



Sex, age, condition and tooth wear of harvested caribou *Rangifer tarandus groenlandicus* in west Greenland, 1995–1998

Authors: Loison, Anne, Cuyler, L. Christine, Linnell, John D.C., and Landa, Arild

Source: *Wildlife Biology*, 7(4) : 263-273

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2001.031>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Sex, age, condition and tooth wear of harvested caribou *Rangifer tarandus groenlandicus* in west Greenland, 1995-1998

Anne Loison, L. Christine Cuyler, John D.C. Linnell & Arild Landa

Loison, A., Cuyler, L.C., Linnell, J.D.C. & Landa, A. 2001: Sex, age, condition and tooth wear of harvested caribou *Rangifer tarandus groenlandicus* in west Greenland, 1995-1998. - *Wildl. Biol.* 7: 263-273.

Managing ungulate populations in a sustainable way requires monitoring plans to provide useful information about population status and trend. Our aim is to evaluate the use of hunters to collect information about the status of caribou *Rangifer tarandus groenlandicus* in Greenland. Caribou have been harvested under a quota system since 1995 in four regions of west Greenland. In each year, hunters were asked to return information on the sex, approximate age and body condition of animals harvested, and lower jawbones were collected from animals shot in 1995. The harvest is strongly sex-biased (90:10) towards males. Jawbone length did not vary among regions. Age-specific tooth wear was, however, most pronounced in the northern region (Sisimiut-Kangerlussuaq), probably due to the nature of the substrate in the area. The condition of animals, based on a rump-fat index, appears to be good over all west Greenland, with some slight but consistent differences between regions. We conclude that information provided by hunters will be useful in monitoring the caribou populations, but validation of their information is required.

Key words: body-condition, caribou, harvest, *Rangifer tarandus*, tooth wear

Anne Loison* & John D.C. Linnell, Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway
L. Christine Cuyler & Arild Landa, Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland

*Present address: UMR CNRS 5558, Biométrie et Biologie Evolutive, Université Lyon 1, F-69622 Villeurbanne cedex, France - e-mail: loison@biomserv.univ-lyon1.fr

Received 13 December 1999, accepted 17 July 2000

Associate Editor: Heikki Henttonen

Caribou *Rangifer tarandus groenlandicus* in western Greenland is an important game species both for recreational and professional hunters, and as such of both economic and cultural importance (Kapel & Petersen 1982), although it has not received as much attention as the marine mammals (Caulfield 1997). The size of Greenland's caribou populations have fluctuated widely during historic times, although it is uncertain what roles climate, resource-limitation and possible overharvest have played (Vibe 1967, Roby, Thing & Brink

1984, Meldgaard 1986). Following two years of protection (1993-1994), a quota-regulated harvest began in 1995. Against the background of these historic population fluctuations, the poor base of scientific knowledge (Linnell, Cuyler, Loison, Møller Lund, Motzfeldt & Landa 1999), and the intrinsic difficulties of surveying and monitoring caribou in wilderness areas (Thomas 1998), it has been very difficult to make harvest-quota recommendations. In order to improve the state of knowledge about these caribou populations it is neces-

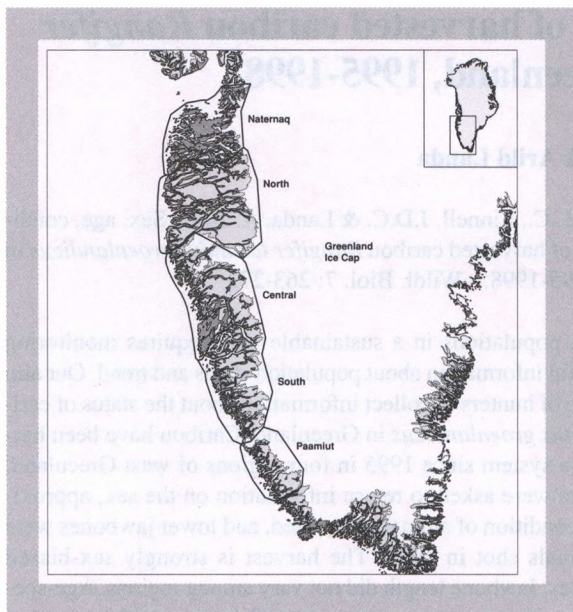


Figure 1. Location of the North, Central, South and Paamiut regions in western Greenland.

sary to utilise information from all sources. In some other countries information provided by hunters provides a valuable source of data to assist in monitoring wild ungulate populations (e.g. Jordhøy, Strand, Skogland, Gaare & Holmstrøm 1997, Solberg & Sæther 1999). In this paper we examine the value of information returned by the caribou hunters in west Greenland during the first four years of quota-regulated harvest.

Monitoring the condition and size of individuals in a population is a potential tool for assessing the relationship between the population and its environment. Decreasing condition of individuals may indicate high population density or unfavourable environmental conditions during some years (Skogland 1985, Kojola & Helle 1996). In order to improve the status of knowledge concerning individual condition and harvesting patterns for caribou in west Greenland, information on harvested animals has been collected since 1995. During these years, hunters reported the sex, the estimated age, the estimated condition and the location of all caribou killed. In addition, in 1995, lower jawbones were collected for measurement of precise age and tooth wear. Using this information, we analysed the sex and age structure of the harvest and compared the size and condition of the caribou in different regions of west Greenland. We evaluated the value of using information provided by hunters as a tool for monitoring the age, sex and condition of individuals in the harvest, and discuss the long-term sustainability of the current hunting strategy.

Study areas

The range of caribou in western Greenland has been separated into the following five, geographically distinct, management regions (see map, Fig. 1):

- **Naternaq (68–69°N):** This population lies north of Nordre Strømfjord. Because of very low caribou density there is no harvest in the region.
- **North (66–68°N; ca 24,000 km²):** Formerly referred to as the Sisimiut-Kangerlussuag herd, this population is found between Nordre Strømfjord and Søndre Strømfjord and in Angujartorfiup Nunaa.
- **Central (64–66°N; ca 13,000 km²):** This population is bounded by Godthåb fjord in the south and the Sukkertoppen glacier to the north.
- **South (62°30'–64°N; ca 10,000 km²):** This population is bounded by Buksefjord in the north and Fredrikshåb Isblink glacier to the south.
- **Paamiut (62°N; ca 3,000 km²):** This small population occurs east and south of the town of Paamiut.

