A life table for female barren-ground caribou in north-central Canada

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Abstract: A survivorship curve and cohort-specific life table were developed for female barren-ground caribou *(Rangifer tarandus groenlandicus)* sampled from the Beverly herd from 1980 through 1987. Significant *(P < 0.05)*differences among yearly samples in the age distributions of females >2.5 years old were attributed to sampling error and real cohort size fluctuations caused by variations in productivity. Pooled data overcame much of that variation and the resultant quadratic-fit curve and life table are believed to yield about average survival/mortality statistics over the 8-year sampling period. Mortality rates increased progressively from 10.6% between age 2 and 3 years to 22.4% between age 10 and 11 years and accelerated thereafter.

Key words: mortality rate, *Rangifer*, survivorship

Introduction

We obtained from 1980 through 1987 a sample of 1284 caribou as part of studies concerned with caribou diet, forage digestibilities, and the effect of forest fires on the winter range of Beverly herd. That herd winters in the southern Northwest Territories (NWT) and adjacent Saskatchewan.

Average mortality rates for specific ages are needed in studies where radio collars are applied and mortality rates are recorded (Edmonds and Bloomfield, 1984; D. Heard, pers. comm., NWT Department of Renewable Resources): is the observed mortality rate about average and, if not, why not? If the ages of collared caribou are known, the expected mortality

can be calculated using data in the life table. Life tables when combined with fecundity tables, and particularly sex-specific fecundity, can yield estimates of rate of increase (Caughley, 1977). Survival curves can be used to assess variations in productivity in past years and relate it to variations in environmental factors.

The purpose of this paper is to provide average survivorship and mortality statistics for a migratory herd of barren-ground caribou subject to hunting and wolf predation.

Methods

From field camps established specifically to sample the herd in early and late winter, local shooters operating snowmobiles collected most

of our caribou samples. We estimated ages up to 2 years by tooth eruption criteria; older caribou from stained sections of the first incisor and first molar. Data for calves and yearlings were excluded from this analysis as our shooters sometimes selected against them (less meat and fat). By weighting the data according to the relative sample sizes of females > 2 years old in December (n = 197) and March (n = 519), we pooled the mean collection dates of December 8 and March 21 and used February 21 (0.71 of a caribou year beginning June 8) as the mean date of the samples.

We pooled data for all years to reduce the variation (tested with G statistic, Sokal and Rohlf, 1981) caused by small sample sizes, heterogeneity of caribou groups, and changes in productivity. Using a quadratic form, we regressed the observed age class frequencies against age using least squares. We then used the quadratic equation to calculate smoothed frequencies in each cohort 2.71, 3.71, ... 14.71 years old in the pooled winter samples. We also calculated age class frequencies at the appropriate birth pulse (Caughley, 1977) of June 8 by substituting in the quadratic equation for ages 2.0 through 15.0 years. Estimates of survival to 1 year and from 1 to 2 years allowed us to complete the life table for all ages.

We then tested by Chi-square the expected numbers at ages 2.71 through 14.71 and observed numbers in each winter sample of 1981-82 through 1986-87. The expected numbers were calculated as the products of sample sizes and the relative frequencies of each cohort $\geq$ 2.71 years obtained from the quadratic equation. Relative frequency is the number in a cohort divided by numbers in all cohorts $\geq$ 2.71 years.

Results

Our fitted ($R^2 = 0.96$) survival curve was: $y = 0.330x^2 - 15.558x + 161.113$, where y was the pooled frequencies at February 21 and x was age 2.71, 3.71, ... 14.71 (Fig. 1A). We calculated
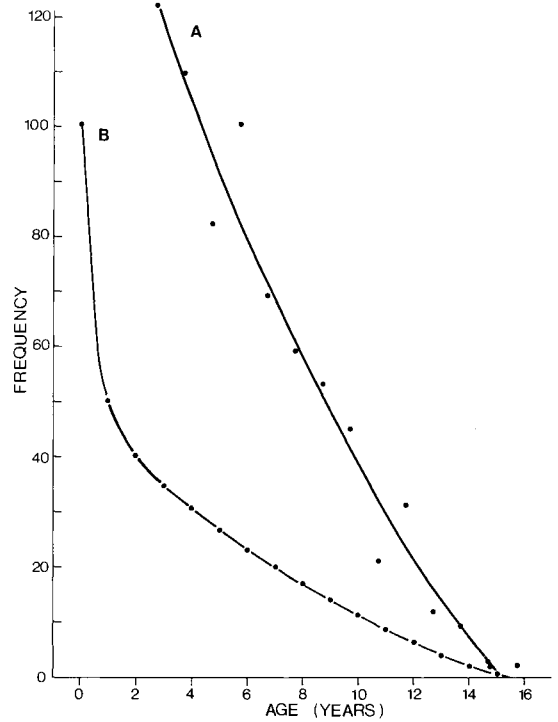

Figure 1. Survivorship curves for female barren-ground caribou 3 years old (A), based on pooled age distributions in samples from the Beverly herd, obtained from 1980 through 1987, and for all ages (B) where assumptions are made concerning survival from birth to 3 years (see Text).

birth pulse values (ages 2, 3, ... 15) using the regression equation and constructed a partial life table (Table 1), which revealed the average mortality pattern of the breeding component over the period of the sampling. Extrapolation to age 2 assumes no change in survival trends (Fig 1A) from age 2 to 2.71 years.

