vary somewhat from area to area. Most areas sat the 1985 prices for non-residents (Norwegian citizens living outside the area) around the following values (NKr. 100 = US$ 12.20); calf 340, female 800, small/medium size male 1000, large male (unspecified licence) 1500. The 1+ year male cohort is separated into small/medium and large males which have different prices. I assume that the two male cohorts are equally represented among the 1-year or older males in the hunting statistics. This allows me to use a common licence price tag of NKr 1250 pr. 1+year male. Resident prices are one half those of non-residents. The number of non-residents who are allowed to hunt reindeer varies between the different areas. The income from sold licences is calculated from non-resident prices and gives area differences in maximum income.

Results and discussion

The average population densities varied from 1.96 in Hardangervidda and 1.8 in Rondane North to below 0.9 in the other areas (Table 2). The variation is the result of management decisions and all the populations would increase if the harvest was reduced. Female body weights and pregnancy rates were inversely correlated with density. Net population increase is influenced by population sex ratio and recruitment rates. Migration between areas is not important and the population sex ratio has remained fairly constant at 60 - 70% females 1+years during recent years (Skogland, 1985 c).

Net population increse was highest in Forelhogna (42.4%) followed by North Ottadalen, Snøhetta and Rondane South, with values between 31.8 and 33.4% (Table 3). A high net population increase implies a high pregnancy rate

Table 1. Wild reindeer carcass mean weights (kg)

Area	Calves	1+ years Males	1+ years Females
Forelhogna[1]	27.0	64.3	42.3
North Ottadalen	26.1	77.5	39.2
Rondane South	24.4	71.2	40.3
Rondane North	19.1	46.1	35.7
Hardangervidda	15.2	44.6	28.8
Snøhetta	18.4	46.0	33.8

[1] Forelhogna weights from Meli (1985).

Table 2. Average population size and density (winter), female carcass weights and pregnancy rates.

Area	Period	Area size (km^2)[1]	Average size of winter population±SD[2]	Corresp. density (anim./km^2)	Winter population 1983-1984	Female carcass weight (kg)[3]		Pregnancy rates[4]	
						Yearlings	2+ years	1-2 years	2-3 years
Forelhogna	1974-1984	1638	1425± 239	0.87	1770	39.2	43.7	100(4)[6]	100(18)
North Ottadalen	1974-1984	3245	2625± 431	0.81	2157	37.6	39.6	50(2)	100(8)
Rondane South	1981-1984	1500	1174± 126	0.78	1000	-	41.1	-	-
Rondane North	1972-1984	1441	1701± 254	1.18	1404	32.7	36.1	63(8)	94(16)
Hardangervidda	1973-1984	8122	15921±2956[5]	1.96	14969	25.6	29.3	60(15)	85(160)
Snøhetta	1977-1984	3295	2591± 441	0.79	2200	30.3	34.3	-	-

[1] Total hunting area (Krafft 1981).
[2] From Holthe (1977), Krafft (1981), Skogland (1985a) and annual reports from the various Reindeer councils.
[3] Forelhogna carcass weights from Meli (1985).
[4] Pregnancy rates: Forelhogna 1984 (Skogland, 1984), North Ottadalen and Rondane 1966-72 (Reimers, 1983) and Hardangervidda 1948-83 (Reimers, 1983; Skogland, 1984).
[5] Calculated from fig. 1 in Skogland (1985a).
[6] Sample size in paranthesis.

as shown in Table 4, and a low prenatal, neonatal and adult mortality. Skogland (1984, 1985d) found the calf mortality to ble low in the Forelhogna and Knutshø herds (Table 4). The relatively low pregnancy rate and the high calf mortality (Table 4) result in a low population net increase in Hardangervidda.

The pregnancy and calf mortality rates in Rondane North fall between those of Forelhogna-Knutshø and of Hardangervidda. In spite of this Rondane North population showed the lowest (18.8%) net increase.

Skogland (1985d) found that the high mortality among Hardangervidda calves was caused by winter food-limitations. Food restriction in late winter reduces fetus growth and calves are born smaller. Smaller new-born calves generally suffer higher neonatal mortality than heavier calves (Rognmo *et al.*, 1983). Winter range quality is very good in Rondane North (Reimers *et al.*, 1983) so that the relatively high calf mortality and the low population net increase in this area must have another explanation.

We have no reason to believe that the Rondane North herd or any other of the herds suffer important adult mortality. Large predators are virtually absent from the areas and the management policy aims to stabilize populations with an annual harvest of the population's net

Table 3. Average population net increase ±SD and annual harvest ±SD.

Area	Period	Population net increase as % of winter population	Harvest			
			Number of animals	% of winter population	% calves	Meat (tonnes)
Forelhogna	1970-1984	42.4±10.0(10)[1]	459± 182(15)[1]	35.2± 9.1(13)	29.4±6.1(15)	21.1± 7.7(15)
North Ottadalen	1972-1984	33.4± 1.5(8)	944± 255(11)	36.4± 6.1(10)	8.6±4.3(11)	52.7±15.0(11)
Rondane South	1969-1984	31.8± 7.2(13)	350± 123(4)	29.2± 8.4(4)	17.2±5.2(4)	17.4± 6.4(4)
Rondane North	1960-1984	18.8± 7.7(16)	357± 112(25)	19.8± 4.4(18)	7.2±6.6(18)	14.5± 4.5(25)
Hardangervidda	1960-1984	24.8± 6.4(22)[2]	4143±2376(25)	32.1±25.9(23)	13.7±1.1(5)	141.0±76.4(25)
Snøhetta	1977-1984	32.1± 5.1(4)	831± 444(7)	26.8±12.8(6)	13.2±6.4(6)	29.4±14.9(7)

[1] Number of years in paranthesis.
[2] Calculated on basis of Fig. 1 in Skogland (1985a).

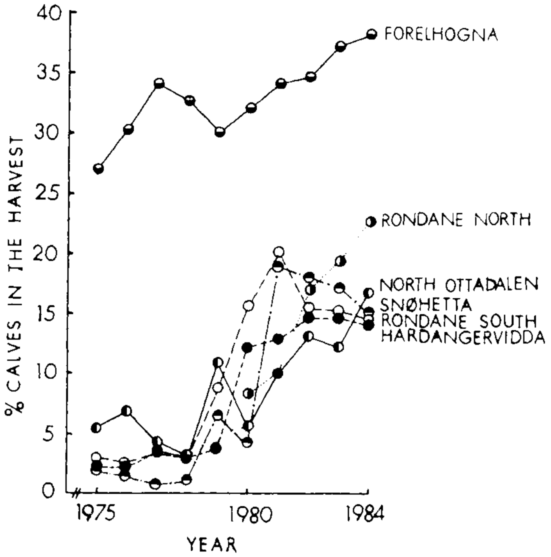

Fig. 1. Harvest of wild reindeer calves from 1975.

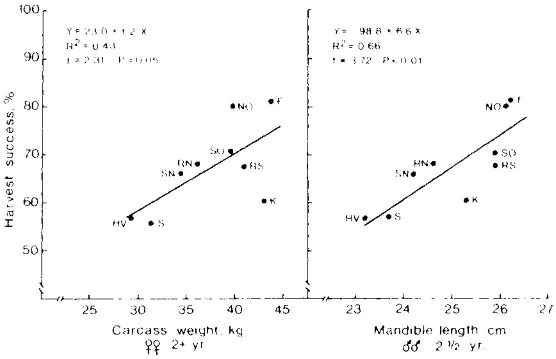

Fig. 2. The relationship between carcass weight (kg) or mandible length (cm) and harvest success. Areas and years: Forelhogna (F) 1964-84, North Ottadalen (NO) 1964-84, South Ottadalen (SO) 1974-84, Rondane North (RN) 1965-84, Rondane South (RS) 1976-84, Setesdal (S) 1964-84, Snøhetta (SN) 1953-84, Hardangervidda (HV) 1960-84, Knutshø (K) 1970-84.

increase. Mortality caused by old age is therefore insignificant and large scale mortality caused by starvation of adults has not been observed.

The average net population increase was 42.4±10.0% in Forelhogna and 33.4±1.5% in North Ottadalen (Table 3). The high variance in Forelhogna may indicate annual variation in reproduction and mortality or, more likely, population count accuracy. Body weights and pregnancy rates are similar (Table 2) and there is no reason to believe that calf survival is different in the two areas. The difference in population growth rate is therefore most likely attributable to harvest strategy differences, in particular calf shooting.

In Forelhogna in order to maximize herd productivity, protect winter ranges and reduce winter mortality of calves, calf shooting has been practiced since 1968 and the average annual kill of calves is nearly 30% of the total harvest (Fig. 1). In North Ottadalen the calf harvest has been kept low and the average percentage during 1974 - 84 was 8.6. The local management of the Forelhogna reindeer herd is very well organized (see Meli, 1985). The management strategy developed in this area, in particular the high calf harvest, has been adopted by the official management authorities and from 1978 there has been a percentage increase in the calf harvest in all areas (Fig. 1).

Table 4. Pregnancy rates among 1-year or older wild reindeer and calf mortality. Sample size in paranthesis.

Area	Pregnancy rates % Jan.-Apr.	Pregnancy rates % At calving	Number of calves/ 100 females 2+ years in late summer	Calf mortality (%) from late pregnancy through summer
Forelhogna and Knutshø	100(45)[1]	-	95(1085)[1]	5[2]
Rondane North	83(24)[2]	85(589)	57(2014)[3]	33[3]
Hardangervidda	83(175)[4]	50(1911)[1]	39(3776)[1]	53[1]

[1] Data from Skogland (1984, 1985d).

[2] Data from Reimers (1983).

[3] Calculated from herd size and composition before calving, pregnancy and herd size and composition in autumn as yearling females and 2+ year were indistinguishable in summer. Data from 1983 - 85.

[4] Data from Reimers (1983) and Skogland (1984).

Table 5. Harvest of animals, meat and sale of licences.

Area	Period	Harvest/100 km^2 Number of animals	Harvest/100 km^2 Meat (kg)	Licences sold[1]/ 100 km^2 (1000 NKr)
Forelhogna	1970-1984	28(33)[2]	1288(1498)	28.6(33.2)
North Ottadalen	1974-1984	29(36)	1624(2005)	35.2(43.5)
Rondane South	1981-1984	23(29)	1160(1487)	31.0(39.7)
Rondane North	1960-1984	25(21)	1004(850)	37.2(31.5)
Hardangervidda	1960-1984	51(26)	1736(886)	85.0(43.4)
Snøhetta	1978-1984	40(51)	892(1129)	33.5(42.4)

[1] Non-resident prices. Local residents pay half the resident price.

[2] Values in parenthesis: harvest of animals, meat and sale of licences adjusted to an animal winter density of 1 animal/km^2 in all areas.

The hunter have not shared the management authorities enthusiasm for the calf harvest strategy. Population net increase values from Forelhogna and North Ottadalen support the calf harvest strategy while total harvest as percentage of the winter population does not (Table 3). Of the two, the population net increase estimate probably is the most reliable. However, the increased calf harvest that took place in all areas from 1978 has not resulted in a net population increase. In the two areas, Forelhogna and Hardangervidda, there was a positive but insignificant relationship while in the other four areas there was an insignificant negative relationship.

The harvest of meat and the income from hunter-licences are 26% and 23%, respectively, higher in North Ottadalen than in Forelhogna (Table 5). This development was predicted in an early simulation study (Reimers *et al.*, 1977). Harvest of animals and income from licences were twice as high in Hardangervidda as in the other areas. Meat harvest was however, not much higher.

At a winter population density of 0.8 - 2.0 animals/km^2 annual harvest (per. km^2) of wild reindeer amounts to 0.23 - 0.51 animals, 9 - 18 kg meat and 286 - 850 NKr from sale of hunting licences.

Table 6. Comparision of domestic and wild reindeer management.

Measurements	Domestic reindeer[1]	Domestic reindeer[2]	Wild reindeer[3]
Range (km^2)	85 000[4]	6000[4]	29 241
Winter population	187 094	11 416	25 437
Animal density (animals/km^2)	2.2	1.9	1.3
Harvest (%) of winter population (Range in parenthesis)	30(12-52)	45	30(20-36)
Harvest of meat (tonnes)	1484	161	276
Average carcass weight (kg)	26	31	36
Meat harvest (kg/km^2)	17	27	14
Meat harvest (kg/km^2) adjusted to a density of 1 animal/km^2	8	14	11

[1] Areas where the Saami population has legal exclusive rights to practice domestic reindeer management.

[2] Areas without the exclusive rights for the Saami population. Includes domestic reindeer herds in southern Norway.

[3] Data presented in this paper.

[4] From Langdal and Rundberg (1979). Other domestic reindeer data from Reindriftsstyret (1984).

Harvest success varied between areas. There was a significant relationship between harvest success and animal body size expressed as carcass weight and mandible length (Fig. 2), possibly reflecting a relationship between behaviour and body size. Animals with a nervous behaviour as in Hardangervidda are more easily disturbed and therefore more difficult to hunt than the less nervous animals in Forelhogna. A high versus a low disturbance threshold probably have the same effect as a low versus a high level of disturbances and result in a low versus a high body growth rate as found by Reimers (1980).

Average population and harvest data from domestic reindeer areas and from the six wild reindeer areas representing ca. 50% of the total wild reindeer range in Norway is compared in Table 6. Meat harvest (kg/km^2) is higher among domestic than wild reindeer due to higher animal density in the former.

Acknowledgement

I thank O. Brøste, J. Hageland, J. Meli, R. Sørumgård and E. Winther for supplying data on herd counts and S. Stavøstrand for language assistance.

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Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus* L.

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Abstract: Polyacrylamide gel electrophoresis was used to analyse transferrin variation in wild caribou *(Rangifer tarandus granti)* and domestic reindeer *(R.t. tarandus)* from Alaska. Eighteen alleles were detected in caribou and ten alleles were detected in reindeer. The most common allele was Tf^{F1} with a frequency of 0.304 and 0.408 in caribou and reindeer, respectively. The allele frequency distributions were significantly different in reindeer and caribou. This finding, together with the absence in reindeer of nine alleles present in caribou, suggests that little genetic exchange has taken place between caribou and reindeer in Alaska. The allele frequency distribution in Alaska caribou and reindeer are compared with those for other populations of caribou and reindeer. This comparison indicates that Alaskan caribou as well as Eurasian reindeer have evolved from a common ancesteral population different from the ancesteral population of Peary cairbou *(R.t. pearyi)* and Svalbard reindeer *(R.t. platyrhynchus)*.

Key words: *Rangifer*, caribou, reindeer, transferrin, polymorphism, Alaska.

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Rangifer, Special Issue No. 1, 1986: 247 - 251

Introduction

In Alaska domestic reindeer, *Rangifer tarandus* L., originate from animals introduced from Eurasia and not from the native caribou. Reindeer have been introduced both from the Soviet Union (Banfield, 1961) and from Norway (Skjenneberg and Slagsvold, 1968). The present domestic reindeer are, however, assumed to originate mainly from the first introduction in 1892, when 1280 reindeer were imported from Eastern Siberia and brought to the Seward Peninsula in Alaska (Stern *et al.*, 1980). These animals subsequently increased in number to approximately 600.000, and had become widespread in large parts of Alaska by the early 1930s (Klein, 1980; Stern *et al.*, 1980, Thomas and Arobio, 1983). A rapid decline in numbers followed this peak population and a loss resulting from intermingling with wild caribou, *R. t. granti*, presumably contributed to the population decline (Klein, 1980; Thomas and Arobio, 1983). This loss led to extensive speculations about the genetic influence of domestic reindeer on wild caribou in Alaska (cf. Greig, 1979; Klein, 1980).

One approach to the study of genetic exchange between populations is to investigate the distribution of alleles at polymorphic loci. The transferrin locus in reindeer and caribou is of particular value since it possesses a high degree of variation. Several studies have used the transferrin allele frequency distribution to test for genetic exchange between populations of reindeer and caribou (Brænd, 1964; Zhurkevich and Fomicheva, 1976; Shubin, 1977; Storset *et al.*, 1978; Soldal and Staaland, 1980; Shubin and

Matyukov, 1982; Shubin and Ionova, 1984; Røed, 1985a, 1985b, in press; Røed *et al.*, 1986). We report here the result of an electrophoretic examination of the transferrin locus in caribou and domestic reindeer in Alaska in order to determine the amount of genetic exchange that has taken place between these populations. The allele frequency distribution is further compared with those in other populations of reindeer and caribou and the results are discussed in relation to the origin of different subspecies of the genus.

Material and methods

Blood samples were obtained from 103 reindeer and 112 caribou. The reindeer samples were from the Seward Peninsula and the caribou samples were from the Central Arctic herd and the Delta herd (see Davis *et al.*, (1983) and Whitten and Cameron (1983) for descriptions of these populations.) The blood samples were centrifuged and the sera removed and stored at — 20°C until analysis. Vertical slab polyacrylamide gel electrophoresis was used to analyse transferrin variation using the Jolley and Allen (1965) buffer system. The acrylamide concentrations in the stacking and separating gels were 2.5% and 7%, respectively. Twenty specimens were run on each gel, beginning at 5 v/cm for the first half hour, and continuing at 30 v/cm for approximately 3.5 hours. To localize the transferrin on the gel most other proteins were precipitated from the serum by pretreatment with rivanol before electrophoresis (Chen and Sutton, 1967). Transferrins were made visible by overnight staining with Coomassie Brilliant Blue R250 (Diezel *et al.*, 1972). Relative mobilities of transferrin bands were confirmed by re-running samples of approximately the same mobility side

Table 1. Transferrin allele frequencies of wild caribou and domestic reindeer in Alaska together with allele frequencies of other reindeer/caribou populations.

Allele	Alaskan wild caribou	Alaskan domestic reindeer	Norwegian domestic reindeer	Norwegian wild reindeer	Peary caribou	Svalbard reindeer
A	0.027	0.005	0.016	0.032	0.041	
B	0.013				0.006	
C1	0.085	0.078	0.331	0.195	0.058	
C2	0.036	0.010	0.036	0.028	0.099	
C3					0.006	
D			0.001			
E1	0.304	0.408	0.269	0.389	0.023	
E2	0.036		0.002	0.019		
G1	0.054	0.053	0.053	0.024		
G2	0.049				0.297	0.745
G3						0.255
G4	0.004					
H1	0.013		0.009	0.051	0.023	
H1b	0.009	0.053				
H2	0.147	0.073	0.051	0.134	0.180	
I	0.134	0.306	0.156	0.096	0.163	
J	0.013				0.006	
K	0.013		0.037	0.027		
K2		0.010				
L	0.018				0.041	
M	0.040	0.005	0.039	0.005	0.017	
N					0.006	
O					0.023	
O2	0.004					
P					0.017	

Table 2. Paired combinations of genetic identity between populations of reindeer/caribou.

Population	A	B	C	D	E
(A) Alaskan caribou	*****				
(B) Alaskan reindeer	0.912	*****			
(C) Norwegian domestic reindeer	0.803	0.778	*****		
(D) Norwegian wild reindeer	0.942	0.864	0.890	*****	
(E) Peary caribou	0.516	0.365	0.345	0.340	*****
(F) Svalbard reindeer	0.120	0.000	0.000	0.000	0.691

by side on the same gel. Reference plasma was from continental Norwegian wild and domestic reindeer, *R.t. tarandus* (Røed, 1985a), from Svalbard reindeer, *R.t. platyrhynchus* (Røed, 1985b), and from Peary caribou, *R. t. pearyi* (Røed, *et al*, 1986.)

Results

The amount of genetic variation at the transferrin locus was high in both Alaskan cairbou and reindeer, with a total of 19 separate alleles resolved. Eighteen of these were present in caribou and 10 in reindeer. Compared with the reference plasma, four new alleles were detected. These have been designated according to their mobility relative to the reference alleles: one with a banding pattern slightly cathodal to Tf^{G3} was labeled Tf^{G4}, one with bands between Tf^{H1} and Tf^{H2} was labeled Tf^{H1b}, one scored between Tf^{K} and Tf^{L} was labeled Tf^{K2} and one between Tf^{O} and Tf^{P} was labeled Tf^{O2}

Table 1 presents the allele frequencies in the Alaskan caribou and reindeer together with previously reported values for Norwegian domestic reindeer, *R. t. tarandus*, (mean frequencies of five herds, Røed, 1985a), Norwegian wild reindeer, *R. t. tarandus*, (mean frequencies of five populations, Røed, in press), Peary caribou, *R. t. pearyi*, (Røed *et al.*, 1986) and Svalbard reindeer, *R. t. platyrhynchus*, (Røed, 1985b), where the same techniques and allelic designations were used.

Tests of goodness-of-fit to the Hardy-Weinberg equilibrium did not reveal any significant deviations either in the caribou or in the reindeer from Alaska.

The most common allele in both caribou and reindeer from Alaska was definitely Tf^{E1}, with a frequency of 0.304 and 0.408 in caribou and reindeer respectively. The same allele is also very common among Norwegian reindeer, but not in Peary caribou and Svalbard reindeer, where Tf^{G2} is the most common allele.

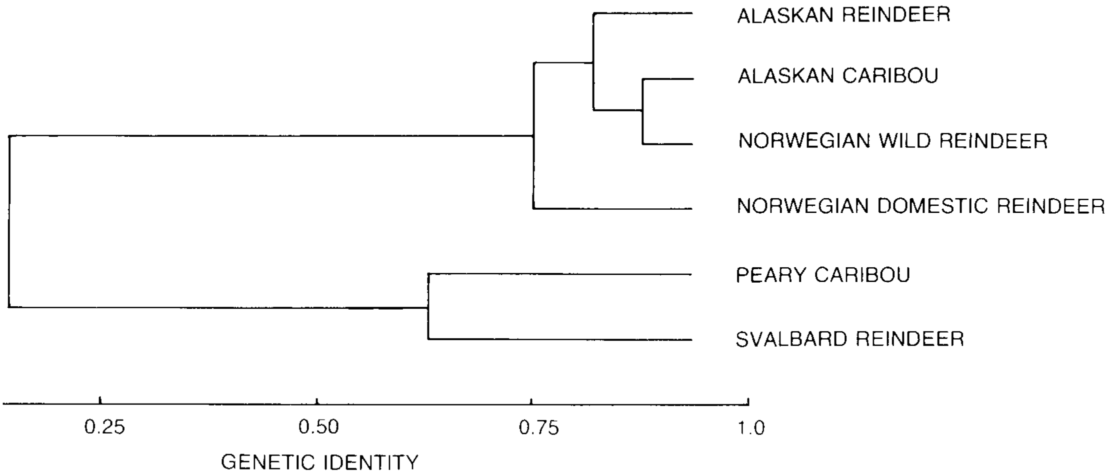

Fig. 1. Genetic identity dendrogram (Nei's coefficient) for transferrin variation of populations of reindeer and caribou.

The pattern of allele frequency distribution in Alaska reindeer and caribou, with an absence in reindeer of 9 alleles present in caribou, indicates considerable genetic difference between caribou and reindeer. Contigency chi-square tests for heterogeneity were an addition highly significant at both Tf^{F1} ($X^2=5.10$, $P<0.05$), Tf^{F2} ($X^2=6.01$, $P<0.05$) and Tf^{F} ($X^2=18.71$, $P<0.01$).

Table 2 gives the coefficient of genetic identity (Nei, 1972) calculated from the allele frequencies in Table 1. The genetic identity between Alaskan caribou and reindeer was 0.912. Alaskan caribou were most similar to the Norwegian wild reindeer and Alaskan reindeer were most similar to Alaskan caribou. Both displayed low identity when compared with Svalbard reindeer and also with Peary caribou. A dendrogram (Fig. 1) summarizing the genetic identities was constructed using UPGMA (unweighted pair group method based on arithmetic averages) cluster analysis (Sneath and Sokal, 1973). As illustrated in Fig. 1 this analysis reveals a major dichotomy between Alaskan and Norwegian caribou and reindeer on the one hand and Peary caribou and Svalbard reindeer on the other.

Discussion

In Alaska the wild caribou appear to have several more alleles coding for transferrin than do the domestic animals. This, in combination with the considerable difference in the allele frequency distribution, indicates low genetic similarity of reindeer and caribou. The previously large loss of reindeer to wild caribou herds in Alaska seems therefore not to have resulted in appreciable genetic exchanges. This study therefore does not support a view of large-scale interbreeding between reindeer and caribou in Alaska. Low breeding success of domestic reindeer joining the wild herds may be explained by several factors. The breeding season of domestic reindeer usually precedes that of caribou by several weeks (Klein, 1980) and synchronous mating and calving appear to be strongly selected for among caribou (Dauphiné and McClure, 1974). Futher, male domestic reindeer are usually substantially smaller than male wild caribou and therefore presumably would be less effective in competing for access to the females (Klein, 1980). Also the weaker migratory urge of domestic animals might work against the interbreeding since the breeding of wild caribou usually takes place during fall migration from the summer to the winter ranges. The long migrations and difficult winter foraging conditons that are often characteristic of wild herds may also reduce the survival of domestic reindeer joining the wild animals. The domestic reindeer are probably also more exposed to predation and hunting, because they are less wary than the wild animals. Relatively higher mortality of domestic reindeer compared with wild animals has been reported in the Taymyr region in the Soviet Union, where considerable numbers of domestic reindeer had been absorbed by the wild herds (Geller and Vostryakov, 1975). In this region considerable genetic differences in the transferrin locus between domestic and wild reindeer have been reported (Shubin and Ionova, 1984). Similar genetic differences have also been reported between domestic and wild reindeer in Norway (Røed, 1985a). It appears therefore that the amount of genetic exchange between domestic and wild reindeer is generally very restricted.

The origin of reindeer/caribou and how they have spread into their present habitats is largely unknown. The genus has been traced back to about 440.000 B.P. in Eurasia and its existance in North America may well be equally long (Banfield, 1961). The caribou in North America segregate several more alleles in the transferrin locus than do reindeer from Eurasia. Eight alleles present in North American caribou are not detected in Eurasian reindeer, while only two alleles present in Eurasian mainland reindeer are not detected in North American caribou. Such a pattern could be explained by a longer evolutionary time of North American caribou and an origin of present Eurasian reindeer from ancesteral populations in North America. Concerning the origin of the different subspecies of reindeer and caribou, it has been hypothezised that continental tundra forms evolved in the Beringia refugium in Alaska-Yukon during the Wisconsin glaciation, the woodland caribou south of the ice sheet, and the Peary caribou in a refugium in the Canadian Arctic Archipelago or in northern Greenland (Banfield, 1961; Macpherson, 1965). A common genetic origin of Svalbard reindeer and Peary caribou has also recently been suggested (Røed, 1985b; Røed *et al.*, 1986). The findings of considerable genetic differentiation between Svalbard reindeer and Peary caribou on the one hand and the Eurasian reindeer and Alaskan caribou on the other (Fig. 1) clearly support the view that Alaskan caribou and Eurasian reindeer have evolved from a common ancesteral population different from the ancesteral population of Peary caribou and Svalbard reindeer.

Acknowledgement

We sincerely appreciate the help of Dr. Robert A. Dieterich in obtaining the reindeer samples.

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Winter ecology of the Porcupine caribou herd, Yukon: Part III, Role of day length in determining activity pattern and estimating percent lying

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Abstract: Data on the activity pattern, proportion of time spent lying and the length of active and lying periods in winter are presented from a 3 year study on the Porcupine caribou herd. Animals were most active at sunrise and sunset resulting in from one (late fall, early and mid winter) to two (early fall and late winter) to three (spring) intervening lying periods. Mean active/lying cycle length decreased from late fall (298 min) to early winter (238 min), increased to a peak in mid winter (340 min) then declined in late winter (305 min) and again in spring (240 min). Mean length of the lying period increased throughout the 3 winter months from 56 min in early winter to 114 min in mid winter and 153 min in late winter. The percent of the day animals spent lying decreased from fall to early winter, increased throughout the winter and declined in spring. This pattern was related, in part, to daylength and was used to compare percent lying among herds. The relationship is suggested to be a means of comparing quality of winter ranges.

Key words: caribou , *Rangifer tarandus*, activity, winter range, daylength, lying period.

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Rangifer, Special Issue No. 1, 1986: 253 - 259

Introduction

The winter activity of *Rangifer* has been the subject of numerous studies in recent years (Segal, 1962; Gaare *et al.*, 1975; Skogland, 1978; Roby, 1978, 1980; Boertje, 1981; Thing, 1984) and comparisons among herds are beginning to emerge (Roby 1978; Russell and Martell, 1984.) Knowledge of the activity pattern (the short-term alternation between active and resting periods) and activity budget (the tabulation of the proportion of time in various activities) enables researchers or managers to assess the relative condition of the winter range, determine the energetic relationship and nutritional status of the herd and, by understanding the factors that determine activity budget, more accurately analyze the influence of human disturbance (Klein and White, 1978).

It is generally accepted that the proportion of time spent lying is inversely related to range quality in relation to either forage quality or availability (Gaare *et al.*, 1975; Roby, 1978; Boertje, 1981; Russell and Martell, 1984). Animals ingesting poor quality forage require longer periods for rumination than those ingesting high quality forage (Blaxter, 1962). When food is scarce (because of either low biomass or adverse snow conditions), animals face an energetic trade-off between the high energy expenditure of obtaining food and low energy intake by increasing lying time. By comparing percent lying (percent of the observation period animals spend lying) among herds or temporally for the same herd, an indirect method of assessing range quality is available.

One factor that complicates a direct comparison of percent lying among studies is the observation that *Rangifer* cue their activity to sunrise (Gaare *et al.*, 1975; Thomson, 1977;

Roby, 1978; Erriksson *et al.*, 1981), and that day length (percent of a day occurring between sunrise and sunset) affects activity pattern (Erriksson *et al.*, 1981). Thus, since winter ranges are located at different latitudes and winter studies have occurred at different times, our objective in this paper is to define the relationship between day length and percent lying and compare studies based on this relationship.

The winter ecology of the Porcupine caribou herd was the subject of a cooperative study between the Canadian Wildlife Service and the Yukon Department of Renewable Resources between 1979 and 1982. Among the study's objectives was to assess the quality of the winter range both on a seasonal basis and in relation to other herds. A thorough treatment of the winter activity budget of the herd will be presented elsewhere (Martell and Russell, unpublished data).

Methods

For the purpose of comparison among seasons, the field season was divided into six periods:

1. early fall: In 1980 field work was conducted October 10-13 to coincide with the rut.
2. late fall: November 6-13 when snow depths were very shallow or snow was absent.
3. early winter: December 5-15 to coincide with the shortest daylight hours.
4. mid winter: January 26-February 6 to coincide with the period of moderate snow accumulation.

Table 1. Length of lying and active periods and active/lying cycle during the study.

Period	Total cycle (min) 1st*	Total cycle (min) 2nd	Lying period (min) 1st	Lying period (min) 2nd	Active period (min) 1st	Active period (min) 2nd
Early fall						
1980-81	206	285	38	102	168	183
Late fall						
1979-80	270		56		214	
1981-82	325		100		225	
Mean	298		78		220	
Early winter						
1979-80	255		54		201	
1980-81	230		47		183	
1981-82	230		68		162	
Mean	238		56		182	
Mid winter						
1979-80	310		93		217	
1980-81	375		101		274	
1981-82	335		147		188	
Mean	340		114		226	
Late winter						
1979-80	360	315	180	98	180	217
1980-81	270	240	124	87	146	153
1981-82	285	—	156	—	129	—
Mean	305	278	153	93	152	185
Spring						
1979-80		195		55		140
1980-81		225		112		113
1981-82		300		132		168
Mean		240		100		140

* Length of 1st and (if applicable) 2nd period from Fig. 1.

5. late winter: March 5-12 to coincide with maximum snow accumulation and increasing day length.
6. early spring: April 5-25 when snowmelt begins and movement rate increases.

We observed caribou with 15x-60x zoom spotting scopes at 17 field camps during the winters of 1979-80 through 1981-82. A band of caribou was defined as a socially interacting group of animals spatially distinct from other bands in the area. Activity data were collected using the instantaneous scan method (Altmann, 1974). We scanned each band at 15-minute intervals and tallied the number of caribou engaged in each of five general activities which were identified primarily by posture. An animal was defined as lying if observed bedded on the ground in a resting or ruminating position, either upright or lying on its side.

For each camp, activity data were pooled and the proportion of caribou lying was plotted in relation to time since sunrise. The length of the active/bedded cycle was calculated as the time between consecutive activity peaks. The area under the curve between activity peaks, when divided by the length of time between the activity peaks, was used to calculate the mean percent of time spent lying during that cycle. This mean was multiplied by the length of the active/bedded cycle to yield the mean length of the lying period.

The proportion of time spent lying for each camp was calculated as a single ratio for each camp with confidence limits as described in Cochran (1977:156). Values were considered significantly different if confidence limits were non-overlapping.

Results

Activity pattern

During the six time periods examined, caribou were most active at sunrise and sunset (Fig. 1). The number of lying cycles was directly related to day length with periods of similar day length yielding similar cyclic patterns. Thus, early winter (15% day length) yielded one indistinct lying period (assessed visually from Fig. 1), late fall and mid winter (25%) yielded one distinct lying period, early fall and late winter (45%) yielded two full lying periods and, through extrapolation, in spring (60%), animals exhibited three lying periods.

The mean length of the active/bedded cycle varied from 238 min in early winter to 340 min in mid winter (Table 1). The mean length of the lying period decreased from late fall to early winter, then increased throughout the winter (Table 1).

Activity budget

The seasonal trend in percent lying was consistent for all years, decreasing from fall to early winter, increasing throughout the winter and decreasing again in spring. In each year values for percent lying in fall and early winter were significantly lower than those from mid winter to spring (Table 2). Furthermore, year three (1981-82) tended to have the greatest percent lying (significantly different from years one and two in mid winter and from year one in spring).

Since activity pattern appeared greatly influenced by day length, we examined the effect of daily observation time on our estimates of percent lying (Table 2). Some of our original observations extended from before sunrise to

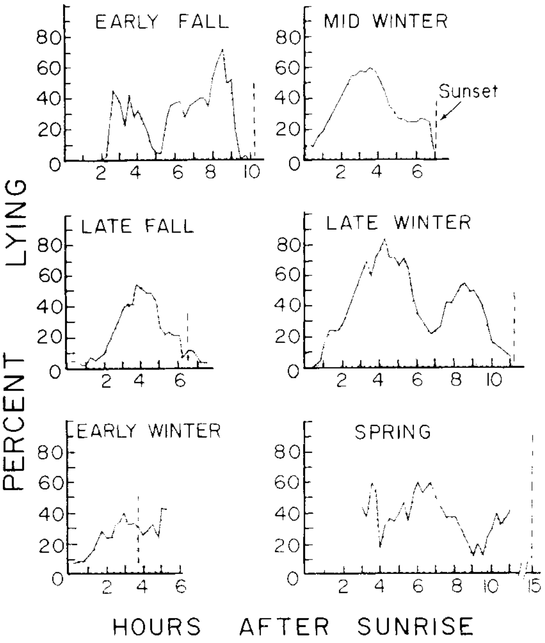

Fig. 1. Percent of animals lying from 15 minute scans in relation to hours after sunrise for the six study periods: early fall (10-13 Oct.), late fall (6-13 Nov.), early winter (5-15 Dec.), mid winter (26 Jan. - 6. Feb.), late winter (5-12 Mar.), spring (5-25 Apr.).

Table 2. Estimation of percent lying[1] from data of different time intervals (n=number of scans).

	All data			Sunrise to sunset		Hour after sunrise to hour before sunset	
Period	n	%	±95%CI[2]	n	%	n	%
1979-1980							
Late fall	82	20	3.9^{a}	80	20 (0)[3]	64	21 (+1)
Early winter	61	15	8.5^{a}	54	15 (0)	27	20 (+5)
Mid winter	89	30	5.9^{b}	88	30 (0)	69	35 (+5)
Late winter	111	45	5.5^{c}	107	47 (+2)	98	51 (+6)
Spring	110	33	5.5^{b}	110	33 (0)	110	33 (0)
1980-81							
Late fall	175	28	14.2^{a,b}	175	28 (0)	159	30 (+2)
Early winter	216	21	6.8^{a}	176	20 (—1)	111	23 (+2)
Mid winter	320	29	5.5^{a,b}	278	31 (+2)	196	39 (+10)
Late winter	155	42	13.0 ^{b}	155	42 (0)	150	44 (+2)
Spring	74	33	13.8^{a,b}	74	33 (0)	74	33 (0)
1981-82							
Late fall	183	28	6.4^{a}	172	29 (+1)	131	33 (+5)
Early winter	154	26	6.9^{a}	104	28 (+2)	47	32 (+6)
Mid winter	293	40	3.7^{b}	279	40 (0)	206	45 (+5)
Late winter	149	47	5.7^{b}	149	47 (0)	149	47 (0)
Spring	94	44	4.4^{b}	94	44 (0)	94	44 (0)

[1] Percent of the observation period animals spent lying (that is, for each winter period, percent lying=total number of animals lying/total number of animals observed in scans x 100).

[2] The 95% confidence interval is based on a single estimate on each band of caribou observed. Within each winter, values with the same subscript are not significantly different at the P=0.05 level.

[3] Bracketed value equals change from «all data» estimation.

after sunset. When we excluded data collected before sunrise or after sunset, the estimates changed little, but using only those data collected between 1 hour after sunrise to 1 hour before sunset we reduced our original sample size by 25% and consistently increased our estimate of percent lying for all time periods (Table 2). The change was not significant, however, for any period. Each spring and in late winter 1981-82 all our observations occurred well after sunrise or well before sunset.

Discussion

Other authors have noted that caribou cue their activity to sunrise producing a conspicuous «midday» peak in lying (Gaare *et al.*, 1975; Roby, 1978; Erriksson *et al.*, 1980). In the present study this «midday» peak generally occurred about 3.5 to 4.5 hours after sunrise, regardless of day length. The pattern of active and bedded cycles for the remainder of the day, however, is constrained by day length since caribou also appear to exhibit another peak in activity at sunset.

Researchers normally employ the «50% rule» when determining mean length of lying and active periods (Roby, 1978; Boertje, 1981). By this method a lying period starts when 50% of animals lie down and ends when over 50% get up again. Utilizing the area under the curve method in our study the length of the lying period increased throughout the winter from 56 min (early winter) to 153 min (late winter). Other researchers maintain that the length of the lying period is consistent throughout the winter (Segal, 1962; Roby, 1978; Boertje, 1981). In fact, Boertje (1981) concludes that his observed differences in percent lying among winter periods must be related to changes in the length of activity periods rather than the length of the lying periods. However, data in Tables 1 and 2 indicate that percent lying is significantly related to the length of the lying period (r=0.83, n=15) and not significantly related to the length of the active period (r=—0.43, n=15). We feel that the

«50% rule» is inappropriate for individual bands during short day length sampling times. Animals are normally active at sunrise and sunset and therefore complete active periods are seldom observed or if they are observed they are biased toward shorter periods. For example, using the «50% rule» we calculate for our study that the mean length of the active period over all winter periods is 109±11.1 min (mean ± SE, n=16) However, we had to disregard 42 incomplete active cycles (mean 200 min). By the area under the curve method the estimate of mean active period for all winter periods is 184 min. The major disadvantage of the area under the curve method is that no estimate of variation is possible.

In contrast, many complete lying periods were observed during the «midday» period. However the 50% rule is not appropriate when lying periods are short and animals are somewhat asynchronous. The combination of these two factors normally results in observers seldom noting 50% of the band lying. The bias in this case is towards longer lying cycles. From our observations these two factors do occur in the early winter period. Using the 50% rule we would estimate a lying period length of 108 min compared to 56 min using the area under the curve.