All populations were surveyed from aircraft using a strip-transect method between 1993 and 1996 (Greenland Institute for Natural Resources, unpubl. data). Because the 1996 survey was the most complete, we used figures from this year for comparing the relative distribution of caribou between regions, with the exception of the Paamiut region where we used the results from the 1995 survey. Although all populations are within the low-arctic zone, local climate varies along north-south and coast-inland gradients, with coastal, and more southerly areas receiving more precipitation (ca 800 vs 200 mm per year) and less extreme temperatures than northern, and more inland areas (Böcher & Petersen 1997). Because the area of ice-free land is so broad in the North region, the inland areas of this region are especially dry. This, together with periodic, dry föhn winds, results in a layer of fine sand/dust which covers the ground and vegetation and is potentially abrasive to caribou teeth. No potential predators of caribou are found in west Greenland (Dawes, Elander & Ericson 1986).

Caribou were harvested during a short season every

Table 1. Age and rump-fat thickness as reported by hunters were converted into categories for use in the analysis.

Category	Reported fat (cm)	Reported age (years)
0		<1
1	<1	1
2	1–2	2–3
3	2–3	≥4
4	3–4	
5	≥4	

autumn from mid-August to mid-September. During the period 1995-1998, the quota was not specific to region or age/sex, so hunters were free to take whatever category they chose anywhere in the four regions, with the exception of 1995 when hunters were not allowed to kill females.

Material and methods

For all years since quota hunting opened in 1995, hunters have been asked to report the location of death, the sex, the thickness of the rump fat, and an estimated age for all caribou shot. Age and rump-fat thickness were then classified into six categories (0-5; Table 1). In 1995, hunters also sent the lower jawbones of the caribou they shot to the Greenland Institute for Natural Resources. These animals were aged using the cementum layers in incisor i_1 (Reimers & Nordby 1968). The total mandible length, the diastema length, and the length of the posterior and anterior part of the mandible, were measured with digital callipers to the nearest mm. The height of the incisor i_1 was measured as an index of tooth wear.

For each year, we calculated the percentage of females in the harvest and the percentage of animals shot in each region. The latter statistic may not be fully representative of the real geographical distribution of the harvest because not all hunters completely filled out their report cards, and 10-20% did not submit any report cards at all. When an animal was reported without information about its location of death (around 10% each year), we attributed the animal to the region in which

the hunter lived. When the sex of the animal was missing, we did not include it in the analysis.

From 1996 to 1998, we could only analyse the age distribution based on the age classes reported by the hunters. For each year, we calculated the proportion of the harvest in each age class, for all regions combined, for each sex, and for males (not enough females were shot to provide equivalent data). We also calculated the proportion of the harvest by year and region. In 1995, we could calculate a more accurate age distribution of the harvest based on precise tooth age determination. Based on this accurate age determination, we compared the age estimated by hunters to the actual age by calculating the percentage of animals misclassified by hunters for each age class.

The age distribution in the harvest can be used to estimate, under some restrictive assumptions, the annual mortality rate. The assumptions are: 1) that the population has a stable age distribution and is neither increasing nor decreasing, 2) that there is no hunter selection for any criteria correlated to age, and 3) that mortality rates are not age dependent. The survival rate can then be deduced from the slope of the linear regression of the logarithm of the proportion in each age class against age (Caughley 1977).

For each year and sex, we analysed the fat index according to region and age class, using ANOVAs when age class was considered as categorical, or ANCOVAs when age class was considered as continuous. Then, we also tested for differences between sexes and years. We did not include age class 0 (calf) in the analyses because of the very low number of calves harvested (less than 1%).

Table 2. Number of harvested caribou reported by region and sex from 1995 to 1998, and percentage of females in the harvest. The sum of the number of males and females does not equal the number in the column 'Total' because some hunters' reports did not indicate the sex of the animal. Similarly, the sum of the region total does not always equal the total of a given year, because sometimes neither the location of death nor the the municipality in which the hunter lived were indicated.

Year	Region	Total	%Region	Male	Female	% Females
1995	North	319	25.4	290	16	5.2
	Central	547	43.6	501	30	5.6
	South	362	28.8	321	29	8.3
	Paamiut	27	2.2	21	2	8.7
	Total	1314		1135	77	6.4
1996	North	841	42.2	766	68	8.2
	Central	390	19.5	350	27	7.2
	South	623	31.2	534	82	13.3
	Paamiut	141	7.1	107	31	22.5
	Total	1995		1757	208	10.6
1997	North	1086	44.0	997	80	7.4
	Central	643	26.1	601	42	6.5
	South	573	23.2	489	64	11.6
	Paamiut	164	7.7	140	21	13.0
	Total	2472		2227	207	8.5
1998	North	1264	42.6	1123	80	6.0
	Central	730	24.6	639	36	5.3
	South	758	25.5	642	69	9.7
	Paamiut	214	7.2	148	33	18.2
	Total	2966		2552	218	7.9

Table 3. Age distribution of females and males, calves and yearlings excluded, as determined from incisor cementum layers (Real) and as estimated by the hunters (Estimated). The totals are lower in the 'Real' age columns, because some yearlings were mistakenly classified in age class 2 (two and three years of age) by hunters. The percentage of individuals misclassified is indicated for each age class.

Age class	Females			Males		
	Real	Estimated	Error	Real	Estimated	Error
2 (2-3 years of age)	21	17	30%	327	186	29%
3 (≥ 4 years of age)	12	16	56%	191	337	58%
Total	32	33		518	523	

A series of strip-transect aerial censuses of all four regions were made between 1993 and 1996 (Greenland Institute for Natural Resources, unpubl. data). These were used to determine the relative distribution of caribou between the four regions, and indicated that in 1996, the total size of the west Greenland population was in the order of 22,000 caribou (95% confidence intervals: 19,500-25,000).

