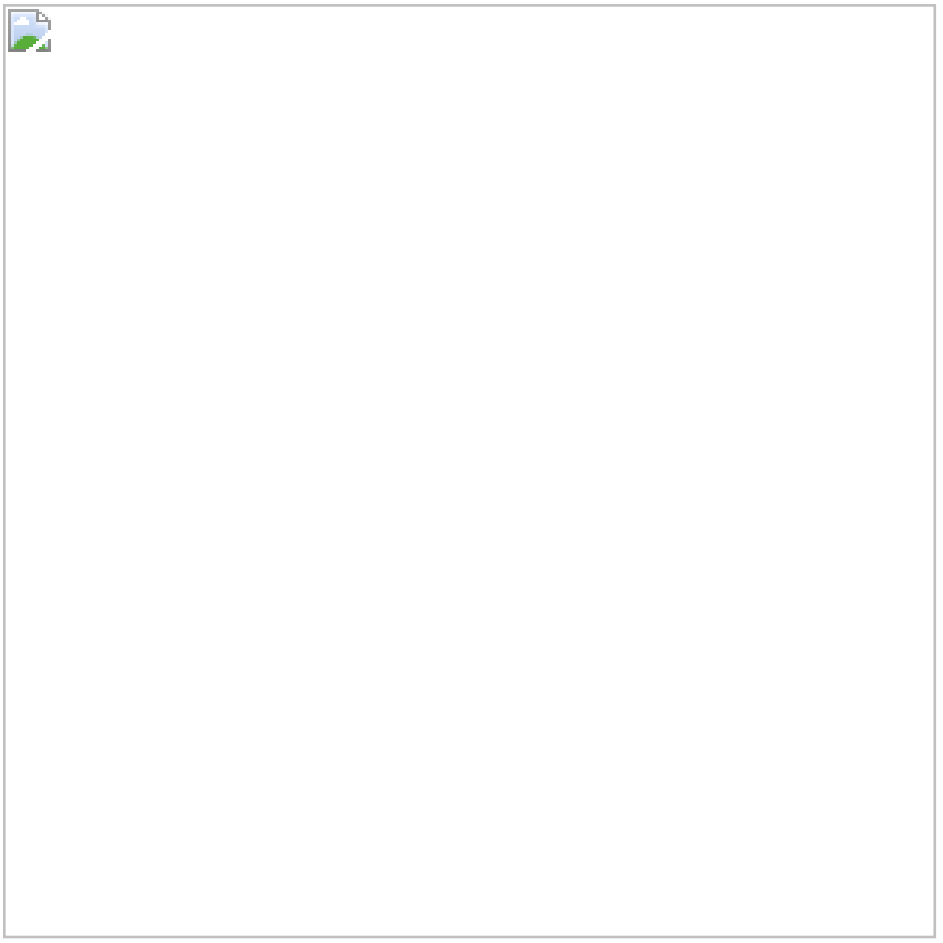

Fertility in two West Greenland caribou Rangifer tarandus groenlandicus populations during 1996/97: potential for rapid growth

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Fertility in two West Greenland caribou *Rangifer tarandus groenlandicus* populations during 1996/97: potential for rapid growth