The fixed and thus predictable pattern of activity/lying peaks in relation to sunrise and sunset must be taken into consideration when comparing activity budgets between studies. In particular, the latitude, date, and time of daily observations are important when comparing winter activity among different herds. For example, comparing our results in early and mid winter to data presented by Gaare *et al.* (1975) could be misleading. They observed Norwegian herds at approximately 60°N compared to 65°N for our study. The day length in early and mid winter in Norway is 25% and 38%, respectively, compared to 15% and 25% in central Yukon. It is not surprising, therefore, that Gaare *et al.* (1975) presented an early winter cycle similar to our mid winter cycle (one very distinct lying peak) and a mid winter cycle similar to our late winter cycle (two distinct lying peaks). Furthermore, Gaare *et al.* (1975) indicated that their observation period in mid winter was only from 1.5 hours after sunrise to 1.5 hours before sunset, thus yielding an overestimate of percent lying compared to our estimates.

An examination of the literature indicates that few studies provide enough data points to compare winter activity patterns (percent lying as the indicator) to day length. However the available data indicate that larger seasonal

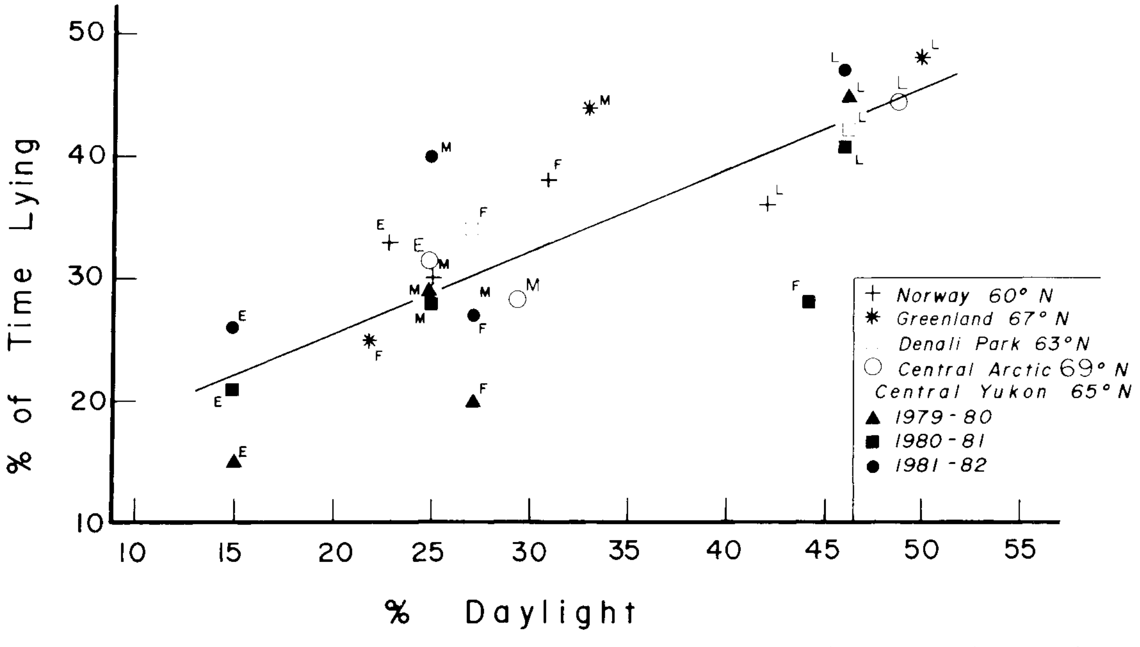

Fig. 2. Relationship between day length and percent lying from various studies for fall (F), early (E), mid (M), and late (L) winter. *Note:* Early fall 1980 for central Yukon not included in estimation of the line since observations occurred during the rut.

fluctuations in day length (i.e., higher latitudes) correspond to larger fluctuations in percent lying (Fig. 2). Herds in Norway (Gaare *et al.*, 1975), which exhibited the least variation in percent lying, were located at the most southerly latitudes. Our data (65°N latitude) generally exhibit a lower early winter minimum in lying and a higher late winter maximum. At even higher latitude, Roby (1978) recorded the greatest increase in percent lying from mid to late winter for the Central Arctic Herd.

The overall relationship between percent lying and day length appears linear for daylight values of less than 50%. Although a straight line has been drawn through the data in Fig. 2, we do not provide an equation because we do not know the exact observation dates for most studies. In Roby's (1978) study, for example, a 5 day change in the midpoint of his observation period could result in a 5% shift in day length.

An important factor that contributes to the variation in percent lying for each day length (Fig. 2) is range quality, as indicated by food availability and/or food quality. Our data indicate that percent lying increases in severe snow conditons (Martell and Russell, unpublished data). Because of this and the fact that diet did not vary significantly between years in our study (Martell and Russell, unpublished data), we hypothesize that this increase in percent lying results in most cases from a decrease in forage availability rather than forage quality. This hypothesis is based on R.G. White's (University of Alaska, pers. comm.) contention that caribou can physiologically reduce rumen volume at times of low food availability, thus requiring less feeding time to fill the rumen. Reduced rumen volumes in winter have been documented for field killed animals (Staaland *et al.*, 1979). Increased lying time therefore should be caused by either longer rumination time (to extract the maximum amount from limited food supply) or by an energy conservation strategy whereby the lying period exceeds time necessary for rumination, as documented by Erriksson *et al.* (1981). Forage quality can also affect percent lying since ingestion of poor quality forage requires longer rumination times for digestion thus longer lying periods (Blaxter, 1962; Cammell and Osborn, 1972). With standardized observations plotted as in Fig. 2, the points above the line should correspond to poorer quality or less available forage and points below the line should indicate higher quality or more available forage.

Studies that indicated poor range conditions do tend to fall above the line in Fig. 2. Roby (1978) indicated that preferred forage (lichens) had low availability on the range of the Central Arctic Herd in northern Alaska. Range quality on Greenland was very poor and animals were near starvation (Roby, 1980). Gaare (1968) indicated that a significant decline in lichen biomass had occurred on the Snøhetta range in southern Norway (fall value for Norway, Fig. 2). As well, estimates of percent lying from the present study indicate poorer quality range in deep snow years (e.g., 1981-82) than shallow snow years (e.g., 1980-81 (Martell and Russell, unpublished data)). Another indication that lower food availability results in higher values is illustrated by comparing values for fall and mid winter for animals on the same range. At similar day length, fall values tend to be lower than mid winter values.

Acknowledgments

Throughout the study many people contributed to the success of the project. Technical field assistance under sometimes severe weather was routinely carried out by Janet MacDonald, Kim Asquith, Christine Boyd, Bob Hayes, Susan Fleck, Wendy Nixon, Catherine McEwan, Hammond Dick, Malcolm Dennington and Heather McLeod. Jim Hawkings assisted in the computer analysis. Advice from John Smith on statistical analysis was greatly appreciated. Funding for the project was received from the Government of Yukon (for whom the senior author worked during the field phase of the project), the Canadian Wildlife Service, the Northern Roads and Airstrips Division of the Department of Northern Affairs and Polar Continental Shelf Project.

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Physiological control of growth, reproduction and lactation in deer.

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Abstract: The physiological mechanisms controlling the growth, lactation and reproductive cycles of cervids, and the control of allocation of energy to different organs are discussed. The growth cycle may be secondary to an appetite cycle, regulated by changes in the secretion of prolactin, gonadal steroids, and possibly unknown factors. The reproductive cycle is controlled by changes in the release at the hypothalamic hormone GnRH, and by changes in the feedback effect of gonadal steroids. These cycles are probably the result of the timing effects of nutrition and changing photoperiod on an endogenous, circannual rhythm. The effect of photoperiod is mediated by the pineal hormone melatonin. The physiological mechanisms controlling the partitioning of substrates between milk production, fetal growth and the tissues of the mother are poorly understood, but may involve changes in the secretion of growth hormone, insulin and triiodothyronine.

Key words: cervidae, seasonal cycles, endocrine regulation

Rangifer, Special Issue No. 1, 1986: 261 - 266

Introduction

In the northern latitudes, where the supply of food changes annually, the rate of production must necessarily change. However, production in these animals does not passively follow changes in food intake, instead the whole physiology of the deer changes seasonally, to be adapted to the environmental conditions. The energetically most costly processes - growth and lactation - take place during the period of highest plant production, whereas fetal growth, which requires less energy, occurs during winter. When various productive processes do occur at the same time, they must compete for energy and substrates.

This review is concerned with how the productive processes of deer are regulated in such a manner as to make best use of the annual cycle of plant production, by correct timing, and by sharing available resources.

Growth

Cervids have a cyclic growth pattern, with rapid weight gain in summer, followed by a winter growth stasis (Ryg, 1983). The annual growth cycle may passively follow an appetite rhytm, although this is not firmly established. Nilssen *et al.* (1984) reported that basal metabolic rate does not change throughout the year. Maintenance requirements of reindeer, measured by the amount of food required to maintain body weight, do not change from winter to early summer (Ryg and Jacobsen, 1982a), and weight gains per unit of food above maintenance is the same in early summer as in winter (M. Ryg, unpublished data). On the other hand, when maintenance requirements of roe deer (Ellenberg, 1978) and white-tailed deer (Holter *et al.*, 1979) was calcluated from energy balance trials, a seasonal cycle was apparent. It is not clear whether these differences are due to methodology or species.

In studies of seasonal appetite, grain-based concentrates have commonly been used as feed. With such diets, the appetite of ruminants is regulated by metabolic signals. The significance of these studies for natural conditions, in which roughage intake is limited more by gastrointestinal factors (Freer, 1981), is unclear. On roughage diets, seasonal appetite could be explained by changes in gastrointestinal capacity (Milne *et al.*, 1978; Mitchell *et al.*, 1976; Staaland *et al.*, 1974.). However, the seasonal regulation of that capacity is unknown, and there may be interactions with metabolic factors.

Although the seasonal growth pattern is entrained by photoperiod (Brown *et al.*, 1979) the controlling mechanisms are unknown. Pinealectomy of white-tailed bucks had no effect on either growth or food intake cycles (Brown *et al.*, 1978), but this could be attributed to the age of the animals, or the limited duration of the experiment. Pinealectomy of young animals affects the seasonal changes in prolactin and gonadal steroids, both of which have been implicated in the control of appetite cycles (Ryg, 1983; Suttie, 1980).

Although cervids may start gaining weight in spring, fat is mostly deposited in autumn and late summer (Dauphiné, 1976; Mitchell *et al.*, 1976). Lipogenic capacity of isolated fat cells parallels changes in food intake (Larsen, Nilsson and Blix, 1985), but from data presented it appears that for a given intake, lipogenic capacity of the fat cells is highest in autumn. This change could be hormonally mediated, since in spring, levels of growth hormone (GH) (which is protein anabolic and lipolytic) are high (Ryg, 1983) and triiodothyronine (T_3) levels increase markedly with increasing food intake, at least in young males (Ryg, 1984b; Ryg and Jacobsen, 1982a). Insulin levels also increase in summer (Larsen, Lagercrantz, Riemersma and Blix, 1985), possibly the result of an increse in food intake. During late summer and autumn, GH leves are usually low in adults, and level of food intake has only a minor effect on T_3 concentrations (Ryg, 1984b). High insulin, and low GH and T_3 levels, in combination with a sustained high food intake, could promote fat deposition. The high GH levels occationally found in calves in autumn might limit lipogenesis. Seasonal changes in T_3 levels in adult females are strikingly different from those found in young males (Bahnak *et al.*, 1981; Nilssen *et al.*, 1984), but whether this is related to differences in metabolic patterns is not known.

Skeletal growth of reindeer is regulated to some degree independent of the appetite cycle. After an obligatory growth stasis from October to January, skeletal growth commences and with good nutrition, the rate of growth may be faster in winter than in summer (Ryg, 1983; Ryg and Jacobsen, 1982a). Food restriction had less effect on skeletal growth in summer than in winter, suggesting that skeletal size may be determined more by winter than summer nutrition. This agrees with the observation of Skogland (1983) that mandible length of free ranging reindeer correlated better with winter than summer conditions, although his results may also be interpreted as an effect of maternal winter nutrition on fetal and early postnatal growth (Skogland 1983, 1984).

Gonadal function and reproduction

Seasonal reproductive cycles are regulated by changes in the secretion of the hypothalamic gonadotrophin releasing hormone (GnRH) (Lincoln and Short, 1980), and by changes in the sensitivity of the hypophysis to the negative feed-back action of gonadal steroids (Karsch and Foster, 1981). Before the rutting season, the secretion of GnRH increases and the feedback effect of steroids decreases, resulting in increased hypophyseal and gonadal activity. Frequently there is a peak of gonadotrophin and steroid secretion in spring (Bubenik *et al.*, 1979; 1982; Ryg, 1984a; Sempere and Lacroix, 1982), suggesting a semiannual cycle of reproductive function. The secondary gonadotrophin peak in spring is possibly attenuated by the negative feedback effect of gonadal steroids, since it was much more pronounced in castrates than in intact white-tailed bucks (Bubenik *et al.*, 1982).

High prolactin (PRL) levels are often associated with infertility, and it has been suggested that sexual quiescence in summer is caused by the seasonal increase in PRL secretion. However, suppression of PRL secretion with bromocryptine did not stimulate gonadal function in the ewe (McNeilly and Land, 1979). Possibly the inverse relation between PRL and gonad function is regulated by the hypothalamus. Recently, it was found that the precursor peptide for GnRH contains a peptide that inhibits PRL secretion (Nikolics *et al.*, 1985). GnRH and the prolactin-inhibiting peptide are located in the same hypothalamic nerve terminals (Phillips *et al.*, 1985) and presumably are released at the same time. Increased activity in these neurons conld simultaneously stimulate gonadotrophins and inhibit PRL secretion.

The most important external stimulus to gonadal development and regression is the photoperiod; the response is probably mediated by melatonin from the pineal gland. Melatonin administered orally or intramuscularly advances the rutting season of red deer *(Cervus elaphus)* (Adam and Atkinson, 1984; Webster and Barrell, 1985) and white-tailed deer *(Odocoileus virginanus)* (Bubenik, 1983). The effects of pinealectomy on the reproductive cycle are variable. It has little effect on old animals (Brown *et al.*, 1978). In young animals, the testicular cycle may be suppressed, although usually gonadal and hypophyseal cycles persist, but become irregular and out of phase with intact animals (Plotka *et al.*, 1984; Schulte *et al.*, 1981; Snyder *et al.*, 1983). This indicates that the annual cycle is timed, but not generated by, the pineal gland. This suggestion is supported by the classical studies of Goss (1969a, 1969b) which showed that an endogenous, circannual rhythm was involved in the control of antler growth in Sika deer *(Cervus nippon)*.

As with other mammals, female deer must reach a critical body weight, or fat content, in order to conceive (Albon *et al.*, 1983; Ellenberg, 1978; Hamilton and Blaxter, 1980; Lenvik *et al.*, 1982; Reimers, 1983; Thomas, 1982.) The effect is most likely on ovulation rates (Leader-Williams and Rosser, 1983). It is not clear, however, what the metabolic signal is. The critical body weight, as a percentage of mature body weight varies between species and subspecies. Albon *et al.*, (1983) reported that the critical body size in red deer hinds increased with increasing populations density, and Lenvik *et al.*, (1982) reported that reindeer *(Rangifer tarandus)* hinds conceived at a later age when 1½ year old bulls were used as breeding males, than when older males were used. So it appears that the metabolic signal can be modulated by other factors, which are at present poorly understood. Finally, it has been suggested that frequent suckling, associated with poor nutrition, could delay or suppress estrus in red deer (Loudon *et al.*, 1983). Whether this mechanism would apply to reindeer, whose «follower» calves normally suck more frequently than red deer calves, is questionable.

Pregnancy

Maintenance of pregnancy depends on the presence of progesterone, secreted by the placenta, or by one or more corpora lutea. In white-tailed deer, the corpus luteum of pregnancy is the most important source of progesterone. Ovariectomy induces abortion as late as 156 days of pregnancy (Plotka *et al.*, 1982). Whether the maintenance of the corpus luteum of pregnancy depends on luteotropic hormones from the hypophysis or the placenta in deer is not known, but a luteotropic and lactogenic hormone (placental lactogen, PL) is apparently secreted by the placenta of fallow deer *(Dama dama)* (Forsyth, 1973). Parturition is probably initiated by a declining luteal function. It is preceded by a decline in maternal progesterone leves (Blom *et al.*, 1983), and injection of the luteolytic substance prostaglandin $F_{2\alpha}$ induces parturition (Langvatn, 1986). The exact timing of birth is influenced by the nutritional status of the dam; poor nutrition delays birth (Reimers *et al.*, 1983; Skogland, 1984). Since parturition is initiated by factors related to the degree of maturity of the fetus (Nathanielsz, 1978), this effect is probably a result of slower fetal growth.

The growth of the fetus depends, of course, on the transfer of substrates across the placenta, and may be regulated by the substrate supply to the feto-placental unit, by the size of the placenta, or by endocrine factors. Inadequate nutrition affects the growth of the fetus. Under a wide range of experimental and natural conditions, the weight of the fetus or newborn calf is correlated with the body weight of the dam (Rognmo *et al.*, 1983; Skogland, 1984; Varo and Varo, 1971), indicating that the energy flow to the fetus is a more or less constant part of total metabolic turnover of the dam. The effects of severe undernutrition in early pregnancy, which could inhibit placental development, has not been studied. Fetal growth may be influenced by hormones from the fetus itself, or from the placenta, e.g. placental lactogen (PL), which affects fetal glucose metabolism (Freemark and Handwerger, 1984) and somatomedin production (Adams *et al.*, 1983) and could act as a fetal growth hormone. However, no studies on the effects of maternal nutrition on plasma levels of PL have been conducted.

Lactation

The development of the milk gland is induced by the presence of a conceptus, but little is known about the endocrine regulation in cervids. Progesterone and estrogen, produced in incresed amounts during pregnancy in deer (Blom *et al.*, 1983; McEwan and Whitehead, 1980; Ringberg and Aakvaag, 1982) are probably important. Peptide hormones secreted by the hypophysis (PRL and GH) or placenta (placental lactogen) may participate as well.

Milk secretion by the fully developed gland is partly under nutritional and partly endocrine control. As with other mammals, progesterone probably inhibits milk secretion in deer. When birth of red deer fawns was induced prematurely by prostaglandin injections, the fawns grew normally (Langvatn, 1986). This suggests that the milk secretion started as soon as the corpus luteum, the most important source of progesterone, regressed.

The energy and substrates needed for milk production must be taken from increased food intake or, especially in early lactation, from the body reserves of the dam (Sadleir, 1984). Both the size of the dam at birth (Jacobsen *et al.*, 1981; Rognmo *et al.*, 1983; Skogland, 1983) and nutrition during lactation (Loudon *et al.*, 1984) affects milk yield and calf growth. It has been pointed out that, since the fertility of the female is related to her condition, extended suckling would diminish the chances of conceiving in the fall. White and Luick (1984) presented some evidence that the growth of the mother may have priority over that of the calf; when food was restricted in mid lacation, milk yield and calf growth rate declined, whereas the restriction had little effect on the growth of the dams. The growth rate of red deer dams was scarcely affected by range quality after midsummer. However, up to 40 days of lactation (about mid July), nutrition strongly affected body weight of the females (Loudon *et al.*, 1984), indicating a shift of priorities about mid summer. Before this time the body condition of the dam will decline when nutrition is poor, in order to maintain milk yield as much as possible, whereas in late lactation, poor nutrition will cause diminished milk yield.

The control of milk secretion in cervids is poorly understood. The declining milk yield in late summer might be a result of the seasonal decline in PRL levels. Although PRL is not considered necessary to maintain established lactation in domestic ruminants (Forsyth and Hayden, 1977) Loudon *et al.*, (1983) found a positive correlation between PRL levels and milk yield of red deer hinds throughout lactation, and results from animals selected for high milk yield may not be applicable to wild ruminants. PRL may simultanously stimulate food intake (Ryg and Jacobsen, 1982b), thus ensuring a sufficient substrate supply, an so, growth and lactation may have some endocrine control in common.

The question then becomes how the flow of energy and substrates is partitioned between the milk gland and the tissues of the mother in early lactation. White and Luick (1984) suggested that, since lactose synthesis may be the pace-setter of milk secretion, the control is exerted via the glucose metabolism of the dam, and endocrine control of glucose metabolism may be important. Growth hormone, which is necessary for maintaining lacation in domestic ruminants (Forsyth and Hayden, 1977), and in the lactating cow shifts nutrient flow from the tissues of the female to the milk gland (Tyrrell *et al.*, 1982) is elevated during lactation in white-tailed does (Bahnak *et al.*, 1981) and reaches maximum levels later than what is seen in males (Ryg, 1983).

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Movements of tagged and radio-instrumented wild reindeer in relation to habitat alteration in the Snøhetta region, Norway

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Abstract: In winter, 1981, 103 reindeer, out of a population of 3600, were herded into a fence by snowmobiles and marked. During the next 4½ years reindeer were followed from the ground, or by radiolocations from an airplane. On the average one animal was tagged per 42 animals in any group. A total sample of 175 locations in all seasons indicated that snow conditions, traffic on a road lying parallel to a railroad, and the damming of a lake significantly affected annual distribution as compared with expected modern as well as prehistoric distribution.

Keywords; reindeer, movements, habitat alterations, demographic effects.

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Introduction

Previous to and during the nineteenth century a single herd, called the Dovrefjell herd wintered in the Rondane and Knutshø region, and moved westward to the Snøhetta region for calving and summer pastures (Skogland and Mölmen, 1980). During the early years of the nineteenth century overshooting had reduced all wild reindeer herds in Norway to a very low level, resulting in 5 years of hunting prohibition. Subsequent to this period, herds increased again and hunting was resumed. By 1920 the Dovrefjell herd had again been severely depleted, perhaps to a few hundred animals in Snøhetta in the fall of 1920 (see Skogland, 1977). In the period 1920-1926 a railroad was built across the migration route (see map in Skogland and Mölmen, 1980) to the fall-winter range in Rondane. At the time of hunting (late August, early September) reindeer were usually found in the central and western parts of Snøhetta and were not shot in any large numbers near the railroad. One might argue that lead animals coming to traditional crossings are the first to be shot so that the crossing tradition is shot out. Since hunting licences are tied to land ownership and many land owners in five municipalities are involved, hunting is distributed relatively even over the entire area. This tends to minimize the shooting out argument. During the construction period no animals were reported crossing eastwards. After the completion of the railroad, during the 1920s, the herd slowly recovered from its low numbers of 1920, probably due to the controlled hunting program that had been established.

During the second World War hunting was prohibited, and the herd increased west of the transportation corridor, reaching more than 8000 individuals in 1950 (Holaker, 1955). By this time, a year-round road, parallel to the railroad track, had also been completed. By the winter of 1956 the herd on the *west* side of the corridor numbered about 15000 head (Holaker, 1955). Starvation was found that winter, the harshest on record (with 250% of normal snow accumulation; meterorological records of Norway), and several hundred animals starved to death (Holaker, 1957). The lichen mats were completely denued (Nordhagen, 1963; Gaare, 1968), and about 2000 animals finally crossed the railroad and road (P. Holaker, pers. comm.). A reduction-shooting program was undertaken to prevent mass starvation on the west side of the corridor, and by 1965 the herd had been reduced to a few thousand (Krafft, 1965).

Since 1971 the herd had been slowly increasing from 1200, to a maximum of 3500 head in the winter of 1981. During the 16-year period, a few to several hundred animals crossed the railroad and highway occasionally or even every winter. In the winter of 1972 - 73 a few hundred adult females failed to return across the transportation corridor, presumably because the Driva river opened up a month earlier than usual. They stayed and calved in the Knutshø region (P. Holaker, pers. comm.), and formed what is now called the Knutshø herd, which today numbers 1000 wintering head. They live on superfluous winter pastures and similar summer pastures as compared to Snøhetta, and attain record size (see Skogland, 1983), whereas the Snøhetta deer are still suffering from the effects of winter range overgrazing.

In the period of population reduction in the 1960s the recruitment rate of reindeer in the Snøhetta area was down to about 20 calves/100 does, and body size was smaller than it is today. The lichen mats in Knutshø today have a mean of 600 g DM (dry matter)/m^2. In Snøhetta in the early 1960s it was about 25 g DM/m^2. It has slowly been restored to about 100 g DM/m^2 by the present time (Skogland, 1983, 1985).

The recruitment rate and body size of Snøhetta reindeer vs. the Knutshø reindeer have been followed for over a period of about 10 years (Skogland, 1985). The mean calf/doe ratio in Snøhetta was about 38 calves/100 does ≥1 yr, whereas the ratio in Knutshø has been about 62/100 (Skogland, 1985). Body size (dressed weight) for adult does ≥3 yr in Knutshø was about 46 kg, compared to about 32 kg in Snøhetta (Skogland, 1983), and represents a rather spectacular demographic effect. The size of Snøhetta reindeer was similar to present-day Knutshø reindeer in the 1950s before the overgrazing took place (Hjelmeland, 1981). The

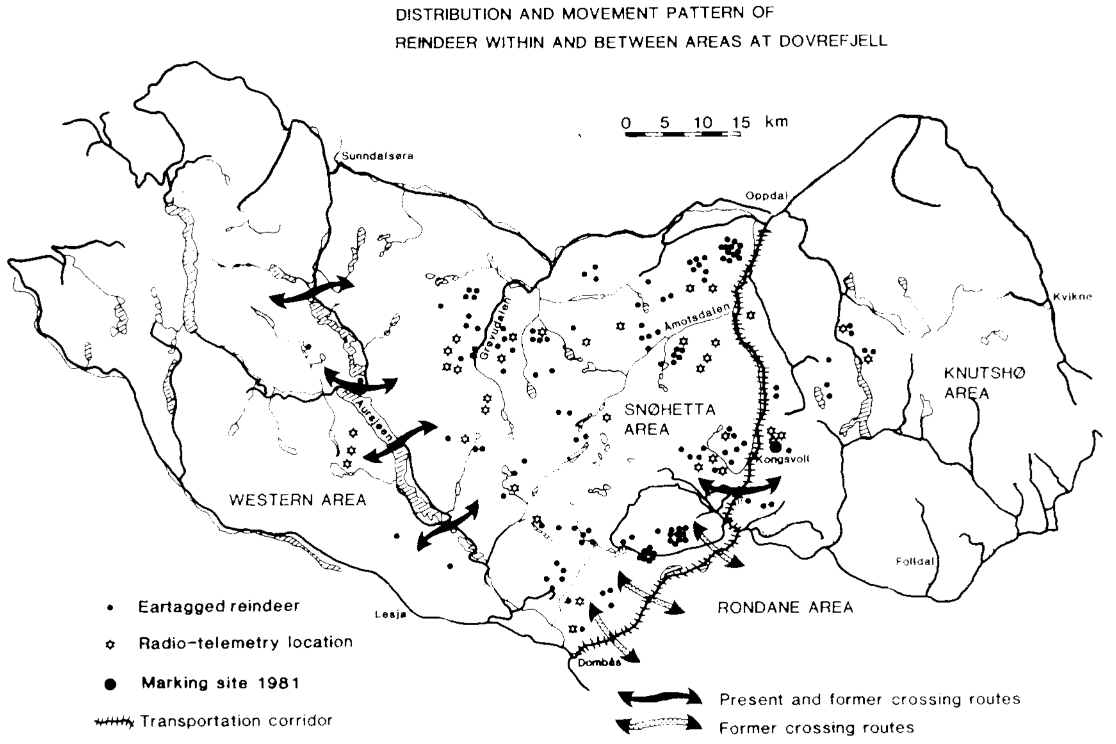

Fig. 1. The distribution of ear-tagged and radio-collared reindeer in Snøhetta - Knutshø 1981 - 85. Roads are shown by a dark line.

lower calf productivity in Snøhetta after this period is due to worse feeding conditions in Snøhetta compared to Knutshø during gestation with subsequent higher calf mortality (Skogland, 1984, 1985).

In the period between 1955 and 1965 a hydroelectric dam was constructed in the western part of Snøhetta. The shores of two lakes, Aursjøen and Torbu, were raised by 28 m (Fig. 1). An access road, two hydroelectric power lines, and an increasing number of cabins for recreational purposes were established along the access road. The two flooded lake valley floors interfered with the lowest altitude portion of the previous calving area, and flooded the seasonal routes of reindeer movement to the western early spring and summer pastures. After dam construction had been completed, a marked drop in use of areas to the west of the lakes was noted, and calving shifted to the east (Skogland and Mölmen, 1980; Skogland *et al.*, 1981).

In order to be able to quantify the effects of habitat alteration on the access to calving — summer range in the western area (Snøhetta), as well as to the winter range in the east (Knutshø), a program of tagging reindeer was initiated. The hypothesis tested was that habitat alteration, in the form of flooded valley floors, and an all-weather road and railway acted as barriers to free passage of reindeer along long established, prehistoric access routes between seasonal habitats.

Methods

The winter of 1981 was as hard as the winter of 1956 and there was evidence of some starvation on the Snøhetta side of the transportation corridor, and 44% of the Snøhetta herd, about 1600 animals, crossed into Knutshø.

About 150 of a group of 600 of these reindeer was herded by snow mobiles into a 2 m high fenced corral where 103 were eartagged and 3 of them also fitted with radio collars. An equal number of both sexes were tagged. About 2.9% of the total population of 3600 wintering reindeer in 1981 was tagged.

After tagging, the animals were followed on the ground and by telemetry locations from a small airplane fitted with receiving antennas on the wings.

Results

During the regular hunting season following tagging, 23 tagged reindeer have been shot by hunters. Included in this number are two of the three radio-collared does (one shot in 1983 and one shot in 1984), while the last one was still transmitting by mid May 1985. A total of 175 relocations representing about 80% of tagged reindeer were recorded, 37 of which were of the three radio-collared females (Fig. 1).

Social dispersal

During the first year following tagging, an attempt was made to record the dispersal pattern of individuals from the winter aggregation in Knutshø. After release the animals stayed in Knutshø until the spring return to Snøhetta during the end of April 1981. During the following year I recorded in Snøhetta an average of one marked individual for evey 42 animals ±9.42 SE, n=58 groups). The mean group size in Snøhetta was 77 animals (Skogland, 1977).

Movments to the western area during spring and summer

During the period following tagging, the mean population size in Snøhetta was 2800 wintering reindeer and 3500 animals after calving (Skogland, unpublished data). During the period after marking, only 8 tagged animals including 4 radio-locations were recorded in the area west of Aursjøen.

A total of 175 observations of tagged or radio-collared animals were recorded in the period following tagging. Out of these five were from animals wintering in Knutshø, and eight from the summer range in the western area. Thus, in the western area about 4.6% of all observations (or 140 animals of the total herd of 3500) were recorded. Annual ground counts from the western area carried out since 1975, have yielded from 130 — 170 animals annually in this area, indicating that the proportion of recorded tagged individuals in this area corresponds to the proportion of the total herd distributed east and west of the dammed Aursjøen area.

Out of the recorded animals in the western area, only 20% were does with calves. A maximum of 10 calves has been counted in any summer since 1975. Thus, the previous calving and summering in the western area has, to a large extent, been relocated further to the east.

Previous distribution patterns have not returned after a period of 21 years following the completion of the dam.

Movements to the winter range in Knutshø

During the period 1976 — 85 I have recorded the annual crossing of the transportation corridor, as far as possible. The historic or traditional crossing places were used. In 1977 recording was made impossible by incessant poor weather conditions. In Fig. 2 I have plotted the proportion of the Snøhetta herd which crossed in relation to the percentage snow accumulation in the first part of winter at which time they normally crossed. The data suggest that there is a positive correlation between snow condition, as influencing foraging conditions, and the chance of crossing the corridor to obtain better food ($r=0.64$, $P<0.05$).

During the years following tagging, 44% in 1981, 5% in 1982, and no animals in 1983, 1984 and 1985 crossed the corridor. In 1982 one radio-collared and five tagged animals crossed. In the 3 following years no tagged animals crossed. The distribution of tagged reindeer thus complements the distributional pattern of the herd in general, both during winter and summer. On approaching the transportation corridor, groups were usually frightened back from distances of 100 — 300 m. This usually led to flight up to ½ — 1 km away. Flight releasers were usually moving cars or trains. Most crossings occurred at night when traffic was minimal.

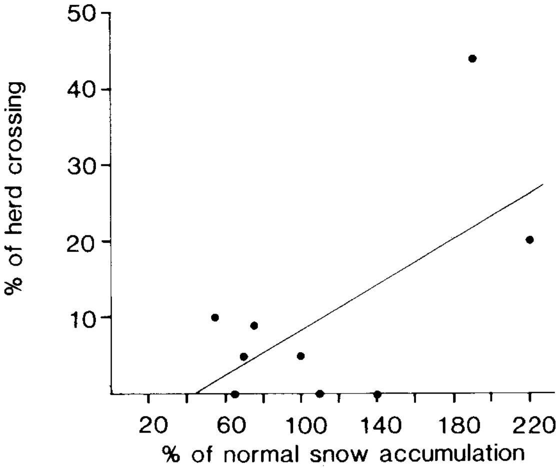

Fig. 2. The percentage of the Snøhetta herd which crossed the transportation corridor (European highway No. 6, and railroad track) across Dovrefjell in relation to percentage normal snow accumulation (data from Norwegian Meteorological Records).

Table 1 shows the distribution of observed tagged reindeer in relation to the three parts of the former reindeer range. Most of the observations were concentrated in the central Snøhetta, where a seasonal pattern of use has been established following the earlier habitat modifications. Compared to the expected observations, the null hypotesis that annual distribution is homogenous in relation to seasonal habitats must be rejected ($x^2=159.15$, $P<0.001$).

Discussion

On the average, the likelihood of recording at least one tagged reindeer in every group in Snøhetta was high. This result indicates a very open social system which would tend to minimize the bias of using tagged individuals which may be expected from a more clumped distribution.

These results support Valkenburg *et al.*'s (1983) hypothesis that the basic social unit of caribou (or in this case reindeer) is a temporary, tenuous association of individuals in an open

Table 1. Observation frequency of tagged reindeer in relation to expected, based on size of different areas and the assumption of a homogenous distribution.

	Size (km^2)	Observations	Expected
Central Snøhetta	2375	162	79
Knutshø (wintering area)	1600	5	54
Western area (summer range)	1225	8	42
Totals	5200	175	175

social system. From the aggregated winter band in which they were caught and tagged a marked social dispersion occurs during the following spring, summer and autumn.

Examination of the distribution of prehistoric trap sites in Snøhetta (Skogland and Mölmen, 1980) reveals a concentration of pit trap sites in the western area which is very high compared to central Snøhetta. A very high concentration of pit trap sites (1200 is also found along the transportation corridor between Snøhetta and Knutshø and Rondane, through which animals previously would move during their annual spring and autumn migrations.

The present distribution of reindeer in Snøhetta in the western area is therefore clearly lower than that found prior to habitat alteration by modern man as suggested by prehistoric evidence.

Fiftynine years after the completion of the railroad, and about 35 years after the opening of an all-weather highway across Dovrefjell, movements across this transportation corridor to wintering areas to the east are far below the prehistoric level (Fig. 2).

Evidence accumulated after nearly 5 years of following tagged individuals strongly suggests that severity of winter weather in the form of snow accumulation, which limits access to the already denuded lichen heaths in the central Snøhetta, is the major driving force initiating crossing of the transportation corridor. Snow levels above 160% of normal accumulation appear to act as a threshold to crossing. In winters of normal or below average snow conditions, reindeer in central Snøhetta prefer to stay within this area instead of crossing the transportation corridor to better winter ranges in Knutshø. All evidence suggests that traffic along the corridor is the inhibiting factor for crossing. Recent work on caribou in Alaska along the trans-Alaska oil pipeline suggests that vehicles act in a synergistic fashion with a pipeline to produce a negative stimulus that resulted in decreased crossing success (Curatalo and Murphy, unpublished data). See also Horjesi (1981).

The consequence of lowered use of the western part of Snøhetta is most likely an additional trampling of the already previously denuded lichen heaths, caused by a year-round existence in the central Snøhetta area. This will slow the recovery rate of the overgrazed lichen heaths.

The study suggests that in the western area that was previously used as a calving-summering area, males have resumed use to a larger extent than females with young. The ratio of males to females in the area was 80:20 while the population sex ratio was on average 40:60 (Skogland, unpublished data). Cameron (1983) and Whitten and Cameron (1983) found that caribou males were found closer to the trans-Alaska oil pipeline and haul road than females. Both in Knutshø and Snøhetta there were access roads with restricted traffic (see Fig. 1). These roads do not appear to hinder movement of reindeer when there was no traffic. In the western area it appears that the combined effects of a dammed lake, roads with some traffic, recreational activity as well as two high-power electrical lines parallel to the lakes and roads could act in a synergistic fashion to prevent the more shy females with young from crossing.

Acknowledgements

Pilot Richard Grefstad and telemetry operator Gunnar Ottem are appreciated for their skillful operations in the air. John Nordfjell and his crew of reindeer herders are acknowledged for their competent handling of the tagging operations. Simen Bretten and his family are acknowledged for their logistic support and hospitality at the Kongsvold Biological Field Station. Marit Helgesen, DN kindly typed the manuscript and Britt Egeland, DN made the drawings.

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Thermoregulation in reindeer

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Abstract: Thermoregulation was studied in Finnish reindeer (*Rangifer tarandus* L) on captive and herded individuals during 1977-85. Newborn calves maintained a high rectal temperature (Tre) (+39-41°C) even at —23°C by increasing heat production 5- to 6-fold through non-shivering thermogenesis, stimulated by cold-induced noradrenaline (NA). Plasma NA and thyroxine (T4) were high (18 ng/ml and 459 nmol/l) in neonatal reindeer. Sensitivity to exogenous NA was lost during the first 3-4 weeks of life. At +20°C and above, calves increased Tre (ca 1°C), oxygen consumption and heart rate, thereby showing poor heat tolerance. Thermal conductance was low in a cold environment, but rose sharply as ambient temperature (Ta) increased above +10°C. The Tre of adults (+38-39°C) was independent of Ta (—28 to +15°C). Coarse (hollow) hair density and length in adults averaged 2000/cm^2 and 12 mm on the legs, 1000/cm^2 and 30 mm on the abdomen and 1700/cm^2 and 30 mm on the back (calves 3200/cm^2, 10 mm), respectively. The dependence of skin temperature on the Ta was linear in excised fur samples, but complex in living animals being strongest in the legs. Serum adrenaline correlated with the weight, age and total lipids. Serum NA and dopamine-ß-hydroxylase were highest in spring and decreased by autumn. Serum T4 was highest in summer and lowest in spring.

Key words: thermoregulation, insulation, catecholamines, reindeer.

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Introduction

The semi-domestic Finnish reindeer (*Rangifer tarandus tarandus* L.) is well adapted to wide seasonal changes in climate, nutrition and photoperiod in the subarctic. Seasonal thermoregulation involves changes in insulation and metabolism. Energy expenditure is lower in winter than in summer and metabolic requirements of thermoregulation are minimal. Heat is saved by effective fur insulation and peripheral heterothermia of the extremities (Irving and Krog, 1955). Consequently, the reindeer endures cold as severe as —62°C without evident difficulty (Gultsjak, 1954).

Calving begins in late April, when pastures are still snow covered. Survival of the calves in the harsh postnatal environment demands the maintenance of a high body temperature. Primary protection against cold is provided by a birth fur. Further, heat production by metabolism of brown adipose tissue, or non-shivering thermogenesis (NST), is assumed to play an important part in cold resistance in neonates (Hissa *et al.*, 1981). Little is known about the heat tolerance of reindeer calves. Hot midsummer weather may cause them considerable heat stress,as it does for adult reindeer.

In this paper we report thermal and metabolic responses of reindeer calves to various ambient temperatures (Ta) during their first weeks of life (Soppela *et al.*, 1986). The structure and insulative properties of reindeer fur and blood chemical constituents that may have thermoregulatory significance are also studied based mainly on works by Nieminen *et al.* (1984) and by Timisjärvi *et al.* (1984).

