Age-specific fecundity of the Beverly herd of barren-ground caribou

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Abstract: The age-specific fecundity of the Beverly herd of barren-ground caribou *(Rangifer tarandus groenlandicus)* was monitored each winter from 1979-80 through 1986-87. Fecundity in 840 females increased with age from 12% in yearlings to 86% at age 5 years and it did not decline in old (>11 yr) females. Significant variations occurred among winters and even between two subherds in one winter. Reproductive abnormalities were detected in 2 of 840 females and a probable resorption in 1 of 420 females collected in March. Only about 5% of the fetuses were conceived late, possibly by repeat ovulators. Combining survival and fecundity data yielded age-specific calf production, which indicated that, for example, 54% of calves were born to females 3-6 years old.

Key words: age, calf production, *Rangifer*, reproduction

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Introduction

The results in this paper are part of a study conducted from 1980 through 1987 on the effects of forest fires on the winter range of the Beverly herd of barren-ground caribou. This herd winters largely in the south central Northwest Territories (NWT) between Great Slave Lake and the NWT-Saskatchewan boundary. Caribou were sampled primarily to assess the quality of the winter range by monitoring changes in fat reserves from December to March (Thomas and Kiliaan, 1990a).

Fecundity is a measure of the energy reserves and nutrition of caribou at the time of breeding in late October (Dauphiné, 1976; Thomas, 1982; Reimers, 1983; Tyler, 1987) and of their general well-being, which is related to environmental conditions including the quantity and quality of summer and winter ranges. Estimates of fecundity are needed as part of the formula to derive herd size estimates from counts of caribou on the calving grounds (D. Heard, pers. comm., NWT Wildlife Service). The best information on age-specific fecundity of barren-ground caribou in Canada was the results of Dauphiné (1976) for the Kaminuriak herd.

The purpose of this paper is to further document the age-specific fecundity of barren-ground caribou; to record annual variations in fecundity over several years; to document variability between subherds in one winter; to estimate the relative production of male and female calves by each age class of females; to assess the extent of reproductive disfunction; and to estimate the proportion of late breeders.

Methods

Caribou were sampled from the Beverly herd each March from 1980 through 1987, in late November 1982, and in early December from 1983 through 1986. The usual procedure was to establish a field camp where the caribou were in greatest concentration or near the front of it if the caribou were in migration or travelling from one part of the range to another. These camps were cooperative ventures with the Fort Smith Hunters and Trappers Association.

Reproductive tracts of females obtained in November and December were frozen in the field and returned to the laboratory for examination. In the November 25 - 28 sample, the uteri of some females were enlarged but in others pregnancy was confirmed by the presence of filamentous membranes and early embryonic stages, some detectable by eye and others microscopic. The uteri of pregnant females collected in early December were distended with fluid and the embryos were visible to the unaided eye. In a few late conceivers, pregnancy was assumed if one or more corpora lutea were present. Ovaries were sliced transversely at about 2 mm intervals after fixing them for several days in AFA (ethanol, formalin, and acetic acid). A book of slices was produced by not cutting through the hilum.

Ages were estimated from eruption schedules (0.5 - 2 yr) and from counts of annuli in stained sections ofthe first incisor and first molar. Among- and within-year (1984) variation in fecundity was analyzed by modified Chi-square (Zar, 1984), as was variation among age classes in low and high fecundity samples and in all samples. We calculated variation (SD and CI) about mean fecundity after Zar (1984:377).

Results

Age-specific fecundity and annual variability

Pooled data for all years provided average fecundity data for 840 females in seven standard age classes used throughout the study and four larger age groupings (Table 1). Two females with reproductive abnormalities were excluded

Table 1. Fecundity of age classes of caribou sampled from the Beverly herd from 1979-80 through 1986-87.

Age class (yr)	Fecundity[a] (%)	Standard deviation[b]	Confidence interval[b]	Sample size
0.5-1	0.0	0.0		37
1.5-2	12.0*	3.4	6.1-20.4	92
2.5-3	71.7	4.1	62.7-79.5	120
3.5-4	81.5	3.8	72.9-88.3	108
4.5-5	85.5	3.9	76.1-92.3	83
5.5-11	87.5[c]	1.8	83.5-90.8	343
>11	90.9	3.9	80.0-97.0	55
>2	83.7[d]	1.4	80.8-86.3	711
>3	86.1[d]	1.4	83.1-88.8	591
>4	87.2[d]	1.5	83.8-90.0	483
>5	87.5[d]	1.7	83.9-90.6	400

[a] The pregnancy rate in unweighted data from all collections.