Results

Spatial distribution of hunting

From 1995 to 1998, the geographic distribution of the harvest has been stable among regions, with the highest proportion of animals harvested in the North region (about 45%), followed by the Central and South regions (about 25% each), and finally a smaller proportion (<10%) in the Paamiut region (Table 2). The aerial surveys from 1996 (Greenland Institute for Natural Resources, unpubl. data) indicated that the relative availability of caribou was 48, 29, 21 and 2% in the North, Central, South and Paamiut regions, respectively. Although there were no major discrepancies in the relative ranking of the regions with respect to the distribution of the animals and the distribution of the harvest, the hunting pressure in the Paamiut region was relatively high for a population which probably consists of <1,000 animals (Greenland Institute for Natural Resources, unpubl. data).

Sex and age structure in 1995 and associated mortality estimates

The distribution of the tooth ages and ages estimated by hunters differed both in males and females (Table

3). Hunters misclassified nearly 30% of age class 2 males and nearly 60% of age class 3 males. The misclassified age class 2 males were actually older than three years of age but had nevertheless been mistaken for young males, whereas 60% of the males thought to be four years old and older by hunters were actually 3 years old and younger. In females, misclassifications were of the same order with 30% and 56% of the females misclassified in age class 2 and age class 3, respectively. Therefore, the age estimated by hunters can only be taken as a rough estimate.

The real age structure of males in 1995 was significantly different from the age structure based on hunter estimates from 1996 to 1998 (comparing age classes 2 and 3: $\chi^2 = 19.12$, $df = 1$, $P < 0.001$). Assuming that age structure in the living male segment of the population was similar in 1995 and 1996-1998 (Figs. 2, 3), this suggests that hunters tended to misclassify males of age class 2 into age class 3 and vice versa in 1996-1998 as well (Table 4). For females, the age structure estimated by hunters in 1996-1998 did not differ significantly from the real age structure from 1995 ($\chi^2 = 1.15$, $df = 1$, $P = 0.283$).

The age distribution of the numbers of males and females harvested indicated a relatively smooth exponential decrease of the proportion of animals in each age class. This was confirmed when plotting the logarithm of the proportion of culled individuals against age as the relationship obtained was well described by a linear relationship (Fig. 4). This relationship did not differ between regions ($F_{2,5} = 0.048$, $P = 0.953$). The slope for all regions combined differed between sexes (interaction between sex and age: $F_{1,35} = 13.994$, $P = 0.001$) whereas the intercept did not (main sex effect: $F_{1,35} = 2.196$, $P = 0.109$), indicating that the proportion

Table 4. Total number of animals aged, calves and yearlings excluded, and the percentage classified as age class 2 (2-4 years of age) and age class 3 (>4 years of age) in 1995 versus 1996-1998 combined. The ageing in 1995 is based on incisor cementum layers, whereas it was based on the hunters' own estimates for 1996-1998. Totals are made for the North, Central and South regions combined.

Age class	Females		Males	
	1995	1996-1998	1995	1996-1998
2 (2-3 years of age)	70.0	77.4	60.8	51.2
3 (≥ 4 years of age)	30.0	22.6	39.2	48.8
Total	40	465	594	5480

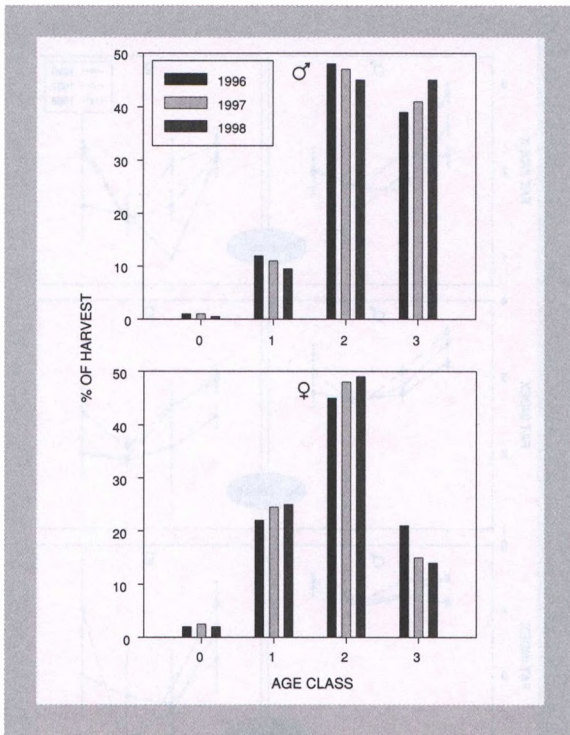


Figure 2. Percentage of the total harvest in the age classes 0-3 (as estimated by hunters) according to sex and year for 1996-1998.

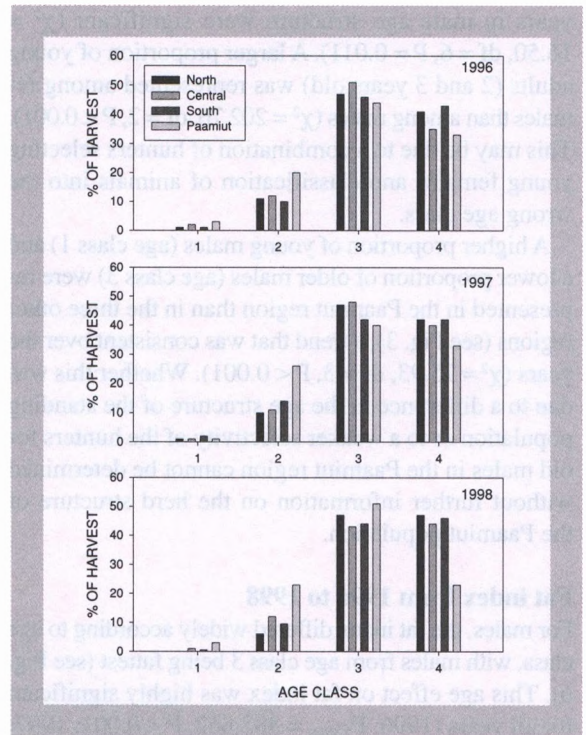


Figure 3. Percentage of males in the age classes 0-3 (as estimated by hunters) according to region and year for 1996-98.