Material and methods

Thermoregulatory capabilities of 51 (50M + 1F) reindeer calves aged 1 to 35 days were studied at the Kaamanen Reindeer Research Station, Finland (69°10' N) in 1981 and 1982. Calves were divided into four age classes: 1-4, 6-9, 16-18 and 27-35 days. Measurements were performed in a metabolic chamber, in which the temperature (Ta) was stepwise decreased or increased in the range —27 to +35°C. At each Ta, stabilized recordings of rectal temperature (Tre), skin temperature (Ts) at various locations, oxygen consumption (VO_2), heart rate and muscle shivering (EMG) were monitored (Hissa *et al.*, 1981; Soppela *et al.*, 1986). Heat loss was estimated by calculating thermal conductance according to the equation of McNab (1980). Non-shivering thermogenesis (NST) was tested by injecting noradrenaline (NA) subcutaneously in newborn and growing reindeer calves at different Ta's.

Fur structure in six adults and four newborn calves was examined using light and scanning electron microscopy. Skin samples were collected from the back, abdomen and foreleg in adults and from the back in calves. Rectal (Tre) and skin temperatures (Ts) at four locations (foreleg, back, abdomen and muzzle) were measured for 216 animals (74 hinds, 142 calves, F, M) at varying Ta's (—28 to +15°C) and seasons in several reindeer herding districts during 1977-82. Ts on excised skin samples were measured *in vitro* attached to a heat sink in the laboratory (Timisjärvi *et al.*, 1984).

Blood glucose and lactate, serum total lipid and triglyceride, thyroxine (T4), adrenaline (A) and NA concentrations and serum dopamine-ß-hydroxylase activity (DBH) were studied in 61 hinds and 81 calves at the Research Station and in several reindeer herding districts during 1977-78. Calves varied in age from 1 day to 10 months; hinds 3-10 years. Ta varied from —28°C to +14°C. Reindeer were penned outside with ample fodder or they grazed freely on pastures. Blood samples were taken from the jugular vein and kept frozen at —20°C until analyzed (Nieminen *et al.*, 1984).

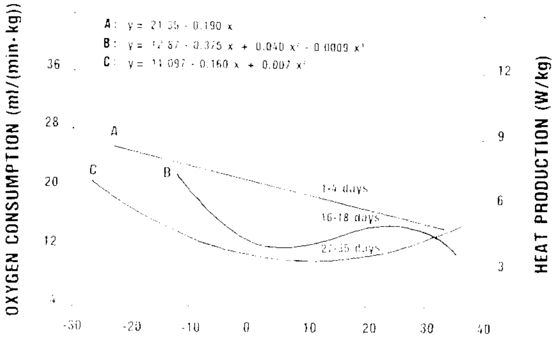

Fig. 1. Relation of oxygen consumption (heat production) and ambient temperature (Ta) in reindeer calves in three age classes, after a 30 min exposure to a given Ta. The goodness of fit of polynomial regression was checked by an F-test after each increment of the polynomial degree. (y = oxygen consumption and x = Ta)(modified from Soppela *et al.* (1986)).

Results

Calves aged 1-4 days maintained a high Tre (+40.2°C) even at —22.5°C by increasing oxygen consumption (VO_2) linearly as Ta decreased (Soppela *et al.*, 1986) (Fig. 1, $r=-0.396$, $n=66$, $P<0.001$). VO_2 varied from 5.7 ml/(min.kg) at +11.0°C to 38.8 ml/(min.kg) at 14.5°C. In calves 16-18 and 27-35 days old VO_2 rose at a lower Ta than in the newborns, but increased 3-fold above the resting level (Fig. 1). Tre remained independent of the Ta. Ts on the forefoot, lumbar and interscapular areas, however, followed changes in Ta. Thermal conductance values in calves aged 1 to 35 days were low at low Ta's, but rose strongly as Ta increased above +10°C (Fig. 2). At Ta above +20°C, VO_2 and heart rate increased sharply and Tre rose approximately 1°C. Calves panted rapidly when removed from the metabolic chamber. Compared with the resting level, VO_2 of calves aged 1-4 days increased 4- to 5-fold and nearly 2-fold in older calves.

Shivering thermogenesis in calves aged 1-4 days was weak and infrequent but it became stronger at low Ta's and attained 50-60 µV. Injection of NA caused a sharp increase in both Tre and VO_2 (Soppela *et al.*, 1986). The colder the Ta, the smaller the effect of NA on heat production. The endogenic NA-induced non-shivering thermogenesis of newborn calves was highest at —15.7°C, which thus appears to be their critical Ta (cf. Hissa *et al.*, 1981). The responses of older calves (7, 16 and 27 days) to NA injection were less than in the newborns.

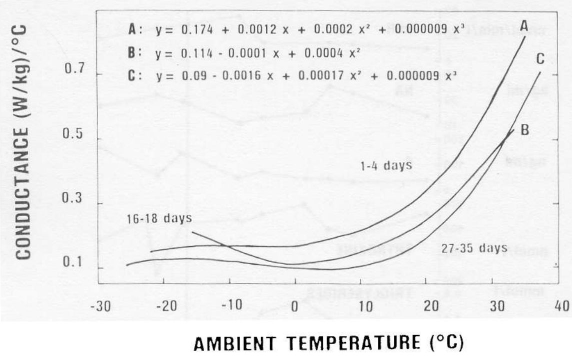

Fig. 2. Relation of thermal conductance to ambient temperature (Ta) in reindeer calves in three age classes, after 30 min exposure to a given Ta. The goodness of fit to polynomial regression was checked by an F-test after each increment of the polynomial degree. (y = thermal conductance and x = Ta)(modified from Soppela *et al.*, (1986)).

NA sensitivity disappeared during the first 3-4 weeks of life (Fig. 3, r=-0.954, n=8, $P<0.001$). Mean Tre over the Ta range +8 to +22°C was highest in newborn calves (+40.3±0.15°C, n=17). It decreased significantly ($P<0.001$) during the first 2 weeks but rose again to +40.0±0.23°C (n=5) in calves about 1-month old (Fig. 3). Mean thermal conductance was greatest (0.32±0.026 (W/kg)/°C, n=11) in calves aged 1-4 days, whereafter it decreased significantly ($P<0.001$) to the lowest value of 0.17±0.077 (W/kg)/°C, n=5) in calves 1-month of age.

The winter fur of adult reindeer consisted of thick guard hairs with air-filled cavities and an underfur of thin and woollen hairs. There was no variation in thickness between the back and abdomen fur, but foreleg fur was thinner ($P<0.001$). The density and length of guard hairs varied considerably and averaged 2000/cm^2 and 12 mm on the legs, 1000/cm^2 and 30 mm on the abdomen and 1700/cm^2 and 30 mm on the back (Timisjärvi *et al.*, 1984). The corresponding counts on the back of calves were 3200/cm^2 and 10 mm. The guard and woollen hairs in calves could not be discriminated. All hairs were wool-like and hollow. The Tre of adults averaged +38.9.±0.2°C and was independent of Ta. Decreases in Ta were followed by decreases in Ts, which were largest in the foreleg and muzzle areas. The behaviour of Ts in calves was similar to that of adults. Ts *in vitro* showed a linear dependence on Ta (Fig. 4). When the wind (10 m/sec) blew along the lay of the back fur, Ts decreased by 1.6°C at +20°C, by 6.7°C at 0°C and by 9.5°C at —20°C. Ts was lowest when the wind blew against the fur at an angle of 45° or perpendicular to the fur. There was a close correlation between surface Ts and thickness of the fur.

Seasonal blood composition (Fig. 5) revealed that blood glucose and lactate concentrations did not correlate with age, weight or Ta. No correlation was found between serum total lipid or triglyceride concentration and age, weight or Ta (Nieminen *et al.*, 1984). In adults total lipids and triglyceride were lowest in spring and highest in autumn ($P<0.001$). Serum total lipids increases significantly ($P<0.01$) in the neontal reindeer. Serum thyroxine (T4) level was not correlated with weight, age or Ta. In adults T4 showed significant ($P<0.001$) seasonal differences except between autumn and winter. T4 was high at birth, whereafter it decreased during the first weeks, then increased towards autumn ($P<0.05$). Serum adrenaline (A) correlated

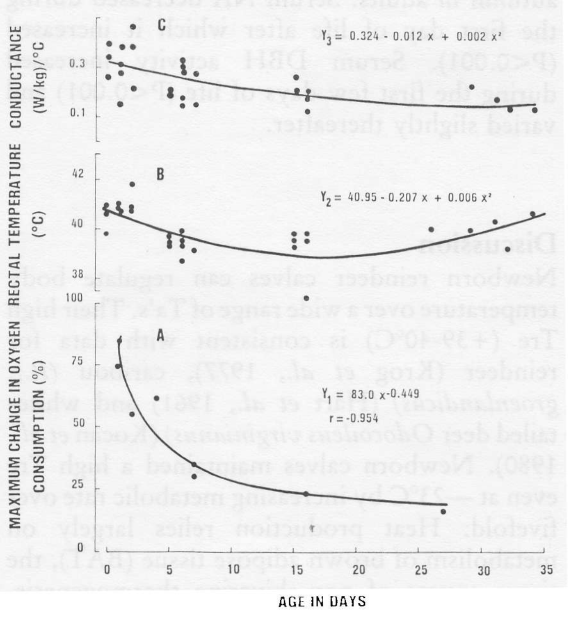

Fig. 3. A. Metabolic response to subcutaneous injection of noradrenaline (0.2 or 0.4 mg/kg) in 1 to 27 days old reindeer calves at 0°C.
B. C. Changes in rectal temperature (Tre) and thermal conductance with age in 1 to 35 days old calves at +8-22°C. (y1 = maximum change in oxygen consumption, y2 = Tre, y3 =thermal conductance and x = age in days)(modified from Soppela *et al.*, (1986).

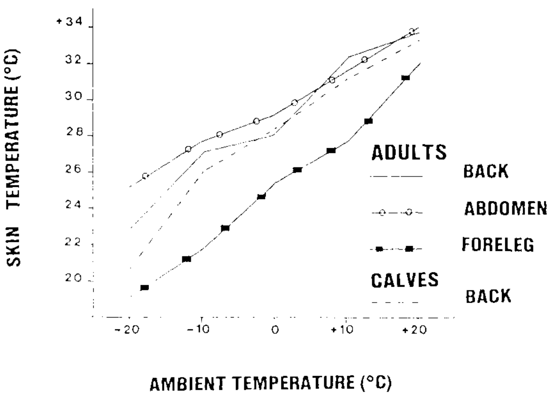

Fig. 4. Skin temperature of excised fur samples of adult reindeer and reindeer calves at various ambient temperatures.

positively with body weight (P<0.001), age (P<0.001), and total lipids (P<0.05), but not with Ta. Serum A varied (P<0.001) seasonally in adults. Serum NA was not correlated with other parameters. Both NA and dopamine-ß-hydroxylase (DBH) were highest in spring (P<0.01 and P<0.001) and decreased towards autumn in adults. Serum NA decreased during the first day of life after which it increased (P<0.001). Serum DBH activity increased during the first few days of life (P<0.001) and varied slightly thereafter.

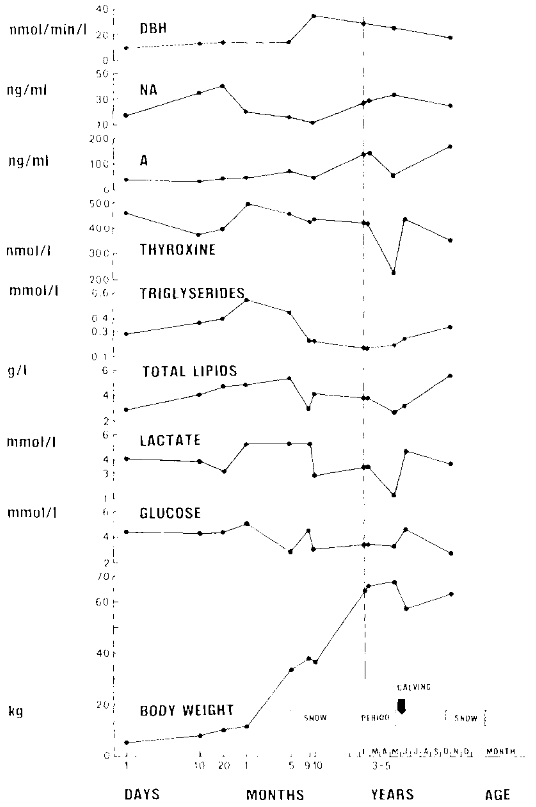

Fig. 5. Changes in body weight and blood constituents in reindeer with age and season. Filled circles represent measurement means.

Discussion

Newborn reindeer calves can regulate body temperature over a wide range of Ta's. Their high Tre (+39-40°C) is consistent with data for reindeer (Krog *et al.*, 1977), caribou *(R.t. groenlandicus)* (Hart *et al.*, 1961) and white-tailed deer *Odocoileus virginianus)* (Kocan *et al.*, 1980). Newborn calves maintained a high Tre even at —23°C by increasing metabolic rate over fivefold. Heat production relies largely on metabolism of brown adipose tissue (BAT), the tissue source of non-shivering thermogenesis, which is stimulated by the cold-induced NA release. The high energy content of reindeer milk supports a high metabolic rate and rapid growth. Shivering thermogenesis seems to be less important in the heat production of calves, as only weak shivering was found, mainly in newborns. Newborn reindeer calves shiver intensively immediately after birth until their birth fur is dry (Krog *et al.*, 1977).

Disappearance of NA sensitivity during the first month of life possibly reflects the concomitant loss of BAT. Growing reindeer calves appear to be more stressed by heat than by cold exposure as indicated by the increase in Tre at high Ta's. Poor heat tolerance was seen also in the strong increase in oxygen consumption and heart rate in a warm environment. Precise Ta leading to heat stress can not be given, since there is no real thermoneutral zone in a neonatal animal. In yearling reindeer Yousef and Luick (1975) found +35°C to be a critical Ta, when water was available *ad libitum*. Most of the heat load in reindeer, as in many other mammals with thick fur, is dissipated by evaporation through the respiratory tract. The great increase in oxygen consumption in reindeer calves at high Ta may result from the high energy demands of panting.

The reindeers birth fur is composed mainly of hollow, woollen hairs. Hair density is similar to that of the caribou calf (Lentz and Hart, 1960). The low and rather constant thermal conductance values at low Ta's reflect the good insulation capacity of the fur. Wind and wetting may, however, increase heat loss by as much as 50% (Lentz and Hart, 1960). Changes in conductance are not directly related to fur insulation (McNab, 1980). Strict comparisons must consider mass, changes in blood circulation and other aspects. The replacement of the birth fur commences in late June at an age of one month, and by late autumn it is adult in structure.

The thickness of winter fur (30 mm) was less than reported by Berge (1950) (35 mm) or by Scholander *et al.*, (1950)(50 mm), and less than in many other cervids (see Berge, 1950; Timisjärvi *et al.*, 1984). The length of individual guard hairs exceeded fur thickness since the hairs were not perpendicular to the skin. They still can be raised to an erect position. Piloerection reduces heat loss in the caribou calf by 30% (Lentz and Hart, 1960). The density of guard hairs varied between animals and depended on the sampling site. Our figures generally exceeded those reported by Berge (1950). The thick underfur is very important, since it effectively prevents air movement within it and thus reduces heat dissipation.

The Tre of adult reindeer agrees with earlier observations (e.g. Irving and Krog, 1955). It is within the normal range of +37-41°C, described for most Cervidae species. A rise in Tre resulting even from slight physical restraint is common in reindeer because of the fur insulation. Ts of extremities in both living animals and excised skin samples showed a strong dependence on Ta. The decrease in surface Ts *in vitro* was due to increased convection at low Ta's. The effect of Ta on Ts was further intensified by wind. A clear difference existed in fur thickness and Ts, the foreleg samples showing the lowest temperatures. A positive correlation between fur thickness and insulation value in arctic mammals has been reported by Scholander *et al.*, (1950).

Many physiological regulative mechanisms present in living animals are lost in excised skin samples. Reindeer are able to regulate leg Ts by adjusting blood circulation, invoking a counter current heat exchange mechanism. This mechanism is also utilized to prevent snow melting on the surface of the legs (Irving, 1951). A resting reindeer chooses a position in which the wind blows against the fur (Skjenneberg and Slagsvold, 1968) to shelter its head and minimize heat loss.

Blood constituents showed few correlations with Ta. Their seasonal differences are more indicative of nutrition than climate. Discrepancies may also arise from different methods of capturing and handling the animals. Serum total lipid and triglyceride concentrations were highest in autumn and may reflect the anabolism of adipose tissue. Autumn is also the rutting season of the reindeer, with associated high levels of gonadal steroids and adrenaline. High serum total lipids and triglycerides in calves may result from the high fat content of milk.

Thyroid secretion appears to elevate in the cold, but the magnitude of increase is species specific. Ringberg *et al.*, (1978) found the highest T4 levels in reindeer in summer and lowest in winter, whereas Yousef and Luick (1971) found no significant seasonal variation. In our work T4 was lowest in spring, indicating an overall lowered metabolic rate. NA was not correlated with other parameters, but A concentration was correlated with age, weight and total lipids, and also showed seasonal variation. No correlation was found with Ta. The high NA concentration in newborn calves supports high endogenous non-shivering thermogenesis. In adult reindeer the role of catecholamines may be involved in the mobilization of energy reserves under stress situations or starvation and may also reflect the body condition. In conclusion, the results suggest that the prime mechanism by which adult reindeer thermoregulate in a cold environment is insulation.

Acknowledgements

We would like to thank Dr. D.C. Thomas and Dr. C. Gates for their valuable criticisms while reviewing of this manuscript.

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Mineral absorption in relation to nutritional ecology of reindeer

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Abstract: This paper addresses the way which absorption of minerals relate to nutritional ecology and mineral conservation processes. A latin square designed experiment was used to assess the effects of diet on mineral (Ca, Mg, K, Na) absorption processes in reindeer (*Rangifer tarandus* L.). Three male calves were fed 3 different diets: concentrate with 25% grass meal (RF-71), lichens, and a mixed diet of lichens and RF-71. Two other male calves were fed the lichen or mixed diet, supplemented with 4 g Ca/day. Ca supplementation significantly increased fecal Ca excretion, reduced the excretion of K and Mg, but had no significant effect on Na excretion. Rates of intake and fecal exretion of Ca, Mg and K were highly correlated ($P<0.001$), while no correlations were found for Na. Negative digestibilities of Ca, Mg and K, and a positive Na digestibility were noted for the lichen diet. For the other diets, all minerals were in positive digestibility, and Ca supplements increased the digestibility of all minerals. Digesta from different sections of the alimentary tract were collected after termination of the experiment. Alimentary pools of Ca and K were equal for animals fed lichen or RF-71, whereas the Na pool was largest on the lichen diet and the Mg pool largest on the RF-71 diet. Rumen turnover time (rumen mineral pool size/daily mineral intake) was consistently less than 3 days for Ca and Mg, but was 22 and 82 days for Na on the RF-71 and lichen diets respectively. Estimates of mineral exchange in various parts of the tract showed that the intestines play and important role in scavanging endogenously secreted minerals. Results are discussed with respect to mineral binding by lichens and the possible role of natural mineral supplements in the nutritional ecology of reindeer.

Key words: reindeer, *Rangifer*, mineral absorption, digestion, calcium, Ca

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Rangifer, Special Issue No. 1, 1986: 279 - 287

Introduction

In northern reindeer and caribou habitats the availability of minerals may vary by season and location. It is generally believed that the staple winter diet of reindeer (lichens, shrubs, etc.) are deficient in nutrients, resulting in the gradual depletion of body energy, protein and Na reserves (McEwan and Whitehead, 1970; White *et al.*, 1981; Staaland *et al.*, 1982). Also, the apparent Na deficiencies experienced by some northern herbivores in spring and summer, may be exacerbated by high dietary K levels which stimulate Na excretion (Weeks and Kirkpatrick, 1976, 1978; Staaland and Jacobsen, 1983). for moose on Isle Royale in Lake Superior, Na balance is maintained on a year-round by eating aquatic vegetation which accumulates Na (Belovsky and Jordan, 1981). Likewise, reindeer and caribou supplement their diets with mineral-rich sources such as aquatic and coastal vegetation, salt licks, soil, and sea water. In fact, these mineral-rich resources may be central to the location of home ranges of moose (Tankersley and Gasaway, 1983) and Dall sheep (Heimer, 1974). The occurrence of such resources within reindeer and caribou ranges could be important factors in establishing routes of seasonal migrations.

The physiological regulation of mineral metabolism in reindeer is poorly understood (White, 1979). However, studies on domestic species indicate that mineral absorption sets the pace for mineral turnover which shows adaption to dietary source (ARC, 1980). In this report, we describe some of the characteristics of mineral absorption in reindeer, and relate these findings to the nutritional ecology of the species.

Material and methods

Five male reindeer calves (9 months old), mean body weight 45±3 kg (±SE), were used in the feeding trials. The animals were brought from semidomestic herds in southern Norway to the Animal Science Laboratory at the Agricultural University of Norway, Ås, in early December 1983. The animals were given a commercial, pelleted feed, RF-71 (Jacobsen *et al.*, 1977), supplemented with lichens (200 g/d) until january 1984 when they were equipped with rumen and abomasal cannulae. During February and March they were kept in large stalls at room temperature (+20°C) and used in a multipurpose experiment (see also Hove *et al.*, 1986). We designed a 3x3 latin square experiment in which 3 animals were subjected sequentially to three dietary treatments: concentrate with 25% grass meal (RF-71), lichens, and a mixture of RF-71 and lichens (Table 1). The other two reindeer were fed lichens or the mixed diet and given a continous intraruminal infusion of calcium acetate equivalent to 4 g Ca/day. Ca absorption potential was estimated using an intravenous injection of absorption stimulant, 1,24 dihydroxy vitamin D_3 (20 µg) (see Hove *et al.*, 1986). All animals received a continous intraruminal infusion of the non-digestible marker Co-EDTA at a rate of 183±7 mg/day.

The reindeer were offered ca. 1 kg dry food/day and water *ad libitum*. At least 8 days conditioning to new diets was allowed before each Ca trial. Food and food remains were weighed daily throughout the experimental period. Total feces was collected and weighed over 5 consecutive days starting at 10:00 h. Fresh food and fecal samples were collected each day and dried overnight at 105°C; subsamples were dried to a constant weight, ashed and analyzed for Co, Ca, Mg, Na and K by conventional Atomic Absorption methods. Acid insoluble ash (AIA) content was determined by dissolving the ash twice in boiling 4N hydrochloric acid, filtering through as-free filter paper, and ashing again at 625°C.

Dry matter digestibility (DMD) was determined by conventional means and was also estimated based on the concentration of none-digestible marker in feces. The two markers used were AIA in the diet and Co-EDTA which was infused into the rumen. These markers were also used to assess cumulative absorption of dry matter, water and minerals down the intestinal tracts of animals fed the lichen and RF-71 diets.

After termination of the feeding trials two animals fed the RF-71 and three fed the lichens were slaughtered. The gastrointestinal tract was removed and divided into 11 sections: rumen, reticulum, omasum, abomasum, small intestine (3 sections), cecum, spiral colon (2 sub-sections) and rectum. For each section, total content was weighed and representative subsamples taken for chemical analysis were analyzed as described above.

Statistical analyzes included the t-test for comparisons of means and Duncans test for a general linear model using ANOVA (Helwig and Council, 1982).

Table 1. Chemical composition of food used in feeding trials (x̄±S.E.)

Diet		Lichens (n=3)	RF-71 (n=3)	Mixed diet[1]
Crude protein	(g/kg DM)	40.6±2	120.0±2.7	77.8
Ca	(mM/kg DM)	29±1	82±3	54
Mg	(mM/kg DM)	12±1	74±1	41
K	(mM/kg DM)	37±1	242±5	133
Na	(mM/kg DM)	6.4±0.3	15.5±1.1	10.7

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[1] The composition of the mixed diet was calculated from the concentrations given for lichens and RF-71, contributing 53.2 and 46.8%, respectively.

Table 2. Feeding regimen, dry matter consumption and comparison of methods for estimating dry matter digestibility (x̄±S.E.)

Diet		Lichens	RF-71	Mixed diet[1]
Food offered	(g DM/day)	1026 (20)	902 (13)	964 (23)
Intake	(g/day)	591±54	823±42	849±20
Food eaten	($g/kg^{0.75}day$)	34±3	45±2	49±1
Dry matter digestibility (%)				
Total collection		68.0±4.4	70.9±2.2	66.4±1.2
Co-EDTA as marker		63.3±6.5	59.7±7.4	69.9±1.8
AIA as marker		72.3±2.0	70.7±2.5	71.4±2.2

( ) number of observations.

Results

The concentration of protein (Nx6.25) and minerals were lowest in the lichen diet, intermediate in the mixed diet and highest in the RF-71 diet (Table 1). Mean dry matter intake was lowest for the lichen diet, but differences in consumption of the other feed were not significant. Mean apparent DMD was not significantly different between diets, irrespective of the methods used to estimate DMD ($P>0.05$) (Table 2). Intraruminal infusion of Ca had no significant effect on DMD; therefore, Table 2 includes all data for each diet.

Although previous studies indicate that vitamin D_3 supplementation may increase Ca absorption (Hove *et al.*, 1986) we detected no significant effect of this treatment on fecal Ca content or apparent Ca digestibility.

Highest concentrations of fecal Na were noted for reindeer fed lichens. Fecal concentrations of Ca, Mg and K were highest on the RF-71 diet. The addition of 4 g Ca/day to the RF-71 diet increased Ca and decreased fecal K and Mg concentrations but had no significant effect on fecal Na (Table 3). Fecal excretion of Na was independent of intake, whereas the intake and excretion of Ca, Mg and K were correlated with intake:

Eq. I: $Ca_{feces} = 0.37 \cdot Ca_{food} + 20.68$; $r^2=0.47$, $n=54$, $P<0.001$

Eq. II: $Mg_{feces} = 0.62 \cdot Mg_{food} + 2.46$; $r^2=0.86$, $n=54$, $P<0.001$

Eq. III: $K_{feces} = 0.15 \cdot K_{food} + 19.23$; $r^2=0.25$, $n=54$, $P<0.01$

A negative apparent digestibility of all minerals, except Na, was noted for reindeer fed the lichen diet (Table 4). Ca supplementation of the lichen diet had a positive effect on Ca, Mg and K digestibility, but had no significant effect on mineral digestibility of the mixed diets or RF-71.

Concentrations of AIA increased from the rumen-reticulum to the abomasum and then decreased to low levels in the duodenum (Fig. 1). AIA concentration increased steadily between the duodenum and the distal colon. Alimentary concentrations of AIA were consistently higher in the lichen fed animals in all sites except the

Table 3. The effects of dietary Ca supplementation of fecal mineral concentration (mM/kg DM) and water content (g/100 g wet weight) (x̄±S.E.).

Diet	Ca	Mg	K	Na	Water
Lichen (n=13)	151±8 ab[1]	45±3a	164±11a	14.3±1.0a	60.1±1.4a
Lichen + Ca (n=9)	443±37c	35±2a	47±7 b	12.2±2.2ab	63.5±2.7ab
Mixed diet (n=13)	142±9 a	96±4b	183±11a	10.2±1.0bc	66.3±1.0b
Mixed diet + Ca (n=10)	254±25d	73±4c	83±13b	12.2±1.6ab	63.6±3.0ab
RF-71 (n=13)	199±15b	181±5d	198±23a	7.4±0.7c	71.7±0.8c

[1] Values in the same column followed by the same letter(s) are not significantly different.

Table 4. Mineral digestibility in reindeer fed different diets ($\bar{x}$% ±S.E.).

Diet	Ca	Mg	K	Na
Lichen (n=10)	—79±32a[1]	—33±27a	—57±22a	16±15a
Lichen + Ca (n=10)	42± 9b	9±24b	52±18b	40±17ab
Mixed diet (n=13)	16± 7b	28± 4b	57± 3b	69± 4bc
Mixed diet + Ca (n=10)	51± 4b	35± 5b	77± 4b	58± 7bc
RF-71 (n=13)	29± 7b	29± 6b	75± 4b	85± 3c

[1] Values in the same column followed by the same letter(s) are not significantly different.

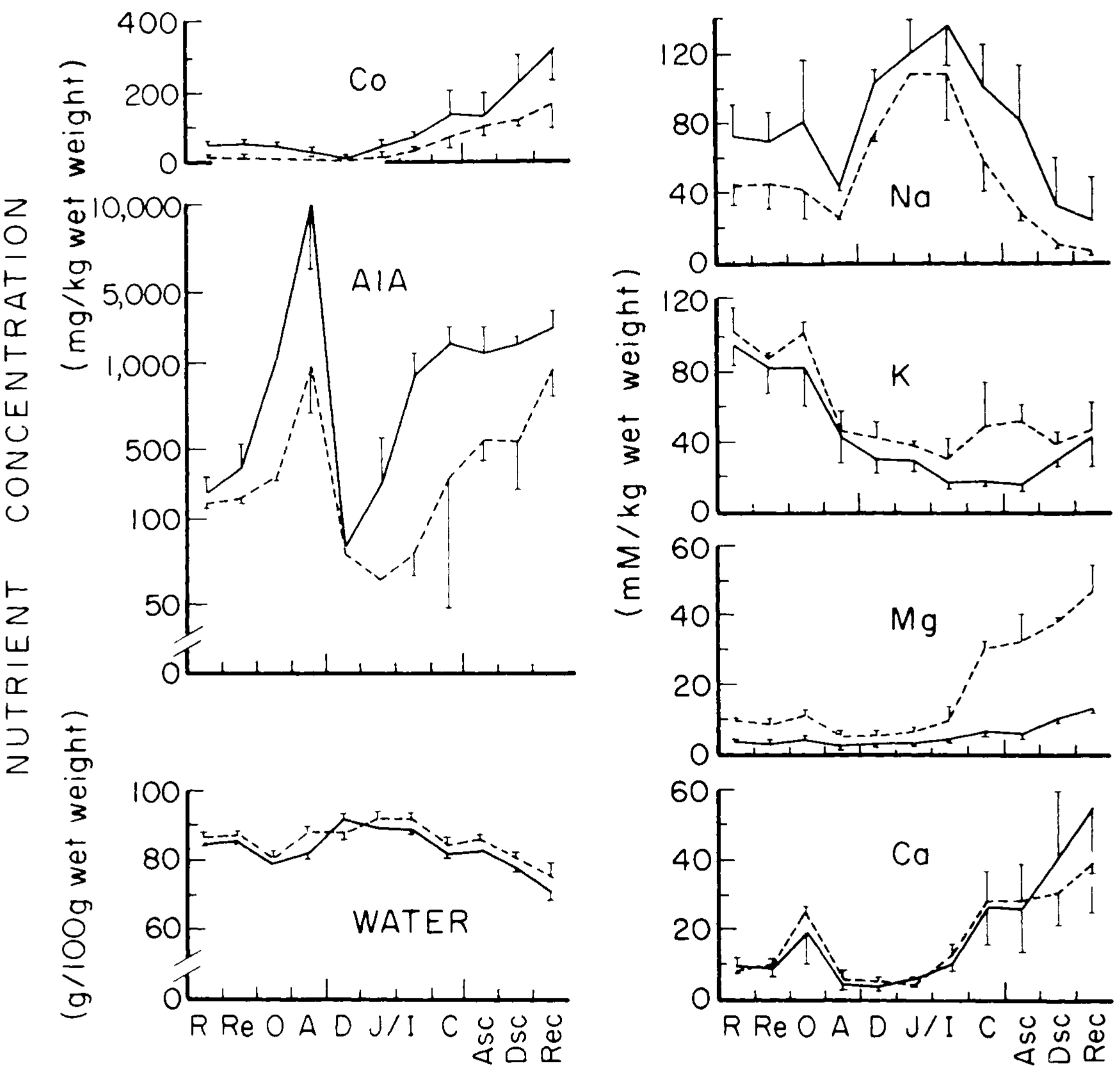

Fig. 1. Mean concentrations of markers, water and minerals in the alimentary tract of reindeer fed two different diets; ———————— Lichens (n=3) and ---------------RF-71 (n=2). Vertical bar represents the SD. R, rumen; Re, reticulum; O, omasum; A, abomasum; D, duodenum; J/I, jejunum/ileum; C, cecum; Asc and Dsc, ascending and descending spiral colon; Rec, rectum.

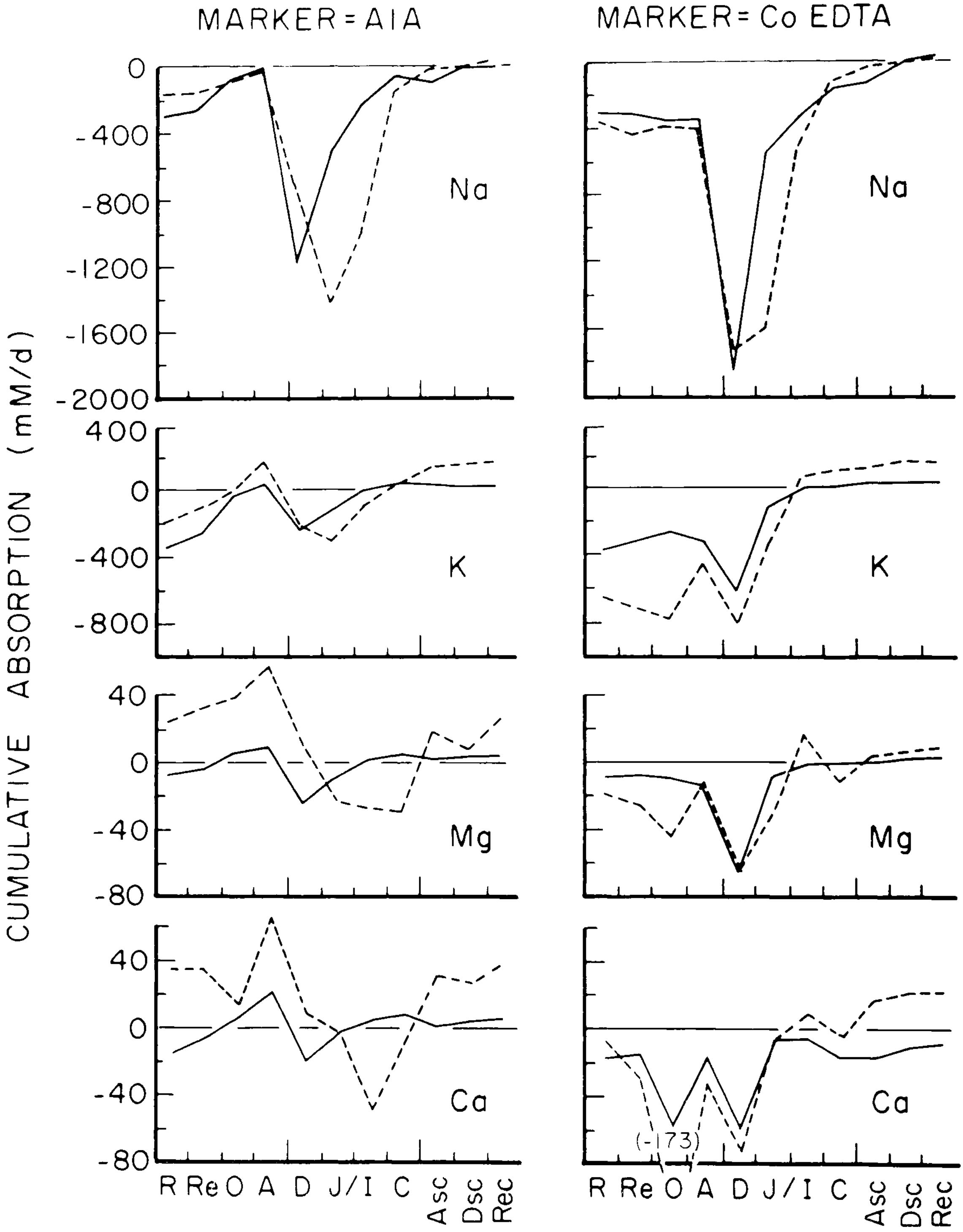

Fig. 2. Cumulative absorption of minerals in the alimentary tract of reindeer fed two different diets: ———— Lichens; - - - - - - - RF-71. Acid insoluble ash (AIA) left, and Co-EDTA right, were used as reference markers. For reasons described in the text, calculations of mineral exchange within the omasum are assumed to be less reliable than those for the rest of the alimentary tract. Negative changes indicate secretion and positive changes indicate absorption. Calculations for each cation are made in relation to the respective dietary intakes. Abreviations are given in Fig. 1.

duodenum. High AIA concentrations in the abomasum can be attributed in part to an accumulation of sand and stones.

Co was derived mainly from the external marker Co-EDTA. The concentration of Co was remarkably constant in the forestomachs, but increased progressively through the intestines (Fig. 1). Co concentrations were higher in the alimentary contents from reindeer fed lichens than from those fed RF-71.

Concentration gradients of Ca and Mg in the alimentary tract were similar to that of Co. In contrast, K concentrations were highest in the forestomachs and remained relatively low in the intestines (Fig. 1). Na concentration decreased markedly in the abomasum, followed by an increase to a peak in the cecum and an abrupt decline in the large intestine. Na concentrations in the lichen-fed animals were consistently higher than those in animals on the RF-71 diet. Water content followed the same general pattern as Na concentration (Fig. 1).

The method of calculating absorption/secretion in the alimentary tract using non-absorbed markers has been described by White *et al.* (1984). Absorption calculations are based on the assumption that equal amounts of markers (i.e. AIA ingested in food or Co-EDTA infused) flow through each section of the alimentary tract per day. However, this method may not be applicable to the omasum, as liquids, separated from solids at the rumen-omasal orifice, are thought to move through the omasum more rapidly than solids. Some accumulation of sand or small stones in the abomasum may increase AIA concentration which would give a spuriously high apparent absorption of minerals using the AIA marker.

Irrespective of these limitations, there was generally good agreement on the calculated absorption/secretion patterns for Na and K between the two markers (Fig. 2). Calculations show a substantial secretion of Na into the proximal small intestine and an efficient absorption in the distal small intestine. K exchange in the forestomachs was small and was secreted in the duodenum, and reabsorbed in the distal small instestine and large intestine. The exchange of Mg and Ca across the wall of the alimentary tract follows a more irregular pattern, and the results differ with the marker used. The pattern of Ca and Mg secretion/absorption resembled that for K when Co-EDTA was used as marker: Co-EDTA is the preferred reference substance for minerals absorbed from the liquid phase. Net absorption of Ca from the small intestine is in agreement with *in vivo* results (Hove *et al.*, 1986), again suggesting that Co-EDTA may be the preferred marker for determining Ca absorption patterns. On a molar basis less endogenous Mg and Ca, compared to Na, was added to intestinal contents during exchange processes in the intestines (Fig. 2).

Standing pool sizes of minerals in the alimentary tract are shown in Table 5. The rumen contained 60 - 70% of the total alimentary pool of all 4 minerals. Turnover time of minerals, calculated as pool size/daily intake, was lower for Ca and Mg (0.6 - 2.4 days) than for Na (21.5 - 81.8 days), while K was intermediate. These results correspond to previous results obtained in earlier experiments (Staaland *et al.* 1984).

Table 5. Alimentary pool size ($\bar{x}$±S.E.) and rumen mineral turnover time[1].

	Total alimentary pool[2]		Rumen pool		Turnover time (d)	
Diet	Lichens	RF-71	Lichens	RF-71	Lichens	RF-71
n	3	2	3	2	3	2
Total content	5.3±0.7	5.4±1.0	4.2±0.7	4.3±0.9	1.1[3]	0.7[3]
Ca	61±10	63±24	38±2	41±11	2.2	0.6
Mg	24±3	64±12	17±2	42±10	2.4	0.7
K	443±88	482±81	408±81	432±56	18.6	3.8
Na	411±82	275±89	311±63	196±70	81.8	21.5

[1] Food intake calculated from average daily food consumption and mineral concentrations in the diet (Tables 1 and 2).

[2] Total content in kg wet weight; mineral content in mM.

[3] DM turnover time = rumen pool x rumen DM/DM intake.

Table 6. Examples of natural sources of minerals (x̄ mM/kg DM ± S.E.).