Christine Cuyler & Jette Buch Østergaard

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Estimates of caribou *Rangifer tarandus groenlandicus* abundance in West Greenland in 2001 were much larger than estimates from the early 1990s. Two caribou populations, the Kangerlussuaq-Sisimiut of the North region and the Akia-Maniitsoq of the Central region, were examined for productivity. In total, 96 female caribou were collected in early and late winter from the subareas Kangerlussuaq and Akia, respectively. Data on reproductive status, reproductive history and animal age were collected. Maximum age observed was 15 years and mean age of death may be 12-13 years, which indicates a natural mortality of approximately 8%. Despite habitat differences in climate and vegetation, the two West Greenland caribou populations had similar pregnancy rates for mature females, i.e. ca 81% ($P = 0.93$). Likewise, mean fertility (total number of all pregnancies) for the age classes 1-10 years (age at breeding season) was not significantly different at 4.77 ± 2.38 and 4.23 ± 2.57, respectively ($P = 0.65$). Although West Greenland adult female pregnancy rates in 1996/97 were similar to those of North American caribou, the Greenland sample showed a high percentage of pregnant subadults. Further there was no significant difference between early and late winter pregnancy rates for either population. Fertility among Greenland females was excellent. Maximum potential number of pregnancies for their lifetime was attained by 25%, while 2-4% exceeded the maximum, and at the age of 10 Greenland females can be expected to have had > 7 calves. The high productivity in both populations may occur through first conception in the second autumn or twinning, both of which suggest summer forage of equal and excellent value for several years preceding this study. The potential for rapid growth in abundance of both populations was present in 1996/97 regardless of the dissimilar range characteristics.

Key words: fertility, Greenland, pregnancy, Rangifer tarandus groenlandicus, reproduction, retrospective ovarian analysis

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Until recently caribou *Rangifer tarandus groenlandicus* studies in Greenland focused on obtaining population size estimates. These estimates changed radically over the last decade. In 1993 the estimated total number of caribou in Greenland was about 9,000 animals (Ydemann & Pedersen 1999). In 2001 and several surveys later the

estimate had grown to approximately 140,000 animals (Linnell et al. 2001, Cuyler et al. 2002, 2003). Although important, estimates of animal abundance provide no answer to how or why abundance changed. Reproduction studies allow greater understanding of a population's capacity for growth, which may explain changes in animal abundance.

Two of the major caribou populations in West Greenland inhabit ranges, which differ in climate, snow cover and vegetation (Hansen 2000, Lund et al. 2000, Aastrup et al. 2001). The west coast of Greenland has a complex topography, which is generally characterised by arctic/alpine tundra habitat and climate, with plant communities and species varying with elevation and proximity to the coast or inland Greenland Ice Cap. Major differences, however, include a dry continental climate lacking fructose macro-lichens in the inland Kangerlussuaq area (Holt 1980), whereas there is greater precipitation accompanied by an abundance of lichens in the Akia area (Trapnell 1933, Hansen 2000, Aastrup et al. 2001).

To investigate fertility, we collected female caribou from two West Greenland caribou populations, i.e. the Kangerlussuaq-Sisimiut and Akia-Maniitsoq populations, in late autumn/early winter 1996 and late winter 1997. Pregnancy was ascertained by presence of foetus or *corpus luteum verum*, and fertility by retrospective analysis of ovaries. The latter provides a reproductive history of the individuals examined. Subsequent combination with individual age permits estimates of reproductive rate for the population. We compare results from the two caribou populations to each other and herds elsewhere. Given the differences in habitat, we discuss possible productivity variations between the two populations, as well as their capacities for population growth.

Material and methods

Study areas

The two study areas were: the Kangerlussuaq area in the North region (66˚-67˚30'N), and the Akia area in the Central region (64˚30'- 65˚45'N; Fig. 1). Neither wolves *Canis lupus* nor any other potential predator (Dawes et al. 1986) have existed in either region for several hundred years.

The Kangerlussuaq area borders the Greenland Ice Cap and has a dry continental steppe climate lacking fructose macro-lichens. There is little precipitation during summer or winter, and drying föhn winds are common. Mean temperatures in February and July are -22˚C and 14˚C, respectively, and annual precipitation is ca 170 mm (Haarløv et al. 1980).

The Akia area, being near the ice-free coasts and fjords, has a more maritime climate, and typically receives abundant precipitation year round. In 1996/97 extensive fructose macro-lichen of *Cladonia* and *Cetraria* spp. were present (Aastrup et al. 2001).