[b] After Zar (1984:377 and 378).

[c] Excludes one barren female and one female with no uterus.

[d] Includes barren females.

from the 5.5 - 11 year class but included in the larger age groups, e.g., >2 years. We excluded them from the standard age classes because their chance occurrence could unduly influence relative age-specific fecundity. We included them in the large groupings of age classes because they affect overall calf production. Fecundity stabilized by the 4.5 - 5 year class (binomial test, $P<0.05$).

Fecundity of yearlings averaged 12% with yearly values ranging from 0 to 31% where minimum n=10 (Thomas and Kiliaan 1990b). Fecundity of females 2.5-3 years old varied from 47 to 90 % and from 64 to 92 % in 3.5-4 year females where n ≥10. In females >4 years old, pregnancy rates varied significantly ($P<0.01$) from 1981-82 through 1986-87, ranging from 78 % (n=50) to 94 % (n=51) (Thomas and Kiliaan, 1990b). The pregnancy rate was 98% in 60 females >4 years old in a subherd sampled in March 1984, excluding one female with no ovaries.

Annual fecundity, including two disparate rates in 1983 - 84, fell into low (1982 -.83; 1983 - 84, subherd A; 1985 - 86; and 1986 - 87) and high categories (1981 - 82; 1983 - 84, subherd B; and 1984 - 85). Fecundity in females 2, 3, 4, 5, 6 - 11, and >11 years old were 2, 64, 77, 80, 81, and 86% (n = 28 - 181) and 34, 86, 90, 95, 94, and 96% (n = 27 - 142) in the low and high groups, respectively (Thomas and Kiliaan 1990b). Fecundity in 1979 - 80 was low (50 and 86% pregnancy rates in 2.5 - 3 and >3 year age classes, respectively) in a segment sampled in the NWT. In 1980 - 81, 14 of 15 females in our sample were pregnant.

Subherd variations in fecundity

In December 1983 and March 1984, a subherd (A) was sampled that straddled the tundra/taiga ecotone all winter. Another subherd (B) sampled in March, remained in the taiga all winter. Yearling pregnancy rates were 0% (n = 10) and 33% (n = 9) in the two subherds; 80% (n = 45) and 99% (n = 74) in older females (Thomas and Kiliaan 1990b). The lower fecundity in subherd A was present in the December sample and was related to poorer fat reserves. For example, average depths of back fat in females >2 years old in the subherds were 10 and 21 mm, respectively (Thomas and Kiliaan, 1990a). This variability was attributed to unknown events on the spring and summer range before the rut in October.

Age-specific calf production

Relative calf production by each age (Table 2) was the product of the frequency of each age class in the breeding population and the fecundity of that class (Table 1). Frequencies were derived from a quadratic regression equation for females >2.5 years old in all collections (mean date February 21) adjusted to the June 8 "birth pulse" (Caughley, 1977) and extrapolated to include females 2 years old (Thomas and Barry, 1990. Our shooters selected against small, lean caribou and therefore calves and yearlings were excluded from the survivorship data.

Relative calf production was highest in females 3 and 4 years old with progressive decreases in older females. Over half (54%) of the calves are produced by age classes 3 through 6 years.

Young females (2 - 4 yr) produced more female than male offspring and the reverse occurred in old females (>10 yr) (Thomas *et al.*, 1989). Apparently 3 - 6 year-old caribou produce 59% of the female calves.

Reproductive abnormalities

A 7-year-old female collected in March 1984 had a small, pale uterus characteristic of calves and nulliparous (never pregnant) yearlings. Ovaries were absent. A female nearing 6 years old, collected in March 1986, had no detectable uterus though its ovaries had developed. A 5-year-old female in the same group as the female with no uterus had about a liter of yellow

Table 2. Relative age-specific production of caribou calves in the Beverly herd from 1980 through 1987 based on estimated frequency of female age cohorts in the breeding population, their mean fecundity, and fetal sex ratios.