of 2-year-old females and males was the same, but that subsequent mortality rates differed. The slope was 0.417 ± 0.058 for males, giving an estimate of annual survival rate of 0.66, with a 95% confidence interval of 0.61-0.75. This means that, if the assumptions were fulfilled, an average of 34% (95% CI: 26-39%) of males between 2 and 13 years of age died each year, either from the hunt or from natural causes. For females, the slope was -0.198 ± 0.051 (all regions combined), giving an annual survival rate of 0.82 with a 95% confidence interval of 0.71-0.91. Under the same assumptions as for males, an average of 18% (95% CI: 10-29%) of females between 2 and 10 years of age die each year.

Sex and age structure from 1996 to 1998

The sex structure in the harvest was strongly biased towards males in all regions and for all years, although hunters in the South region and especially in the Paamiut region tended to shoot a significantly higher proportion of females than hunters in other regions ($\chi^2 = 95.56$, $df = 3$, $P < 0.001$; see Table 2).

The age structure for the female segment of the harvest showed no significant differences between years ($\chi^2 = 1.01$, $df = 6$, $P = 0.985$), with most animals belonging to age classes 2 and 3 (≥ 2 years old; see Fig. 2). Given the large sample size, the differences between

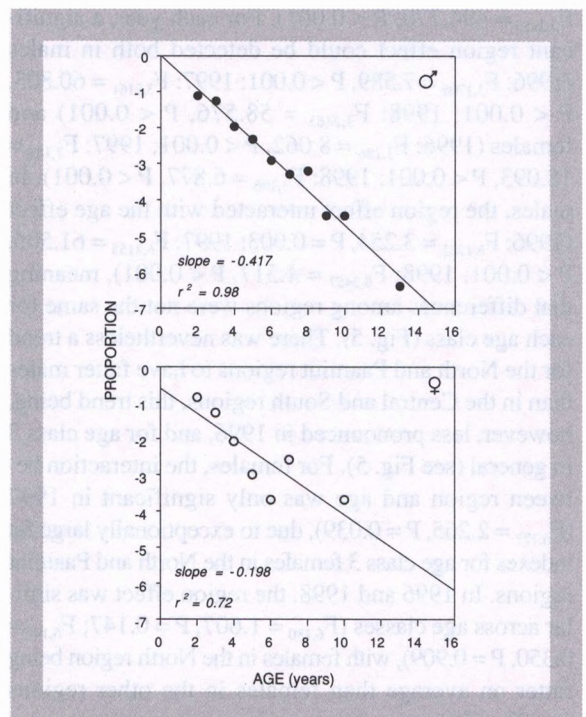


Figure 4. Proportion (ln-transformed) of harvested males and females according to age (based on cementum annuli in incisors), in 1995 for all regions combined. Regression lines between the ln-transformed proportion and age are shown.

years in male age structure were significant ($\chi^2 = 16.50$, $df = 6$, $P = 0.011$). A larger proportion of young adults (2 and 3 years old) was represented among females than among males ($\chi^2 = 202.76$, $df = 2$, $P < 0.001$). This may be due to a combination of hunters selecting young females and classification of animals into the wrong age class.

A higher proportion of young males (age class 1) and a lower proportion of older males (age class 3) were represented in the Paamiut region than in the three other regions (see Fig. 3), a trend that was consistent over the years ($\chi^2 = 75.93$, $df = 3$, $P < 0.001$). Whether this was due to a difference in the age structure of the standing population or to a weaker selectivity of the hunters for old males in the Paamiut region cannot be determined without further information on the herd structure of the Paamiut population.

Fat index from 1996 to 1998

For males, the fat index differed widely according to age class, with males from age class 3 being fattest (see Fig. 6). This age effect on fat index was highly significant for all years (1996: $F_{2,1708} = 382.662$, $P < 0.001$; 1997: $F_{2,2155} = 494.770$, $P < 0.001$; 1998: $F_{2,2457} = 512.808$, $P < 0.001$). The same results hold for females (1996: $F_{2,187} = 6.051$, $P = 0.003$; 1997: $F_{2,177} = 8.113$, $P < 0.001$; 1998: $F_{2,2155} = 494.770$, $P < 0.001$). For each year, a significant region effect could be detected both in males (1996: $F_{3,1708} = 7.589$, $P < 0.001$; 1997: $F_{3,2161} = 60.803$, $P < 0.001$; 1998: $F_{3,2463} = 58.576$, $P < 0.001$) and females (1996: $F_{3,186} = 8.062$, $P < 0.001$; 1997: $F_{3,183} = 18.093$, $P < 0.001$; 1998: $F_{3,196} = 6.877$, $P < 0.001$). In males, the region effect interacted with the age effect (1996: $F_{6,1702} = 3.254$, $P = 0.003$; 1997: $F_{6,2155} = 61.505$, $P < 0.001$; 1998: $F_{6,2457} = 4.517$, $P < 0.001$), meaning that differences among regions were not the same for each age class (Fig. 5). There was nevertheless a trend for the North and Paamiut regions to have fatter males than in the Central and South regions, this trend being, however, less pronounced in 1996, and for age class 3 in general (see Fig. 5). For females, the interaction between region and age was only significant in 1997 ($F_{6,177} = 2.265$, $P = 0.039$), due to exceptionally large fat indexes for age class 3 females in the North and Paamiut regions. In 1996 and 1998, the region effect was similar across age classes ($F_{6,180} = 1.607$, $P = 0.147$; $F_{6,190} = 0.350$, $P = 0.909$), with females in the North region being fatter on average than females in the other regions (see Fig. 5).