Study animals

Females were sampled from the Kangerlussuaq-Sisimiut and Akia-Maniitsoq caribou populations and mature adults ≥ 3 years of age were selected. A population was defined as all the animals of the same species living in a specific region, which do not mix with animals from other regions, i.e. they are reproductively isolated. We collected 25 caribou in each study area in early winter (November 1996) and again in late winter (March-April 1997), i.e. in total 100 caribou; 96 of these were females and 79 were mature females.

Age

The term, adult female, refers to animals ≥ 3 years of age. Adult age was determined by counting cementum rings from the root of the first incisor (McEwan 1963a, Reimers & Nordby 1968). Cementum is the bony substance covering the root of a tooth, lines of which are used to obtain accurate animal age. Since cementum deposition in a permanent incisor does not commence until the time of eruption, about eight months after birth, one year may be added to the number of growth rings when determining the age of the animal (McEwan

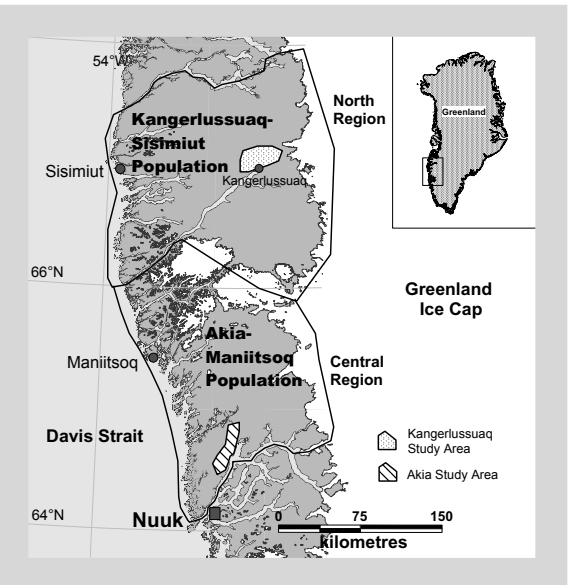

Figure 1. Location of the two West Greenland study areas within the North and Central regions with indication of the respective population.

1963a). Subadults, i.e. individuals < 3 years of age, were aged using tooth eruption.

Pregnancy rates and fertility

Ovaries were weighed, sliced longitudinally, and placed in a formaldehyde solution, which was later exchanged for a 70% alcohol solution. A retrospective analysis of ovarian activity examined for the presence or absence of the following ovarian structures as per Heggberget (1998):

- *corpus luteum verum* (CLV) - true yellow body, present during current pregnancy;
- *corpus luteum accessorium* (CLA) - true secondary yellow body, assists a current pregnancy;
- *corpus albicans* (CA) - regressing luteal structure and a relatively large discoloured mark remaining after a CLV, indicating previous pregnancies;
- *corpus albicans accessorium* (CAA) - regressing luteal structure and a small, discoloured mark remaining after a CLA, indicating an aid to a previous pregnancy.

Pregnancy rate for a population is defined as the percentage of females which were pregnant out of the total collection of females for that population. Pregnancy was identified by the presence of CLV or foetus.

The effect of time of sampling, early versus late winter, was compared with pregnancy rates within and between populations.

Maximum potential number of pregnancies for a female first conceiving as a yearling was defined as one less than the number of years she has lived (age n-1 year).

Fertility of a population is the number of live births over a time period, usually a year, e.g. the number of live births per female, or the number of female young born per female. Calculations of fertility usually employ average litter size, average number of litters produced per time interval (year) and the sex ratio at birth (Caughley 1977).

In this study, we define fertility as the realised reproduction, i.e. the number of live births per female caribou over her reproductive life span, which was cautiously defined as actual age minus one year. We assumed that the number of live births was equal to the ascertained number of pregnancies found through retrospective ovarian analysis, plus if present, a current foetus.