Source	N	Ca	Mg	K	Na
Lichens[1]	17	19±2	10±1	42±11	12±1
Horsetail[1]	14	331±38	140±6	617±65	25±5
Grass[1]	55	49±2	36±3	330±20	10±1
Aquatic herbs (leaves)[1]	14	214±33	97±15	717±85	102±25
Aquatic herbs (roots)[1]	17	127±6	34±1	346±44	125±30
Sea water (34‰)[2]		10	52	10	459
Salt licks[3]		3	1.4	0.2	7
Salt licks[4]		0.15-2.15	0.07-1.15	0.01-0.19	1.8-37.0

[1] From Staaland and Sæbø (1985).
[2] In mM/1 sea water.
[3] From Fraser and Reardon, 1980; in mM/1 water.
[4] From Fraser *et al.* (1980), in mM/1 water.

Discussion

Adaptions in mineral ecology of herbivores can occur at the detection-acquisition, absorption and retention-recycling levels (White, 1979). This study addresses absorption function since the winter pasture of reindeer and caribou is generally low in minerals (Staaland *et al.*, 1983; Staaland and Sæbø, 1985). Furthermore, minerals are not evenly distributed within the food base or soil substrate, and reindeer appear to obtain extra minerals through the selective use of plants and inorganic material. Some terrestrial plants (buck-beans, *Menyanthes trifoliata* and horsetail, *Equisetum* spp.) and aquatic vegetation sought by reindeer are known to contain high levels of Na (Skjenneberg and Slagsvold, 1968; Staaland and Sæbø, 1985). Thus, it can be argued that a diverse flora provides for the best overall mineral balance.

Plants also change in chemical composition during the growing season; for example, K, P and N concentrations are high in rapidly growing vegetation but decrease substantially during senescence (Staaland and Sæbø, 1985). Habitats with some snowbeds and large altitudinal variations with plants in different phenological stages, should therefore also contribute to maintaining a high availability of most minerals, notably K and P (Klein, 1970; Skogland, 1980, 1984). The occurrence of certain types of bedrock and soil, as well as arctic seabird rookeries can also influence the effective quality of pasture and increase the overall value of some isolated areas to reindeer (Staaland *et al.*, 1983; Staaland 1985). Other potentially important sources of minerals are mineral licks and sea water (Table 6). Also it is well known that reindeer are attracted to urine on snow, may chew on shed antlers, or may even eat small mammals such as lemmings. Presumably these dietary novelties serve to supplement the minerals in forage, thereby improving mineral balance.

Lichens apparently have a special effect on mineral absorption. Fecal concentration of Na is frequently higher when anmimals are consuming lichens in winter than when grazing summer pasture (Staaland *et al.*, 1980). One might speculate that lichens bind some minerals, particularly Na and Ca, and lower their net absorption (White *et al.*, 1984). Indeed, it has been shown that the efficiency of Ca absorption is lower on lichen than high Ca diets (Hove *et al.*, 1986). Therefore mixing of lichens with vegetation higher in mineral resources, e.g. mosses and dead leaves, may serve to saturate these binding sites and maintain mineral balance in the wild.

It was reported previously that lactating reindeer on summer pastures in Interior Alaska depleted their body reserves of Na (Staaland *et al.*, 1982). Subsequent field studies in Norway showed that the rumen-reticulum can function as a reserve for Na; ruminal Na is gradually exchanged for extraruminal K to maintain osmotic balance. This may occur when intake of Na is too low to meet body requirement or when increased K intake in spring stimulates Na excretion in urine (Staaland and Jacobsen, 1983). It has also been shown that depleted body reserves of Na can be rapidly restored by the consumption of forages or other materials that are rich in Na (Staaland *et al.*, 1982). Na, and probably also K, may be replenished by different mechanisms than Mg and Ca. The slow ruminal turnover of Na (Table 5) indicates that most Na in the alimentary tract is of endogenous origin. Furthermore, considerable Na is involved in exchange between the alimentary tract and the body pools (Fig. 2). In fact, the daily addition of salivary Na may easily equal that in the entire total body pool (Bartley, 1976; White *et al.*, unpublished data) and serves to maintain rumen function even when animals become Na depleted.

In contrast to the Na and K pools, the ruminal Ca and Mg pools are turned over rapidly (Table 5), and there is a strong correlation between intake and fecal excretion (Eq. I and II). Although Ca supplementation increases fecal Ca content (Table 3), fractional Ca absorption from the small intestine increases (Hove *et al.*, 1986) giving an overall positive effect on Ca digestibility. The present study shows that increased dietary Ca also stimulates absorption from the spiral colon (Fig. 2). It is possible therefore that the consumption of Ca-rich soils or vegetation enhances short-term Ca absorption. The intake of highly soluble Ca has a stimulating effect on the absorption and digestibility of Mg and K (Tables 3 and 4), particularly when animals are eating lichens.

In conclusion, the results of this study show that the absorption of the major mineral elements Ca, Mg, Na and K can be stimulated by increasing the respective dietary intakes of each. This suggests that reindeer utilize mineral-rich licks and vegetation in relation to need. In addition, the present results indicate that supplementation with Ca in a highly soluble form can stimulate the absorption of other minerals. This observation highlights the complexity of events that occur when an animal feeds sporadically on mineral-rich substances.

Acknowledgements

This study was supported by grants from «The development fund for reindeer herding in Norway» to the Agricultural University of Norway. The study was carried out when R. G. White, was on a 3 month sabbatical leave to the Agricultural University of Norway in a «Senior Scientist Visiting Program. sponsored by the Norwegian Science Council for Agriculture (NLVF).

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Review of forestry practices in caribou habitat in southeastern British Columbia, Canada

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Abstract: Woodland caribou *(Rangifer tarandus caribou)* in southeastern British Columbia feed mainly on arboreal lichens in winter. Some modified forestry practices that have been used or proposed for caribou ranges are reviewed. Partial cutting results in the retention of some forage lichens. Partial cutting and small patch harvesting may improve lichen growth on the remaining trees. Retention of advanced regeneration and some residual trees may improve lichen growth in the remaining stand. Extension of the rotation age increases the amount of harvestable forest useful to caribou at any one time. Progressive cutting minimizes road access to caribou ranges, and may be combined with partial cutting. Most forestry practices intended to maintain lichen production will result in increased human activity in caribou ranges, unless road access is controlled. The management strategy selected depends on site conditions and on the relative importance assigned to the impact of habitat alteration and human activity on caribou.

Key words: *Rangifer,* caribou, forestry practices, lichens, British Columbia, Canada.

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Rangifer, Special Issue No. 1, 1986: 289 - 295

Introduction

In British Columbia, there are broad geographic areas in which certain forage types predominate in the winter diet of woodland caribou (*Rangifer tarandus caribou).* In northern and western British Columbia, the snowpack is usually shallow enough to permit cratering for terrestrial lichens and vascular forage. In the southeast, the snow is much deeper, and caribou feed mainly on arboreal lichens. This paper is limited to a consideration of caribou habitat in southeastern British Columbia (Fig. 1). There, caribou occupy forested mountain slopes and plateaus, avoiding the most rugged terrain. Heavy precipitation results in snowpacks of 3 m or more on high elevation ranges. The major tree species are western red cedar *(Thuja plicata),* western hemlock *(Tsuga heterophylla),* and lodgepole pine (*Pinus contorta)* at low elevations, and Engelmann spruce *(Picea engelmannii)* and subalpine fir *(Abies lasiocarpa)* at high elevations. The transition from low- to high-elevation forest types ranges from 1000-1500 m, depending on latitude.

Two broad patterns of winter habitat use by caribou occur in southeastern British Columbia. When snow is soft, as in early winter, the animals use low-elevation forests. They feed on vascular plants and on lichens that are available as litterfall, on windthrown trees, and on trees felled by loggers (Edwards and Ritcey, 1960; Freddy, 1974; Bloomfield, 1980; T. Antifeau, pers. comm.) At low elevations, lichens are rarely abundant on the lower branches of trees. In high-elevation forests, where the canopy is more open, lichens are usually abundant in both lower and upper portions of the crowns. When a deep, settled snowpack is present, caribou usually use high-elevation forest, where they feed almost exclusively on arboreal lichens. The crusted snowpack supports caribou and improves access to lichens. The strategy of feeding on

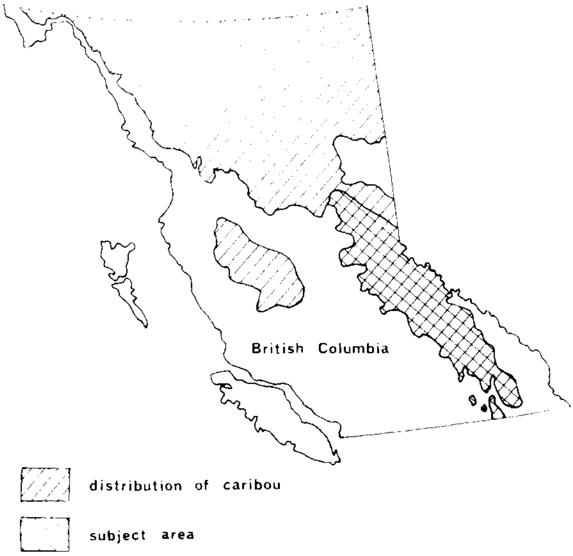

Fig. 1. Caribou range in British Columbia.

arboreal lichens in subalpine forests during winter removes caribou from the ranges of other ungulates, reducing competition and predation.

The arboreal lichens used by caribou, such as *Alectoria sarmentosa* and *Bryoria* spp., are markedly more abundant in older forests than in second growth. When a lichen-bearing stand is harvested, large amounts of lichen are briefly available on felled trees, and are readily used by caribou. After clearcut logging, arboreal lichens from adjacent stands of mature timber colonise the regenerating trees, but do not become abundant for at least 100 years, and often longer (Scotter, 1962; Edwards *et al.*, 1960; T. Antifeau, unpublished data). It is unclear why the lichens do not become abundant earlier. Microclimatic conditions in the young stand, unsuitability of the bark of rapidly growing young trees as a substrate, dispersal limitations in large clearcuts, and the slow growth rates of lichens may all play a part.

The impact of logging on lichen abundance has caused conflict over the management of caribou ranges. Researchers and managers have sought forestry practices that allow timber extraction while maintaining caribou habitat. Although most concern has focussed on maintaining arboreal lichen production, it is important to consider other consequences of logging. Increased road access, direct disturbance, altered snow conditions, and changes in numbers of other ungulates and predators may affect caribou. Research needs regarding those relationships have been identified by Stevenson and Hatler (1985). In this paper, several proposed techniques for integrating forestry and caribou management are reviewed. The special logging practices are assessed for their impact on arboreal lichen production and other aspects of caribou habitat, and their forest management implications.

Standard forestry practices

All timber harvested in southeastern British Columbia is old growth. Before 1966, a variety of partial cut systems were used, all of which left considerable amounts of residual timber. Since 1966, when new utilization standards were introduced, clearcutting has been the usual practice. Clearcutting is done in patches, leaving mature timber between patches for later harvest. Patches range from 40 to several thousand hectares. After clearcutting, logging debris is usually burned, and commercial tree species are planted.

Partial cutting

Partial cutting is a term applied to a variety of logging systems that leave a residual stand of trees distributed throughout the cutblock. Diameter-limit logging, a partial cutting system in which only trees above specified diameter limits are felled, has been applied in some caribou ranges.

The use of partial cutting rather than clearcutting is thought to reduce adverse impacts of logging on caribou for three reasons. First, some arboreal lichen remains available as forage. Taking into consideration the removal of harvestable trees, felling of snags, damage to residuals, and loss of forested areas to roads and landings, Stevenson (1979) estimated that in three spruce-fir stands, a cut to 51 cm minimum diameter at stump height would result in the retention of 20-32% of the lichen biomass that was originally available. The value of that forage supply to caribou is unclear. Caribou have been observed to travel through logged areas in winter and to feed on lichens from residual timber (Stevenson, 1979). However, the consequence of a reduced and dispersed forage supply is an increase in the energetic cost of feeding.

The second advantage of partial cutting is that lichens should regenerate more quickly than after clearcutting. Lichens on residual trees provide a source of propagules for dispersal to the remaining timber. Advance regeneration left after harvesting will provide a suitable substrate for lichen colonisation sooner than would new seedlings. Third, partial cutting may increase lichen growth rates in the lower part of the residual canopy. Improved growth of *Alectoria* and *Bryoria* spp. is expected in moist or dense stands, but not in xeric or open-canopied stands, which would become too dry for optimum lichen growth after partial cutting.

The potential effects of partial cutting on caribou range must be assessed within the overall harvesting plan. If a second cut is planned within 20-40 years, lichens may never recover to preharvesting levels, and the period during which they are abundant is likely to be brief. The long-term effect on lichens of successive partial cuts is even less certain. Also, any partial cutting system is likely to result in larger areas being harvested at any one time, so that government commitments of timber volume to industry can be met. The concomitant increase in road access may offset benefits to caribou derived from partial cutting. Furthermore, where successive entries are planned, roads must be maintained for a long time.

The use of diameter-limit logging and other partial cutting systems rather than clearcutting has implications for forestry. Road and harvesting costs increase, and windthrow may be a problem. Alexander (1973, 1974) prepared detailed recommendations for achieving a windfirm, partially cut stand in spruce-fir types through a series of light preparatory cuts which open the stand gradually.

Several silvicultural problems may result from partial cutting. First, the residual stand may be damaged during logging or may fail to release. Alexander (1974) recommended measures for protecting residuals. Second, the presence of an overstory tends to favour subalpine fir, a species of lower commercial value than spruce. However, an overstory may benefit spruce on some sites. At high elevations in the Rocky Mountains of the United States and southern Canada, mortality of spruce seedlings has been related to high light intensity, high soil surface temperatures, summer drought, and frost damage (Alexander, 1974; Utzig and Herring, 1974). In contrast, high soil temperatures and soil moisture deficits are not problems in the northern part of the study area (McMinn, 1982). Because a residual stand can help prevent damage to spruce seedlings from temperature extremes, partial cutting is suggested as a viable silvicultural option on suitable sites in the southern part of the study area.

Partial cutting has the potential of minimizing the loss of lichens, but not without some costs to timber management. If partial cutting is accompanied by an increase in the area harvested at any one time, then the benefits to caribou of lichen retention must be weighed against the risks that result from increased access.

Retention of advanced regeneration and non-merchantable trees

An alternative to partial cutting is managing for future lichen crops by protecting the advanced regeneration and by retaining as many lichen-bearing snags and low-value subalpine fir trees as possible. Some mature, lichen-bearing subalpine fir trees are not merchantable, and could be left standing with no short-term loss. Stevenson (1979) reported that 13-25% of the lichen biomass available to caribou in three mature spruce-fir stands occurred on snags. Acknowledging that some dead trees present a safety hazard to workers, retention of as many lichen-bearing snags as possible is recommended. From the standpoint of caribou management, this approach offers an advantage over other harvesting systems: since successive entries are not required, closure of roads after harvesting is an option.

The short-term cost of the approach is limited to the measures required to protect the advanced regeneration. The silvicultural consequences are variable. Advanced regeneration in Engelmann spruce-subalpine fir stands is dominated by subalpine fir. Although reforestation programs at high elevations have generally been aimed at spruce, they have suffered from inconsistent seed sources for natural regeneration, and high failure rates in planted stock (Utzig and Herring, 1974). On some sites, the use of advanced regeneration may be a cheaper and more reliable method of restocking (Utzig and Herring, 1974). Recent studies indicate that on appropriate sites, management of subalpine fir advanced regeneration is a viable silvicultural option (Herring, 1981). On the other hand, retention of large, unmerchantable subalpine fir trees is silviculturally undesirable - they occupy growing sites without contributing to the value of the stand, and may be a source of poor genetic material.

Retention of advanced regeneration and non-merchantable trees would not significantly increase short-term lichen availability, but would probably hasten lichen recovery. The technique is suggested where management for lichen crops is important, but where partial cutting is unacceptable.

Harvesting of very small patches

Clearcutting of very small patches (1-2 ha) has been recommended for subalpine forests where water yield is a primary consideration (Alexander 1973, 1977). The practice also has the potential of enhancing lichen production.

Creating a number of small, dispersed openings would increase light penetration into the remaining stand of mature timber. Except in stands that are already open or very dry, increased sunlight should improve the microclimate for lichen growth. Dispersal of lichen propagules would not be a limiting factor, as it might be in large clearcuts. As in the case of partial cutting, the long-term consequences for caribou would depend on the timing of later cuts, as well as on the response of the lichens to the changed microclimate. Small patch harvesting requires more road access than does block cutting — a serious drawback from the standpoint of caribou and forest management.

In terms of timber economics, Alexander (1977) rated small patch clearcutting as less favourable than block clearcutting, but more favourable than any partial cutting system. Initial road costs are high. Silviculturally, the chances of natural regeneration are greater in very small openings than in larger clearcuts (Alexander, 1974). Small patches should be favourable to spruce regeneration. Since the wind does not normally reach ground level in openings of that size (Alexander, 1973), windthrow should be minimal. On sites where slash burning is required, fire control may be a problem.

Small patch harvesting, like partial cutting, may enhance lichen production in the remaining timber, but would result in increased harvesting costs and increased road access.

Extended rotation

The second-growth spruce-fir forests of the future will ordinarily be harvested when their growth rate culminates, at age 120-150 years. Because arboreal lichens are not abundant in stands younger than 100-150 years, logging will occur before or shortly after stands become useful to arboreal lichen-eating caribou. For that reason, an extended harvesting rotation of 250 years has been proposed for caribou ranges (Ritcey, 1976).

Assuming that only stands older than 150 years are useful to caribou and that all stands are clearcut, Ritcey (1976) calculated that under a 200-year rotation, 25% of the harvestable forest would be useful to caribou at any one time; under a 250-year rotation, 40% of the harvestable forest would be useful to caribou. Extended rotations could also be used with a partial cutting system, so that harvested areas had value to caribou for a longer period.

The cost of extending the harvest rotation is high in terms of growth and yield of timber. If no growth is assumed after 150 years, then changing the rotation from 150 to 250 years would decrease the contribution of a stand to the annual rate of harvest from 1/150 to 1/250 of the mature volume — a drop of approximately 40%. Although the assumption of no growth after 150 years is incorrect, it is true that the annual increment of volume decreases after the optimum rotation period — older forests grow slowly. Furthermore, older forests are more susceptible to windthrow, disease, and insect infestations than are young forests.

Despite the cost to the timber resource, some sort of extended rotation, perhaps in combination with other special practices, is the technique most likely to ensure long-term lichen production. It is unlikely that special practices, such as partial cutting or very small patch logging, will ensure a usable supply of forage lichens if the stands are harvested as soon as they become merchantable.

Progressive partial cutting

In large unlogged areas where caribou management is a high priority, progressive cutting, at least some of which must be partial cutting, is an option to consider.

Progressive cutting concentrates harvesting in a single watershed until its timber supply is exhausted, leaving other watersheds undisturbed for some time. The advantage to caribou is that the adjacent drainages continue to provide undisturbed, unroaded habitat while the first area is under development. If the first drainage is clearcut, then lack of suitable substrate and of propagules may prevent lichen re-establishment in the second growth. But if partial cutting is practised in spruce-fir forests where lichen abundance warrants it, and topography and stand structure allow it, then acceptable lichen crops may be present when the stands mature. There must also be a commitment to delay reharvesting past the time when the lichen supply becomes adequate; without such a commitment, this approach does nothing more than to buy time. This option is feasible only where little development has occurred previously, and unlogged areas are available to remain undisturbed for some time.

A potential disadvantage to caribou is the possibility that the presence of very large areas of unsuitable habitat within their range for many years will result in the abandonment of traditions of use. After the second growth becomes suitable as habitat, there may be a delay before caribou begin using it.

Concentration of timber harvesting through progressive cutting has advantages from the standpoint of forest management (Pearse, 1976: 279 - 284). Logging and road costs are substantially decreased. A reduction in the amount of exposed forest edge is expected to reduce losses due to escaped slash fires, unsalvaged blowdown, and epidemics of insects that breed in fallen trees. Although partially cut areas would be vulnerable to those hazards, the net losses would probably not be as great as they are under a patch logging system.

Silviculturally, the consequences of progressive cutting would be variable. Opportunities for satisfactory natural regeneration would be limited. Some foresters have argued strongly for progressive clearcutting in silvicultural grounds. However, in some areas and on some sites, especially at high elevations, growing conditions in a progressively clearcut watershed would be severe. In those situations, partial cutting might benefit silviculture as well as caribou management.

Progressive cutting is more often favoured by foresters than by other resource managers. Progressive cutting which incorporates partial cutting at high elevations is likely to be viewed less favourably by foresters. The inclusion of partial cutting in spruce-fir stands would mitigate the impact of the practice on some resources, such as watershed values. It would not mitigate its impact on the habitat of most other wildlife species. The advantages to caribou of such an approach must be weighed against its consequenses for other forest resources.

Access control

The development of roads in previously inaccessible areas is a serious consequence of logging in caribou habitat. Roads invite human activity in wilderness areas. They lead to increases in legal and illegal hunting. The negative effects of harassment on caribou, intentional and unintentional, have been described by Geist (1978) and Klein (1980).

Closure of roads after the completion of logging is inconvenient, but is generally possible. Signs, gates, felled trees, and trenches reduce public use but often do not eliminate it. Drivers of all-terrain vehicles are known for their ability to remove or circumvent obstacles. More complete physical barriers are necessary for complete closure. Closing roads is accomplished most easily if the need for closure was considered before the road was constructed. Roads can be planned to cross streams where they cannot be forded after the bridge is removed, or located along cutbanks that can be blasted onto the roadway.

Deliberate closing of roads after logging has some benefits other than the protection of wildlife: it reduces the risk of man-caused fire, and allows roads and skid trails to revert more quickly to growing sites. On the whole, it is undesirable from the standpoint of forestry because it eliminates access for purposes of stand tending, fire fighting, and other management activities. Road closure is also strongly resented by the public. Despite its drawbacks, it is technically feasible in most cases, and is an option that should be considered where caribou management is a high priority. The effects of access on caribou may be so severe that there is little value in modifying logging practices to maintain caribou habitat unless road closure is included in the management plan.

Conclusions

The special forest management practices considered here involve a tradeoff between forest economics and the objectives of caribou management. In general, those most likely to be effective in maintaining caribou habitat have the most severe economic consequences. In caribou ranges that are managed for lichen production, it will probably be necessary to defer some harvesting past the time that is optimum for timber production. There are no easy solutions to the problem of extracting timber from caribou ranges while maintaining caribou populations, at least where arboreal lichens are judged essential.

Wildlife managers must consider the trade-off between special forestry practices intended to encourage lichen production, and increased road access to caribou ranges. Unless the rate of timber harvest is reduced, the use of practices such as partial cutting and very small patch logging will result in an increase in the area that is under development at any one time. The result will be greater human disturbance for an extended period of time, unless access control is practised. To a great extent, the management strategy selected must depend on the relative importance we assign to the effects of habitat alteration and human disturbance.

Research is currently underway or proposed on several topics that could greatly alter the conclusions presented here: the development of techniques to enhance lichen production in managed stands (Stevenson, 1985), the relationship between predation and man-caused habitat changes, the impact of access on caribou, and the winter forage needs of caribou (Stevenson and Hatler, 1985). However, given the current state of knowledge, a prudent strategy for caribou management requires that key ranges be managed conservatively. Where caribou management is a high priority and arboreal lichens are the major winter food, both access control and practices intended to enhance lichen production should be incorporated into the management plan.

Acknowledgments

The review forms part of a larger study that was funded by the British Columbia Ministry of Forests, Research Branch and the British Columbia Ministry of Environment, Wildlife Branch. I thank R. Ellis, D. Eastman, and D. Hatler for advice and criticism, and T. Antifeau, Department of Animal Science, University of British Columbia for permission to cite unpublished data.

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Antler possession by west Greenland female caribou in relation to population characteristics

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Abstract: The frequency of antlerless adult female caribou *(Rangifer tarandus groenlandicus)* was studied in four separate populations in west Greenland. Between the herds antlerlessness varied from 21% to 79%. An inverse relationship between winter range quality and percentage of unantlered cows is demonstrated. Relationship between calf percentage and maternal antler status was studied in one population and antlerless cows showed higher reproductive rate than antlered ones. In another population antlerless cows were almost absent outside the calving area. Calves of antlerless mothers were more susceptible to diseases and had significantly higher summer mortality than other calves, 42% and 27% respectively. The relative importance of factors influencing antler development under various environmental conditons are assessed and a close relationship between antlerlessness, physical condition, lactation, and length of period between calving and midsummer is discussed.

Key words: caribou, *Rangifer*, Greenland, antler, reproduction, calf mortality, antler status, antler cycle.

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Rangifer, Special Issue No. 1, 1986: 297 - 304

Introduction

As an exception in *Cervidae* both sexes in genus *Rangifer* normally grow antlers. The female antler might be largely of social importance. When adult bulls loose their antlers in early to midwinter they are also deprived of their previous rank in the feeding hierarchy. During winter adult antlered females acquire highest ranks, thereby getting access to the best forage patches (Espmark, 1964, 1971; Henshaw, 1968; Shea, 1979). Development of antlers as a defensive structure in female *Rangifer* has been proposed by Bubenik (1975) and Espmark (1964). Parturient cows often still have antlers and are therefore capable of defending their calves against predators (Espmark, 1964). *Rangifer* often aggregates in big groups during insect season and migration and resulting intra-specific interactions might account for the development and function of antlers in the females (Clutton-Brock *et al.*, 1982). Goss (1976, 1977) demonstrated antler development to be dependant on day length in white-tailed deer. To our knowledge similar experiments have not been done with *Rangifer.* Skjenneberg and Slagsvold (1968) stated that antlers are shed earlier in strong and healthy individuals than in animals in poor physical condition. Bergerud (1976) reported that even pregnant cows might have antlers in velvet and the same may occur in Greenland. (P. Aastrup, unpublished data).

In the Hardangervidda (Norway) and Ameralik (Greenland) populations antler chewing on both shed and unshed antlers is widespread decline an epidemical summer mortality caused by E. coli arthritis has removed up to 65% of the calf crop annually (Clausen *et al.*, 1980, Thing and Clausen, 1980). Hunting pressure is very strong during the fall and winter seasons and the populations are apparently still decreasing (Ministry for Greenland, 1985; C.R. Olesen, unpublished data). The calving season is from 29 May to 23 June.

Sermilik herd: This herd is close to the present southern limit of caribou distribution in Greenland. Little data have been available for this population. Herd size was around 400 animals in July 1980 (Reimers, 1980; Aastrup, 1983). Very strong hunting pressure prevents animals from extending their home range into adjacent, more favorable range. Carrying capacity of the present range is believed to have been exceeded during recent years. Range lies in the coastal zone and heavy precipitation as well as above-zero temperatures are part of the winter weather pattern. The calving season is around early-mid June.

Materials and methods

Each of the four populations has been surveyed on foot. Field work took place in July-September 1977-84 in all ranges except Nuuk where data were collected in April 1979.

To minimize possible biases in registration of long-term antler status data collected between early May and early July were not used in the tables because parous females drop their antlers at various times.

Whenever adult females were encountered (during mid July - early April) at close range antler status, calf-leading, not calf-leading, and physical conditon of the calf was registered using 10 x 50 binoculars or 25 x 60 spotting scope. An adult female with no antlers nor any visible pedicles protruding through the skin was recorded as antlerless.

(Fig. 2C). Half-antlered cows were characterized by the absence of just one antler beam including pedicle either left or right (Fig. 2B). Fully antlered cows showed a complete set of antlers (Fig. 2A). Antlerless individuals may sometimes have dark-colored hairs on the spot where the pedicles should have protruded.

Close examination of their skull revealed that some of them were in fact truly antlerless while some had a small but detectible raised part of *os frontale* interpreted as the reminiscence of a resorbed pedicle (Fig. 2D).

Results

Antler and range data

Table 1 shows the percentages of antlerless and half-antlered females at various localities in Greenland together with reported percentages from Canada and Svalbard. Using the range as an indicator of the nutritional status of the herds we have furthermore tried to rank the localities.

Accordingly there seems to be an inverse relationship between range quality and the frequency of individuals without antlers. The two exceptions to this, the Disko and Itinnera herds, are both of *R. t. tarandus* origin and both calve 3-4 weeks before the *R. t. groenlandicus* herds. The Ameralik herd seems to be genetically influenced by the Itinnera herd.

Calf production and mortality in relation to antler status

Table 2 shows the relation between calf production and mortality parameters and antler status of the Sisimiut herd, July 1979.

The frequency of disease and mortality among calves is assumed to be an indicator of the health and nutritional status of the mother.

Four trends are apparent: 1) More antlerless females and fewer antlered females than expected were leading calves (X^2-test; P (x) <<0.005). 2) More antlerless and fewer antlered cows than expected were leading *sick* calves (X^2-test; P (x) <<0.005). 3) The disease frequency among calves lead by antlerless cows was greater than among calves lead by antlered cows (X^2-test; P (x) <0.025,) and 4) 80.2% of the diseased calves were lead by antlerless cows compared to 6.3% lead by half-antlered and 13.5% by antlered mothers.

Furthermore, summer mortality among calves was greatest among calves lead by antlerless cows (P (x) <0.05). In mid-August the calf ratio per 100 antlered adult females was 37.5 (N = 66) compared to 31.3 in July (N = 71) and for antlerless cows 36.4 (N = 75) compared to 55.9 in July (N = 238). The indicated increase in calf ratio for antlered cows is not absolute but purely a result of relative dependency of the decreasing calf ratio of unantlered cows.

(Wika, 1982; Aastrup, 1984). Antler growth might therefore be interpreted as part of a mineral saving strategy. In several *Rangifer* populations in Eurasia, Svalbard, Greenland, and North America a varying percentage of females are antlerless. Antlerlessness in this context is defined as the condition in which no sign of an antler is visible. The question of whether the absence of antlers is an inherited or environmentally determined condition has not yet been discussed. This paper presents circumstatial evidence that 1) in some years antlers may fail to sprout depending on the nutritional status of the individual and 2) that pedicles may be partly or fully resorbed in periods of antlerlessness. The scars from a dropped antler may heal so well that they can not be detected by ordinary field observations.

We set forth to examine and discuss the following:

I. The status of antlers in different herds in Greenland.
II. Possible correlations between this and range conditions.
III. A hypothesis that possession of antlers is environmentally determined.
IV. Testing this across subspecies.

Study areas

This paper deals with data collected between 1977 and 1984 in four populations of west Greenland caribou (*Rangifer tarandus groenlandicus*): 1) Ameralik, 2) Nuuk, 3) Sisimiut, and 4) Sermilik (Fig. 1). These areas exhibit various range conditions based on assessment of the amount of fruticose lichen stands. The Ameralik range is documented to be a near optimal condition (Aastrup, 1983), whereas the Nuuk, Sisimiut, and Sermilik ranges represent an increasing deprivation of the winter food resource of lichens (Reimers, 1980; Thing, 1983). All study areas have bordering topographical features that render exchange of animals between neighbouring herds unlikely.

Ameralik herd: The population was estimated at 2100 animals in 1983 (Aastrup, 1984). Winter climate in recent years has been very adverse with heavy snowfall which seems to have prevented access to the lush lichen stands (2-250 g dry weight/m^2) in the coastal areas. The history of the population is unknown until 1982 but the herd is apparently stable or slightly increasing. Fall hunting pressure is relatively light. Calving season is from 18 May to 15 June.

Nuuk herd: This herd numbered approximately 8000 in March 1982 (Strandgaard *et al.*, 1983) and population size is stable or slowly decreasing. Hunting pressure is strong - recently approaching 30% of the fall population (Ministry for Greenland, 1985). There are reports of many animals in poor physical condition in recent years but heavy winter mortality has not been recorded. Calving time is from early to late June.

Sisimiut herd: Latest peak in this population occurred around 1970 with ca. 30 000 animals. Since then the herd has decreased to 3000 in March 1982 (Thing, 1982; Strandgaard *et al.*, 1983). Long-term carrying capacity is believed to be around 10-12 000 individuals (Strandgaard *et al.*, 1983). During at least the last 8 years of

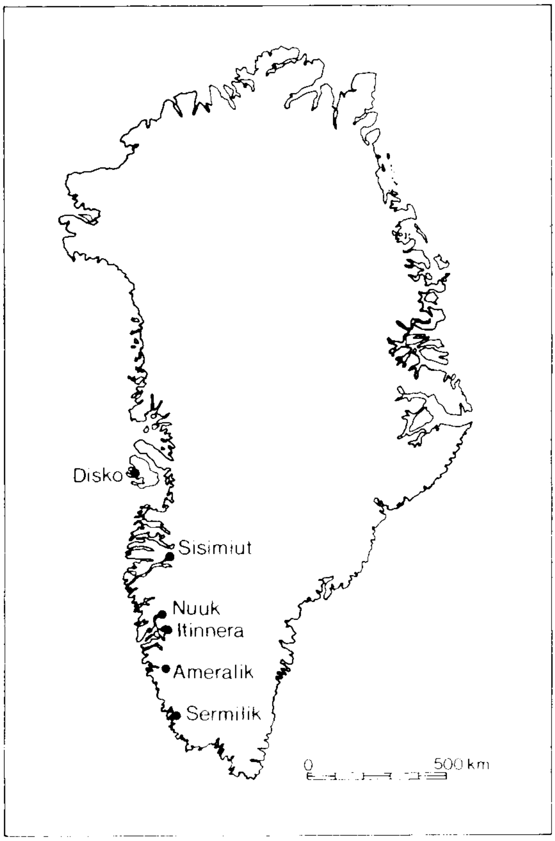


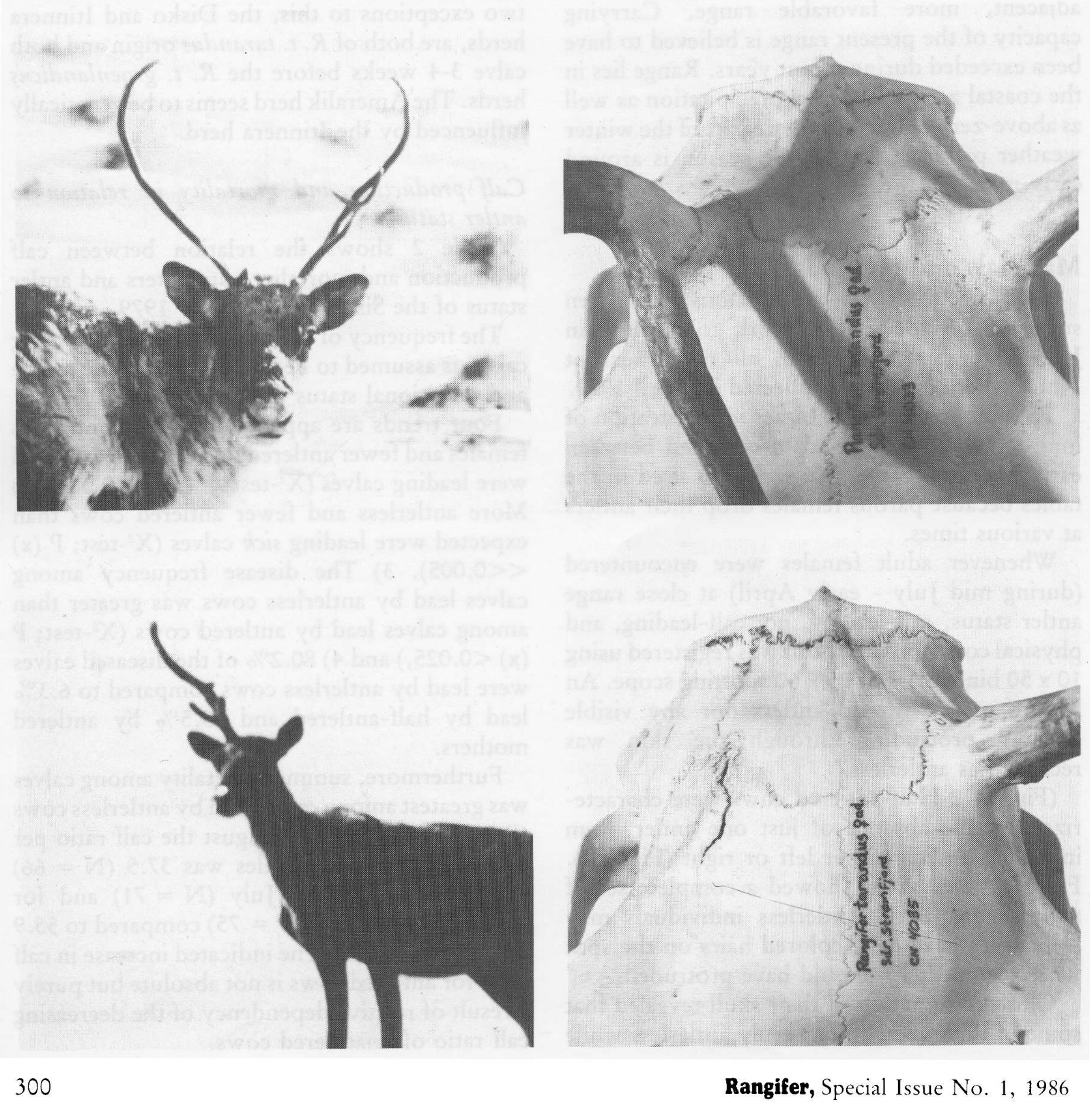
Fig. 1. Map of Greenland showing location of the six study herds. Disko: c. 70°N; Sisimut: c. 67°N; Nuuk: c. 65°N; Itinnera: c. 64°N; Ameralik: c. 64°N; Sermilik: c. 62°N.

Discussion

The annual antler cycle in female caribou has been studied by several authors and time differences in antler shedding and initiation of new growth have been related to hormonal and behavioral parameters (Lent, 1965; Henshaw, 1968; Espmark, 1964, 1971). The pattern of antler shedding in parturient caribou cows in the Sisimiut and Ameralik herds is not in accordance with that reported by Lent (1965), Espmark 1971), and Bergerud (1976) but rather complex. Around calving time cows exhibited all possible stages of antler status in the immediate *post partum* period (Table 1) similar to the situation described long ago by Müller (1906) in west Greenland.

Some females had growing antlers up to 10 cm long at the time they gave birth. Since the mid 1970's winter forage conditions in the Sisimiut range have been very poor with virtually no lichens to be found (Thing, 1983). Frequency of polled cows in 1977-84 varied between 45% and 64% with a general increase during the period.

The Nuuk and Sermilik herds both occupy ranges where winter food regime is comparable to the situation in the Sisimiut herd and high percentages of antlerlessness were observed. The different populations of *Rangifer* in west Greenland are fluctuating out of phase (Strandgaard *et al.*, 1983). In the Ameralik range good quality winter food is still abundant and the animals are generally in good physical condition



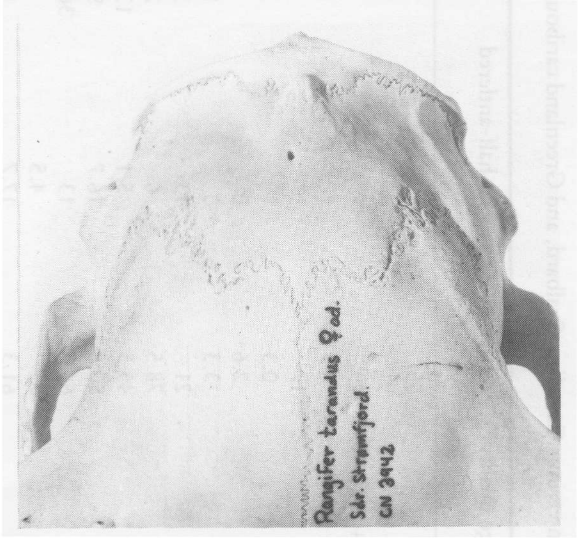
(Aastrup, 1984) and a relatively low frequency (21%) of polled females was recorded. Thus the frequency of antlerless adult females appears to be inversely related to winter range quality (Table 2). This would support the theory of competitive mineral use between gestation/lactation and antler development (Wika, 1980).