When testing for sex effects, accounting for age and region, we detected a strong effect of both sex (1996: $F_{1,1894} = 99.408$, $P < 0.001$; 1997: $F_{1,2344} = 58.853$, $P <$

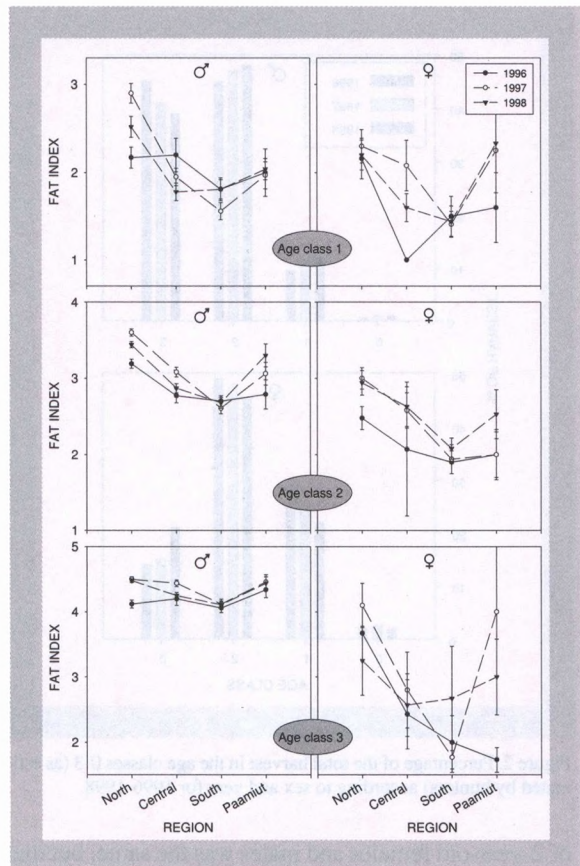


Figure 5. Mean fat index (\pm SE) for males and females according to age class and region (as estimated by hunters) for each of the years 1996–1998.

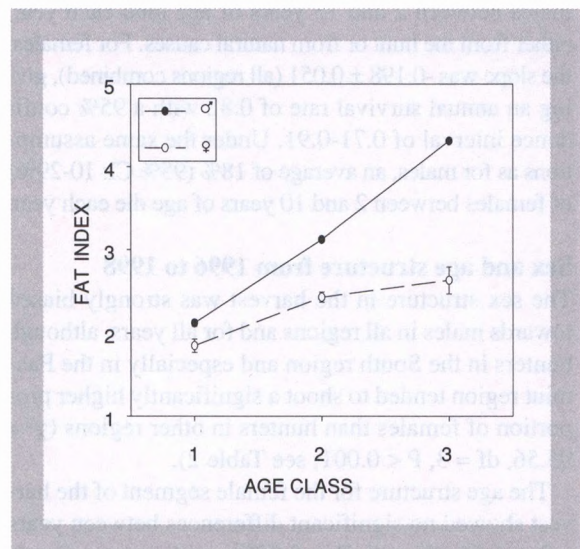


Figure 6. Mean fat index (\pm SE) for males and females according to age class (as estimated by hunters) for all regions combined during 1996–1998.

0.001; 1998: $F_{1,2662} = 75.777$, $P < 0.001$) and interaction between sex and age (1996: $F_{2,1894} = 13.383$, $P < 0.001$; 1997: $F_{2,2344} = 11.999$, $P < 0.001$; 1998: $F_{2,2662} = 14.383$, $P < 0.001$), showing that females had a lower fat index than males, and that this difference increased with age (Fig. 6). The mean difference between sexes, when accounting for year and region effect, was 0.246 ± 0.097 for age class 1, 0.657 ± 0.059 for age class 2 and 1.617 ± 0.106 for age class 3.

We then tested for year effects across age classes, regions and sex. The year effect was highly significant in both sexes (males: $F_{2,5766} = 10.207$, $P < 0.001$; females: $F_{2,517} = 5.411$, $F = 0.005$) with a significant interaction between region and year for males ($F_{6,5766} = 5.672$, $P < 0.001$; see Fig. 5) (e.g. there is no year effect in the South region for age class 2 whereas for all other regions, males in age class 2 had a lower fat index in 1996). When accounting for sex, region and age effects, we can conclude that the fat index of 1996 was slightly lower than in the other two years (1996 vs 1998: -0.161 ± 0.031). In addition, there was a very slight tendency for animals to be fatter in 1997 than in 1998 (1997 vs 1998: 0.090 ± 0.029), however, this was not consistent over age classes and regions (see Fig. 5).

Jawbone measurements and tooth wear in 1995

Age was the only significant effect resulting from a two-way ANOVA testing for region and age effects (Region: $F_{2,523} = 1.232$, $P = 0.293$; Age: $F_{6,523} = 11.438$, $P < 0.001$). The examination of contrasts following the ANOVA of jawbone length according to age showed that no significant differences in jawbone length could be detected after males were five years old. Therefore, we grouped all males 5-years old and older into the same age class. Among adults five years old and older, the mean jawbone length was 262.09 ± 1.20 mm (Fig. 7).

The jawbone's morphology was compared among regions by examining the diastema length and the length of the posterior part of the jawbone. The diastema length increased with age, and was best predicted by a model simultaneously incorporating effects of age ($F_{1,522} = 110.629$, $P < 0.001$), jawbone length ($F_{1,522} = 1050.753$, $P < 0.001$) and region ($F_{2,522} = 15.776$, $P < 0.001$). Both age and jawbone length had positive effects on the diastema length, meaning that for a given jawbone length, the older animals have the longest diastema. The region effect showed that animals have relatively small diastema lengths in the North region compared to the Central and South regions.