Statistical analysis

Significance testing and predictability were tested using Chi-squared tests, two-tailed t-tests (two sample assuming unequal variances) or linear regression analysis where applicable. When testing for relationships between pregnancy and age and/or study area, a SAS GLM analysis (PROC GLM in SAS, Type 3 Sum of Squares, SAS Institute Inc. 1990) was used to model the three independent variables (age, study area and interaction between these) versus the dependant variable, number of pregnancies.

Results

Age

The oldest caribou in our study sample from the Kangerlussuaq-Sisimiut and Akia-Maniitsoq populations were approximately 13 and 15 years old, respectively (Fig. 2). The data suggest that mean age of death was 12-13 years. The relative age distribution of the animals collected from Kangerlussuaq and Akia reveals that more young females were collected in Akia than in Kangerlussuaq. Of the 47 females collected from the Kangerlussuaq-Sisimiut population, 60% were ≥ 8 years old, whereas of the 49 females collected from the Akia-Maniitsoq population, 67% were ≤ 8 years old. Combining the autumn and winter collections, mean age was ≈ 8 years for the Kangerlussuaq-Sisimiut females (7.80 ± 3.2), while mean age was ≈ 6 years for the Akia-Maniitsoq females (6.20 ± 3.7), owing to the many subadults and young adults taken in Akia. In Akia, 13 subadults were collected, but only four were collected in Kangerlussuaq. The difference in mean age was significant ($t = 1.986$; $df = 93$; $P = 0.024$).

Pregnancy rates and fertility

Considering only adult females ≥ 3 years old, pregnancy was identified in 35 out of 43 adult cows in Kangerlussuaq and 29 out of 36 cows in Akia. Pregnancy

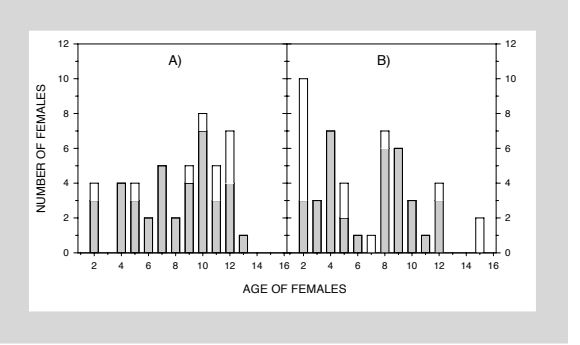

Figure 2. Numbers of pregnant (■) and non-pregnant (□) caribou females for a specific age class in the Kangerlussuaq (A) and Akia (B) populations during 1996/97.

rates for the winter of 1996/97 were 81.4% ± 0.39 for the Kangerlussuaq-Sisimiut females and 80.6% ± 0.40 for the Akia-Maniitsoq females (see Fig. 2). The difference was not significant (t = 1.9925; df = 74; P = 0.926).

For adult females in Kangerlussuaq-Sisimiut pregnancy rates were 90 and 77% in early and late winter, respectively. In Akia-Maniitsoq pregnancy rates were 77 and 88%, respectively. There was no significant difference between the proportion of pregnant females in early and late winter in either the Kangerlussuaq-Sisimiut females (χ^2 = 0.4773; df = 1; P = 0.4897 with Yates' correction) or the Akia-Maniitsoq females (χ^2 = 0.2152; df = 1; P = 0.6427 with Yates' correction). Similarly, when comparing between populations, there was no significant difference (χ^2 = 0.02325; df = 1; P = 0.8788 with Yates' correction).

In both populations pregnancy was sometimes observed in subadults; three of the four Kangerlussuaq-Sisimiut subadults collected were pregnant in contrast to six of the 13 Akia-Maniitsoq subadults sampled. If subadult females < 3 years of age were included, then the pregnancy rate was 80.9% ± 0.40 for Kangerlussuaq-Sisimiut, but decreased to 71.4% ± 0.46 for Akia-Maniitsoq. Differences were still not significant (t = 1.9858; df = 93; P = 0.283).