Two west Greenland *Rangifer* populations originating from domestic Norwegian reindeer, the Disko and Itinnera herds, have high quality winter ranges available and just one antlerless cow has been observed in the Itinnera herd (Reimers, 1980; Lassen and Aastrup, 1982). These observations are remarkable when compared with *R. t. groenlandicus* herds as calving occurs three to four weeks earlier than in caribou and because of possible genetical differences.

Gossow (1977) reported 17% antlerless cows in the Sassendalen herd on Svalbard (*R. t. platyrhynchus*). Winter range quality in Sassendalen was considered sub-optimal when compared to the range of the Nordenskiöld Land herd and an inverse relationship between winter range quality and percentage of unantlered cows was documented.

Antlerlessness in female caribou was also observed on Newfoundland (Bergerud, 1971, 1975, 1976) but lack of range quality data made correlation between antler and range status impossible.

In Greenland antlerless females are extremely rare in the Itinnera and Disko herds while both



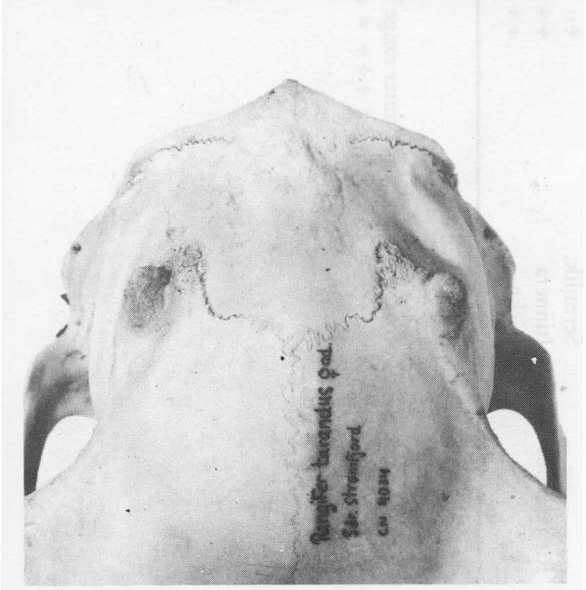


Fig. 2 A-D. The four types of antler status of adult females on live animals and skulls. A: Fully antlered (live, March 1982; skull, November 1978). B: Half-antlered (live, August 1977; skull, November 1978). C: Antlerless (live, August 1979; skull, November 1978). D: Skull from cow appearing antlerless but with partly resorbed pedicles (November 1978).

Table 1. Summary of comparative range and antler data in various Canadian, Svalbard, and Greenland caribou herds.

Subspecies	Locality	Range quality°	Antlerless %	% half-antlered	N	Sample time	Reference
R.t.caribou	Interior, N.fl.*)**	++	55	?	?	1958-63	Bergerud, 1974, 1975
—	Avalon, N.fl.	+	91	?	?	1962-64	Bergerud, 1974, 1975
—	Humber, N.fl.	+++	29	?	?	?	Bergerud, 1974, 1975
—	NE Alberta	?	8	?	?	?	Fuller and Keith, 1980
R.t.platyrhynchus	Sassendalen**	++	17	17	59	Aug.1972	Gossow, 1977
—	Nordenskiöld Land**	++	0.3	?	?	Aug.1972	Gossow, 1977
—	Adventdalen	++	2.6	0	78	Oct.1980	Tyler, pers.comm.
—	—	++	3.3	0	171	Oct.1981	Tyler, pers.comm.
R.t.groenlandicus	Ameralik, W.Greenland**	++	21	13	316	Aug.1983	Aastrup, 1984
—	Tasersuaq, — **	+	78.5	6	240	Apr.1979	H. Thing, unpubl.data
—	Sisimiut, — **	+	45.5	5.1	1373	Aug.1977	H. Thing, unpubl.data
—	—	+	50.6	16.7	925	Aug.1978	H. Thing, unpubl.data
—	—	+	64.3	13	3684	Aug.1979	H. Thing, unpubl.data
—	—	+	55	4.5	43	Aug.1982	Aastrup, 1983
—	—	+	61.3	17.7	181	Jul.1984	H. Thing, unpubl.data
—	Sermilik,	+	74	11.7	77	Jul.1980	Reimers, 1980
R.t.tarandus	Itinnera	+++	≤0.5	0	480	Sep.1977	Aastrup, unpubl.data
—	Disko	++	0	0	?		Reimers, 1980

* N.fl. = Newfoundland, Canada,

** late calving

° subjective appraisal of relative quality of winter range based on available data on fruticose lichen quantities.
+ = heavily exploited; ++ = sub-optimal; +++ = optimal.

Table 2. Calf production and mortality parameters in relation to antler status of cows in the Sisimiut herd, July 1979.

Antler status of mother	No. of calf-leading cows: Observed	Expected	P (x)*	Calf/cow ratio: July	mid-Aug.	No. of cows leading sick calves: Observed	Expected	P(x)*	Disease freq. among calves %	Distribution of diseased calves
Polled	213	186		55.9	36.4	89	68		41.8	80.2
Half-antlered	36	33	<.0005	53.7		7	12	<.0005	19.4	6.3
Fully antlered	55	86		31.3	37.5	15	31		27.3	13.5

* Significance levels tested with X^2 test.

belong to *R. t. tarandus*. The Itinnera herd has winter ranges comparable to the Amaralik herd where unantlered cows are as frequent as 20%. Calving time occurs 2-3 weeks earlier in the Itinnera herd than in the Ameralik herd. Besides, they are genetically different.

Herds where females without antlers occur frequently seem to have late calving date in common. In our examples, these herds belong to the *R. t. groenlandicus* subspecies which might lead to the conclusion that the phenomenon is genetically determined. However, we feel that the evidence for environmental control is so strong that another explanation is more likely.

Goss (1976) suggests that the shift of antlers in deer is triggered by the alteration of increasing and decreasing daylength. We assume that the initiation of antler growth in *Rangifer* is dependent on the shift between increasing and decreasing light at midsummer. We hypothesize that a late calving date and subsequently late antler shedding might result in a high probability of the animal not being physiologically capable of initiating new antler growth because the triggering date was passed before initiation of new antler growth.

In the process of antler shedding osteoclastic erosion occurs at the line between the dead antler and the pedicle (Goss, 1963). This process might proceed to the pedicles in case new antler development was not commenced resulting in resorption of the pedicles.

According to our theory late calving combined with pregnancy and poor nutritional status would be expected to lead to at high proportion of antlerless females in the herd.

The demonstrated difference in proportion of antlerless females in the Sisimiut herd in 3 consecutive years corroborates that being antlered is not a permanent condition in the individual and that pedicles may be resorbed (Fig. 2D). It seems likely that the nutritional status of the individual in part determines whether the antlers sprout. This is further supported by the fact that antlerless non-pregnant females from the Ameralik herd were rare outside the calving ground at calving time. Non-pregnant females are most often in better nutritional condition and grow new antlers before pregnant or maternal females. Skjenneberg and Slagsvold (1968) state that in bad years antlers shedding and development are delayed and that females shed the antlers before calving on good ranges. According to Bergerud (1976) females may grow new antlers earlier when in good nutritional condition following e.g. mild winters. This might apply to non-pregnant females too.

The higher than expected calf/cow ratio and heavier than expected calf mortality for antlerless females in the Sisimiut herd (Table 2) also points towards a relation between antler status and nutritional status.

Acknowledgement

This work was funded by the Ministry for Greenland, Commission for Scientific Research in Greenland and Greenland Fisheries and Environmental Research Institute. The K. Højgaards foundation is also gratefully acknowledged for financial support. Morten Meldgaard, Zoological Museum, Copenhagen, is thanked for supplying the photographic material on caribou skulls.

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The late winter diets of barren-ground caribou in North-Central Canada

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Abstract: Rumen samples from 104 barren-ground caribou *(Rangifer tarandus groenlandicus)* collected in March 1980 and 1981 at 18 sites on the winter range in south-central Northwest Territories (NWT) and northern Saskatchewan were examined microscopically for relative occurrence of plant fragments. The composition of plant fragments in the rumens of calves did not differ from that in older caribou. Samples were homogeneous within sites and among them. Therefore we analyzed composite samples for each site and then pooled the data. Terricolous fruticose and foliose lichens averaged 68.5 ± 1.5% (SE) of tallied fragments at all 18 sites, followed by conifer needles (11.9 ± 1.2%), green leaves of *Vaccinium* spp., *Ledum* spp., and other shrubs and forbs (5.6 ± 0.6%), twigs and bark (5.5 ± 0.4%), bryophytes (4.9 ± 0.6%) and 3.6% unidentified. The lichen component consisted of 8.4 ± 1.5% *Stereocaulon* spp., 46.9 ± 2.6% other fruticose lichens (largely *Cladina* spp., *Cladonia* spp., and *Cetraria* spp.), and 13.2 ± 1.5% foliose lichens (largely *Peltigera* spp.). A comparison of rumen contents with the average relative abundance of plants found in feeding craters at 13 sites suggests that use of plant species was not always proportionate to their occurrence.

Key words: caribou, winter diets, Northwest Territories, *Rangifer*, rumen samples.

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Rangifer, Special Issue No. 1, 1986: 305 - 310

Introduction

In 1980, the Canadian Wildlife Service began a study of the winter ecology of barren-ground caribou *(Rangifer tarandus groenlandicus)*. The Beverly Herd was selected as the study herd because hunters and trappers, notably in Fort Smith, Northwest Territories (NWT), voiced concern over the effects on the herd of the extensive fires that occurred on the winter ranges in the summer of 1979 (Northern Affairs Program, 1980).

The first priority was to obtain information on the winter diet of the study herd. The only existing data for caribou herds in north-central Canada were analyses of rumen contents of: 1) 302 caribou collected from the adjacent Kaminuriak Herd in November (126), February (14), and April (162) of 1967-1968 (Miller, 1976a); 2) 28 caribou killed in northern Manitoba and Saskatchewan in February and April of 1972 and 1973 (Miller, 1976b); and 3) 20 caribou collected from various locations in Manitoba, Saskatchewan, and the NWT (Scotter, 1967).

Data on feeding locations and the frequency occurrence of plants in craters dug in the snow by caribou can provide insights into their food habits. Some conclusions about food preferences are possible if such data are combined with information from rumen analyses.

Miller (1976a) provided data on the frequency occurrence of plant genera at feeding sites in northwestern Manitoba and northeastern Saskatchewan in early, mid, and late winter. Miller (1976b) also obtained cover values of species at feeding sites used by caribou in February and April in the same region. The sites were fenced for examination in the summer.

Kelsall (1968) collated data on frequency occurrence of vegetation at several sites cratered by caribou in the NWT and northern Saskatchewan. He also compared data on frequency of occurrence of plants in craters with their frequency in the same general region.

This report gives the results of an analysis of the rumen contents of 104 caribou obtained in March 1980 and 1981 in conjunction with a study of *in vitro* digestibilities of plants using rumen fluids of caribou (Thomas and Kroeger, 1981; Thomas *et al.*, 1984). We also sampled vegetation in caribou craters to investigate the relationship between crater and rumen contents.

Methods

In March 1980, 75 rumen samples (50 fresh and 25 frozen) were obtained from 12 locations in the NWT and one in Saskatchewan. A year later, 29 samples were obtained from five locations in the NWT.

The site locations were on the following lakes which are named on 1:500 000 scale National Topographic Series maps of the area: Bedareh, 22 km south of Bedareh, 10 km southwest of Van Dyke, Van Dyke (two locations), Imogen, Brazen, Huntington, Dardier, Dunvegan, Carleton, and Scott (two sites). The sites were in a 58 x 160 km rectangle between 59°48'N and 60°20'N and between 106°09'W and 109°38'W.

In the laboratory, the half litre samples were thawed and 120 ml subsamples were thoroughly washed in a no. 20 sieve (0.85 mm) (Bergerud and Russell 1964) to remove particulate matter. A sample of the sieved material was spread in a dish and examined under a stereomicroscope (6X) equipped with a grid ocular. Plant fragments under 50 grid intersections were recorded and the process was repeated on another five sub-sub-samples to yield data for 300 point samples from each rumen subsample.

Species fragments were grouped in the following categories: terrestrial fruticose lichens except *Stereocaulon* spp., *Stereocaulon* spp., terrestrial foliose lichens, conifer needles, bryophytes, leaves of *Ledum* spp., leaves of *Vaccinium vitis-idaea* var. *minus*, other evergreen leaves (e.g. *Arctostaphylos* spp. and *Empetrum nigrum)*, twigs and bark, and unidentified fragments. Other species groups, including arboreal lichens, graminoids, and forbs were not present or not detected.

Age, site and yearly difference were tested by: (1) comparing the results from three calves and six older caribou obtained at one site in 1980 (*t* test); (2) degree of homogeneity within two sites (five and nine samples) and among sites (N=13) examined in 1980 (ANOVA and Kruskal-Wallis); and (3) comparing the results of pooled samples in 1980 (N=13 sites) with those of 1981 (N=5 sites) (*t* test).

Several hands-full of vegetation present at the base of 100 craters dug by caribou in late March, 1980 were placed in paper bags, labelled and returned to the laboratory for sorting. Ten bags were obtained at each of seven sites and five bags at each of six sites. Four of the sites were at caribou collection sites and the other nine in the same study region.

The relative abundance of plant species in feeding craters were subjectively rated at four levels and given a class symbol: 1 = trace amount, 2 = scarce, 3 = moderately abundant, and 4 = abundant. Average abundance values were then calculated for each site by pooling the data. Average relative abundance values were obtained by pooling the data from all 13 sites.

Snow thicknesses were measured adjacent to the 10 caribou craters that were sampled for plant species abundance at each site. At a few additional sites a minimum of 10 measurements were obtained in small clearings where the forest canopy and drifting did not affect snow thickness.

Results

Age, site and year variations

The fragment composition in rumens of three calves did not differ ($P<0.5$) from that of six older caribou. Fragment proportions of *Stereocaulon* spp., other fruticose lichens and foliose lichens were 7.3 and 9.8%, 61 and 59% and 4.7 and 5.2% in calves and older caribou, respectively.

Variations in fragment composition of the five most abundant plant groups within the two sites examined were not significant.

Variations in rumen composition were not significant among the 13 and 5 sites examined in 1980 and 1981, respectively. Much of the variability among sites in 1980 was caused by the sites at Dunvegan and Carleton lakes where 24% of the fragments were *Stereocaulon* spp. compared with a high of 14% elsewhere. The proportions of other lichen species at those two sites, located in a region of drumlins (ridges of till), were the lowest of all sites. Proportions of *Stereocaulon* spp. were low (2-7%) at the seven sites west of 108°W but the total lichen values were similar at all sites, varying from 55-80% of all fragments.

The results for the five sites obtained in March 1981 were similar ($P<0.05$ for all classes) to those for 1980. The results for identified plant groups were all within 3% of one another except that fruticose lichens varied from 44% in 1980 to 54% in 1981, and *Stereocaulon* spp. decreased from 13 to 8%.

Diet

Pooled results from March 1980 and 1981 (Table 1) reveal the importance of terricolous lichens to caribou in the study herd. We believe that the conifer needles (mostly dead) are eaten incidentally because they are interspersed among the lichens. Similarly mosses are intertwined with lichens and cannot be avoided. Exclusion of those two groups increases the relative importance of the other components.

Frequency, relative abundance and availability of forage

Lichen genera and species occupied 7 of the 10 top positions in the list of the most frequent and most abundant species present in craters dug by caribou in search of forage in March 1980 (Table 2). *Cladina mitis* was by far the most abundant species in the craters.

Average snow thichnesses in 1980 at 14 sites varied from 31 to 56 cm and averaged 42 cm. The thickest snow was in the southeast in the Grollier and Robbins lakes region of Saskatchewan and the thinnest in the southwestern limits of the study area. Snow thicknesses in March 1981 averaged 31 cm (range 27-36 cm) at four sites (Brazen, Abitau, Hurricane and Porter lakes).

Discussion

Age, location and year variables

Minor differences in diet between calves and older caribou reflect use by calves of craters dug by older caribou, the close association of calves with their mothers, the limited variability in major vegetation groups among sites and the probable need to eat a variety of plant species to meet nutritional requirements. Miller (1976a) also found no dietary differences between sexes of caribou and therefore age and sex differences can be ignored in comparisons between individuals or in pooling rumen samples from a site.

Table 1. Proportionate occurrence (percent) of plant fragments in composite samples of rumen contents obtained in March 1980 and 1981 from barren-ground caribou at 18 locations on the winter range east of Fort Smith, NWT.

Plant species or groups	% occurrence Mean	SE	Range
Fruticose lichens	46.9	2.6	25-70
Foliose lichens	13.2	1.5	3-24
Conifer needles	f1.9	1.2	3-23
Stereocaulon spp.	8.4	1.5	2-24
Twigs and bark	5.5	0.4	2- 9
Bryophytes	4.9	0.6	0-10
Vaccinium vitis-idaea	2.4	0.3	1- 4
Evergreen leaves[a]	1.4	0.3	0- 4
Ledum spp.	1.8	0.3	0- 4
Unidentified	3.6	0.5	0- 7
Total lichens	68.5	1.5	55-80

[a] Other than conifer needles, *Vaccinium* spp., and *Ledum* spp.

The insignificant regional and annual differences in diet reflect the similarity of vegetation throughout the study area and the similar snow conditions in both years. Snow was relatively shallow compared with average range-wide values between 53 cm and 57 cm in March of 1982 through 1985 (Thomas, unpublised data). Miller (1976a) found a few significant differences between sites in a given season and differences between years in the proportion of lichens in rumens obtained in April.

Diet

Our findings differed little from those of Scotter (1967) who found that lichens accounted for 69% of the dry weight of plants in the rumens of 20 caribou collected in the winter in Saskatchewan, Manitoba, and the NWT. Woody plants (24%), bryophytes and fungi (4%), and grass-like plants (3%) completed the list.

Miller (1976a, 1976b) obtained data on the relative dry weights of plants in the rumens of 28 caribou obtained in February and April of

1972 and 1973 in northern Manitoba and Saskatchewan. The major difference was in total lichens (46-49% versus our 68%) and grass-like plants (8%) and mushrooms (2-3%) in Miller's (1976a) samples and not detected in ours.

Miller's (1976a) data for 302 rumen samples from barren-ground caribou collected on winter ranges in northern Manitoba from 1966 to 1968 are also comparable to ours. The approximate average composition by dry weight was lichens 49%, twigs 20%, leaves 21%, grass-like plants 8%, and mushrooms 2% (Miller, 1976a). The lower proportion of lichens in his samples may relate to the much deeper snow in semi-open coniferous stands in midwinter (February): 74-79 cm in 1967 and 60-80 cm in 1968 (Miller 1976a). Data extracted from his Fig. 5 indicate virtually no difference in broad classes of forages consumed by the Kaminuriak Herd between February and April of those years.

The proportionate ingestion of terricolous lichens is undoubtedly higher than is indicated by the above results because of their relatively rapid digestion (Bergerud and Russell, 1964; White and Trudell, 1980). Furthermore, the relative value of lichens as an energy source is higher than that of most other forages because lichens are highly digested by caribou (Person *et al.*, 1980a, 1980b; Thomas and Kroeger, 1981; Thomas *et al.*, 1984). Those factors in combination with the data on rumen contents provide overwhelming evidence that terricolous lichens are the most important forage item for barren-ground caribou on winter ranges in north-central Canada.

Our data on frequency of occurrence of plants in caribou craters differs markedly from Miller's (1976a) data. In general, the occurrences of lichens were much higher in our samples. For example, *Cladina mitis* occurred in 96% of the craters we examined compared with 56 and 61% for *Cladina* spp. in his February and April-May samples, respectively. *Peltigera* spp. occured in 39% of the craters we sampled compared with 0 and 4% for combined *Peltigera* spp. and *Nephroma* spp. in his February and April-May sampling periods. *Vaccinium vitis-idaea* occurred in 76% of craters that we examined compared

Table 2. Frequency of occurrence and average relative abundance[a] of plant genera and species in 100 caribou craters examined in March 1980 at 13 sites on the winter range of the Beverly Herd in the southern NWT and northern Saskatchewan.

Plant genus, species or group	% occurrence		Relative abundance[a]	
	Mean	SE	Mean	SE
Cladina mitis	96	14	3.6	0.1
Vaccinium vitis-idaea	76	6	1.7	0.2
Cetraria nivalis	69	8	2.0	0.3
Cladonia spp.[b]	69	6	1.1	0.2
Cetraria ericetorum	59	7	1.2	0.1
Stereocaulon spp.	57	8	1.6	0.3
Needles	42	11	1.4	0.2
Cladonia uncialis	40	7	1.1	0.4
Peltigera spp.	39	8	0.9	0.2
Cladonia cornuta	34	5	0.7	0.1
Cladonia amaurocraea	24	6	0.7	0.2
Cladina rangiferina	24	7	0.7	0.2
Ptilidium ciliare	24	6	0.9	0.2
Ledum spp.	23	8	0.5	0.2
Cladina gracilis	19	4	0.4	0.1
Cladonia coccifera	10	3	0.2	0.1

[a] Where 1 = trace, 2 = scarce, 3 = moderately abundant, and 4 = abundant

[b] Exclusive of *Cladonia amaurocraea*, *C. cornuta*, *C. coccifera* and *C. uncialis*, which were treated as individual species.

with 13 and 23% occurrence in Miller's (1976a) samples for the two periods. Kelsall's (1968) data on occurrence of plants in 428 feeding craters also varies considerably from ours, with much lower frequencies in most categories, except for *Carex* spp. Sampling differences may account for these differences in crater contents. We removed vegetation from the surface of the ground at the base of the crater whereas Miller (1976a) recorded the species occurrence of grazed and browsed plants.

Rumen contents versus crater contents

A conclusion derived from examination of the data in Tables 1 and 2 is that caribou ingested less *Vaccinium vitis-idaea*, *Ledum* spp., and bryophytes than would be expected by their frequency in the craters. For example, *Vaccinium vitis-idaea* occurred in 76% of the craters but its fragments constituted only 2.4% of all fragments tallied in rumen samples. Habitat studies in summer reveal that it is the most common vascular plant on the winter range (Miller 1976a), occurring in almost every ½ x ¼ m quadrat used for cover and biomass estimations (Thomas, unpublished data). *Ledum* spp. are usually not browsed when exposed in craters. There appears to be selection for foliose lichens, a group dominated by *Peltigera* spp. in the study area.

Conclusions

1. The diet of calves and older caribou were similar.
2. There was little variation in the diet of barren-ground caribou among years and on different parts of forested winter ranges in north-central Canada.
3. Rumen contents of barren-ground caribou indicate that lichens that grow on the ground dominate the diet in late winter on forested ranges in north-central Canada.
4. Shrubs and bryophytes were not eaten to the extent that they are available at caribou feeding sites.

Acknowledgements

Aircraft support was received from the Northwest Territories Wildlife Service and Indian and Northern Affairs Canada. We thank the Fort Smith Hunters and Trappers Association for help during the collection of samples and Dr. W.E. Stevens and E.S. Telfer for manuscript reviews.

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The relationship between the fat content of Svalbard reindeer in autumn and their death from starvation in winter.

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Abstract: The relationship between body fat reserves in autumn and age-specific mortality in winter were examined in Svalbard reindeer *(Rangifer tarandus platyrhynchus* Vrolik). Total dissectible fat (TDF) was measured in 17 females, 1-12 years of age, shot on Spitsbergen (78°N lat.) in autumn 1980-1981. TDF declined with age in reindeer 2 years and older. The youngest females which died in winter, with the exception of calves, were aged 7 years old. A direct causal link between low autumn TDF and mortality in winter seemed unlikely. Mortality was clearly associated with the degree of wear of molariform teeth. Perhaps severe tooth wear results in inefficient mastication of low quality forage and a decline in the rate of passage of digesta, thereby restricting the amount of food that reindeer can eat. A simple model of the energy balance of female Svalbard reindeer in winter shows that they must obtaine not less than about 74% of their total energy requirements from forage. Consequently, differences in the ability of individual reindeer to feed in winter are potentially more important for survival than differences in their fat content in autumn.

Key words: body composition, energy balance, mortality, reindeer, *Rangifer,* starvation, Svalbard, tooth wear

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Rangifer, Special Issue No. 1, 1986: 311 - 314

Introduction

Reindeer and caribou (*Rangifer tarandus)* store fat during summer and autumn which they use in winter when the quality and abundance of their forage declines. In some wild populations starvation is an important cause of natural mortality. However, although there is usually considerable variation in the size of fat reserves within a population (Dauphiné, 1976; Leader-Williams and Ricketts, 1981), it is not clear to what extent the fat content of an animal in autumn predjudices its chances of surviving winter. Fat may be an important source of energy but it is not their principal one. Individual differences in the ability to find food in winter, or actually to feed, might also be expected to have an important effect on survival.

Most natural mortality in Svalbard reindeer *(R.t. platyrhynchus* Vrolik), a sub-species known to have large amounts of subcutaneous fat in autumn (Reimers, *et al.,* 1982), is due to starvation in winter (Tyler, 1986). In this paper, age-specific patterns of variation in (1), the fat content of female Svalbard reindeer in autumn and (2), the condition of their molariform teeth, are compared with age-specific patterns of natural mortality.

Methods

Fat content and energy store.

Total dissectible fat (TDF) was measured in a sample of 17 females aged 1-12 years old shot in September and October 1980 and 1981 on Nordenskiold Land, Spitsbergen (78°N lat.)

(Tyler, 1986). The total amount of retrieval energy contained in this was calculated assuming that dissectible adipose tissue was composed of 92% triacylglycerol, by weight (Reimers, Ringberg and Sørumgaard, 1982), which yielded 9.4 kcal·g^{-1} on complete oxidation.

Energy budget in winter.

The average daily energy expenditure (DEE) of a non-pregnant, adult female reindeer during winter was estimated from the mean live body weight of females during winter (55 kg, Tyler, 1986), assuming a resting metabolic rate (standing) of 4.03 W (Watt) $kg^{-0.75}$ (Nilssen, *et al.*, 1984) and adding on increments for different activities. Activity patterns in winter were measured by watching reindeer continuously for periods of ≥24 hours (Tyler, 1986). Total energy expenditure during winter was calculated by multiplying DEE by 211 days (21 October to 29 May).

Age-specific pattern of mortality.

A discrete sub-population of between 400-800 reindeer lives all the year round in the valley of Adventdalen and its associated side valleys (Tyler, 1986). There is usually negligible net dispersal of reindeer either into or out from this area. The entire area was searched each summer (1979-1984) for carcasses of reindeer which had died during the preceding 12 months. Age at death was determined by counting annulations in the cementum of first incisor teeth (Leader-Williams, 1979).

Tooth wear.

The degree of wear of the first mandibular molar, m 1 (normally the most worn tooth), of each dead reindeer was measured using a dimensionless index devised for this purpose (Tyler, 1986).

Analysis of data.

The homogeneity of samples collected in different years was examined by analysis of variance. The degree of association between TDF, tooth wear and reindeer's age (in whole years) was measured using Spearman's rank correlation coefficient. Comparisons between age classes were made using the Mann-Whitney 'U' test (Siegel, 1956). The null hypothesis was rejected in all cases at the 5% level.

Results

Fat content and energy store.

There were no significant differences in the mass ($F_{(1,15)}=3.19$) or TDF ($F_{(1,15)}=2.36$) of reindeer shot in 1980 and 1981, so results from the two samples were combined. TDF increased with age up to 2 years but declined after that. The correlation between TDF and increasing age was weak, though, and not significant in females aged 4 years and older (females ≥2 years old, $r_s=$ —0.58, n = 15, P <0.05); females ≥4 years old, $r_s=$ —0.35, n = 13, n.s. (P >0.05).

Two 2-year olds each had 16.0 kg TDF in autumn. Females aged 4 years and older had a mean of 10.6 kg TDF (range = 6.4 - 14.5 kg, n = 13). In autumn, therefore, full grown females carried sufficient dissectible fat to yield, on average, approximately 92 000 kcal standard free energy. Their gross energy store (including intramuscular fat and protein) was approximately 105 000 kcal (Tyler, 1986).

Energy budget in winter.

The total energy expenditure of non-pregnant female Svalbard reindeer during winter was approximately 400 900 kcal. Hence, in autumn, females had reserves of energy sufficient to contribute, on average, 26% of their total requirement for winter, not including the cost of gestation, They must, therefore, have had to obtain not less than 295 900 kcal, or 74% of their requirement, by feeding.

Age-specific pattern of mortality.

The youngest females found dead (excluding calves) were 7 years old (N = 127). Age-specific rates of mortality increased almost linearly from the age of 8 years (Tyler, 1986). No reindeer lived more than 15 years.

Tooth wear.

The degree of wear on the first mandibular molar increased linearly with age up to 8 years old after which there was no significant increase in tooth wear (females aged 2-7 years: $r_s=$ 0.84, df = 44, t (one tailed) = 10.27, (P <0.005); females ≥9 years: r_s = —0.12, df = 35, t (one tailed) = —0.72, n.s. (P >0.1). The m1 of females aged 8 years and older was invariably badly worn: in most cases, for example, the infundibulum between the anterior and posterior cusps had disapeared completely (Tyler, 1986).

Fat content and mortality.
Females aged 4 to 7 years old (i.e. those which normally survived winter) were fatter in autumn than females aged 8 years and older but the difference was only just significant ($z = -1.68$, $P = 0.047$). There was no sign of a marked decline in fatness in the latter group, corresponding with the onset of mortality.

Tooth wear and mortality.
All reindeer which starved to death had badly worn molar teeth. The first mandibular molars of reindeer which had starved were significantly more worn than those of animals of the same age which had been shot ($z = -1.90$, $P = 0.029$).

Discussion

Svalbard reindeer undoubtedly need fat in winter but their principal source of energy, nevertheless, is their food. Consequently, individual differences in fat content in autumn are likely to have less significance for survival than differences in rates of food intake in winter. Adult females, for example, would need approximately 6.5 kg more fat (an increase of 60% on the mean autumn value) to compensate for a 20% reduction in their average daily intake of energy from food. However, they would need to eat only about 6% more food per day to compensate for a 20% reduction in autumn TDF.

Both the onset of mortality and age-specific differences in the survival of adult females were associated with increasing wear of the first mandibular molar teeth. Ruminants have evolved hypsodont (high crowned) teeth for grinding forage and the efficiency of mastication presumably decreases as their teeth wear down. The importance of thorough mastication has been demonstrated indirectly in both wild and domestic species (Dean *et al.*, 1980, Freer and Campling, 1963; Campling *et al.*, 1963). Cattle eat less when fed bulky, low quality roughage than when the same ration is finely ground and pelleted (Campling and Freer, 1966). Sheep eat less when their jaw-movements are restricted artificially during rumination (Pearce and Moir, 1964). In both of the above cases voluntary food intake was thought to have been limited by the rate of passage of digesta from the reticulo-rumen, a rate which itself is related to the specific gravity of particles (Campling and Freer, 1960). Conceivably, reindeer whose teeth are in good condition are able to masticate coarse winter forage better, pass the digesta through the gut more rapidly and, hence, eat more than those whose teeth are worn.

An alternative explanation for reduced survival after 7 years of age is that there exists a threshold fatness above which reindeer are safe from starvation. Females 1-7 years old, inclusive, had 10 or more kg dissectible fat in autumn and suffered negligible mortality; most females aged 8 years and older, by contrast, had less than 10 kg fat and many died. The minimum amount of fat a reindeer needs in winter depends on how much food it can find, eat and digest. Consequently, the decline in fatness with increasing age is likely to be sufficient by itself to explain the pattern of mortality *only* if all adult reindeer had the same rate of food intake. This is almost certainly not the case. An individual whose teeth are in good condition is likely to be able to eat more and, hence, to need less fat than one whose teeth are worn. Thus, it does not necessarily follow that reindeer with less than 10 kg TDF suffered increased rates of mortality because their reserves were too small *per se*. The main conclusion from this study is that it is misleading to assume a direct causal link between mortality in winter and body fat content alone.

Acknowledgements

This work was carried out as part of the Norwegian MAB (UNESCO Programme on Man and the Biosphere) project on Svalbard, managed by the Norwegian Polar Research Institute. A Special Research Grant awarded to me by the Eco-Sciences Division of NATO provided additional support. I am grateful to the Cambridge Philosophical Society, the Lightfoot Fund of Selwyn College, Cambridge and especially to ARCO Alaska Inc., for grants which enabled me to attend this meeting. Dr. M.G. Murray kindly read an earlier draft of this paper.

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Calving distribution of Alaska's Steese-Fortymile caribou herd: A case of infidelity?

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Abstract: The Steese-Fortymile caribou *(Rangifer tarandus granti)* herd has changed its calving distribution frequently during the past 30 years. A «traditional» calving area, used for decades, west of the Steese Highway (Preacher Creek) was abandoned after 1963. By the early 1970's, a new calving area had been established 74 km to the southeast in the Birch Creek drainage. This new calving area was abandoned after 1976. From 1977 through 1983, calving occurred in annually variable locations approximately 136 km southeast of the Birch Creek calving area. In 1984, however, the herd again calved in the general vicinity of the Birch Creek calving area. General characteristics of the various calving areas are described, and calving distribution is discussed in relation to herd size, development and disturbance, predator abundance, and other factors. Location of calving in recent years was unpredictable, which warrants reconsidering the merit of protecting only previously important calving grounds.

Key words: caribou, Steese-Fortymile herd, calving, Alaska, wolf.

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Rangifer, Special Issue No. 1, 1986: 315 - 323

Introduction

Caribou *(Rangifer tarandus* L.) have been shown to be more faithful to their calving grounds than to other seasonal ranges (Skoog, 1968:121; Fleck and Gunn, 1982; Valkenburg *et al.*, 1983; Cameron et al., 1986). Also, caribou seem most sensitive to disturbance during calving (DeVos, 1960; Lent, 1964; Kelsall, 1968; Bergerud, 1974; Miller and Gunn, 1979), and severe disturbance during calving may be of greater consequence to the population (through direct mortality of calves) than disturbance at other times. Presumably there are advantages, leading to increased survival, for caribou to annually use traditional calving areas.

For the above reason, calving areas are generally considered «critical habitat» and are frequently excluded from mineral exploration and production by land managers. There is often intense pressure from industry to keep these excluded areas as small as possible, but there is mounting evidence that caribou may select different calving areas over time (Davis *et al.*, 1985). Short-term studies, especially on northern herds where historical information is lacking, may fail to identify important potential calving areas. With this in mind, we examined the historic pattern of calving ground use by the Steese-Fortymile caribou herd (FCH) in east-central Alaska (Fig. 1) and discuss it in relation to population size, tradition, predation, development, interaction with other herds, habitat, and weather.

Methods

We examined the historical information on calving ground use in the FCH as presented by Skoog (1956, 1968), Hemming (1970), and Davis *et al.*, (1978). Data since 1976 are from unpublished reports in the Alaska Department of Fish and Game (ADF&G) files and Shrier (1983). Information from radio-collared caribou was not available until October 1980, when four

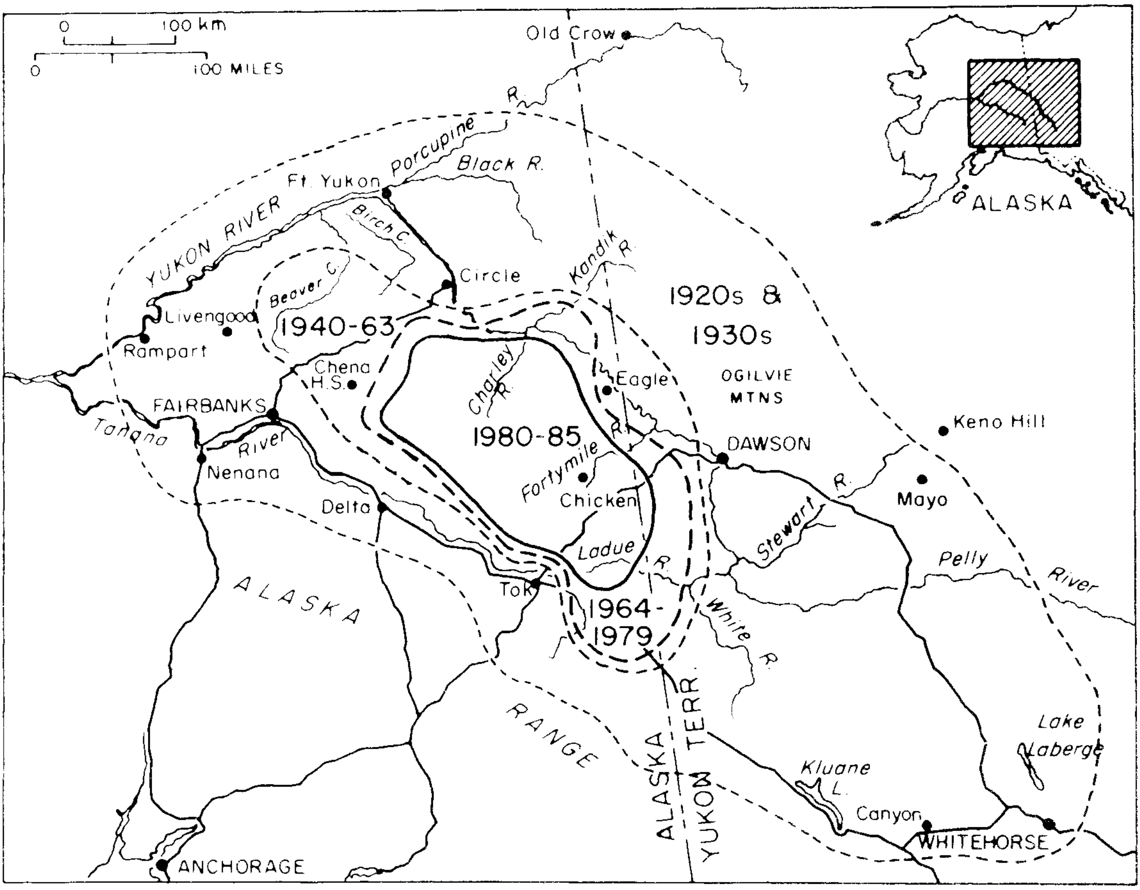


Fig. 1. Greater range of the Fortymile caribou herd, 1920-1985.

females were radio-collared. From December 1981 through April 1982, 16 more caribou (14 females and 2 males) were collared to investigate the interaction between Porcupine herd and FCH caribou that were wintering together. Seven of these caribou left with the caribou from the Porcupine herd as they returned north in May, one female died from capture-related causes shortly after tagging, one was killed by wolves (*Canis lupus*), and one died of unknown causes, leaving 10 caribou with functioning radio collars during calving in 1982 in the range of the FCH.

During September 1983, 16 more females were radio-collared, and in December 1984, 2 females and 10 males were radio-collared. The radio-collared caribou have contributed to substantially better documentation of calving areas since May 1982.

Delineation of calving grounds from old reports was subjective and often depended upon interpretations of various different observes over the years. In this paper, the main calving area is the area in which the density of calving caribou was highest and/or including over 50% of all calving caribou, based on ocular estimates during aerial reconnaissance ranging from intensive to extensive. Secondary calving areas were those areas, usually on the periphery of the main calving areas, where additional calving caribou were seen.

FCH calving areas have been aerially surveyed annually since 1950. In general, these surveys were designed to estimate initial productivity and to determine roughly where calving occurred. Little effort was made to count caribou on calving areas. The FCH was generally censused (Table 1) 10-30 days after 15-25 May, which is the normal peak of calving.

Results

Calving areas of the FCH where not accurately mapped before the advent of aerial surveys in the late 1940's. From 1920 to 1950, the area

Table 1. Estimates of the size of the Fortymile caribou herd since 1920.