The estimated survival curve for all ages (Fig. 1B) was developed by assuming 50% survival to 1 year and 20% mortality from age 1 to 2 years. The long-term average recruitment of the Beverly herd (Kelsall, 1968; Beverly and Kaminuriak Caribou Management Board, 1987; Thomas and Kiliaan, 1990) equates to about 50% survival of calves to age 1 year (Thomas, unpubl. data.) Survival and mortality values

Table 1. Contracted life table for female caribou >1.5 years old that were collected from the Beverly herd from 1980 through 1987.

Age[a] (yr) x	Observed frequency Feb 21 of $_x$	Frequency from Quadratic[b] Feb 21 f_x	June 8 f_x	Survival[c] l_x	Mortality[d] d_x	Mortality rate[e] q_x	Survival rate[f] p_x
2		135.5	131.3[e]	100.0	10.6	10.6	89.4
3	120	121.4	117.4	89.4	10.0	11.3	88.7
4	109	107.9	104.2	79.4	9.6	12.1	87.9
5	83	95.2	91.6	69.8	9.2	13.0	87.0
6	101	83.0	79.6	60.6	8.5	14.1	85.9
7	70	71.6	68.4	52.1	8.1	15.5	84.5
8	59	60.8	57.8	44.0	7.6	17.2	82.8
9	52	50.6	47.8	36.4	7.1	19.4	80.6
10	45	41.2	38.5	29.3	6.5	22.4	77.6
11	21	32.3	29.9	22.8	6.1	26.6	73.4
12	31	24.2	21.9	16.7	5.6	33.3	66.7
13	12	16.7	14.6	11.1	5.0	45.4	54.6
14	9	9.8	8.0	6.1	4.6	75.0	25.0
15	2	3.7	2.0	1.5	1.5	100.0	0.0
16	2						
Totals	716	853.9	813.0		100.0		

[a] Ages at June 8. Ages at February 21 are *Age − 0.29*. E.g., 1.71/2 yr.
[b] From quadratic equation: $y = 0.330x^2 − 15.558x + 161.113$ where y is frequency and x is age.
[c] Each frequency divided by 131.3 and converted to percent (X 100).
[d] Difference between survival at successive age classes.
[e] $100\ d_x/l_x$. These values were rounded from three decimal places.
[f] $100 − q_x$.

changed (Table 2) but their rates did not. Weighted mean mortality rates ($\Sigma d_x/\Sigma l_x$) calculated for various age groups: >0, >1, >2, ... >10 years were 25.2, 16.8, 16.2, 17.2, 18.5, 19.9, 21.6, 23.7, 26.2, 29.5, 33.5%, respectively.

Extrapolation of the quadratic to age 1 year yields 145.9 caribou as a starting number and a mortality rate of 10.0% at age 1 to 2 years. These values are provided as recent results from radio-collared caribou in Alaska indicated that mortality rates were similar in age classes 8 - 12, 12 - 24, and >24 months (Davis *et al*., 1988). Readers can construct a new life table where mortality rates are given (Caughley, 1977).

There was significant variation (G test, P <0.05) among years 1981-82 through 1986-87 and in 1981-82 through 1985-86 when sample sizes were largest. Two sources of variation are apparent upon close examination of the age distributions (Table 3): sampling error and cohort variation. Relatively large or small cohorts that are consistent in successive years indicate variation in numbers entering the 2.5 - 3 year class. Other variation is caused by non-random distribution of age and sex classes within herds. Large sample sizes are needed to overcome heterogeneous distributions.

Strong and weak cohorts were examined statistically (Table 3) by comparing observed fre-

Table 2. A life table for female caribou in the Beverly herd, 1980 through 1987.