Maximum potential number of pregnancies was realised for 24.4% of the Kangerlussuaq-Sisimiut and 24.5% of the Akia-Maniitsoq females, while 2.2 and 4.1%, respectively, exceeded the maximum.

Fertility, expressed as the mean total number of all pregnancies for all females, was 5.76 ± 2.75 for Kangerlussuaq-Sisimiut females, which was greater than the 4.45 ± 3.41 for the Akia-Maniitsoq females (t = 1.986; df = 91; P = 0.043).

In order to make comparisons to North American caribou, fertility was also expressed as the total mean of each cohort's mean fertility, using only cohorts aged 1-10 years (age n-1 year). Then mean fertilities were 4.77 ± 2.38 for Kangerlussuaq and 4.23 ± 2.57 for Akia. The difference between the two Greenland populations was not significant (t = 2.1098, df = 17, P = 0.646).

Fertility was often close to the reproductive lifespan, which was actual age minus 1 year (Figs. 3 and 4). Fertility did not decrease with age in the Akia-Maniitsoq females. Although one 12-year old Kangerlussuaq female had pregnancies equal to her reproductive lifetime age (n-1 year), eyeballing the figures suggests that fertility may have decreased slightly for the sampled Kangerlussuaq-Sisimiut females > 8 years of age.

The positive relationship between the total number of pregnancies and age was significant (Kangerlussuaq-Sisimiut: $F_{1,43}$ = 171.71, P < 0.0001; Akia-Maniitsoq: $F_{1,47}$ = 619.36, P < 0.0001). The regressions had excellent predictive power (Kangerlussuaq-Sisimiut: r^2 = 0.80 (SE = 1.24); Akia-Maniitsoq: r^2 = 0.93 (SE = 0.92)). The respective linear regressions describing the positive relationships for all females in Kangerlussuaq-Sisimiut and Akia-Maniitsoq were:

$$y = 0.7749x + 0.1935$$
$$y = 0.8811x - 0.4059,$$

where y is the predicted number of pregnancies and x is a given female's age (n-1 year).

Modelling the three independent variables, age, study area and interaction between these, versus the dependant variable, number of pregnancies, showed an overall significant effect ($F_{3,90}$ = 233.54, P < 0.0001). The number of pregnancies revealed a significant linear increase with age ($F_{1,90}$ = 620.38, P < 0.0001). There was no significant difference between study areas ($F_{1,90}$ = 1.49, P = 0.2249) or regression line slopes ($F_{1,90}$ = 2.55, P = 0.2249).

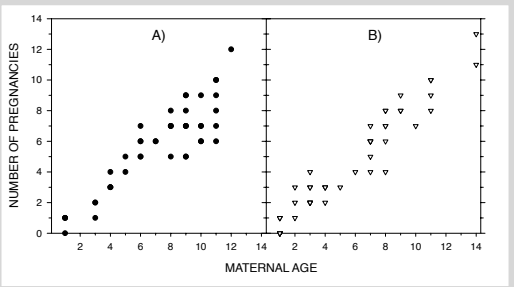

Figure 3. Fertility expressed as the number of pregnancies female^{-1} in Kangerlussuaq-Sisimiut (A) and Akia-Maniitsoq (B) females during 1996/97. Overlapping data points occur and account for the disparity in total number of points versus total number of females collected. Age is given as reproductive lifespan (age n-1 year).

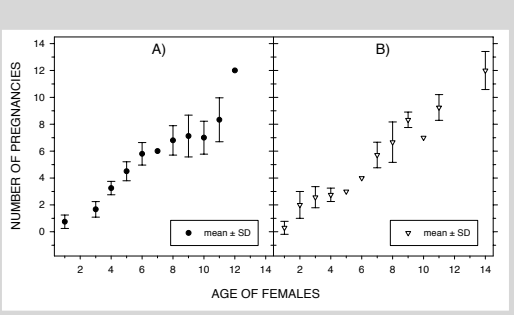

Figure 4. Fertility expressed as number of pregnancies female^{-1} (mean ± SD) within age classes in the Kangerlussuaq-Sisimiut (A) and Akia-Maniitsoq (B) females versus reproductive lifespan age (n-1 year), during 1996/97.