The ratio of the posterior part of the jawbone to the total jawbone length can be used to illustrate the difference in jawbone proportions according to age and

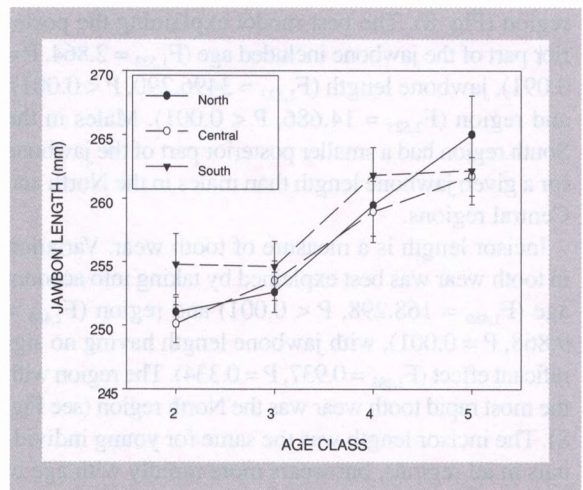


Figure 7. Male jawbone length (\pm SE; in mm) according to region and age class (based on cementum annuli in incisors) in 1995. The age classes 1-4 cover one year each, whereas age class 5 included all males >4 years old.

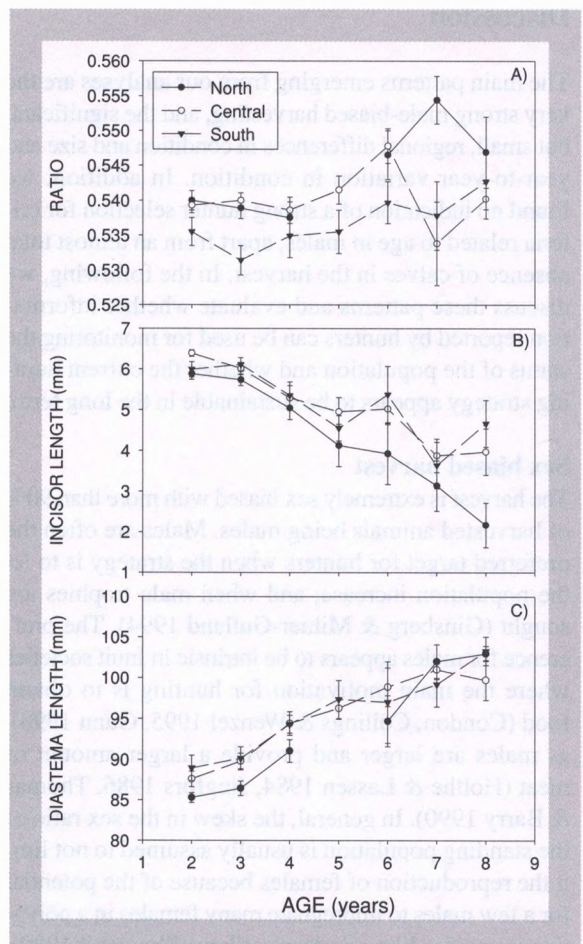


Figure 8. Ratio of the posterior length of the jawbone to the total length (A), incisor length (B) and diastema length (C) (\pm SE; in mm) according to region and age in years (based on cementum annuli in incisors) in 1995.

region (Fig. 8). The best model explaining the posterior part of the jawbone included age ($F_{1,523} = 2.864$, $P = 0.091$), jawbone length ($F_{1,523} = 3496.290$, $P < 0.001$), and region ($F_{2,523} = 14.686$, $P < 0.001$). Males in the South region had a smaller posterior part of the jawbone for a given jawbone length than males in the North and Central regions.

Incisor length is a measure of tooth wear. Variation in tooth wear was best explained by taking into account age ($F_{1,489} = 168.298$, $P < 0.001$) and region ($F_{2,489} = 9.868$, $P = 0.001$), with jawbone length having no significant effect ($F_{1,488} = 0.937$, $P = 0.334$). The region with the most rapid tooth wear was the North region (see Fig. 8). The incisor length was the same for young individuals in all regions, but wears more rapidly with age in males coming from the North region than for males coming from the Central and South regions.

Discussion

The main patterns emerging from our analyses are the very strong male-biased harvesting, and the significant, but small, regional differences in condition and size and year-to-year variation in condition. In addition, we found no indication of a strong hunter selection for criteria related to age in males, apart from an almost total absence of calves in the harvest. In the following, we discuss these patterns and evaluate whether information reported by hunters can be used for monitoring the status of the population and whether the current hunting strategy appears to be sustainable in the long term.

Sex biased harvest

The harvest is extremely sex biased with more than 90% of harvested animals being males. Males are often the preferred target for hunters when the strategy is to let the population increase, and when male trophies are sought (Ginsberg & Milner-Gulland 1994). The preference for males appears to be intrinsic in Inuit societies where the main motivation for hunting is to obtain food (Condon, Collings & Wenzel 1995, Gunn 1998), as males are larger and provide a larger amount of meat (Holthe & Lassen 1984, Jingfors 1986, Thomas & Barry 1990). In general, the skew in the sex ratio of the standing population is usually assumed to not limit the reproduction of females because of the potential for a few males to impregnate many females in a polygynous species like reindeer/caribou (Skogland 1989). In addition, for the same number of individuals harvested, the population will contain a higher proportion of females that produce a larger number of calves than if the sex

bias in the harvest was more balanced. Nevertheless, when conducted to an extreme and over the long term, a male-biased harvesting strategy may not be without costs and risks for the dynamics and genetics of a population (Ryman, Baccus, Reuterwall & Smith 1981, Ginsberg & Milner-Gulland 1994). Although the aim of the management in Greenland during the 1990s has been to allow the population to increase after an apparent low in population size, both managers and hunters are also concerned by the potential development of 'boom and crash dynamics' (Swanson & Barker 1992, Mallory & Hillis 1998). The potential for this type of dynamics is favoured by a male-biased harvest because it keeps the growth rate at a maximum for a given harvest rate. A more conservative strategy would be to harvest a higher proportion of females to keep the population growing, but at a slower rate.