Year	Number of caribou counted	Estimated population size	Source
1920	13 200	568 000	Murie, 1935
1953	40 000	60 000	Skoog, 1956
1956	30 000	45 000	Olson, 1957
1960	28 000	50 000	Jones, 1962
1961	— —	50 000	Jones, 1963
1962	— —	50 000	Jones, 1963
1963	26 000	50 000	Skoog, 1964
1964	— —	30 000	Lentfer, 1965
1969	— —	20 000	Alaska Department of Fish and Game files
1973	— —	5 300	Davis *et al.*, 1978
1983	12 150	12 500	Alaska Department of Fish and Game files
1984	13 073	14 000	Valkenburg and Davis, 1985

northwest of Eagle Summit and Twelvemile Summit was regularly used for calving (Murie, 1935), but calving was also reported in the upper Salcha, upper Charley, and upper Goodpaster River drainages in some years (Skoog, 1956) (Fig. 2a). Between 1950 and 1954, most calving occurred north of the Steese Highway in the White Mountains (Skoog, 1968; Hemming, 1970) (Fig. 2b). From 1955 through 1960 there was considerable calving along the ridges on Birch Creek and some on the upper Salcha and Charley rivers, although the White Mountains were still heavily used (Skoog, 1968; Hemming, 1970) (Fig. 2c).

From 1961 through 1963 there was a definite shift to the southeast. What had been the main calving area in the White Mountains became a secondary calving area, and most caribou calved in Birch Creek and the upper Chena and Salcha rivers (Skoog, 1968; Hemming 1970) (Fig. 2d). After 1963, little calving occurred northwest of the Steese Highway, and the southeastward trend in location of the calving area continued (Hemming, 1970; Davis *et al.*, 1978) (Figs. 2e and 2f.) After 1979, the Clums Fork-Birch Creek calving area, which had been regularly used for 16 years, was abandoned, and calving was dispersed in the upper Salcha, Charley and Seventymile river drainages and the Slate Creek drainage (Alaska Department of Fish and Game files) (Fig. 2g).

In 1984 many caribou calved in the head of the Salcha River and the South Fork of Birch Creek, near the old Clums Fork calving area. In 1985, the spring weather was unseasonably cold and during calving the only areas that were snowfree were muskegs along the Charley River. Most calving occurred on these snowfree muskegs. However, calving also occurred in the Middle Fork of the Fortymile River and upper Charley River drainages, which was along the migration route from winter range.

Discussion

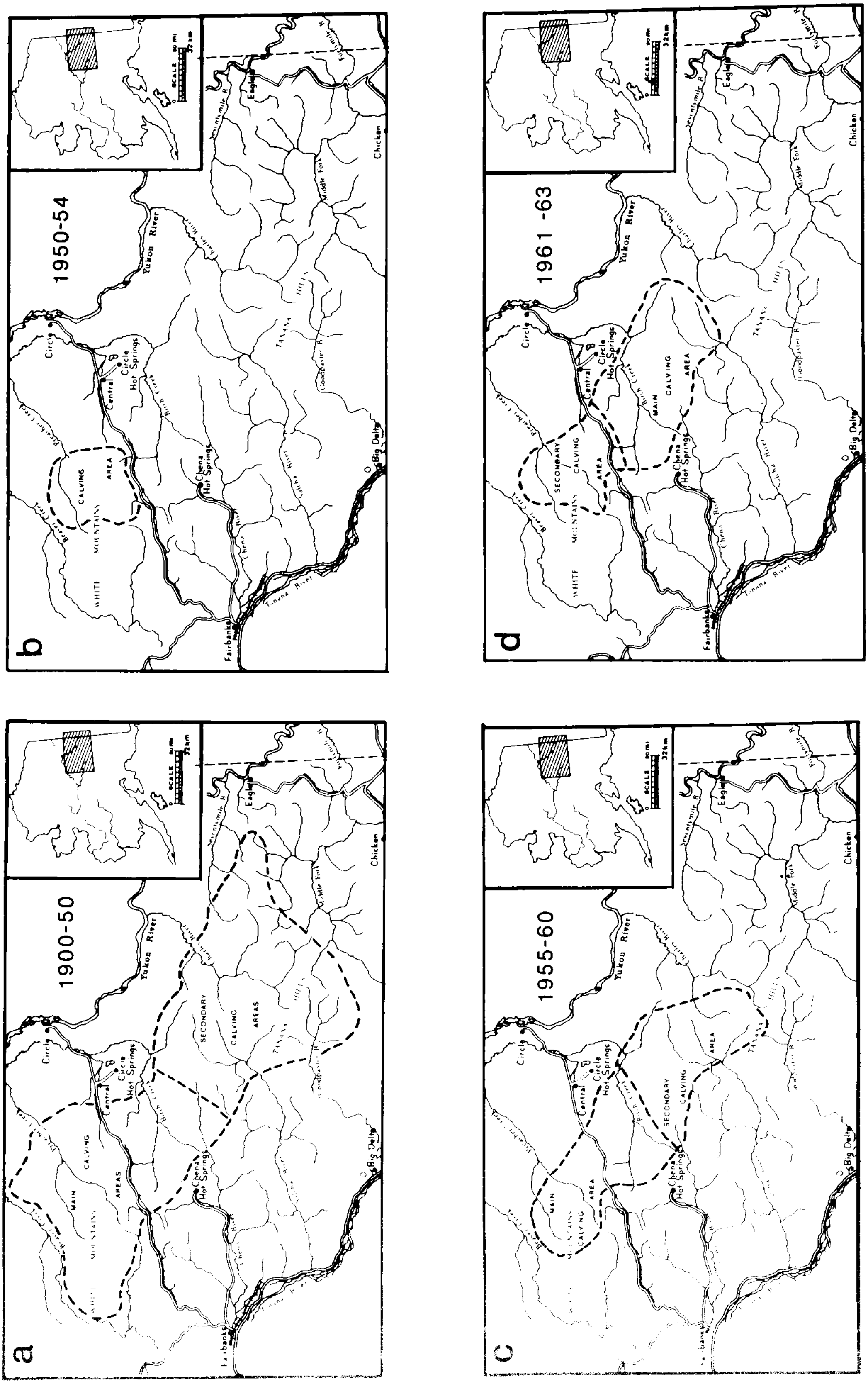
During the mid-1950's some factor(s) apparently caused caribou of the FCH to select calving areas other than the traditional calving area in the White Mountains. Various influences have been proposed as reasons why caribou select calving areas, but few of the proposed influences have been substantiated. Experimentation is necessary to determine the influence of some of the factors currently thought to affect caribou behaviour. For example, restocking calves to new ranges in Newfoundland demonstrated the importance of learning and tradition to caribou movement behaviour (Bergerud, 1974).

Population size

Population size and range size appear to be positively correlated in the FCH (Fig. 1 and Table 1), but the extent and/or location of calving areas seems poorly correlated with population size. During the early 1950's the herd was relatively small (40 000 - 60 000) compared to historic size, the calving area was relatively small, and calving took place at the western extreme of the herd's range. In the late 1950's, calving distribution shifted to the southeast. This shift, which persisted into the early 1960's, occurred as the population was stable or possibly increasing (Table 1). Later, as the population declined during the 1960's and early 1970's, the size and location of the calving area apparently remained stable. After 1977, when the herd was again increasing (albeit slowly), calving appeared to be more scattered and calving distribution had shifted farther southeastward.

Tradition

Tradition probably has a strong influence on the location of calving areas from year to year.


a
1900-50
MAIN CALVING AREAS
SECONDARY CALVING AREAS
b
1950-54
CALVING AREA
c
1955-60
MAIN CALVING AREA
SECONDARY CALVING AREA
d
1961-63
MAIN CALVING AREA
SECONDARY CALVING AREA
WHITE MOUNTAINS
TANANA HILLS
Yukon River
Tanana River
Chena River
Birch Creek
Charley River
Salcha River
Goodpaster R.
Middle Fork
Fortymile R.
Seventymile R.
Beaver Creek
Preacher Creek
Circle
Central
Circle Hot Springs
Chena Hot Springs
Fairbanks
Big Delta
Eagle
Chicken
SCALE 20 mi 32 km

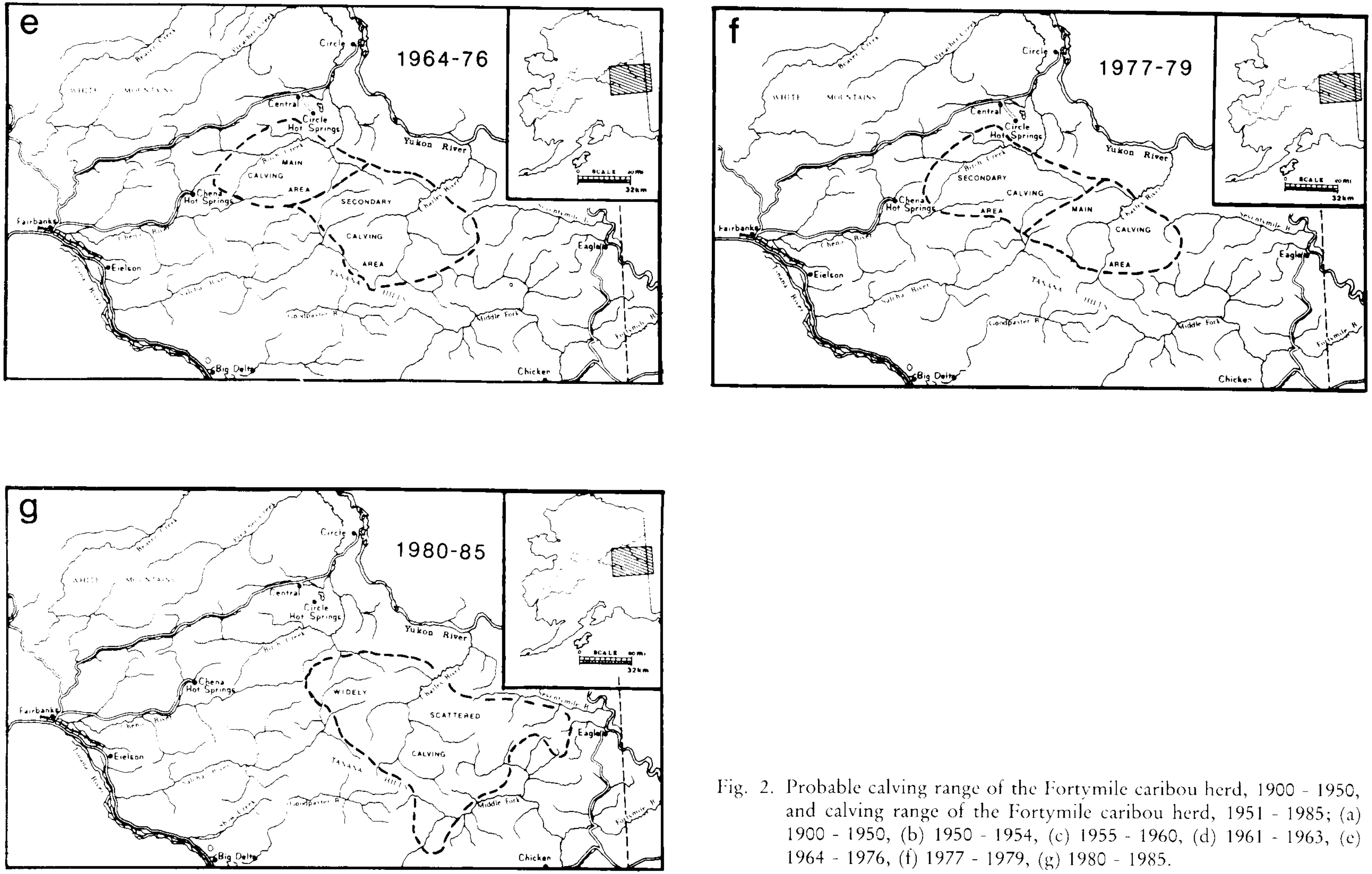


Fig. 2. Probable calving range of the Fortymile caribou herd, 1900 - 1950, and calving range of the Fortymile caribou herd, 1951 - 1985; (a) 1900 - 1950, (b) 1950 - 1954, (c) 1955 - 1960, (d) 1961 - 1963, (e) 1964 - 1976, (f) 1977 - 1979, (g) 1980 - 1985.

Some individual radio-collared caribou return to specific calving sites year after year (Alaska Department of Fish and Game files), and most return to the same general area unless weather conditions are particularly adverse (Lent, 1964; Skoog, 1968; Hemming 1970; Fleck and Gunn, 1982; Whitten and Cameron, 1983; Valkenburg *et al.*, 1983; Davis *et al.*, 1985). This strong affinity of female caribou for their calving areas was graphically demonstrated by the movements of one radio-collared cow from the Teshekpuk herd (for her locations see Davis, 1980) on the Alaskan arctic coastal plain in 1982. She had wintered with Western Arctic and Central Arctic herd caribou near the Trans-Alaska Pipeline until late April, but was observed 160 km west of the area, in early May, migrating with Western Arctic herd caribou enroute to the Utukok calving area. Between early May and late May she must have returned to her traditional Teshekpuk calving area 240 km to the northeast where we found her in early June.

Caribou abandon calving ranges relatively rarely, although small annual shifts within the greater calving area are common (Skoog, 1968; Bergerud, 1974; Fleck and Gunn, 1982; Davis *et al.*, 1985). Major long-term shifts in calving distribution, such as that which occurred in the FCH beginning in the early 1960's, are not common and certainly not well-documented. In view of the affinity that caribou have for calving areas, there must have been a good reason for the shift, at least initially.

Predation

We could not determine if caribou of the FCH successfully avoided wolves by shifting calving areas. Calf numbers were chronically low between 1961 and 1975, and available data suggest a strong inverse correlation between wolf numbers and calf survival and a weak correlation, if any, between shifting calving areas and calf survival (Valkenburg and Davis, 1985).

Shifting the location of calving areas could be advantageous to caribou if wolves key in on regularly used calving areas. This may be especially true if alternate prey species, e.g., Dall sheep (*Ovis dalli*) and moose (*Alces alces*), support the wolves when caribou are absent. However, wolves can also shift seasonal ranges to take advantage of a seasonal abundance of prey (Kelsall, 1968:248; Stephenson, 1979).

Predators, especially wolves, may influence the selection of calving areas by caribou (Lent, 1964; Kelsall, 1968; Skoog, 1968; Bergerud, 1974). Wolves are relatively uncommon on the calving grounds of large, migratory herds (Kelsall, 1968; Bergerud, 1974; Fleck and Gunn, 1982; Davis and Valkenburg, 1985). Wolves were extensively shot and poisoned in the White Mountains between the late 1940's and 1954 (Davis *et al.*, 1978; Harbo and Dean, 1983). Wolf control was discontinued between 1954 and 1957. During these 3 years, wolves apparently increased dramatically (Davis *et al.*, 1978; Olson, 1958) in the White Mountains calving area, and the number of calves present in the caribou population in autumn plunged (Davis *et al.*, 1978). It may be significant that the shift in calving distribution was detected shortly after the wolf population increased after 1954.

In response to the dramatically lowered calf numbers between 1955 and 1957, poisoning and aerial hunting of wolves was resumed in 1957 and calf recruitment again rebounded (Davis *et al.*, 1978). In 1960, predator control was terminated in all of Alaska except the Seward Peninsula reindeer ranges, and wolves again became numerous and remained numerous until the mid-1970's (Davis *et al.*, 1978). Based on the lack of observations of large packs of wolves by pilots and hunters and the general decline in moose and caribou after the early 1970's, it appears that the wolf population has declined on the White Mountains calving area since the mid-1970's (Alaska Department of Fish and Game files). The FCH has been increasing slowly since the mid-1970's (Valkenburg and Davis, 1985).

Development and disturbance

The range of the FCH has remained relatively free from development and human activity although it is traversed by two major highways. The Steese Highway (Fig. 1) was built in the 1920's and has been gradually upgraded. Before major reconstruction in the early 1980's it was a narrow, winding gravel road. Caribou crossed this highway regularly going to and from their calving grounds until 1963. There was never any significant hunting from the highway in spring. Caribou also often crossed the Steese Highway in August and September because they periodically used the surrounding area as summer range, and they were commonly hunted. However, there is no evidence that the Steese Highway acted as a barrier to movements, nor did cessation of caribou crossing of the Steese Highway correlate with a significant increase in traffic.

In contrast to the Steese Highwasy, hunting was heavy along the Taylor Highway in October, especially in the late 1960's and early 1970's. «Firing line» situations were common and groups of caribou were often temporarily prevented from crossing the highway by hunters and associated traffic. Nevertheless, the caribou have continued to cross the Taylor Highway. In the absence of caribou hunters, traffic on the road is light.

Interactions with other herds.

Two major emigrations from the FCH have been reported. In the 1957 emigration, approximately 30 000 caribou of the FCH that wintered with the Porcupine herd in the Ogilvie Mountains supposedly went north to calve with the Porcupine herd. Olson (1958) implied that calving in the FCH was late that year and only 5000 calved in the White Mountains. A «large» segment of the herd also calved in the Charley River drainage, however. If the 1957 emigration indeed occurred, the caribou must have returned almost immediately because the 1958 and 1960 censuses revealed no net loss of animals (Olson, 1959; Jones, 1962; Skoog, 1968). Skoog (1968) mentioned that, in 1964, most of the FCH wintered in the Ogilvie Mountains and had moved north in the spring. These caribou were thought to have returned (Skoog, 1968). A general population decline was recognized throughout the late 1960's and by 1973 only 5312 caribou were found (Davis *et al.*, 1978). This population decline can be adequately explained by an imbalance between mortality and recruitment (Davis *et al.*, 1978).

In 1982, approximately 20 000 Porcupine herd caribou crossed the Yukon River and wintered in the FCH's range (Whitten and Cameron, 1983). Only one radio-collared caribou was among the 20 000, and at the time there were only four radio-collared caribou of the FCH on the air. In May, the one known Porcupine caribou returned north and the four known caribou of the FCH stayed. Censuses of the FCH in 1983, and 1984 did not reveal that any unexpectedly large increases in population had occurred.

So far, the evidence for large-scale interchanges between ranges and herds is anecdotal and speculative. Despite the presence of hundreds of radio-collared caribou in various herds throughout Alaska, there have been few documented interchanges of individuals even through it is common for caribou from different herds to share winter range (Davis and Valkenburg, 1985; Cameron *et al.*, 1986).

Habitat

Although few data have been recorded on selection of habitat by calving caribou of the FCH until recently, there has been an apparent trend away from using generally treeless, higher elevation habitat to more forested areas. The old White Mountains calving area was almost entirely treeless tussock and alpine tundra above 800 m elevation. The Birch Creek calving area has considerably more timbered habitat than the White Mountains calving area. Farther east, the upper Salcha River drainage is treeless and many ridges along the Yukon Fork, Birch Creek, and Charley River are treeless, but most of the area is at least sparsely forested. In 1983, 1984 and 1985, when radio-collared caribou were monitored, 56% of the relocations ($n = 52$) in late May were in treeless habitats and 44% were in sparse or closed-canopy forest habitats.

Whether caribou use open, higher elevation habitat for calving or lower elevations muskegs interspersed with spruce, the *Eriophorum* flower buds which are their main food prior to leaf emergence are still widely available. However, at lower elevations, caribou may have more ready access to birch (*Betula* spp.) and willow (*Salix* spp.) leaves when they first emerge. In the absence of a compelling reason to go to the White Mountains calving area, like avoiding predators, it may be advantageous for the cows to remain farther east at lower elevations to take advantage of earlier leaf emergence (Kuropat and Bryant, 1980; Bergerud, 1984).

Weather

Selection of calving habitat is partially dependent on weather (Lent, 1964; Kelsall, 1968; Skoog, 1968), and snowmelt patterns (Lent, 1980; Fleck and Gunn, 1982). If snowmelt is late, caribou may be forced or prefer to remain at lower elevations where snow disappears sooner. They may also be prevented from reaching traditional calving areas and be forced to calve en route (Lent, 1964; Kelsall, 1968; Skoog, 1968; Davis and Valkenburg, 1985). Spring 1985 was about 2-3 weeks later in the FCH's range and many caribou calved farther east than ever recorded. They also used primarily muskeg and forested habitats at low elevation for calving but climbed in elevation to open areas as soon as the snow receded.

Although weather may influence yearly variations in use of calving area, it is unlikely that it has caused long-term shifts in use of calving areas by the FCH. Perusal of weather records for Fairbanks indicates that although there were some particularly severe winters in the 1960's and early 1970's, they were interspersed with some rather mild winters. With the exception of 1974-75 and 1984-85, winters have been mild in the Fairbanks area since 1971-72.

Landsat data have been available only since the early 1970's, so it is not possible to determine whether or not snowmelt patterns changed during the mid-1950's when the first major shift in calving ground use was detected.

Acknowledgements

This study was funded through the Federal Aid in Wildlife Restoration program (Project W-22-3) as part of an investigation of factors limiting the growth of the Fortymile herd. The National Park Service contributed additional funding. W. Regelin and S. Peterson reviewed the manuscript. R. Boertje, D. Grangaard, D. Kelleyhouse, S. Ulvi, and L. Adams assisted with the field work.

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Groups versus individuals in the determination of caribou distribution

K.R. Whitten[1] and **R.D. Cameron**[1]

Abstract: Studies of caribou *(Rangifer tarandus)* habitat selection based on group analyses have led to erroneous conclusions. Convenient designations such as «male-» or «female-dominated» group encompass a wide array of possible sizes and compositions which change continuously and erratically. Whenever individuals of at particular sex/age class can occur in more than one group type, and/or whenever groups within a type vary in size, an analysis based on groups alone is fallacious. Data must be based on individual caribou for most, if not all, determinations of distribution.

Key words: caribou, distribution, groups, habitat selection, sampling

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Rangifer, Special Issue No. 1, 1986: 325 - 329

Introduction

Caribou *(Rangifer tarandus)* are social animals and usually occur in groups. Over short time periods, at least, caribou groups are cohesive units. Behavior of individuals within a group tends to be uniform and synchronous, and groups often respond to various stimuli as a unit. Also, many groups are relatively homogeneous, e.g., predominantly adult males or predominantly cow/calf pairs. Thus, it appears reasonable to analyze caribou behavior or distribution patterns by studying caribou groups.

There is another, more practical reason for recording data on groups rather than individual caribou. It is easier to assign an entire group some general category of composition, activity, or location than it is to record the same data for each individual in the group. This is particularly true when groups are large or far away, when the observer is flying rapidly past the group in an aircraft, and/or when the terrain does not permit full view of all individuals in a group.

However, certain characteristics of caribou groups render them inappropriate for describing the distribution of a population. In this paper we demonstrate how failure to consider variations in group size and composition has led to erroneous conclusions on differential habitat use by male and female caribou.

Caribou groups

Lent (1965) and Bergerud (1974) concluded that caribou groups are loose social units characterized by temporary and tenuous social bonds. Recent radio-telemetry studies in Alaska and the Yukon Territory indicate that caribou captured together frequently change groups and seldom reassociate with each other (Valkenburg *et al.*, 1983; D. Russell and R. Farnell, pers. comm.) Miller (1974) and Miller *et al.* (1975), on the other hand, concluded that small groups, or «winter bands», are the basic units of caribou social organization, and that affinity to these bands persists for many years, perhaps for life; caribou groups observed during the rest of the year are either aggregations or fragments of these winter bands. Thus, the concept of winter bands is not entirely inconsistent with the general conclusion that caribou groups are dynamic.

Virtually all studies of caribou social organization confirm that group size and composition change seasonally and that, within any one season, groups vary considerably in both size and composition. Large groups generally behave differently from small groups, and male-dominated groups behave differently from female-dominated groups. Moreover, convenient categories of group type may sometimes be inappropriate. For example, the distribution of males cannot be determined by examining only the distribution of male-dominated groups because males occure in female-dominated groups as well.

Differential habitat use and reactions to disturbance by male and female caribou

Recently, Carruthers *et al.* (1984) and Curatolo (1985) concluded that female and calf caribou in the Central Arctic region of Alaska avoid riparian habitats. These authors further suggested that one would therefore expect to find few cows and calves along the Trans-Alaska Pipeline System (TAPS) where it is closely associated with the Sagavanirktok River. Such conclusions conflict with our earlier findings that the proportion of cows and calves among caribou along the Dalton Highway (TAPS haul road) was lower than that among caribou observed along all major rivers and the coastline within the range of the Central Arctic Herd (CAH) (Cameron *et al.*, 1979; Cameron and Whitten, 1980; Whitten and Cameron, 1983). If the conclusions of Carruthers *et al.* (1984) and Curatolo (1985) are valid, we should have seen relatively few cows and calves anywhere along our survey route, except possibly along the coast. This was decidedly not the case. How then could our conclusions be so different?

Analyses based on groups

Both Carruthers *et al.* (1984) and Curatolo (1985) assumed that the distribution of male and female caribou could be determined by sampling the distribution of male- and female-dominated groups. Both used similar categories of group type. Curatolo (1985) defined a cow group as comprising more than 70% cow/calf pairs and a bull group as more than 70% bulls. Carruthers *et al.* (1984) defined a female group as one in which more than 67% of the caribou were classified, and more than 67% of the classified adults were female; in a male group, more than 67% were classified, and of those, more than 67% were males. Under either definition, some bulls could occur in cow groups, and vice versa. In fact, by the Carruthers *et al.* (1984) definition, a male or female group could theoretically contain mostly members of the opposite sex (e.g., 0.67 x 0.67 = minimum of 44% males in a male group). Differences in group size were not considered in either study, and all groups were weighted equally in determining habitat use. Both studies demonstrated that a significantly higher proportion of male *groups* than of female *groups* was found in riparian habitat.

Riparian habitats covered 9% of the regional aerial strip transects used by Carruthers *et al.* (1984) to determine caribou distribution. More than 9% of the male groups were in riparian habitat during all seasons, and less than 9% of the female groups used riparian areas during most seasons (Table 1). Furthermore, female groups were, on average, farther than expected from riparian habitats (based on mean distance available) while male groups were usually closer. Thus, Carruthers *et al.* (1984) concluded that females avoided areas within and near riparian habitats. Curatolo (1985) reached the same conclusion based on the observation that 37% of bull groups were in riparian habitat during summer, versus only 19% of the cow/calf groups.

These results can be extrapolated to the population as a whole only if individual male and female caribou were distributed similarly to male and female groups. The problems outlined above suggest that such an assumption is, at best, tenuous. Curatolo (1985) reported only summarized results, but Carruthers *et al.* (1984) presented sufficient data to test this assumption.

Analyses based on individuals

Reanalysis of the data presented by Carruthers *et al.* (1984) indicates that the distribution of *individual* male and female caribou was quite different from the distribution of male- and female-dominated *groups*. On average, female groups were larger than male groups. Assuming that group sizes were similar among habitats, caribou in female groups would have outnumbered those in male groups in riparian areas during much of the year, even though a smaller proportion of female groups than of male groups was observed in riparian habitat (Table 1).

Table 1. Distribution of caribou in male and female groups relative to riparian habitat, Central Arctic Slope, Alaska.[a]

	Mean group size in all habitats		Occurrence in riparian habitat[b]					
			No. of groups		% of total groups seen		No. of individuals[c]	
Season	male[d]	female[d]	male	female	male	female	male	female
Winter	7.6	6.7	22	7	33	31	167	47
Spring	5.8	3.8	3	6	14	8	17	23
Calving	3.6	10.2	84	23	26	4	302	234
Postcalving	5.7	40.6	43	25	33	30	245	1015
August dispersal	1.6	8.0	74	21	25	6	118	168
Pre-rut	3.2	6.5	21	10	17	5	67	65
Rut	1.4	6.1	14	19	10	10	20	116

[a] Based on data presented by Carruthers *et al.* (1984).

[b] 9% riparian habitat available.

[c] (number of groups) X (mean group size). Does not take into account possible differences in group size between riparian and nonriparian habitats.

[d] Group type.

Carruthers *et al.* (1984) reported numbers and composition of individual caribou for only 1 year of their 3-year study. In 1983, they compared caribou observed during regional aerial surveys with caribou observed along a transect flown directly over TAPS, but unfortunately reported data on caribou within 2 km of riparian habitat rather than in riparian habitat only. An analysis based on the distribution of individuals shows that caribou consistently preferred riparian areas, both along TAPS and in the surrounding region (Table 2). Use of areas in or near riparian habitats by all caribou and by calves was high relative to availability of riparian habitat. The higher proportions of individual caribou in or near riparian habitats (Table 2), than of caribou groups in riparian habitats (Table 1), could indicate that groups in riparian habitats were larger, or that many groups occurred close to (<2 km), if not within, the riparian zone. Either case negates the conclusion that one would expect to see few cows and calves along a major river.

Most striking, however, is that percentage calves among caribou along TAPS was consistently lower than in the surrounding region (Table 2). Within or near riparian habitat, calves were less abundant along TAPS except during calving. In nonriparian habitats, calves were less abundant along TAPS except during August dispersal and pre-rut.

In summary, there is no clear evidence that calves (and, by inference, their mothers) consistently used riparian habitats differently than did other caribou. All caribou preferred riparian habitats, and cow/calf pairs avoided all habitats along TAPS. This reanalysis of the findings of Carruthers *et al.* (1984) corroborates our own conclusions (based on data from individual caribou) that cow and calf caribou are underrepresented along TAPS, but not in similar habitats elsewhere. Local disturbance by traffic and construction activity is likely the major cause of this cow/calf avoidance (Cameron *et al.*, 1979; Cameron and Whitten, 1980; Whitten and Cameron, 1983).

Curatolo (1985) reported the distribution of individual CAH caribou in demonstrating that calf percentages in study sites along the Kuparuk River were only ca. 40% of those in nonriparian study sites farther west near Oliktok Point. Petroleum development was considered to have influenced distribution in both areas equally. Therefore, Curatolo (1985) concluded that the relative scarcity of cows and calves along the Kuparuk River was due to their natural avoidance of riparian areas, a conclusion supported elsewhere in his paper by the analysis of caribou *group* distribution. Curatolo failed to note, however, that the area near the Kuparuk River had been disturbed for at least 10 years

Table 2. Distribution of individual caribou relative to habitat type along the Trans-Alaska Pipeline (TAPS) and in the surrounding region, Central Arctic Slope, Alaska[a].

	% occurrence within 2 km of riparian habitat				% calves							
	All caribou		Calves		All habitats		Within 2 km of riparian		Nonriparian		No. of caribou	
Season	TAPS[b]	REG[c]	TAPS	REG	TAPS	REG	TAPS	REG	TAPS	REG	TAPS	REG
Winter	48	42	70	32	3	25	5	20	2	29	287	583
Spring	99	33	100	48	17	17	17	25	0	13	156	326
Calving	57	20	89	6	9	26	14	8	2	30	208	745
Postcalving	87	19	95	21	10	14	11	16	4	14	560	299
August dispersal	93	16	67	11	8	26	5	17	33	28	80	874
Pre-rut	74	18	56	13	15	23	11	17	25	25	122	651
Rut	42	28	44	23	7	19	7	18	7	19	359	1376

[a] Based on data presented by Carruthers *et al.* (1984).
[b] 34% riparian habitat available
[c] 9% riparian habitat available

before his study began in 1982, whereas the Oliktok Road in the nonriparian area had been built just that year. Furthermore, calf percentages in the Kuparuk River area declined from levels similar to regional estimates in 1978 to ca. 40% of regional estimates by 1980 (Cameron *et al.* 1981). Thus, we believe disturbance to be the primary cause of cow/calf underrepresentation along the Kuparuk River, rather than any natural avoidance of riparian areas.

The cause hypothesized by both Carruthers *et al.* (1984) and Curatolo (1985) for cow/calf avoidance of riparian habitats in general (i.e., instinctive avoidance of predator-concealing habitat) is not operative in the range of the CAH. While predators may ambush caribou in tall riparian willow (*Salix* spp.) stands in the ranges of many herds (Curatolo, 1975; Bergerud, 1974; Boertje, 1981), both predators and tall willows are scarce on the summer range of the CAH. Riparian areas are more often characterized by terraces with cushion tundra vegetation consisting mainly of *Dryas*, legumes, forbs, and low (<0.5 m) willows. Tussock or wet sedge tundra often extends to the very edge of a watercourse, and islands in braided streams often have typical tundra vegetation. Lack of predators and a mosaic of habitat types, including both foraging areas and vegetation-free areas for insect relief, may in fact explain the *preference* for riparian areas noted here for all caribou, including cows and calves.

Conclusions

Data based on groups are not appropriate for describing population distribution or habitat preference. Our reanalysis of the data of Carruthers *et al.* (1984) demonstrates that individual bulls and/or cow/calf pairs were not distributed similarly to male- and female-dominated groups. Extrapolations based on treatment of groups as equivalent units yielded erroneous results. By inference, Curatolo's (1985) conclusions based on similar methodology are also suspect.

Few researchers would make the mistake of treating unequal areas as equivalent sample units. For example, no one would compare caribou density in two areas by determining the number of caribou per linear km using 1-km wide transects in one area and 2-km wide transects in the other. Yet this is precisely the sort of error made when caribou distribution is described by weighting all groups equally.

Caribou groups vary in size and composition, and members of the same sex/age class usually occur in more than one group type. Therefore, an analysis based on groups alone will not be representative of a population. Individual caribou must serve as the basis for most, if not all, studies of distribution.

Acknowledgements

This report was prepared under the auspices of Federal Aid in Wildlife Restoration Project W-22. We are grateful to J.D. Wadland, Fairbanks; R.D. Boertje, W.L. Regelin, and W.T. Smith, Alaska Department of Fish and Game; M.C.S. Kingsley, A.M. Martell, and J. Smith, Canadian Wildlife Service, for their critical reviews of the manuscript.

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Special papers

Differences in the ecology and behaviour of reindeer populations in the USSR

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Abstract: The population differences in ecology and behaviour of reindeer (*Rangifer tarandus* spp.) is closely paralleled by the characteristic features of reindeer husbandry which reveals the close relationship between behaviour and husbandry. The western portion of the reindeer husbandry region in the USSR is vast. The reindeer are maintained on a semi-loose basis; the herd is scattered over the range; the social activity of the reindeer is lower; the herdsmen gather the herd using dogs, the herdsmen migrate together with the herd during the summer, grazing the herd in the vicinity of the tent for 2-5 days at a time. In the eastern portion of the region (Yakutia, Chukotka, Kamchatka), the ranges are more restrictive; the reindeer are grazed in a compact mass in summer; their feeding and movement are rigidly regulated; their social activity is high; the herd is gathered in foot without dogs. In summer, herdsmen follow the herd with light tents, the place of grazing being changed almost daily. In the taiga reindeer are raised mostly for transportation, although the hides and meat are also important; the reindeer are bigger, tamer and can be used for riding. The herds are small and the management of them is aimed at retaining the reindeer near home or the camp; migrations are short; often forest reindeer husbandry is of a sedentary nature. Attempts to change the pattern of reindeer husbandry and the methods of herding are not always successful. The harmony of environmental conditons, morphology, physiology, ecology and behaviour of reindeer and methods of husbandry are more easily disrupted than altered.

Key words: reindeer, wild, domesticated, USSR, behaviour, ecology.

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Rangifer, Special Issue No. 1, 1986: 333 - 340

There are sharp distinctions between tundra and forest forms of reindeer (*Rangifer tarandus* spp.) in the USSR. The tundra reindeer include the Novaya Zemlya (*R.t.pearsoni)* and Lapland *(R.t. tarandus)* subspecies, and the Siberian tundra reindeer *(R.t. sibiricus)* which may be divided further into regional forms: the Taimyr-Bulun, Yano-Indigirka and Novosibirsk islands (Egorov, 1971). Flerov (1952) and Sokolov (1959) divided forest reindeer into Siberian *(R.t. valentinae)* and Okhotsk *(R.t. phylarchus).* Egorov (1971), Vodopyanov (1970), Stremilov (1973) and Mukhachev (1981), however, inferred from their studies that the forest reindeer of Evenkia, Trans-Baikal Territory, Southern Yakutia and Far East are the same subspecies. Domestic reindeer are sharply distinct in conformation and coloration and their morphological and ecological characteristics vary regionally. Like their wild conspecifics, regional variation in domestic reindeer may be explained by environmental conditons.

The present paper is based on the author's personal studies in 1962-1965, 1966, 1967, 1969, 1980, in Murmansk Region, Taimyr, Vrangel Island and Kamchatka as well as published data.

Population differences due to peculiarities of the environment

Differences in ecology and behaviour of reindeer from different populations are revealed by habitat preferences. Reindeer avoid cliffs and talus slopes, characteristic of the ridges of Eastern Siberia and the Trans-Baikal Territory. The tundra reindeer migrating from Taimyr to winter taiga pastures in Evenkia and the Putoran Mountains do not ascend the goletzes (alpine tundra - *Note:* all materials appearing in brackets are editorial additions) beyond the mountaine zone, because of the mountain wastes (rock barrens). Near Lake Ayan (Putoran Mountains) where such mountain wastes reach the water, bulls detoured the obstacles by walking uphill, while cows svam around the slopes along the lake shore (Lineitzev, 1983). Sobansky (1981), however, noted that reindeer dwelling on the uplands of Altai readily cross talus slopes.

Sobansky (1981) recorded two different reindeer populations in Altai. The northern population uses ranges at an altitude of 400-1500 m, where snow cover ranges from 130 to 250 cm. Those reindeer prefer the dense coniferous forests, where they feed on arboreal lichens, despite the availability of clearings, burns and felled areas.

The southern Altai population uses alpine tundra (2500-2700 m) where reindeer moss (*Cladonia rangiferina*) is abundant and the snow is only 50-70 cm deep. Those reindeer readily move downhill to the taiga where arboreal lichens are plentiful. Reindeer in the Trans-Baikal Territory avoid regions of sharp alpine relief and preferre areas of gently-rolling topography (Vodopyanov, 1970).

The taiga zone has richer reindeer moss pastures and more accessible green feed. The greater abundance of food is likely responsible for the larger size of forest reindeer compared wiht tundra conspecifics. Another reason is that reindeer migrate south 5-7° latitude where snow melts 20 days earlier, and the autumn is later, so green vegetation is available for 40-50 days longer. In the forest, mushrooms are more abundant.

Young tundra reindeer transplanted to forests grow more rapidly. The metapodia respond the most rapidly to physiographic changes and migration conditions (Egorov, 1971), hence, forest reindeer have longer legs. Although the characteristic conformation is reached at 3-4 years of age, reindeer continue to grow until 5-6 years old when ossification is complete. The transplant of Murmansk tundra reindeer aged 1-2 years to the forest zone of Karelia resulted in an increase in size (Segal, 1962). Druri (1952) also reported that after transplantation to the forest, tundra reindeer become taller with longer legs, a more compact body and a better developed chest.

Forest reindeer have a darker coat and smaller antlers than their tundra conspecifics. The terminal tines of antlers from forest reindeer are bent inside while supraocular tines are bent backward, particularly in cows. The antlers of forest reindeer are shorther because of the flat lateral and antero-posterior curve of the main beam. According to Egorov (1971), these features are particularly useful in the forest life. The European forest reindeer *(R.t. fennicus)* is also characterized by a flattened shape of the antlers (Sokolov and Chernyavsky, 1962). Reduced development or absence of antlers in females is relatively common (up to 25%).

Reindeer in the taiga eat more lichens (terrestial and arboreal) and fewer graminoids than tundra reindeer. The diet of some populations of tundra reindeer (Novaya Zemlya, Malozemelskaya tundra, Yamal) is 40% or more green vegetation in winter (Sdobnikov, 1935, Aleksandrova, 1937; Avramchik, 1939). Nevertheless, previously more importance was attached to feeding on lichens such as reindeer moss in winter, as the very existence of reindeer was thought to be based on a reindeer moss diet. Correspondingly, under a program for range management optium numbers of reindeer were estimated (Sochava, 1934; Andreev, 1940, 1948).

In the 1960s, the actual numbers of wild and domestic reindeer considerably exceeded the estimated numbers in some areas, with no detriment to the ranges. Syroechkovsky (1975) accounted for this phenomenon on the Taimyr, by describing differences between the diets of domestic and wild reindeer. In the latter, reindeer moss was only 30% of the winter diet, and green plants were 70%, a pattern which was the reverse in the diet of domestic reindeer (Andreev and Galaktionova, 1983).