Table 1. Comparison of age-class specific pregnancy rates of females collected from two West Greenland and three North American caribou populations. Sample size (N) is given in parentheses.

Age at breeding season (years)	West Greenland		North America					
	Kangerlussuaq-Sisimiut	Akia-Maniitsoq	Kaminuriak[1]		Beverly[2]		Beverly[3]	Nelchina[4]
1	75 (4)	30 (10)	2	(57)	33	(3)	12 (92)	13 (31)
2	No data	100 (3)	48	(69)	50	(16)	72 (120)	61 (46)
≥ 3	81 (43)	81 (36)	90	(280)	78	(69)	85 (534)	89 (335)

[1] Dauphiné 1976; [2] McEwan 1963b; [3] Thomas & Barry 1990; [4] Skoog 1968

Discussion

Age

Although specifically mature females were desired during animal collection, a large number of subadult females were sampled. Relatively large body size, similar to adults, caused the subadult females to be mistaken for adults. The data suggest a mean age of death of 12-13 years, and a natural mortality of approximately 8%. Despite the lack of predators, longevity in Greenland was similar to that of North American caribou.

Pregnancy rates and fertility

The ca 81% pregnancy rate for mature Greenland females in the winter of 1996/97 lies in the middle of the normal range for *Rangifer tarandus*, which is 70-90% (Dauphine 1976; Table 1). The mean pregnancy rate for eight North American herds was 82% (Bergerud 1980), while that of the Porcupine herd during 1982-1992 was 80% (Fancy et al. 1994). Age-specific pregnancy rates for subadults were greater for Greenland caribou than for several North American herds, but our sample size was small. The data did not reveal possible abortion rates in the populations. Early and late winter pregnancy rates within a population did not differ significantly, nor did they differ between populations.

Although the ranges of the two West Greenland caribou populations differ dramatically, these differences were not reflected in the productivity of the two populations. Pregnancy rates and fertility did not differ significantly. Although the Kangerlussuaq-Sisimiut fertility value appeared higher than the Akia-Maniitsoq, the explanation lies in the greater number of subadults not pregnant plus the large proportion of young adults in the Akia-Maniitsoq collection. When total means of all cohorts are compared, there was no difference ($P = 0.65$). The lack of fructose macro-lichens in the dry steppe-like Kangerlussuaq area had no discernable effect on calf production.

West Greenland caribou cohorts ≤ 10 years (age n-1 year) typically had greater mean fertility than the Kaminuriak caribou from North America (Table 2). However, Greenland total mean fertility values were not significantly greater than those of Kaminuriak caribou (Kangerlussuaq-Sisimiut: $t = 2.1098$; $df = 17$; $P = 0.409$; Akia-Maniitsoq: $t = 2.1009$; $df = 18$; $P = 0.719$).

Fertility, defined as the number of actual births, was excellent in the two West Greenland caribou populations studied. Fertility often equalled and even exceeded a female's reproductive lifespan (age n-1 year). Almost 25% of the females collected achieved maximum potential number of pregnancies, while a further 2-4% exceeded the maximum. Only 19% of Kaminuriak females achieved maximum potential number of pregnancies (Dauphiné 1976) and none exceeded the maximum. Using linear regression analysis we found that the average cow aged 10 would have produced 7.2 and 7.5 calves for Kangerlussuaq and Akia, respectively. In contrast, an average North American caribou female of the Kaminuriak herd aged 10 produced only 6.9 calves (Dauphiné 1976). The high lifetime fertility rate in Greenland suggests that sexual maturity by the second autumn and/or giving birth to twins is common.