Mortality patterns

The mortality rates estimated using the proportion of males and females in each age class from the sample of animals harvested in 1995 has to be interpreted with caution as it is based on the assumption that the population and age structure are stable. The populations may have been in an increasing phase in the mid-1990s. If this is the case, the result is an overestimation of mortality rates. However, it was interesting to find that the plot of the logarithm of the proportion of males harvested per age class against age was so linear. This suggests that there is no selection for any specific age category of males. This is not conclusive as a linear trend could also be produced if hunter selection increased proportionally to age. More information about mortality patterns and population dynamics based on independent data are required to further interpret these results.

The age estimated by hunters can only be taken as a rough estimate of age, especially in the case of females. Males can be categorised relatively more easily than females into broad age categories because they have antlers that increase in size with age. Nevertheless, both body growth and antler growth are very variable among individuals of the same age. By comparing the age distribution estimated by hunters with the actual ages in 1995, it appeared that hunters tended to overestimate the age of males. Males categorised in the oldest age class were also the biggest (i.e. had the thickest rump-fat layer), which supports the hypothesis that animal size is a criteria used by hunters to estimate age. Thus, young males in good condition, probably carrying relatively large antlers for their age class, are susceptible to be misclassified as 'old' males (age class 3, males >4 years of age). Further investigation will have to be conducted to

better evaluate how hunters classify animals into different age categories, and extra criteria will have to be developed to increase the value of the data they provide.

Tooth wear and jawbone length

Tooth wear as measured by the height of the incisor appeared to be well correlated to age in a linear fashion, a result found earlier in caribou from North America (Miller 1974) and for molar height in Norwegian wild reindeer (Skogland 1988). These measurements might be useful for classifying animals into age classes, although the height of the incisor may not be the best measure to indicate age changes. Miller (1974) showed that the third premolar and the first molar were the best teeth to correlate with age. Any tooth measurement would nevertheless have to be calibrated for each region, and periodic re-calibration would be required to correct for temporal changes in age-specific tooth wear. There was a clear regional difference in the rate of decline in incisor height. This may either be due to different food quality (Skogland 1988) or to the nature of the substrate in each region. In the North region, where tooth wear was faster, a layer of fine sand and dust covers vegetation and is therefore chewed along with forage. Skogland (1988) showed by comparing two Norwegian populations that more rapid tooth wear was associated with higher density, lower quality of winter forage, and lower individual physical condition (measured by kidney fat). In our material, there was no indication that the more rapid tooth wear in the North region was associated with a lower body condition of animals as males were actually relatively fatter than males from the other regions.

The total jawbone length did not differ among regions, but the relative proportions did, with males from the South region having a smaller posterior jaw length for the same total jaw length than males from the North and Central regions. This difference was very clear, but the implications and causes are not easy to determine.

Rump-fat index and condition

The rump-fat thickness estimated by hunters, and classified into categories *a posteriori*, appeared to capture some general patterns found in other caribou populations (Dauphiné 1976, Holthe & Lassen 1984, Crête, Huot, Nault & Patenaude 1993) in that the fat index increased with age for males and was larger for males than for females. Because the mean we studied was calculated from the fat index categories, we cannot directly transfer these numbers into centimetres. However, considering that category 1 corresponded to a fat layer of less than 1 cm, and that the following categories corresponded to increments in fat thickness of 1 cm until

category 5 that corresponded to more than 5 cm of fat, we can approximate the real fat thickness by subtracting 0.5 cm (half of the 1 cm range for category 1 to 4) from our average to obtain a rough estimate of the real fat thickness. This estimate may represent an underestimation because it assumes that animals classified in fat index category 5 had a fat thickness of 5.5 cm while it actually groups all animal having an estimated thickness of 5 cm and more. Nevertheless, we approximated the rump-fat thickness to be 2.6 cm for males 2-4 years old, 3.8 cm for older males, 1.9 cm for females 2-4 years old and 2.1 cm for older females. This is more than reported for males and females harvested in the North region during 1977-1978 (Holthe & Lassen 1984), where the mean for males >2 years of age was 2.4 cm rump fat and the mean was 0.7 cm and 1.7 cm for lactating and non-lactating females >2 years of age, respectively. Values reported for the Kaminuriak population in northern Canada (Dauphiné 1976) are of the same order of magnitude, with the mean fat layer of adult females (>2 years of age) being 1.5 cm, and the fat index of males increasing with age for males, from 1.3 cm, to 2.4 cm, 2.8 cm and 4.0 cm for males aged 2, 3, 4 and >5 years of age, respectively. The fat thickness of caribou in all regions surveyed is within the normal range of variation previously reported for caribou and indicates that animals have been in good condition throughout the sampling period (1996-1998).

Rump-fat deposits have been shown to vary seasonally in caribou (Dauphiné 1976) and to be at a maximum in September-October for both caribou males and females. Measuring the fat deposit during these months is likely to give a measure that will be the most sensitive to year-to-year and region-to-region variation. The data presented here suggested that animals had slightly less fat in 1996 and that animals from the South region have less fat than animals from other regions, although we cannot explain these differences with the current information.

Management implications and perspectives

Information contributed by hunters is increasingly being used in the monitoring of wildlife populations (Solberg & Sæther 1999). Such information is a very valuable data source which can be used in monitoring the condition of individuals and thus may contribute to management planning. The validity of this information, however, must be tested. From our analysis, we deduced that hunters often overestimated the age of hunted males. The fat index that they assessed appeared to be sensitive to expected differences in age and sex. This indicates that this information could be very useful to

monitor the condition of individuals across years and regions if continued over the long term. An evaluation of the relationship between the hunter's assessment and the real fat thickness remains to be made. The caribou population in west Greenland is probably in an increasing phase, but so far nothing indicates that the increasing density is having negative effects on their condition. The differences among regions observed in jawbone morphology and tooth wear need to be better explained, but are subtle and do not indicate large differences in condition. It was interesting to note that the most rapid tooth wear was not associated with a low fat index in the North region, a fact that challenges the commonly assumed inverse relationship between tooth wear and body condition (Skogland 1988). Actually, this emphasises the need for caution when using such an index to compare different populations. We hypothesise that within a region, the relationship between tooth wear and condition should hold. This relationship will be tested in the future.