Further observations have revealed that as the domestic ranges deteriorated the reindeer increased their feeding on undersnow green plants and dry herbs. On Chukotka, a range management program run in 1950-1953 and in 1976-1979 revealed that, although the biomass of lichen feed was halved, the number of reindeer increased (Arefyev and Chechunov, 1981).

Comparison of the feeding of domestic reindeer of different breeds can shed light on the time and number of generations required to develop a preference for green plant consumption in winter. The Yakutia population is segregated into three groups: Koryak, Evenki and Khargin. The Koryak reindeer are small and thin but wiry and strong, quick and hardy and good draft animals. The Evenki reindeer are light-coloured, big, rough and hardy animals used for riding by hunters. The Khargin reindeer are dark-coated, fleshy, with a big head, thick legs and antlers. They are bred for meat, lard and for pulling heavy loads (Kokoring and Soskin, 1984).

The Khargin reindeer are of Chukotka origin and have different foraging habitats than the Evenki reindeer. The Khargin reindeer graze intensively, sometimes eating the vegetation to bare ground. The Khargin reindeer eat more green plants in winter compared with the Evenki reindeer and lose less weight than the Evenki reindeer (by 25-30%) during the winter. At the beginning of winter, the Khargin reindeer diet is 21% reindeer moss, 53.8% green feeds, while that of the Evenki reindeer is 56.0% reindeer moss and 21.8% green feed (Rumyanzev, 1976).

The Khargin reindeer developed a feeding pattern as a result of long-term maintenance on ranges with little or no reindeer moss. By contrast, the Evenki reindeer are raised on reindeer moss-rich forest ranges. The Chukchi exclusively hunted wild reindeer as late as the turn of the 18th century, whereupon they acquired reindeer husbandry from Koryaks. After they turned to reindeer husbandry, they moved to Yakutia with their reindeer which were already different in conformation, feeding habits and behaviour from their Koryak ancestors. In Yakutia, the Khargin reindeer found themselves alongside Evenki reindeer which were raised in the forests of the Okhotsk Sea coast and differed from their Chukotka conspecifics.

On the Chukotka itself, two reindeer breeds are now distinguished: Chukotka and Evenski. The major ranges of Chukotka have a harsh climate: in winter, strong winds blow and it may warm up unexpectedly to form a snow crust. The summer is cold, with few blood-sucking insects. Lichens are few and the major forage during the year is sedges, dwarf willows *(Salix* spp.) or birches (*Betula* spp.) and in drier areas, grasses and forbs. Up to 20% sedges remain green under the snow (Ustinov, 1956).

Characteristically, the tendency of Chukotka domestic reindeer to eat little reindeer moss in winter has become more pronounced over the last 20 years. The wild reindeer of Chukotka, which migrate south to forests have, however, retained their preference for reindeer moss (Pomishin, 1981)

Little use of reindeer moss is also characteristic of reindeer dwelling on the islands of Novaya Zemlya and Novosibirsk. During the whole year, reindeer feed on grasses and sedges but rarely on dwarf willow (Egorov, 1971)

Consumption of reindeer moss is an important species- specific adaptation of the reindeer. The enzyme lichenase in their stomachs promotes the scarification of the carbohydrate lichenine (the main component of reindeer moss). The morphology of the teeth (Sokolov, 1959), the thin intestines and their larger size compared with other ruminants (Akaevsky, 1939), the hoof structure of the front legs adapted to digging up the snow (Tarasov, 1956) - all these features indicate that reindeer are adapted to consuming a forage for which it barely competes for with other animals.

Forest reindeer also have characteristic feeding patterns. In Yakutia, reindeer gather in groves of Chosenia (willow) along river beds to feed on horsetails *(Equisetum* spp.) which do not freeze. In Tofalaria, reindeer eat long-rooted onion *(Allium schoenoprasum)* on a mass scale as early as February while the Stanovoy Ridge reindeer, typically eat horsetails, the major source of protein, which they find at river shallows and near the ice. During the first half of May and the first half of June, larch needles *(Larix daurica)* are consumed in relatively large amounts (up to 40% of the gut content) (Vodopyanov, 1971, 1975; Pomishin, 1972).

In a number of regions, moss is important - up to 36% in the Putoran Mountains (Michuring and Vakhtina, 1968) and up to 15% in Altai (Shaposhnikov, 1955). Between 24 and 39% of the diet of domestic tundra reindeer is moss but possibly only wild reindeer are adapted to feeding on moss (Michuring and Vakhtina, 1968).

Forest reindeer suffer from mineral nutrient deficiency, which Segal (1962) relates to the small amount of undersnow green plants in their forage and also to leached moor soils. Presumably, indigenous forest reindeer are better adjusted to salt deficiency compared with the reindeer which came from the tundra. In Karelia 50 - 60% calves born by cows which came from tundra regions of the Murmansk Region to the forest part of Karelia died.

In the mountain regions of Siberia, reindeer regularly visit natural areas of loamy solonetzic soil and in March the reindeer are concentrated on mineralized ice. In the Trans-Baikal Territory, reindeer eat the contents of the middens of flying squirrels *(Pteromys volans)* at the base of trees, where frozen masses of feces and urine accumulate (Vodopyanov, 1971.)

The patterned use of space is not only and adaption to environmental factors but also to the history of the development of the behaviour of populations and the passing on of traditions from generation to generation. I regard as spatial structure the use of (annual) home ranges and seasonal tanges, commonly including several home ranges and also major migration routes.

The USSR has many small reindeer populations, which find their requirements in a relatively small space and have only short migrations. In the Trans-Baikal Territory, in Sayany and Altai, reindeer migrate less then 50 km. Rarely do they move from one mountain system to another and migrate up to 150 km (Vodopyanov, 1970; Sokolov, 1983). In Sayany, during winters of shallow snow, reindeer stay on small home ranges in the taiga. After the snow is crusted, the reindeer move uphill to the subalpine zone, but as early as April they descend to calve on the south-facing slopes. In summer, the reindeer move to the exposed hilltops and ridges to avoid blood-sucking insects and return at the end of summer to the lower tree-line (Sokolov, 1983).

Tundra reindeer migrate great distances over routes largely determined not by terrain landmarks, but by availability of forage, changes in snow cover, dates of river freezing and breakup, climate, and the impact of blood-sucking insects.

A great deal of attention has been given to migrations of reindeer on the Taimyr. The winter ranges are the forest-tundra (transirion-zone) and taiga from the river Taz in the west and to the Anabar in the east. In the 1960s up to 80% of reindeer wintered in the Putoran Mountains, but in the late 1970s most animals moved to the mountain taiga of the northern Evenkia and the western region of Yakutia. The shift in winter distribution occurred after the increase in population size, which resulted in deterioration of forage (Kuksoc, 1981).

Lineitzev's (1983) observations at the biological station at Ayan Lake in the Putoran Mountains revealed the pattern of reindeer distribution in the piedmont. After some critical density was exceeded, migration was initiated through the Putoran plateau to the south.

The new wintering grounds of the Taimyr reindeer are 1000-1200 km away from the calving grounds, and consequently the reindeer reach the Taimyr lowland later. The reindeer linger where the snow melts earlier on the winter mountain ranges. Then the reindeer have to migrate quickly but frequently do not reach the rivers before breakup. Then the reindeer have to stop at the river barrier to calve along the right bank of the Pyasina River and at the bend of the middle flow (central section) of the Agape River (Kuksov, 1981).

In years with a warm autumn, reindeer were observed to linger on the southern Taimyr tundra until December (up to 100 thousand head). Those animals headed for new winter ranges at the left bank of the Enisei River, and when the ice conditions prevented them from crossing, they dispersed southward along the Enisei bank up to Turukhansk (Yakushkin *et al.*, 1970).

The variation in timing of the Taimyr population's migration suggests that migration dates are not fixed by constant factors such as the photoperiod. Temperature, dates of snow melting and abundance of food may trigger or delay migration as may chance reasons such as ice conditions, loose and deep snow, gas-main construction, sudden decline or, conversely, enhancement of forage, and sudden increase in population density, due to the arrival of new animals. Undoubtedly, both the passive submission of reindeer to the environmental conditions and their active correction of the trends and times of movements may be equally adaptive and useful.

Population traditions play an important role. The death of most of the Novosibirsk Island populations in the 1930s resulted in the loss of the tradition of crossing the straits to the mainland (Verkhoyansk Ridge mountains, and Primorie arctic tundra). By 1970, the population on the island was restored, and the numbers reached 17-18 thousand, but the reindeer do not cross the straits.

In many regions, reindeer from different populations use the same winter range but the reindeer subsequently leave for their own ranges. In the Putoran Mountains both forest and tundra reindeer winter on the same range but disperse before the summer (Yakushkin, *et al.*, 1975). On the Verkhoyansk Ridge are the winter ranges of reindeer from several populations (Egorov, 1971; Kischinsky, 1971.)

Reindeer may repeat their previous year's experience of using certain ranges the next year. For example, by 1970 reindeer learned to pass round the railway Norilsk-Dudinka, the gas-main and the settlement Talnakh, but during 1967 to 1969, the herd lingered at the gas-main line and the railway for more than a month (Geller and Borzgonov, 1975.

In 1967, a part of the Taimyr tundra population (50-60 thousand) came for the first time to winter on the right bank of the Enisei River. In 1968, the reindeer attempted to follow the same route, but ice conditions stopped them (Yakushkin *et al.*, 1970).

Reindeer do not invariably migrate north in the spring or towards the sea, and south in the autumn. On the Gydan Peninsula on Novaya Zemyla, tundra reindeer migrate north in the autumn because forage is more abundant and available, as winds expose the vegetation (Naumov, 1933).

The variability in dates and routes of migration is of practical importance, as most of the harvest of the Taimyr population is during migration across rivers. The Taimyr State Reindeer Ranch is the leading reindeer harvesting enterprise, it harvests 50 thousand reindeer annually.

Population properties of behaviour

There are many differences between the behaviour of wild and domestic, forest and tundra reindeer and between breeds and from different regions as well as between herds of dissimiliar sex and age composition. Those differences may stem from external differences: the presence of effective stimuli causing a definite behaviour (wolves(*Canis lupus*), greening-up of cottongrass (*Eriophorum* spp.), differences in communication conditions especially visual communication in open space.)

The strongest stimuli causing defensive and related social response is the sight of a predator, frightened reindeer, or the sight, noise or odour of a frightened herd. A herd of domestic reindeer gathered in a forest shows a different level of excitement than a herd gathered on the tundra. On the tundra, the herdsman has only to call loudly at several of the nearest reindeer for the rest of the reindeer to become excited and come together which takes several minutes. In taiga where reindeer cannot see one another, almost every individual has to be pursued with dogs. Collecting the reindeer takes one or occasionally several days, unless the animals are grazing in a large clearing. In the Murmansk Region, some herds are grazed in winter on the slopes of high hills, so that changes in the behaviour of the reindeer can be seen in moving the herd from the forest uphill to the exposed top of the ridges (Baskin, 1970).

Forest reindeer live in small groups similiar to the family groups of red deer (*Cervus elaphus*). The deer are largely sedentary with only short migrations. In forests with shallow snow and abundant food, the deer live together for several weeks until the forage is exhausted (Shaposkhnikov, 1955; Vodopyanov, 1971; Stremilov, 1973.)

The more abundant tundra reindeer have often been transplanted to the forest to replenish or establish local populations. Those transplants demonstrate the difference in the behaviour between the tundra and forest reindeer, and the poor and difficult adaption of tundra reindeer to the taiga.

During the first year, the transplanted reindeer invariably wander in their unfamiliar areas, though the wandering will familiarize the reindeer with their new habitat. To tie the reindeer to the desired site, they have to be enclosed during the first year (Segal, 1962).

When moved to taiga, tundra reindeer readily disperse, without forming herds and are frequently lost by herdsmen (Poltoradnev, 1932). The dispersion and movements create many problems for the herdsmen which are aggravated by the different methods of grazing reindeer in taiga or tundra. The herdsmen only check where the reindeer are located on the tundra to turn back those that advanced far ahead and chase the animals which lag. No efforts are made to keep permanent guard on the herd and maintain it in a compact mass.

On many occasions, the above reasons were responsible for the failure of transplants of tundra reindeer to taiga. Large numbers of reindeer strayed and died (Vostryakov and Brodnev, 1964; Baskin, 1970).

Tundra reindeer are more excitable than their forest conspecifics, hence are more responsive to the approach and calls of herdsmen, but more agitated when saddled or in a team. In the forests as reindeer are largely bred as draft animals needed for hunting, tame, calm reindeer are needed that will be quiet when ridden and will not stray away when released for grazing.

There are differences in the behaviour between the Taimyr reindeer (western reindeer husbandry, involving dogs) and Kamchatka (eastern) reindeer husbandry which does not rely upon dogs. My personal experience of working for experimental purposes as a herdsman on one of the Taimyr collective reindeer ranches was that it provided impossible to graze the deer in the Kamchatka and Chukotka pattern, i.e. maintaining the animals in a rather compact mass without using dogs. The reason was vast ranges with scanty forage and weak defensive response of the reindeer.

The eastern Bolshezemelskaya Tundra has continuous summer ranges compared to the bands of ranges along the rivers of the Olutosky Peninsula in the Bering Sea. Hence, the herds have to be moved daily to new places, up to 15 km on the latter ranges.

A compact herd structure during grazing in the eastern type of reindeer husbandry determines the retention of a high level of social motivation in the herd and preservation of the herd as a single unit. This type of structure makes it possible for the herdsman to manage the herd continuously - his call addressed to a particular animal will alert other nearby reindeer.

If the animals are scattered, they only respond slightly to their neighbours and a stronger stimulus is required such as the sight of a predator or a dog. Use of a dog has, however, disadvantages as the reindeer become unresponsive to weaker stimuli and it is difficult if not impossible to elicit defense response by calls and gestures. Inadequate defense motivation may be obvious in early summer and in the autumn mushroom season, when feeding behaviour dominates.

Herds of varied sex and age composition behave differently, related to the difference in the number of potential leaders among different sexes and ages. The number of potentlal leaders may be determined in spring when cows are separated from yearlings and bulls, which interfere with calving and rearing of newborn calves. The herd is corralled, with a herder harassing them while the other herdsmen form «a living corridor» at the exit. The cows, many of which are potential leaders, escape outside through the corridor, but the reindeer which try to follow the leader are frightened away or lassoed for return to the corral.

A large proportion of the cows leave on their own, while others seemingly less independant, follow them after some period of time. Still others do not leave and have to be lassoed to be taken out of the corral (Baskin, 1970).

There are few leaders among young animals (Baskin, 1970). Calves rarely become leaders and their behaviour is motivated more by the desire to find their mother than by fright. There proved to be many breeding bulls that could leave the herd on their own, but normally herders leave only a few breeding bulls in their herds (Baskin, 1970.)

The need to drive reindeer is frequent as reindeer are driven to butchering points, from herd to herd, and also for formation of herds. Sex and age structure of the driven groups may vary which allows comparison between the behaviour of herds with different age and sex structures. Herds composed of only calves or yearlings are passive with respect to the environment and respond to any stimulus in a similar manner by walking in a definite direction only (e.g. downwind, uphill, to a familiar place, towards some landmark). It is impossible to drive such herds or even keep them at some place. If a single young cow or a few riding reindeer are added to the herd, or a bull is driven in front of the herd (an artifical leader), the behaviour of the group is drastically changed. The group becomes manageable as the potential leader which appeared in the herd actively responds to the environment and takes the lead. The leader brings along its experience, its peculiar attitude to the environment and a behavioural pattern: the leadership operates as an adaptive mechanism as the leader's adaptations become common to the entire herd (Baskin, 1970).

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Development of the technology for producing reindeer in the USSR

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Rangifer, Special Issue No. 1, 1986: 341 - 343

Reindeer breding occupies a significant place in the combined agricultural and hunting economy of the Far North. The prospects for development in this field are determined by important economic goals such as strengthening northern economy, improving the prosperity of indigenous peoples, establishing a local food supply and grazing plants species not utilized by other species of agricultural animals. The cost of producing reindeer meat is several times lower than production costs of meat from other agricultural animals raised in the North. Besides meat, reindeer provide leather, hides, velvet antlers, and other valuable products. Thanks to Lenin's national policy which is being carried out by the Soviet government, reindeer breeding is developing successfully and the standard of living in the indigenous peoples of the North is gradually improving.

Further increases in production of reindeer products in the USSR and improvements in social and economic conditions of northern peoples will be based mainly on intensifying production, the more complete utilization of reserves and improving the working and living conditions of reindeer breeders.

Natural forage reserves (pastures) serve as the basis for the development of reindeer breeding. Land management measures have already been carried out at all the reindeer farms. Land improvement projects are being introduced to promote efficient use of pastures and to keep their productivity at a high level. Over 150 million hectares of calving grounds are air-patrolled at local expense every year to prevent fires. All the farms have received instructions on the efficient use of pasture land.

In order to provide the reindeer with a fully supply of nutrients during the winter-spring period, the No. 67-IBMD protein-mineral supplement is being used in a daily dose of 100g/100kg/reindeer.

When a crust of frozen snow and ice makes pasture grazing impossible, using the specialized K-67-3 mixed feed (2 kg daily/animal) helps to prevent death and avoids the need to relocate reindeer to places where feed is available.

Supplementary feeding of reindeer during the snow free period with at feed mixture consisting of the special P-67-1 premix, table salt and fluorine-free phosphorus (30 g daily/animal) normalizes the physiological function of the animal, improves grazing, heightens the herding instinct and makes it easier to herd and control the animals.

Fattening of reindeer with below-average fat reserves with the help of specialized mixed feeds (K-67-1, K-67-2) enables us to increase their live weight and fat reserves. Fattening prior to slaughtering yields an additional 80-100 centners of first-grade meat (live weight) from each one thousand reindeer. That represents a profit of about 70 000 - 90 000 roubles.

Supplementary feeding and fattening of reindeer is carried out in accordance with instructions available at each farm.

Improvement of reindeer husbandry technology in the tundra and forest-tundra zones encompasses the following main measures: keeping the size of the herds at an optimal level in relation to regional conditions, with a simultaneous increase in the proportion of breeding cows in the herd to 60-65%; constantly monitoring the upkeep of the animals with a team-shift system of labour organization; grouping draft reindeer into a separate herd during the late autumn-winter-spring period; grouping of infertile animals during the calving period; and using fences and enclosures in those areas where mass autumn migration of wild reindeer take place.

A promising reindeer husbandry technology has been developed in recent years for the taiga zone.

It has been established that a high degree of safety is ensured for even unfenced animals during the winter when the basic organizational-zootechnical and geobotanical requirements are adhered to; daily controlled grazing of the animals by a 2-man duty shift; utilization of the pastures in proper sequence; monthly counting of the animals, and when necessary more frequent counting (along a path or over the fence of a corral); daily food supplements; grouping of draft reindeer into a separate herd; introduction of measures to prevent predator attacks, etc. In connection with this, it is recommended that a stationary or mobile housing and working complex be built in the centre of pasture land designated for winter maintenance of reindeer (the holding capacity of these pastures should be at least 3000-4200 reindeer, i.e. a 3-year rotation should be ensured for the grazing of a herd numbering 1000 - 1400 head). Radially from this complex, the pastures are divided into three areas with an equal grazing capacity. The areas are used in sequence, changing each winter. A stationary dwelling is also built on each wintering area for the herdsmen and they also use a mobile dwelling. In order to ensure the well-being of the animals and the maintenance of a good degree of fat during winter, extra measures are recommended, measures which are called for by the zonal systems of reindeer breeding in taiga conditions.

During the spring-summer-autumn season, it is recommended that the reindeer be kept in fenced pastures, in a specialized complex. The technology of this complex includes the following elements: a contoured (closed) fence extends along the perimeter of the areas set aside for keeping reindeer during the spring-summer-autumn period and prevents the animals from going beyond these boundaries; an interseasonal enclosure separates the pastures of two seasons (spring from the summer, summer from the early autumn and the early autumn from the late autumn ones) and prevents the animals from going into a pasture of another season; an interseasonal dividing enclosure in the spring and late autumn pastures makes it possible to utilize each area every other year (the size of each corresponds to the grazing norms during a season); an intraseasonal separating enclosure separates the pasture area for the grazing of infertile animals in the spring pastures and separates the pasture area for fattening in the late autumn pastures; a therapeutic-prophylactic (quarantine) enclosure makes it possible to organize more leisurely grazing of sick animals and improves the organization and efficiency of reindeer with below-average fat reserves; a supplementary feeding area includes a small frame hut for the herdsmen on duty, mobile feed boxes and fodder sheds (temporary covered structures for the storage of mixed feeds); stationary and mobile feeders which make it possible to rationalize the supplementary feeding of the animals, utilize the pastures according to plan and to spend less time and energy on herding and controlling the animals; corrals are stationary, or a mobile enclosure made of a nylon fabric; mobile veterinary station; mobile slaughterstation; traps for catching the reindeer; folding travelling sheds; a service complex (dwellings, bath and laundry, garage and power station, storehouses, helicopter platform).

The techonolgy of reindeer husbandry within the complex calls for adherence to all the planned geobotanical and organizational economic measures, including inspection of the enclosures and other facilities.

The introduction of the recommended system for keeping a herd numbering 1000-1400 head guarantees high production results with a meat yield exceeding 30 centners (live weight) for every 100 January reindeer. This results in an annual profit of more than 30 000 roubles while simultaneously improving the living and working conditons of the reindeer breeders.

Development of this reindeer husbandry technology is being carried out against the background of pure-strain breeding which has been given a great deal of attention in recent years. The varieties of reindeer (Nenets, Chukchi, Evenki, Evensk) have been certified and approved; 4 pedigree stock farms and one pedigree plant have been established, 123 pedigree herds have been formed, long-term plans of pure-strain breeding have been developed and introduced for regions, territories and autonomous republics for the period extending up to 1990. A regular exchange of pedigree stock is being carried on.

Planned production of velvet antlers has been initiated in order to increase the efficiency of this branch of industry and to utilize this product to a fuller extent.

Further development of this industry is being carried out by annual improvement of machinery and the housing and service complex, as well as by an increase in material incentives on the basis of an increase in the quantity and quality of produciton and the introduction of a brigade system of work.

The workers of the reindeer breeding industry are making a worthy contribution to the common cause of fulfilling the agricultural program of the Communist Party of the Soviet Union.

The management and utilization of reindeer in China

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Rangifer, Special Issue No. 1, 1986: 345 - 346

Reindeer *(Rangifer tarandus)* are economically valuable in China for their hides, meat, velvet antlers and milk. Reindeer are raised and trained by the Owenke, a minority nationality who depends on the reindeer for their food and livelihood. Thus, reindeer have an important role in economic and cultural development of the Owenke.

Since the founding for the People's Republic of China in 1949, the Communist Party and the People's Government have given attention to the protection and development of reindeer resources. The regional veterinary station sent veterinarians to the countryside to inspect the reindeer and, in 1960, set up a branch veterinary station. In 1967 a «Dongfanghong» (Red in the East) hunting team was organized which has worked hard to protect reindeer and to construct Oluguya village.

Owenke hunters have a complex system to manage and raise reindeer based on the annual biological cycle of the animals, as follows.

Spring (April-May)

Reindeer fawning begins with snow melt and greening of vegetation. The Owenke choose a sunny, sheltered site near water to live in preparation for the birth of fawns. They herd the reindeer back near their tents and feed them salt. For those reindeer that are about to give birth, the Owenke hang sticks about 40-50 cm long and 5-6 cm thick on their necks. The sticks hinder the movement of the reindeer and therefore they will not get loose and wander away. At the same time, the Owenke look after the reindeer during the critical period of birth. When the reindeer have fawned, they and their newborn are tied up to prevent them from running away. If some reindeer refuse to nurse or have a weak maternal instinct, the Owenke will force them to nurse and care for the fawn or will find a substitute reindeer mother whose newborn has died. Sometimes they also use artificial feeding. To individualize the newborn reindeer, the Owenke usually give them names. The newborn fawns are usually 6.5-7.5 kg in weight and can follow their mothers about 4 h. after their birth.

Summer (June-August)

Rising temperatures create favourable conditions for the spread of disease and the production of mosquitoes, gadflies and other insects (reindeer are also chased by wolves or bears). To help the reindeer grow well, each day the Owenke herd them back, feed them with salt, and burn moistened mosses for smoke to keep blood-suckings insects away. They also practice disease prevention and cure: for example, they often cure reindeer arthritis by acupuncture treatment or local medicines.

Around the end of May and the beginning of June, velvet antlers are ready for collection. The Owenke get antlers first from stags then from does. The reindeer is tied to a sturdy tree, and the Owenke put the reindeer's head in a frame made from two sticks about 4 m long and 10 cm thick crossing into a «V» form, and saw the antlers off. The Owenke boil the antlers and hang them in a shady and windy place to dry to keep them from rotting.

Since 1961, China has begun to systematically use reindeer antlers in Chinese medicines. The average annual collection of antlers in China has been about 300 kg. In recent years the output has declined slightly from about 400 kg in 1974 to slightly more than 200 kg in 1985 because of low prices.

During the lactation period (May-October), the Owenke milk reindeer once a day in the morning. When doing this, the Ownke leave the front two nipples for the fawn and milk the other two nipples. Each time, they obatin 200-300 g of milk. The milk contains a high percentage of protein, and the Owenke usually boil it for making tea.

Autumn (September-October)

The main work of the Owenke in autumn, as the weather becomes cool, is to prepare for the reindeer rut. In early September, the yearling male reindeer are castrated by pressing the reindeer down on the ground, wrapping its testes, and then biting the testes to pieces. As well, the herders saw off the ossified tips of the antlers of male reindeer to prevent injuries during the rutting fights. The rut starts in early October and lasts about a month during which time breeding males eat little or nothing, but drink more and chase female reindeer constantly. As at that time, it is easy to lose reindeer, the Owenke keep them in pens until evening when they are let out to look for food.

Winter (November-March)

The weather becomes cold and temperatures can reach —50°C. Reindeer excavate craters in the snow with their hooves for lichens. They also can eat tender branches of bushes or withered grass. For the Owenke, winter is the main hunting season, primarily for gray squirrels *(Sciurus vulgaris)*. Owenke hunters move camp from time to time to hunt. Therefore, reindeer carry women and children or goods weighing 30-35 kg, and even up to 60 kg. Five to 10 and even up to 15 reindeer are fastened in a row and follow a person through forest and marshlands at an average speed of 5-6 km/h. To train a draught reindeer, a castrated male reindeer 3-4 yr old is tied up for several days to make it exhausted, hungry and thirsty. It is then fed with lush grass but kept hungry and thirsty and accessible to man. Finally it is led to a river to drink while loaded with some goods. This is done repeatedly until it obeys people and carries a heavy load. The whole process takes about 10 days.

Reindeer are exhibited in large zoos in China. According to incomplete statistics, the sale of reindeer to zoos from 1971 to 1984 totaled 324.

As previously mentioned, the utilization of reindeer in China is restricted primarily to living animals for antlers, milk, draught and exhibition. Meat and hides are seldom used because of the small historical increase in numbers (Table 1), due to a variety of reasons.

In June 1985, The First Symposium on the Development of Reindeer Resources in China was convened in Erguna Zuoqi County. At the Symposium, measures to improve reindeer management and to develop reindeer resources in China were advanced. I believe that the development of reindeer resources in China has a positive prospect.

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Table 1. Numbers of reindeer and Owenke in China over the last 50 years.

Year	Population of Owenke	Numbers of reindeer	Data sources
1939	253	853	Nagata (1939) pp. 9-10
1945	170	400±	Qiu Pu (1962) p. 6
1957	146	629	Qui Pu (1962) pp. 31-32
1967	—	795	Helin, Oct. 1967, records
1976	167	955	Surveys in July-Oct. 1976
1985	195	904	Helin, April 1985, records

Wild reindeer in the USSR, their protection and utilization

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Rangifer, Special Issue No. 1, 1986: 347 - 349

The wild reindeer is one of the most valuable species of our country's natural resources. With the intensive development of the Far North and Far East, the problems of protecting and propagating this species have become more complicated. Therefore, the reserves of wild reindeer, their protection and a scientifically based approach to the management of the populations being utilized are the question with which Soviet theriologists and game management experts are most concerned.

Because of the measures taken by our country to protect wild reindeer, their numbers have increased more than 3-fold over the past 20 years, from 308 000 head in 1965 to 980 000 head in 1985. Reindeer are the most abundant of all the wild hoofed mammals in the USSR. It should also be said that in comparison with other countries, northern reindeer breeding is quite a developed industry in the USSR. Besides the 980 000 head of wild reindeer, we have 2 230 000 head of domestic reindeer, which naturally poses certain difficulties in determining the ecological policy regarding this species. Whereas the numbers of domestic reindeer have remained stable over the past 10 years, those of wild reindeer have shown a tendency to increase and to occupy the ecological niches free of domestic animals. The solution to this problem in different regions of the country is coordinated with the given situation.

In the *European North* as a whole, there are 30 000 - 33 000 head of wild reindeer and 380 000 head of domestic reindeer, and we observe a definite regeneration of reindeer populations. We also observe the revival of the Kola population which was undermined by unreasonable utilization at the beginning of the 1970's, as well as a growth in the numbers of forest reindeer in the Karelian and Komi taiga pastures which are free of domestic reindeer. Reindeer hunting is prohibited. The ecological capacity of the reindeer areas of the European North allows for a 4 to 5-fold increase in the number of wild reindeer in this region.

Western Siberia is a region with well-developed reindeer husbandry numbering 450 000 animals in the tundra and forest-tundra zones. The wild reindeer in this region occupies the taiga pastures at the watersheds of the Western Siberian lowland. Its numbers are fairly stable and stand at 24 000 - 25 000 head. Reindeer hunting is prohibited, and a number of zakazniki has been set up at the calving and wintering grounds.

On the whole, the taiga zone of this region has all the prerequisites for a significant increase in the number of wild reindeer.

The mountainous areas of southern Siberia are populated by wild reindeer in individual isolate localities, predominantly in the alpine or mountain tundra and in the taiga at its upper boundary. Approximately 25 000 head of reindeer inhabit the extensions of the Altai, the Eastern and Western Sayan mountains and the mountain ranges of the eastern coast of Lake

Baikal. Hardly any reindeer hunting is allowed in this area. About 300-350 animals have been killed over the past hunting seasons.

Domestic reindeer breeding is poorly developed in this region (30 000 head), and with an improvement in protection measures, one can expect an increase in the number of wild reindeer here. The establishment in this region over the past 10 years of the *zapovedniki* «Sokhondinsky», «Azassky» and «Sayano-Shushinsky» and the long-existent «Altaisky» will definitely promote an increase in the abundance of the mountaine-taiga forms of wild reindeer.

Central and Eastern Siberia are the main regions with a mass population of wild reindeer. In the tundra and taiga pastures from the Yenisei to the Indigirka rivers, we find the largest tundra populations of wild reindeer: the Taimyr population numbering 570 000 - 575 000 head, the Bulun population numbering 55 000 - 60 000 head, the Yana-Indigirka population numbering 100 000 - 110 000 head, and the Sundrun population numbering 25 000 - 27 000 head.

The nmbers of wild forest reindeer are also quite high here (100 000 - 110 000 head).

A new branch of game management, commercial reindeer harvesting, has developed in this zone on this basis of the utilization of tundra populations. Up to 80 000 head are utilized commercially each year from the Taimyr population and up to 25 000 head from the Bulun and Yana-Indigirka population (Table 1). Mass tagging of reindeer from the Taimyr population and analysis of the results have enabled us to establish its range (1 500 000 km^2), distance of migrations (1500 km), populations size and the presence of contact and exchange of animals with the Bulun population.

Annual aerial surveys, monitoring of the population structure, aerial surveillance of the seasonal migrations and the capacity of the seasonal pastures give us reason to believe that the commercial utilization of these populations can be increased within the next 2-3 years.

The under-utilization of the tundra populations in this region has the danger of triggering a self-regulating mechanism which will be followed by a decrease in numbers.

This region is characterized by highly competitive relations between the wild and domestic reindeer, the numbers of which stand at 107 000 head in the Krasnoyarsk Krai and 360 000 head in the Yakut ASSR[2].

A number of *zapovedniki* (Taimyr, Central Siberian, Ust'-Lena) and zakazniki (Putoransky, Puro-Pyasinsky) have been set up or are in the process of being established in this region. Among other things, they are responsible for protecting the calving and wintering grounds of the wild reindeer.

The Far East is the principal area of developed domestic reindeer breeding. The northeastern part of this region has 830 000 domestic reindeer which utilize the pastures resources almost completely. As a result, the numbers of wild reindeer are quite low.

In the central part of the Chukotka region, an isolated herd has remained at a level of 5000 - 6000 head for a long time.

On the eastern coast of Kamchatka, wild reindeer have stabilized at a level of 4000-4500 head.

In the Khabarovsk Krai and in the Amur and Sakhalin Oblasts, wild reindeer have varied from 20 000 to 25 000 head over the past 20 years, and hunting is prohibited[3].

There is a possibility of increasing the numbers of reindeer in the mountaine-taiga areas of the southern regions of the Far East where domestic reindeer breeding is not carried on.

Table 1. Population size and commercial utilization of the Taimyr population.

Years	Size prior to commercial utilization (1000's)	Recommended quota of utilization (1000's)	Actual utilization (1000's)	Less than recommended quota (1000's)
1981	510	80	80	—
1982	525	100	76	24
1983	540	100	80	20
1984	575	120	80	40

Arctic islands

Novaya Zemlya. By the 1950's, only a few of Novaya Zemlya subspecies of the wild reindeer have survived, and so these animals were added to the *«Red Book of the USSR»*.[4] The population has risen now about 6000 head, which has made it possible to allow limited utilization with annual monitoring of the numbers of this unique population (B.V. Novikov, 1983. Current status of island northern reindeer populations. Collection of scientific works, Central Research Laboratory of the Glavokhita, RSFSR Moscow. 101-107.)

Severnaya Zemlya. The three islands of Severnaya Zemlya have long been inhabited by several hundred wild reindeer. The absence of predators and the extremely limited productivity of the pastures have resulted in a stable small population.

The Novosibirsk Islands are inhabited by one of the largest island populations of reindeer, which maintains constant contact with the mainland during the winter. The present numbers stand at 7500 - 10 000 head (Kupriyanov, A.G. and Belikov, S.S. 1985. Northern Reindeer in the Arctic Islands, Priroda (Nature) No. 3: 46-51.)

On the Wrangel Island zapovednik, the reindeer population originated from domestic reindeer brought in from Chukotka. Its population stabilized at 2000 - 2100 head (Novikov, 1983).

It is possible to significantly increase the wild reindeer population in the USSR. In the opinion of Soviet theriologists, the wild reindeer herds can actually be increased to the level of the domestic herds within the next 25 years in the vast unoccupied taiga and tundra. Therefore, the priority measures at this stage consist of protecting and restoring the wild reindeer populations, and then solving the questions concerned with the economic utilization of large populations.

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[1] *Editor's note:* There are several types of protected areas in the Soviet Union. The two important types include the *zapovedniki* nature reserves which are natural areas set aside for research in the natural sciences and *zakazniki* (wildlife preserves) concerned generally with a specific species found within ist protected boundaries. The zakazniki may be temporary or permanent in nature depending on the purpose of the protection. Permanent zakazniki are generally used to protect wintering or nesting birds and calving and wintering grounds for wildlife.

[2] *Editor's note:* A «Krai» is an administrative unit with a level of political jurisdiction immediately under the republic. There are six Krais in the Russian Soviet Federated Socialist Republic (RSFSR). An «ASSR» - Autonomous Soviet Socialist Republic - has the same level of political jurisdiction as a Krai, but is formed on the basis of a nationality grouping as well. There are 20 ASSR's in the USSR, 16 in the RSFSR.

[3] *Editor's note:* An «Oblast» is an administrative district with the same jurisdictional level as a «Krai». There are 122 Oblasts in the USSR, 49 in the RSFSR.

[4] *Editor's note:* The «Red Book of the USSR». It refers to a catalogue of rare and endangered species.

Expanded abstracts & abstracts

Index measurements of carcass composition for Coats Island caribou

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Rangifer, Special Issue No. 1, 1986: 353

During a 2-year study of the ecology of barren-ground caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada, 27 side dissections were conducted; bone, muscle, and fat were separated and weighed. Mature female caribou made up 17 of the 27 dissections and the remaining 10 were calves ranging in age from 1 week to 11 months. The extreme cycle of body condition in Coats Island caribou permitted the study to span the range from fat fall animals to emaciated spring animals near starvation. Weight of the gastrocnemius muscle (a small, readily identifiable muscle in the hind quarter) was an accurate predictor of total muscle weight (1n (total muscle in kg) = —2.791+1.071 1n (gastrocnemius weight in g); $r^2=0.98$). The regression was not affected by age or condition, and muscle composition varied little with season except in very lean animals, in which intramuscular fat decreased. Weight of the femur was an equally useful predictor of total bone weight (1n (total bone in kg) = —4.878 + 1.137 1n (femur weight in g); $r^2=0.98$). This regression was also unaffected by age or condition. Three carcass fat depots — subcutaneous, intermuscular, and pelvic — and two internal depots — omental and perirenal — were graphed against the total fat in these depots for each animal. Age and body condition again had little effect on the curves for each depot. Subcutaneous fat was the latest maturing but the earliest depleted. A multiple regression using depth of back fat and weight of kidney fat to predict dissectable fat in the 5 depots was developed (weight of total fat in kg = —0.178+1.058 (d.b.f. in cm) + 24.147 (weight of kidney fat in kg); $r^2=0.98$). These allometric relationships based on anatomical dissection permit relatively accurate prediction of body composition using simple index measurements. Comparison with similar studies on domestic reindeer (*R. t. tarandus*) and Svalbard reindeer (*R. t. platyrhynchus*) gave comparable predictions when adjustments were made for technique. The relationships between weights of components of the three tissues and total tissue weight are relatively constant across subspecies of *Rangifer tarandus*, as would be expected from studies with domestic sheep (*Ovis aries*) and cattle (*Bos taurus*).

Factors regulating energy expenditure and heat balance in reindeer

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Rangifer, Special Issue No. 1, 1986: 354

Reindeer are able to maintain a thermogradient between body core and the environment of up to 100°C. This is in part due to prime insulation by fur (Hammel, 1955; Moote, 1955), controlled peripheral cooling by means of counter-current vascular heat exchange in the legs (Irving & Krog, 1955) and counter-current vascular heat exchange in the nasal passages (Blix & Johnsen, 1983). By such protective means the lower ciritical temperature of the Svalbard reindeer, for instance, is as low as —50°C in winter, when resting metabolic rate is only 66% of the summer value (Nilssen *et. al.*, 1984). The seasonal changes in metabolic rate are hardly a result of reduction of basal metabolic rate, but are rather due to seasonal changes in food intake which in turn is determined by seasonal changes in appetite, regulated by photo-period (Nilssen *et al.*, 1984). In reindeer with prime winter insulation and few avenues of heat loss grave thermal problems are incurred when the animal is forced to run to avoid predators, since a trotting speed of only 10 km·h^{-1} increases metabolic rate some 4 times (Nilssen *et al.*, 1984; Fancy & White, 1986). In such situations skin temperature is brought close to core temperature, allowing heat to be dissipated through the fur, and the counter-current vascular heat exchange in legs and nose eliminated (Johnsen *et al.*, 1985, Folkow & Mercer, in press). Moreover, the vascular heat exchanger in the nose is now operated in conjunction with a carotid rete for selective cooling of the brain, while heat is stored in the rest of the body (Johnsen *et al.*, 1985).

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The effect of changes in fur insulation and activity on different modes of heat loss in reindeer

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Rangifer, Special Issue No. 1, 1986: 355 - 356

Climatic conditions in the natural habitats of reindeer (*Rangifer tarandus tarandus*) may show large seasonal fluctuations. At one extreme, low ambient temperatures may prevail in combination with wind and precipitation, which imposes a large negative thermal load on these animals. At the other extreme, high ambient temperatures in combination with intense solar radiation may, especially when combined with heavy exercise, cause reindeer to be severely heat stressed.