Age class[a] (yr)	Frequency[b]	Fecundity (%)	Calf production/100F	
			Males & females	Females only
2	16.2	12.0	1.9	1.2
3	14.4	71.7	10.3	6.4
4	12.8	81.5	10.4	6.5
5	11.3	85.5	9.7	4.7
6	9.8	85.9[c]	8.4	4.1
7	8.4	79.7[c]	6.7	3.2
8	7.1	94.9	6.7	3.3
9	5.9	92.3	5.4	2.7
10	4.7	88.6	4.2	2.1
11	3.7	85.0	3.1	1.0
12	2.7	90.0	2.4	0.8
13	1.8	91.7	1.7	0.5
14	1.0	100.0	1.0	0.3
15	0.2	100.0	0.2	0.1
16	0.0	50.0	0.0	0.0
Totals	100.0		72.1[d]	36.9

[a] Age when calf produced (conceived when 7 months younger).
[b] Based on a smoothed survival curve at June 8 (Thomas and Barry, 1990).
[c] Excluding two females with reproductive tract malformations.
[d] Total is 72.3 where calculations carried to three decimal places.

Table 3. Statistics of three female caribou with reproductive abnormalities in relation to mean values for others in the same sample from the Beverly herd of barren-ground caribou.

Month/ year	Age class (yr)	Condition	Weight (kg)	Back fat (mm)	Kidney fat (g)	Femur length (mm)
Mar 84	7	No ovaries	97	26	163	297
Mar 84[a]	6-11	Pregnant	88.1	21.5	127	274
Mar 86	6	No uterus	111.5	1	114	304
Mar 86	5	Resorption	91.5	21	119	271
Mar 86	6-11	Pregnant	87.6	12.8	107	279
Mar 86	6-11	Not pregnant	76.8	5.8	63	276

[a] Subherd B, 1984, in which all other females 6-11 years old were pregnant.

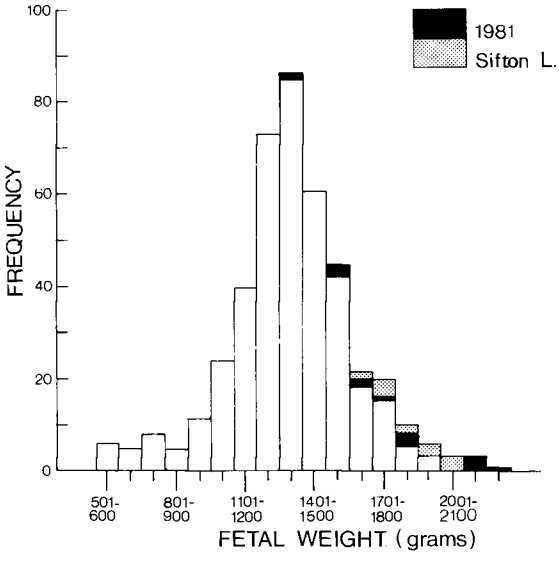

Figure 1. Distribution of fetal weights of barren-ground caribou sampled from the Beverly herd in March, 1980 through 1987.

fluid in its uterus and no fetus. A resorption was suspected. Statistics for the three females (Table 3) reveal that the female with no ovaries was heavier, larger, and fatter than average. The female with no uterus was the heaviest of 591 females >3 years old that we collected over the 8 years, even though it had little mantle fat.

Fetal weights and late conceptions

The frequency distribution of fetal weights (Fig. 1) included late-March samples obtained in 1981 and 1984 (Sifton Lake sample). Fetuses less than 800 g were attributed to late breeders, probably females that cycled more than once before they became pregnant. Late breeders accounted for 4.8% of 420 females. Their exclusion and exclusion of the 1981 and Sifton Lake samples produced a normal distribution of weights. One female aged 5 years had conceived in January based on its 9.2 g fetus collected in March.

Fetal weights were unrelated to age of dam (Table 4). Only in the >5 year class was fetal weigh influenced ($P<0.01$) by sex. Weights increased through the first four age classes but not significantly so (Table 4).