Acknowledgements - funding for our study was provided by the Greenland Directorate for Fisheries, Hunting and Agriculture, the Greenland Institute of Natural Resources and the Norwegian Institute for Nature Research. We thank all the hunters for returning their report cards. S. Jeremiassen, L. Odgaard, M. Heim and M. Solem provided technical support with age determination and measurement of incisors and jawbones.

References

- Böcher, J. & Petersen, P.M. 1997: Greenland. - In: Wielgolaski, F.E. (Ed.); Polar and alpine tundra. Elsevier, New York, pp. 685-720.
- Caughley, G. 1977: Analysis of vertebrate populations. - John Wiley, London, pp. 234.
- Caulfield, R.A. 1997: Greenlanders, whales, and whaling: sustainability and self determination in the arctic. - University Press of New England, London, pp. 203.
- Condon, R.G., Collings, P. & Wenzel, G. 1995: The best of life: subsistence hunting, ethnicity, and economic adaptation among young adult Inuit males. - *Arctic* 48: 31-46.
- Crête, M., Huot, J., Nault, R. & Patenaude, R. 1993: Reproduction, growth and body composition of Rivière George caribou in captivity. - *Arctic* 46: 189-196.
- Dauphiné, T.C. 1976: Biology of the Kaminuriak Population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. - *Canadian Wildlife Service Report Series* 38: 1-69.
- Dawes, P.-R., Elander, M. & Ericsson, M. 1986: The wolf (*Canis lupus*) in Greenland. A historical review and present status. - *Arctic* 39: 119-132.
- Ginsberg, J.R. & Milner-Gulland, E.J. 1994: Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. - *Conservation Biology* 8: 157-166.
- Gunn, A. 1998: Caribou and muskox harvesting in the north-west territories. - In: Milner-Gulland, E.J. & Mace, R. (Eds.); Conservation of biological resources. Blackwell Science, London, pp. 314-330.
- Holthe, V. & Lassen, P. 1984: Vækst, kondition og dødelighed hos vildren (*Rangifer tarandus groenlandicus*) i Sisimiutbestanden, Vestgrønland. - *Rangifer* 4: 35-42. (In Danish).
- Jingfors, K. 1986: Inuit harvesting levels of caribou in the Kitikmeot region, Northwest Territories, Canada, 1982-1984. - *Rangifer Special Issue* 1: 167-172.
- Jordhøy, P., Strand, O., Skogland, T., Gaare, E. & Holmstrøm, F. 1997: Oppsummeringsrapport, overvåkingsprogram for hjortevilt - villreindelen 1991-95. - Norwegian Institute for Nature Research Fagrapport 22: 1-57. (In Norwegian).
- Kapel, F.O. & Petersen, R. 1982: Subsistence hunting - the Greenland case. - Reports of the International Whaling Commission Special Issue 4: 51-73.
- Kojola, I. & Helle, T. 1996: Size-related changes in winter condition of female and male reindeer calves. - *Canadian Journal of Zoology* 74: 1174-1177.
- Linnell, J.D.C., Cuyler, L.C., Loison, A., Møller Lund, P., Motzfeldt, K.G. & Landa, A. 1999: The scientific basis for managing the sustainable harvest of caribou and muskoxen in Greenland for the 21st century: an evaluation and agenda. - *Pinnngortitaleriffik, Grønlands Naturinstitut Teknisk Rapport* nr. 27, 58 pp.
- Mallory, F.F. & Hillis, T.L. 1998: Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints, releases and population dynamics. - *Rangifer Special Issue* 10: 49-60.
- Meldgaard, M. 1986: The Greenland caribou - zoogeography, taxonomy and population dynamics. *Meddelelser om Grønland*. - *Bioscience* 20: 1-88.
- Miller, F.L. 1974: Biology of the Kaminuriak population of barren-ground caribou Part 2: Dentition as an indicator of sex and age; composition and socialization of the population. - *Canadian Wildlife Service Report Series* 31: 1-88.
- Reimers, E. & Nordby, O. 1968: Relationship between age and tooth cementum layers in Norwegian reindeer. - *Journal of Wildlife Management* 32: 957-961.
- Roby, D.D., Thing, H. & Brink, K.L. 1984: History, status, and taxonomic identity of caribou (*Rangifer tarandus*) in Northwest Greenland. - *Arctic* 37: 23-30.
- Ryman, N., Baccus, R., Reuterwall, C. & Smith, M.H. 1981: Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. - *Oikos* 36: 257-266.

- Skogland, T. 1985: The effects of density dependent resource limitations on the demography of wild reindeer. - *Journal of Animal Ecology* 54: 359-374.
- Skogland, T. 1988: Tooth wear by food limitation and its life history consequences in wild reindeer. - *Oikos* 51: 238-242.
- Skogland, T. 1989: Comparative social organisation of wild reindeer in relation to food, mates and predator avoidance. - *Advances in Ethology* 29: 1-74.
- Solberg, E.J. & Sæther, B-E. 1999: Hunter observations of moose *Alces alces* as a management tool. - *Wildlife Biology* 5: 107-117.
- Swanson, J.D. & Barker, M.H.W. 1992: Assessment of Alaska reindeer populations and range conditions. - *Rangifer* 12: 33-42.
- Thomas, D. 1998: Needed: less counting of caribou and more ecology. - *Rangifer Special Issue* 10: 15-23.
- Thomas, D.C. & Barry, S.J. 1990: A life table for female barren-ground caribou in north-central Canada. - *Rangifer Special Issue* 3: 177-184.
- Vibe, C. 1967: Arctic animals in relation to climatic fluctuations. - *Meddelser om Grønland* 170: 1-227.