Maintenance of homeothermy under these circumstances is possible due to the physical, physiological and behavioural characteristics of the animal, *i.e.* a large seasonal change in the insulative value of the fur (Moote, 1955), a great capacity for changing the physiological insulation (*e.g.* by use of nasal heat exchange (Blix & Johnsen, 1983) and of counter current circulation in the extremities (Irving & Krog, 1955)) and finally adequate behavioural temperature regulatory responses.

The purpose of this study was to investigate how some of these thermoregulatory mechanisms respond to changes in the thermal environment of the reindeer. This was achieved by examining changes in the relative importance which different modes of heat loss have under various conditions.

Thus, partition of heat loss was performed in winter and summer insulated reindeer during rest (standing) and exercise (running on a level treadmill at 9.2 km·h^{-1}) in a climatic chamber set to an ambient temperature (T_a) of —30, 0 or 25°C. The experiments involved determining values for the parameters in the following heat balance equation:

$$S = MR + mo \pm W - E - R - K - C$$

The methods involved were as follows:

S (rate of change in heat storage) was calculated from the body weight of the animal and from changes in its body core (rectal) temperature

MR (metabolic rate) was determined by indirect calorimetry, using an open circuit system.

mo (heat produced by micro-organisms inside the gastrointestinal system of the reindeer) was not measured. However, a value of 0.05 W·kg (body weight)$^{-1}$ was used, the value taken from a previous study in the reindeer by Hammel *et al.* (1962).

W (work). The work exerted both by a standing reindeer and by an animal running on a level surface is zero.

E (evaporative heat loss), represented by respiratory evaporative heat loss, was determined by indirect calorimetry, using an open circuit system.

R (radiant heat loss) was calculated from the effective radiating surface area and the mean radiative temperature of the reindeer, (determined with an AGA Thermopoint 80 Infrared radiometer) according to a formula presented by Porter (1969).

K (conductive heat loss) was considered negligible as the contact area between the reindeer and the floor was very small.

C (convective heat loss) was calculated by subtraction.

Of the above parameters, S, MR, E and R were simultaneously determined.

Results showed that the resting winter insulated reindeer lost heat mainly through radiation and convection at the two lower T_a's (92.6% of total heat loss at T_a —30°C and 87.7% at T_a 0°C). At a T_a of 25°C, however, the importance of evaporative heat loss increased to 44.6% of total heat loss. During exercise in winter, ca. 90% of total heat loss occurred through evaporation and convection at T_a's —30 and 0°C. No measurements were made on the winter insulated reindeer exercising at T_a 25°C, as the animals refused to run at this temperature. The resting summer insulated reindeer lost heat according to a pattern similar to that found in the resting winter insulated animal. However, during summer, the importance of evaporative heat loss was smaller than during winter, evaporative heat loss never representing more than 16% of total heat loss in the resting summer insulated animal. In the exercising summer insulated reindeer the importance of radiant heat loss was approximately twice the value found during exercise in winter.

Acknowledgements

This study was supported in part by the Norwegian Reindeer Administration and the Norwegian Research Council for Science and Humanities.

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Does grazing influence growth of the reindeer lichen *Cladina mitis*?

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Rangifer, Special Issue No. 1, 1986: 357 - 358

Objectives

Reindeer (*Rangifer tarandus* spp.) commonly use areas dominated by lichen mats for winter habitats. Dependent on lichen richness, 40 - 70% of the winter diet consists of variable proportions of *Cetraria nivalis*, *Cladina mitis* and *C. stellaris*. Areas with poor snow cover on Norwegian wild reindeer ranges are commonly dominated by these lichens and it is often this lichen grazing resource which restricts the carrying capacity.

Where the lichen grow in the microhabitat depends on the duration of snow cover, and how fast they grow depends on the precipitation and moisture regime in the snow free period. When moist they grow from the top but rot at the bottom. Young, small individuals grow fast, about 20% per year, but they taper off as the mat becomes thicker. When fully grown, they grow and rot at the same speed and no net gain in size is made. How these lichens get their moisture: dew and frequent light rainfall versus infrequent, but heavy rainfall, influence biomass stabilization. In coastal climates in Norway pure mats of *Cladina mitis* have standing biomasses of 1100 gDM (Dry Matter)/m^2, in continental climates, lichen mats have up to 1800 gDM/m^2.

Grazing by reindeer works in two different manners. Heavy grazing tends to clip the mat, but light grazing tends to thin it. To measure the growth of grazed mats I set up an experiment where the two grazing effects are simulated separately, and report here some results from the *Cladina mitis* tests, one of the most preferred species.

Methods

Samples of about 10 gDM were separated out from a *Cladina mitis*-mat, and placed in round trays with a bottom size 0.9 dm^2. The most rotten bottom part was carefully removed. Care was taken not to alter the density of the lichen, to avoid influencing the conditions of growth or decomposition. Three treatments were applied — each in five parallels.

(1) Untreated: As above, weight was 10.69±2.48 gDM, this corresponds to 1188±276 gDM/m^2.

(2) Clipped: Top, about 50% of original weight removed by clipping, resulting weight 5.85±1.20 gDM, this corresponds to 649±133 gDM/m^2.

(3) Thinned: Regular removal of lichen individuals to about 50% weight. Resulting weight 4.42±0.50 gDM, this corresponds to 491±55 gDM/m^2.

Trays were left to grow in ± natural microhabitats in an experimental field in the low alpine region 980 m at the Dovre mountains, Norway (62°16'N, 9°36'E).

Trays were brought in the lab and weighed (dried at 30°C) at the start and end of the snow free period with a standardized procedure starting in May 1979. Correcting factors for water content at 30°C is obtained from parallels, dried at 70°C, repeated each time.

Results

For comparison I have recalculated weight data on a relative basis (Fig. 1). I used data from weighings in May, so that new growth over the years appear. There is a clear tendency shown, however, that rotting causes weights to decrease over the winter.

I found a significant difference between treatments. Clipping causes the growth to be less than untreated samples, whereas thinning causes it to be higher. The most probable explanation is thought to be that clipping removes a greater part of the living material. Compared to untreated samples the rotting thus becomes relatively higher. The reason thinning improves growth may be that the light conditions will be better for the growth of the remaining lichen individuals.

Consequences for management

Management practices try to stabilize reindeer populations in several rather small separated ranges in Norway. Calculations of carrying capacity are based upon reserves of lichen grazings and the average yearly removal of lichen by one animal (Gaare & Skogland 1980). These data for lichen growth will help refine the algorithm. We also try to use them to define and describe what an optimally used lichen pasture should look like.

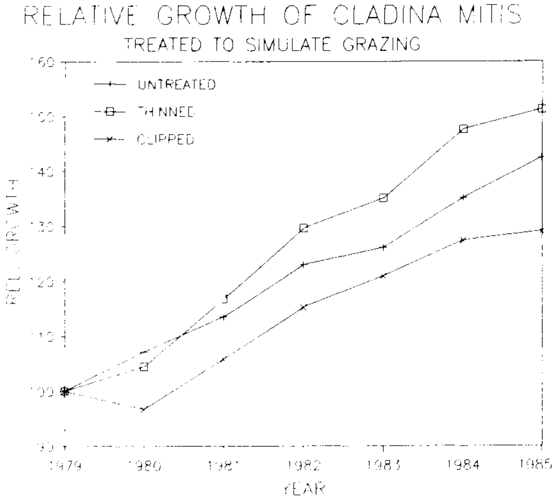

Fig. 1. Relative growth of 5 parallell samples of *Cladina mitis.* Average weight of untreated samples were 11 g DM, clipped 6 g DM and thinned 4.5 g DM, all at to 100 to facilitate comparison.

One may also find them interesting when hypothesizing on the reasons for population variations: To make simulation models over decades and centuries of the reindeer - lichen interaction, like the one presented at the 1st International Reindeer/Caribou Symposium by «Buda Himimi McPapescwa», closer to life (Bunnell *et al.* 1975).

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Comparison of body composition and growth potential in two related island populations of caribou

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Rangifer, Special Issue No. 1, 1986: 359

Body growth in *Rangifer* is governed by the complex interaction of environmental factors and genetic potential. The relative importance of nutrition in different seasons is difficult to partition, but studies have shown that both summer and winter nutrition can influence mature body size. We undertook a study of winter nutrition, body growth and body composition of two genetically related populations of barren ground caribou (*R. tarandus groenlandicus*) on Coats and Southampton Islands in Hudson Bay, Canada. The Southampton Island population was introduced in 1967 using caribou transplanted from Coats Island. Temporally paired collections of adult females and calves were carried out on the two islands in fall (October - November) 1983, and late winter (March - April) 1983 and 1984 (adults=54, calves =10).

Analysis of plant fragments in rumen contents revealed that lichens were a major component of the fall (67%) and late winter (46 - 49%) diet on Southampton Island. Lichens were less important in the fall on Coats Island (36%) and were a minor component in late winter, 12% and 2% in 1983 and 1984 respectively. Dietary prevalence of lichens reflected differences in availability. In the Dryas-lichen community lichen biomass was eight times greater on Southampton Island. Deeper snow in late winter 1984 was correlated with a lower representation of lichens in the diet on Coats Island. Diet quality was determined by analysing acid detergent fibre and nitrogen concentration in rumen contents. Caribou on Southampton Island were able to maintain a higher quality winter diet because of a greater availability of lichens.

The greater severity of the second winter was reflected in lower values for all fat depots. In both winters depth of back fat, mass of kidney fat and percentage femoral fat were lower for Coats Island females. Based on comparing late winter with fall gastrocnemius muscle weights, muscle was catabolized to a greater extent during the second winter. For Coats Island, the fall to late winter difference was —6.5% and —13% for the first and second winters; for Southampton Island females it was —4% and —10% respectively. Coats Island caribou attempted to compensate for low winter diet quality by increasing the volume of digesta in the reticulorumen. Late winter full reticulorumen weight was 19 - 21% of whole body weight on Coats Island and only 10 - 12% on Southampton Island. Body composition was similar in the fall on both Islands, except that females on Coats Island tended to be slightly fatter. Calves on Coats Island depleted virtually all fat depots by late winter in both years, with femoral fat levels of 2% and 0% in 1983 and 1984 respectively; muscle was catabolized to the extent of 28% and 39%. For the single calf collected on Coats Island in late winter 1983, gastrocnemius muscle weight was 26% greater than the mean found for four calves collected on Coats Island in the fall, and some dissectable fat still remained in the carcass (0.69 kg).

Analysis of linear measurements of adult females showed that caribou on Coats Island were smaller than Southampton Island caribou. Calves collected on Coats Island were also smaller than the calf collected on Southampton Island. Caribou on Coats Island acheived less of their growth potential than genetically related caribou on Southampton Island. Population dynamics also differed, with sporadic high winter mortality occurring on Coats Island, but no reported deaths due to starvation on Southampton Island. On Coats Island overwinter losses occurred at different densities and hence were density independent, resulting from snow accumulation and a sparse food supply. As caribou density increases on Southampton Island we predict that grazing will reduce lichen availability (a density dependent process), leading to an ecological state similar to Coats Island.

Taxonomy and history of arctic island reindeer with special reference to Svalbard reindeer - A preliminary report

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Rangifer, Special Issue No. 1, 1986: 360

The study is based on the cranial measurements from 114 adult wild reindeer. A series of 21 measurements was carried out for each complete skull (see: Aquilo Series Zoologica 23:1-11. University of Oulu). The material is mainly concerned with the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik) and the northernmost populations of the Eurasian tundra reindeer (*R. t. tarandus* L.). Remarks are also included on characteristics of skulls from Greenland and the Canadian High Arctic Islands. Sharp differences exist between Svalbard reindeer and the Novaya Zemlya form. The latter resembles more the tundra forms of Eurasian mainland as demonstrated by Banfield (Banfield 1961).On the other hand, Svalbard reindeer shows essential similarities to the specimens from Ellesmere and Axel Heiberg islands, and especially the extinct reindeer of East Greenland. These three populations represent in extreme form the morphology typical on arctic islands. From the taxonomic point of view this would confirm their close affinity and common high arctic origin with Svalbard reindeer. In the light of new geological evidence and radiocarbon dates, and of archeological finds of dwarfed caribou from Southeast and Southwest Greenland the Greenland origin of Svalbard reindeer seems probable. Ice-free pastures in northwestern Svalbard and northern or eastern Greenland theoretically may have created possibilities for accidental immigration as early as 20 000 - 40 000 years ago.

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Calcium absorption in reindeer: Effect of diet and vitamin D

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Rangifer, Special Issue No. 1, 1986: 361 - 362

Calcium is an extremely important element with both structural and metabolic roles depending on tissue function. Therefore, Ca metabolism is well regulated. Ca absorption rate can change with metabolic requirement, and the process is actively regulated by vitamin D. However, there are few studies which describe these mechanisms in wild species in which both the Ca availability and requirements change seasonally. Previous studies indicated that there is a potentially high fecal loss of Ca when reindeer are fed a lichen based diet (Staaland *et al.*, 1984, White *et al.*, 1984) suggesting that Ca regulation may not always counter nutritional insufficiencies. How the absorption process has coevolved with dietary specialization is only poorly known in mammalian species.

This study was to determine the relative role of the rumen versus the small intestine as an absorption site and to test the degree to which absorption is modulated by the active form of vitamin D, 1,25-dihydroxyvitamin D_3 (1,25 D). It was hypothesized that the absolute amount of Ca absorbed would increase with Ca intake but the efficiency of absorption (equivalent to Ca digestibility) would increase as the dietary intake declined and that the role of 1,25 D would be maximal.

Three reindeer calves fitted with cannuli in the rumen and abomasum were kept in metabolism stalls for a 2-month period. In consecutive 2-week periods the animals were fed 1 kg Dry Matter/d of the following diets: lichens, lichens + RF-71 (1:1) and RF-71 (reindeer pellets concentrate and grass meal 3:1). Intakes of Ca on the three diets wee 22, 49 and 67 mmol/d. Ca absorption was measured after 10 d on each diet by deconvolution analyses of plasma radioactivity curves following injections of $^{47}CaCl_2$ into the abomasum, $^{45}CaCl_2$ into the rumen and $^{85}SrCl_2$ iv. 1,25 D (20 ug) was then given intraruminally to stimulate absorption. New measurements commenced 48 h later. The $^{45}CaCl_2$ was injected to determine the role of the rumen relative to the intestines as absorption sites.

Results of Ca absorption in relation to diet and stimulation by 1,25 - dihydroxyvitamin D_3 are: (Mean and s.e.m.)

Diet	^{47}Ca-absorption (% dose)		Net Ca-absorption (mmol/d)	
	Unstimulated	Stimulated	Unstimulated	Stimulated
Lichen	0.23±0.05	0.39±0.03	—3	0
Lichen+RF-71	0.27±0.06	0.50±0.08	1	16
RF-71	0.38±0.07	0.57±0.06	18	26

In spite of low Ca intake the efficiency of Ca absorption was low on the lichen diet. Therefore our hypotesis that fractional absorption would increase with declining intake is refused. Upon stimulation by 1,25 D Ca absorption increased but for lichens the stimulation was only to the level observed in unstimulated calves fed RF-71. Our results suggest that lichens possess Ca binding properties which may be of nutritional significance. In addition, analysis of the data where ^{45}Ca was injected into the rumen suggest that the ruminal route of absorption was relatively unimportant in reindeer.

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Regulation of nasal heat exchange in reindeer

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Rangifer, Special Issue No. 1, 1986: 363 - 364

Previous studies have shown that reindeer are able to restrict respiratory heat loss by use of nasal heat exchange (Blix and Johnson, 1983). This mode of heat conservation, which is based on cooling of the expired air, and thereby condensation of water, particularly at low ambient temperatures, is possible because of the existence of a temperature gradient along the length of the nasal passages (Johnsen *et al.*, 1985a). Furthermore, Blix and Johnsen (1983) have shown that there is a summer to winter difference of about 12°C in exhaled air temperature at, for instance, —10°C ambient temperature, in these animals. At this ambient temperature respiratory minute volume and frequency were the same in summer and winter. This therefore indicates that the temperature gradient along the nasal mucosa in reindeer must be under physiological control.

We have recently investigated the vascular anatomy of the reindeer head with particular emphasis on the nasal mucosa. Based on ideas which emanated from this work we have put forward a hypothesis for the operation and control of nasal heat exchange in reindeer (Johnsen *et al.*, 1985a).

In order to visualize the vascular system of the reindeer head we have made use of uni-lateral plastic casts. These casts revealed that the nasal mucosa in reindeer consists of a network of frequently anastomosing arteries running the full length of the nasal turbinates in the anterior direction. This rete runs adjacent to and in close contact with a venous rete of similar complexity with which it communicates by way of capillaries and arterio-venous anastomoses. It was also evident from the plastic casts that the effluent from the venous rete can be drained through the deep sphenopalatine group of veins at the posterior end, and through the superficial dorsal nasal vein at the anterior end of the nasal cavity. The dorsal nasal vein in turn has a possibility to drain either directly into the jugular vein via the facial vein, or to the carotid rete for selective cooling of the brain.

In situations of extreme heat conservation in the cold we suggest that the blood runs in opposite directions in the arterial and the venous rete of the nasal mucosa, whereby the temperature gradient along the nasal mucosa, which is necessary for cooling of the expired air, is maintained due to counter-current heat exchange. In this situation arterial inflow to the rete is low, and the dorsal nasal vein and the vessels of the anterior end of the venous rete are constricted. Accordingly, the venous effluent from the nasal mucosa is primarily drained through the sphenopalatine group of veins at a temperature close to that of the arterial blood.

On the other hand, when the animal is in a state of extreme heat dissipation (in a hot environment, or during running), respiratory minute volume will increase substantially (Blix and Johnsen, 1983). However, an increase in respiratory minute volume without circulatory adjustments, will result in a substantial decrease of nasal mucosal temperature and a subsequent reduction in expired air temperature, which would compromise the dissipation of heat by way of the respiratory tract. Under such heat stress conditions we therefore suggest that concomitant with heat induced panting the arterial inflow to the nasal mucosa is increased. We moreover suggest that the arterio-venous anastomoses are open and that both retia are now perfused undirectionally in the anterior direction, and that the venous effluent is drained primarily by way of the dorsal nasal vein while the sphenopalatine group of veins are constricted. It follows that the nasal mucosa may now be perfused counter-current with respect to the inspired air, and heat loss from the mucosal surfaces is thereby optimized. The venous effluent in the dorsal nasal vein will then be colder than the arterial blood, and may now be distributed either to the carotid rete for selective cooling of the brain, or, directly to the right atrium of the heart for general body cooling.

With the animal in a state between the above described extremes the need for accurate control of the temperature gradient along the nasal mucosa arises. Thus, changes in ambient temperature, metabolic heat production, respiratory minute volume and seasonal changes in fur insulation must be accounted for if fine tuning of thermal balance is to be achieved. In this respect we have previously found indications for an active regulation of the temperature gradient along the nasal mucosa in reindeer (Mercer *et al.*, 1985b).

Our results suggest several ways by which the temperature gradient along the nasal mucosa may be controlled. With the ventilatory volume kept at a constant level, the temperature gradient along the nasal mucosa may be changed in response to changes in the arterial inflow to the nose, and/or as a result of changes in the distribution of the venous effluent between the dorsal nasal and the sphenopalatine group of veins.

Acknowledgement

This study was supported by the Norwegian Research Council for Science and the Humanities (grant no. 14.57.45.057), and by the Norwegian Reindeer Administration.

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Selective factors in the determination of leg length in *Rangifer*

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Rangifer, Special Issue No. 1, 1986: . 365

Leg length shows considerable variation among both domestic reindeer and the wild forms of *Rangifer,* and it appears to be under the control of several selective factors. These include nutritional constraints, the energetic efficiency of foraging through snow of varying depths, the efficiency of locomotion where long migrations occur, and fleetness in relation to predator avoidance. The net energy cost of walking or running a given distance on a hard surface decreases with increasing leg length, and the advantage of increased leg length in decreasing the cost of locomotion is even more pronounced in deep snow. However, the energetic advantages of long legs for movement in deep snow and for migration are counteracted by the energy costs to the animals for growth and maintenance of the additional tissues and possible decreased efficiency in foraging at ground level in the absence of snow. The cline of decreasing leg length in *Rangifer* with increasing latitutde is apparently the product of these selective mechanisms. Evidence from domestic and feral reindeer, insular populations, and feeding experiments indicate that changes in the nutritive quality of the diet can account for short-term changes in leg length, although the changes are usually of an allometric nature. This is consistent with palaeontological material from Greenland which also suggests that relatively rapid changes in body size (i.e. «dwarfism») may result from nutritional stress associated with climatic change.

Adaptation of the microflora in the rumen and caecum of the high arctic Svalbard reindeer

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Rangifer, Special Issue No. 1, 1986: 366 - 367

The Svalbard reindeer relies on a highly active rumen microbial population of bacteria, fungi and protozoa for the utilization of cellulose and hemicellulose, the major components of growing plants (Rogers and Perkins, 1968). On Svalbard the availability and quality of food changes during the year, ranging from fresh young forage in summer (July - September), to a highly concentrated diet, including seedheads with a high content of protein and starch at the end of the summer, to a highly fibrous diet in the long, harsh winter (October-June).

The Svalbard reindeer have developed a large caecum constituting 12% and 7% by weight of the total intestinal tract in winter and summer respectively (Staaland *et al.*, 1979), but the nutritional importance of the caecum as a fermentation chamber is poorly understood in ruminants.

Optimal utilization of available plants in the rumen and caecum in summer, when body energy stores are deposited, as well as in winter, when food is in short supply, could be of crucial importance for the survival of these animals.

We have therefore presently characterized the dominant bacteria in the rumen and caecum of Svalbard reindeer, in summer (September) and winter (April) (Orpin *et al.*, 1985, Mathiesen *et al.*, unpublished data).

The population density of viable rumen bacteria was 181 ± 124 x 10^8 ml^{-1} in summer and 35 ± 29 x 10^8 ml^{-1} in winter. The winter experiments were conducted after a long period during which the vegetation had been covered with ice, and in spite of that, the winter population density was suprisingly high, with the percentage of cellulose digesting bacteria increasing from 15% in summer to 35% in winter. The percentage of bacteria utilizing hemicellulose constituted 30% and 58% of the viable bacterial population in summer and winter respectively.

The dominant cellulolytic bacterium in the rumen was *Butyrivibrio fibrisolvens* which constituted 10% of the viable population of rumen bacteria in summer and 18% in winter. Of the total *B. fibrisolvens* population 45% and 60% isolates showed cellulolytic capacity, in winter and summer.

The viable bacterial population density in the caecum was 8.9 ± 5.3 x 10^8 ml^{-1} in summer, but it decreased to 1.5 ± 0.7 x 10^8 ml^{-1} (17%) in winter, a similar percentage decrease to that shown by the rumen microbial population. Of the total caecal population, 10% of summer isolates had cellulolytic properties compared with 6% of winter isolates. The percentage of caecal bacteria utilizing hemicellulose was 33% of isolates in summer and 48% in winter.

The dominant cellulolytic caecal bacterium in summer was *B. fibrisolvens,* and in winter, *Ruminococcus albus.* These species represented 7% and 5% of the viable bacterial population density in each season, respectively (Mathiesen *et al.,* unpublished data).

The caecal bacterial population contained large numbers of species which have the potential to degrade plant material, including plant cell wall polysaccharides, which have escaped ruminal fermentation. While we have no data yet on particle flow rates from the rumen, we have observed large, relatively intact, plant tissues in the caecum of animals sampled in the summer. It is likely therefore that plant tissues entering the caecum are subject to extensive microbial fermentation.

The Svalbard reindeer clearly shows seasonal changes in the microflora of both the rumen and caecum. The adaption of these microbial populations helps to maximize the utilization of the diet in summer, when the nutritional demand and food intake of high quality forage is high, and during winter when, despite the poor nutritional conditions, the animal still needs to meet the bulk of its energy requirements from the diet.

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Role of predators in reindeer brucellosis in Alaska

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Rangifer, Special Issue No. 1, 1986: 368

Abstract: Brucellosis caused by *Brucella suis* type 4 is endemic in Alaskan reindeer (*Rangifer tarandus*) herds. Predators and small mammals were collected on the fawning grounds of a known-infected herd during the springs of 1977 — 1984. Serologic reactions were detected in red foxes (*Vulpes vulpes*), arctic foxes (*Alopex lagopus*), grizzly bears (*Ursus arctos*) and arctic ground squirrels (*Spermophilus parryii*). *Brucella suis* type 4 was isolated from red and arctic foxes. Red foxes were orally challenged with *B. suis* type 4 in controlled experiments. Shedding of the organism was detected in fecal samples several days post-challenge. Antibody titers were detected up to several months post-challenge, and *B. suis* type 4 was isolated from several tissues at necropsy. Reindeer confined with infected foxes became infected. Transmission of brucellosis among reindeer and their predators needs to be addressed in a brucellosis control program.

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A suspected virus infection of the oral mucosa in Swedish reindeer (*Rangifer tarandus* L)

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Abstract: In 1980 a rather high frequency of reindeer, supplementarily fed in pens, were taken ill and deaths occurred as well. In five out of eight carcasses necrophsied oral lesions were observed. Histologically the mucosa, surrounding these lesions, was charasterized by the presence of intracytoplasmic inclusion bodies, inter- and intracellular oedema and vesicle formation. *Fusobacterium necrophorum, Coli,* betahaemolizing streptococci, and *Corynebacterium pyogenes* found in the lesions were all considered secondary invaders. Serological samples from disease stricken herds were tested for antibodies against BVD-, Pi3-, and IBR-virus as well as *Chlamydia.* Low positive titres were observed but for BVDV. The result indicates that a thus far unidentified virus might be the primary cause of this enzootically occurring disease.

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Rangifer, Special Issue No. 1, 1986: 369 - 373

Introduction

During the winter 1980 the Tornedalen area along the Swedish/Finnish border was hit by grazing difficulties for the reindeer herds. Thus supplementary feeding was organized at several places from December through April. Mostly this turned out well but at some places animals were taken ill, mostly showing loss of appetite and signs of fever. Sudden deaths also occurred.

This paper deals with the pathological lesions found in animals sent in for necropsy at the National Veterinary Institute, Uppsala, Sweden. In addition blood samples, for serological investigation, were obtained from flocks or reindeer on feeding sites where animals had succumbed (Rehbinder *et al.* 1985).

Material and methods

1. Animals

The eight reindeer autopsied in this investigation had all been subjected to artificial feeding in groups of different sizes and at different places. For most of the reindeer this feeding started up in mid-December. The feed usually consisted of a minor amount of commercial feed-mixture and hay *ad lib.*

For most of the reindeer the feeding period was spent in permanent pens but at some places the pens were regularly shifted to untouched land in order to provide the animals with fresh snow as water supply.

2. Pathological investigations

The eight dead animals which were sent to the National Veterinary Institute, were all in a state of beginning decomposition. Age was estimated on the basis of dental wear.

The preparation of tissue samples for histological as well as ultrastructural studies were performed according to commonly used techniques.

3. Serological investigations

Bloodsamples (2 samples, 6 weeks interval, from each animal) were drawn from the jugular vein of 26 animals at selected feeding sites where sudden deaths had occurred. From three of these herds dead animals were brought in for necropsy, from Hedenäset, Övertorneå I and Männikkö.

Serological tests were carried out against bovine virus diarrhoea (BVD), parainfluenza-3 (Pi3), and infectious bovine rhinotracheitis (IBR) virus as well as against *Chlamydia*.

Results

The results of *post mortem examination* of eight reindeer have been put together in a condensed form in Table 1. From a pathological point of view two reindeer (nos 2 and 5) differed from the rest of the animals autopsied as they had succumbed to differing diseases, a sequestered hoofbone and inanition, respectively. Of the remaining six animals, intracytoplasmic inclusion bodies were seen in the tissue surrounding oral ulcers in four animals.

The ultrastructural examination was affected by the fact that the material obtained showed varying degrees of post mortal changes. The presence of intracytoplasmic inclusion bodies, however, was confirmed. Some cells contained more than one inclusion body. They appeared round or oval with a single membrane and with a granular proteinlike content. Many inclusions, however, were only partly filled or almost empty. Inclusions were regularly located close to and compressing the nuclei into a crescent shape. The compressed nuclei showed a marked condensation of the chromatin but with areas of less electrone density in which varying patterns of granular and fibrillar components were present. In these areas were also regularly observed oval or elongated structures with an average diameter of 40 - 50 nm. Cells either revealed dispersed cytoplasmic organelles or a condensation of the cytoplasm with an increased electron density. A constant feature was clumping of tonofilaments and inter- and intracellular oedema.

A Fusobacterium necrophorum infection was histologically and/or bacteriologically establis-

Table 1. Pathological findings and bacterial infections.

No.	Sex	Age	Diagnosis	Bacterial infection
1	♀	8 months	Necrotizing gingivitis Alveolar cell pneumonia Purulent pleuritis	Beta-haemolyzing streptococci (gingiva) Coli (lungs)
2	♂	8 months	Sequestration of hoofbone Sepsis	*Corynebacterium pyogenes* (hoof) Coli
3	♀	6 years	Inanition. Ulcerative stomatitis. Vesicle formation, intracytoplasmic inclusion bodies.	Coli (whole case)
4	♀	6 years	Ulcerative necrotizing glossitis and gingivitis. Vesicle formation, intracytoplasmic inclusion bodies.	*Fusobacterium necrophorum* (gingiva, tongue) (by histology) Non-haemolyzing streptococci (lung, spleen)
5	♂	8 months	Inanition	— — —
6	♀	5 - 6 years	Purulent necrotizing glossitis. Vesicle formation, intracytoplasmic inclusion bodies. Purulent necrotizing pleuropneumonia	*Corynebacterium pyogenes* (tongue) Coli (lung, liver, spleen)
7	♀	10 months	Necrotizing pleuropneumonia and pericarditis	*Fusobacterium necrophorum* (lung) (by histology and bacteriology)
8	o	2 years	Necrotizing stomatitis and glossitis Vesicle formation, intracytoplasmic inclusing bodies. Necrotizing ruminitis.	*Fusobacterium necrophorum* (mouth and rumen) (by histology and bacteriology)

hed in three of the four reindeer with inclusion bodies.

The result of the *serosurvey* is shown in Table 2. Only a few mild reactions against the IBR, Pi3 and *Chlamydia* antigens were recognized.

Discussion

In reindeer mouth lesions, not seldom infected with *Fusobacterium necrophorum,* has been observed several times in connection with supplementary feeding (Rehbinder and Nordkvist, 1983), while outbreaks of foot rot, which earlier were rather common (Horne, 1897; Nordkvist, 1966; Skjenneberg and Slagsvold, 1968), today are rare (Rehbinder and Nordkvist, 1983).

In the majority of the cases autopsied (five out of eight) mouth lesions (glossitis, gingivitis and stomatitis) were found and of these two were infected with *F. necrophorum* (Table 1). One of the remaining animals had died from a necrotizing pleuropneumonia and a pericarditis caused by *F. necrophorum.* The entrance port of the infection could not be determined. Of the additional two animals one died from sepsis emanating from a hoof lesion infected by C.

Table 2. Results of serological investigation

Herd	Animal no.	Sex	Age	BVD		Pi 3		IBR		*Chlamydia*	
				3/3	17/4	3/3	17/4	3/3	17/4	3/3	17/4
Hedenäset	1	♀	ad	<5	<5	<8	<8	0	0	0	0
	2	♀	ad	<5	<5	<8	16	0	0	4	0
	3	♂	ad	<5	<5	8	<8	0	0	8	0
	4	♀	ad	<5	<5	<8	<8	0	0	0	2
	5	♂	ad	<5	<5	<8	<8	0	0	0	2
	6	♂	ad	<5	<5	8	16	8	16	0	0
	7	♀	22 m	<5	<5	8	16	0	0	16	2
	8	♀	10 m	<5	<5	<8	<8	0	0	4	0
	9	♀	10 m	<5	<5	16	16	0	0	4	0
Övertorneå I	10*	♀	ad	<5	<5	<8	<8	0	0	0	2
	11*	♀	22 m	<5	<5	16	16	0	0	0	0
	12*	♀	ad	<5	<5	8	8	0	0	0	0
Männikkö	13	♀	ad	<5	<5	16	16	0	0	2	0
	14	♀	10 m	<5	<5	8	8	0	0	0	0
	15	♂	10 m	<5	—	<8	—	0	—	0	—
	16	♀	ad	<5	<5	8	8	0	0	2	2
	17	♀	ad	<5	<5	<8	<8	0	0	0	8
	18	♀	ad	<5	<5	16	16	0	0	0	0
	19	♀	10 m	<5	<5	<8	<8	0	0	0	0
	20	♀	ad	<5	<5	<8	<8	4	4	8	0
	21	♀	ad	<5	<5	8	16	0	0	0	0
	22	♀	ad	<5	<5	<8	<8	0	0	0	4
Övertorneå II	23*	♀	ad	<5	<5	0	<8	0	0	0	0
	24	♀	ad	<5	<5	8	8	0	0	0	0
	25	♀	ad	<5	<5	8	8	4	8	2	0
	26*	♀	ad	<5	<5	16	16	0	0	0	0

ad = adult.
m = months.
* = has shown clinical signs of disease.

pyogenes while the other died from inanition most probably due to indigestion. Thus the main findings in the autopsied animals are the epithelial lesions of the oral cavity. The histological and electron microscopical investigations may be indicative of a virus infection but the micrographs, however, did not reveal any virus particles.

As the material, concerning all cases, was obtained a considerable time after the death of the animal no conclusive alterations but for intracytoplasmic inclusions, vesicle formations and epithelial ulcers could be established.

The prevalence of antibodies against BVD-virus in reindeer has earlier been demonstrated (Elazhary *et al.*, 1981; Dietrich, 1981). None of the animals tested in this investigation had antibodies against BVD.Neither did the histological picture of the lesions found in the necropsied animals indicate infection with BVD-virus.

Some animals had a low antibody titre against Pi3-virus (Table 2) but the oral lesions found in the necropsied animals cannot be connected with this disease.

In Finnish reindeer Ek-Kommonen *et al.* (1982) found a high frequency of antibodies against IBR and Dietrich (1981) reports on similar results from Alaska. According to Ek-Kommonen *et al.* (1982) the presence of a closely related cross-reacting herpes-virus cannot be excluded.

Antibodies against *Chlamydia* has been reported in Finnish reindeer (Neuvonen, 1976). Its significance for the health of reindeer has not been established. Of the animals tested eight were considered mildly positive. The morphology of the oral lesions did not, however, indicate any *Chlamydia* infection.

It seems apparent that none of the serologically investigated agents are responsible for the epithelial lesions found in the oral cavity of five out of eight animals necropsied. The histopathological and electron microscopical investigations rather indicate some similarities with pox-virus infections (Crandell and Grosser, 1974; Fenner, 1979; Pospischil and Bachman, 1979).

Already in 1897 Horne described the entity of «foot rot» in reindeer as often producing two different diseases at the same time, one affecting the hoof and the other affecting the oral cavity. Also Skjenneberg and Slagsvold (1968) reports on a mouth disease which can be quite reminiscent of calf diphteria.

Principally, any lesion of the oral mucosa whether caused by traumata, foreign bodies, parasites or a primary infection may give different wound bacteria the opportunity of penetrating into the submucosa and underlying tissues. Thus the varying pattern of the mouth lesions may depend on the type of the secondarily invading bacteria.

The possibility of a primary virus infection, as indicated in this paper, may explain the rapid spread of mouth lesions in herds of reindeer as reported by Horne (1897), Nordkvist (1966) and Skjenneberg and Slagsvold (1968) and observed in this investigation. Attempts to isolate a virus have, however, not yet been performed.

Fig. 1. Tongue of reindeer. Note numerous vesicles (V) and oedema HEx70

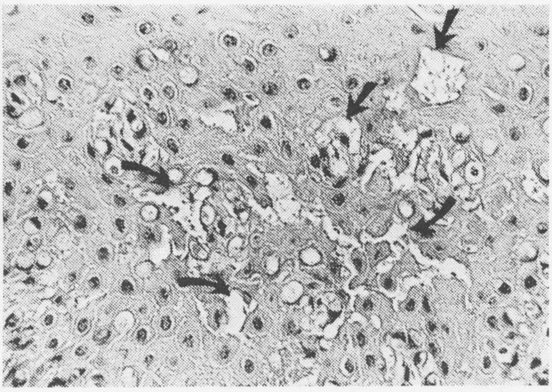

Fig. 2. Tongue of reindeer. Note vesicle formation (arrows) HEx280

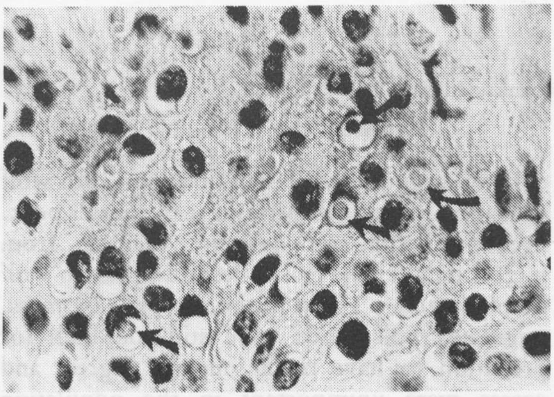

Fig. 3. Lip of reindeer. Note numerous intracytoplasmic inclusion bodies (arrows) HEx1000

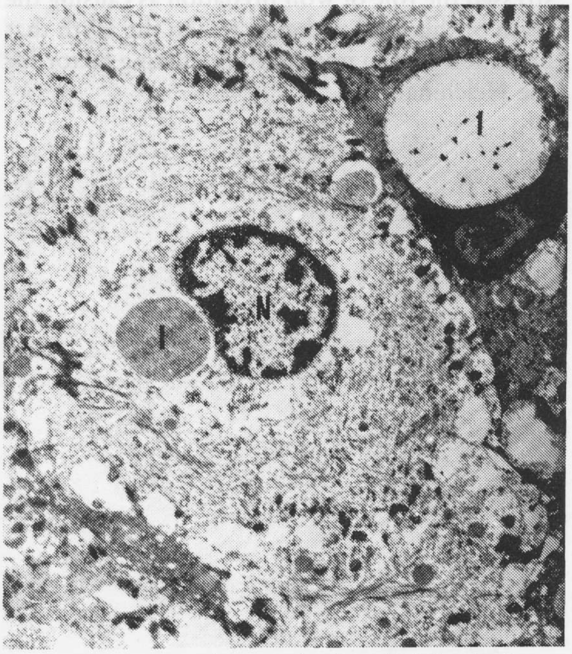

Fig. 4. Electron micrograph of epithelial cells from tongue of reindeer. Note inclusion bodies (I) and compressed nuclei (N) x6000

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Wolf predation on caribou: The myth of the Nelchina herd.

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Rangifer, Special Issue No. 1, 1986: 374

The Nelchina caribou (*Rangifer tarandus*) herd of southcentral Alaska erupted, crashed, and increased again during the period 1950 to 1981 (see: Van Ballenberghe, V. 1985. — Wolf predation on caribou: The Nelchina herd case history. *J. Wildlife Management 49: 711 - 720).* Annual survival of calves, an important determinant of population trends, was high during periods of increase but low when the herd peaked and during some years of the decline. Poor survival of calves and adults, the former related to winter severity, the latter due to hunting mortality, contributed importantly to the decline. It is unlikely that wolf (*Canis lupus*) control triggered the eruption nor did wolf predation reduce calf survival at the herd's peak. Predation did not prevent caribou from increasing after the crash; despite a peak in wolf numbers and a 3-fold decline in prey biomass, ungulate: wolf ratios were still too high for predation to have much impact. Ingress and egress were unimportant in the population dynamics of this herd. Previous publications stressed the role of wolf predation as causing the crash of this herd and gave rise to the myth that predation was an important regulating factor for the Nelchina Herd.

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