Although caribou may breed as yearlings, they do not breed as calves (Bergerud 1980), and the age of female sexual maturity and first conception is typically at the end of the third summer (Dauphiné 1976, Valkenberg

Table 2. Mean fertility (± SD) per cohort for two West Greenland and one North American caribou populations. Data are from females 1-10 years of age (age n-1 year).

Cohort	West Greenland				North America	
	Kangerlussuaq-Sisimiut		Akia-Maniitsoq		Kaminuriak[1]	
Age	N	Mean fertility	N	Mean fertility	N	Mean fertility[2]
1	4	0.75 ± 0.50	10	0.30 ± 0.48	20	0.1
2	--	No data	3	2.00 ± 1.00	15	0.8
3	3	1.67 ± 0.58	7	2.57 ± 0.79	6	1.3
4	4	3.25 ± 0.50	4	2.75 ± 0.50	4	3.0
5	2	4.50 ± 0.71	1	3.00	4	3.7
6	5	5.80 ± 0.84	1	4.00	8	4.2
7	2	6.00 ± 0.00	7	5.71 ± 0.95	10	5.4
8	5	6.80 ± 1.10	6	6.57 ± 1.51	5	6.3
9	8	7.13 ± 1.55	3	8.33 ± 0.58	2	6.5
10	5	7.00 ± 1.22	1	7.00	1	6.9
Total	38	4.77 ± 2.38	43	4.23 ± 2.57	75	3.82 ± 2.48

[1] Dauphiné 1976; [2] Standard deviation not available.

1999). The percentage of pregnant subadults, and the observed number of CAs (regressed CLVs of previous pregnancies) in our collection, indicate that first conception at the end of the second summer may be common in West Greenland caribou. Further, caribou give birth to single calves in May or June (Dauphiné & McLure 1974, Bergerud 1975, Adams & Dale 1998b) and twinning is not considered typical in wild caribou (Skoog 1968, Bergerud 1969, Dauphiné 1976). Yet cows with two calves at heel may be observed in either Greenland population. Two-egged twins, a female and male foetus, were observed in the uterus of a Kangerlussuaq-Sisimiut female, aged 9-10 years, in late winter 1998, and an earlier observation of twin foetuses occurred in March 1984 (C. Cuyler, pers. obs.). Greenland females may have better fertility than their counterparts elsewhere.

Typical for other caribou populations (Dauphiné 1976, Thomas & Barry 1990), fertility did not appear to decrease with age. Still, there were indications that fertility may decrease slightly for Kangerlussuaq-Sisimiut females > 8 years of age. Since the data represent cohorts, this observation indicates poor autumn physical condition in some of the previous eight years, as physical condition in females at the time of breeding is the main determinant of reproduction (Dauphinè 1976, Reimers 1983, Allaye-Chan 1991, Cameron et al. 1993, Cameron & Ver Hoef 1994, Gerhart et al. 1997, Adams & Dale 1998a). Alternatively, a decrease in fertility may indicate that breeding pauses are common in Kangerlussuaq females > 8 years old. If breeding pauses among females > 8 years old are true, this would differ from Alaskan caribou whose reproductive pauses, when occurring, were amongst 3-6 year olds or those ≥ 14-years old (Adams & Dale 1998a).

Potential for rapid population growth

We found a high fertility and therefore an excellent potential for rapid growth in both populations despite habitat differences in climate and vegetation. Many authors have stated that females in well-nourished *R. tarandus* populations ovulate and conceive at an earlier age than females in poorly nourished populations (Klein 1959, Skoog 1968, Reimers 1972, Reimers 1983, Creté et al. 1993). Forage quality and availability on summer range determine caribou growth, body condition and reproduction (Reimers 1996, Post & Klein 1999). The pregnancy rates among subadults, twinning and high fertility observed in West Greenland, suggest that summer forage in both areas has been excellent for several years preceding this study.

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