Discussion

Fecundity of the Beverly herd from 1980 through 1987 was similar to that of the adjacent Kaminuriak herd in 1966 - 68. Fecundity was

Table 4. Weights of male and female fetuses sampled from the Beverly herd of caribou in mid-March, 1980 through 1987.

Age class (yr)	Fetal weight (g)					
	Males			Females		
	Mean	SE	n	Mean	SE	n
1.5-2	1160	32	6	1021	61	2
2.5-3	1287	55	22	1294	46	35
3.5-4	1454	57	18	1321	46	29
4.5-5	1435	31	25	1401	39	21
>5	1397	19	120	1318	21	108
>1	1387	16	191	1320	17	195
>2	1395	16	185	1323	17	193
>3	1409	16	163	1330	18	158

[a] Excludes fetuses probably conceived late (<800 g) and fetuses in samples obtained late in March (1981 and 1984, subherd A).

higher in young females in the Beverly herd but slightly lower in older (e.g., >5 yr) caribou compared with Dauphiné's (1976) results. Parker (1981) reviewed age-specific fecundity in several caribou herds. His values for the George River herd in April 1980 were higher than the others: 43% in 21 yearlings, 90% in 20 females 2.5 - 3 years old, and 95% in older females. Messier *et al.* (1988) gave fecundity values of 12, 70, and 80% for 2, 3, and >3 year females in the George River herd. The previous estimate for the Beverly herd (McEwan, 1963) did not deviate from the present results among females >3 years old. Limited data in the younger age classes prohibit comparisons.

There was no decline in fecundity with age in the Beverly herd (McEwan, 1963; this study) in contrast with declines in the Kaminuriak herd (Dauphiné, 1976) and apparently in the George River herd in 1980 (Parker, 1981). Parker's results were influenced by the chance sampling of 3-year-old females with superior energy reserves and insufficient numbers of old caribou.

The observed low and high fecundity could not be explained by environmental conditions on the winter range, as the caribou maintained their fat reserves in all five winters (Thomas and Kiliaan, 1990a). The fecundity of Svalbard reindeer *(R.t. platyrhynchus)* was either low or high and, with one exception, alternated between the categories (Tyler, 1987).

The incidence of resorptions and abortions is difficult to obtain. Early loss of embryos would go undetected. Our rate of 1 resorption or abortion in 420 would apply to the gestation period between about months 2 and 5. Dauphiné's (1976) rate of 0 - 2% may have been artifacts because of poor fixation or multiple cycling. McEwan (1963) listed 3 cases in 52, but criteria used to identify absorptions were lacking. Tyler (1987) suspected that abortions were common in undernourished Svalbard reindeer.

The >5 year age class of females best reflects annual variations in fecundity caused by environmental factors. Females in young age classes (2-4.5 years) may have their energy reserves depleted by successfully rearing a calf and fail to breed the following October (Dauphiné, 1976). High pregnancy rates in young females in one winter could be followed by low rates the following year with equivalent environmental conditions. Therefore, assessing environmental conditions by the performance of females 2 - 5 years old must be done with caution. The pregnancy rate in yearlings probably is a sensitive barometer of the environment in the preceding 2 years.

Conclusions

1. Average fecundity (pregnancy rate) of the Beverly herd from 1980 through 1987 increased progressively with age. Overall, fecundity was comparable to that of the Kaminuriak herd in 1966 through 1968, being somewhat higher in young females and lower in those over 5 years old.
2. There was no decline in fecundity in old (>11 yr) females in contrast with the results from some previous studies.
3. Fecundity varied considerably from year to year where n≥10: from 0 to 31% in yearlings, 47 to 100% in the 2.5 - 3 year class, 64 to 90 % in the 3.5 - 4 year class, and 79 to 98% (in a subherd) in the >4 year class.
4. The fecundity of two subherds varied significantly in 1983 - 84.
5. Intrauterine mortality between 2 and 5 months of gestation was exceedingly low, involving one suspected resorption in 420 (March samples).
6. Light (<800 g) fetuses, possibly arising from failure to conceive at first estrus, comprised 4.8 % of 420 fetuses obtained in March collections. A fetus weighing 9.2 g was estimated to have been conceived in January by the 6-year-old female.
7. Estimates of age-specific calf production

were obtained by combining data on survivorship of females and of age-specific calf production.

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