Age x	Frequency at June 8 f_x	Survival l_x	Mortality d_x	Mortality rate q_x	Survival rate p_x
0	100.0	100.0	50.0	50.0	50.0
1	50.0[a]	50.0	10.0	20.0	80.0
2	40.0[b]	40.0	4.2	10.6	89.4
3	35.8[c]	35.8	4.0	11.3	88.7
4	31.8	31.8	3.9	12.1	87.9
5	27.9	27.9	3.7	13.0	87.0
6	24.2	24.2	3.4	14.1	85.9
7	20.8	20.8	3.2	15.5	84.5
8	17.6	17.6	3.0	17.2	82.8
9	14.6	14.6	2.9	19.4	80.6
10	11.7	11.7	2.6	22.4	77.6
11	9.1	9.1	2.4	26.6	73.4
12	6.7	6.7	2.3	33.3	66.7
13	4.4	4.4	2.0	45.4	54.6
14	2.4	2.4	1.8	75.0	25.0
15	0.6	0.6	0.6	100.0	0.0
Totals	337.6	337.6	100.0		

[a] Approximate frequency based on data in the literature (see Text).
[b] Assumes mortality rate of 20% between ages 1 and 2.
[c] Values for ≥ 3 years calculated using mortality rates in Table 1.

quencies in each cohort of each winter, 1981 - 82 through 1986 - 87, with frequencies expected from the survivorship curve for February 21. A significant difference between observed and expected frequencies in the 1979 cohort was sampling error because it only occurred in one of six samples from that cohort. Similar cases appeared in the 1977 and 1975 cohorts. Real difference in cohort sizes occured in 1978 (underrepresented) and 1973 (overrepresented). Strong trends towards over- and underrepresentation were present in 1982 and 1980 cohorts, respectively.

Discussion

Strictures on data that can be used to develop mortality tables are sufficiently rigid that most life tables are faulty to some degree (Caughley,

1966, 1977; Miller and Zammuto, 1983). The key requirement is that the age structure must be derived from a stationary age distribution. This requirement is not necessarily satisfied if the population size remains about constant. It is satisfied if the numbers in each class do not change significantly. If the rate of population change is known, data can be adjusted accordingly, provided that the age distribution is stable (Caughley and Birch, 1971). But how can the age distribution remain stable under conditions of population change? The possibilities are remote in nature, e.g., changes in mortality proportional to age-class frequencies. Stationary age distributions are rare in natural populations. There was a perception that the Beverly herd was increasing in the 1980s (Williams and Heard, 1986) but a review of the survey

Table 3. Analysis of cohort relative strengths in samples obtained from the Beverly herd of caribou from 1981-82 through 1986-87.

Cohort	1981—82		1982—83		1983—84		1984—85		1985—86		1986—87		Totals	
	O[a]	E[b]	O	E	O	E	O	E	O	E	O	E	O	E
1984											15	13	15	13
1983									20	23[c]	11	11	31	34
1982							29	26	28	21	16	10	73	57
1981					19	21	31	23	14	18	13	9	77	71
1980			15	20	13	19	15	20	14	16	8	8	65	83
1979	11	11	17	18	17	16	28	18*	15	14	6	6	94	83
1978	4	10	10	16	19	14	10	16	5	12*	4	5	52	73*
1977	10	9	19	14	20	12*	10	13	11	10	1	4	71	62
1976	5	8	7	12	7	11	12	11	13	8	0	3	44	53
1975	5	7	19	10**	6	9	3	9*	3	6	2	3	38	44
1974	10	6	8	8	7	7	1	7*	5	5	0	2	31	35
1973	6	5	9	7	9	6	10	5*	5	3	0	1	39	27**
1972	6	4	5	5	3	4	1	4	4	2	0	0	19	19
1971	3	3	7	4	2	3	2	2	0	1	0	0	14	13
1970	4	2	2	3	2	2	2	1	0	0	0	0	10	8
1969	2	2	1	2	0	1	1	0	0	0	0	0	4	5
1968	0	1	0	1	0	0	0	0	0	0	0	0	0	2
1967	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Totals	66	68[c]	120	120	124	125	155	155	137	139	76	75	678	682

[a] The observed (0) numbers are females ≥ 2.5 years old in pooled December and March samples.

[b] Expected (E) numbers are the relative frequencies of the age classes at February 21 (weighted mean date of samples) based on the smoothed distribution (quadratic) for females ≥ 2.71 years. E.g., 1984 cohort, 1986-87 sample, E = 76 × 121.4/718.4, where 76 is the total number of females ≥ 2.71 years in the 1986-87 sample, 121.4 is the derived number in the 2.71 year (1984) cohort and 718.4 is the derived total sample size for all ages > 2.71 years (853.9 - 135.5, Table 1).

[c] Differs from observed because of rounding.

* $P < 0.05$.

** $P < 0.02$ (Chi square).

data suggests little change has occurred since 1967. The most recent analysis of survey data suggests that the herd has remained about stable in numbers since 1982 (D. Heard, pers. comm.).

A second stricture that is seldom met with large mammals is the need to distinguish between natural mortality and hunting mortality. Total mortality is the most important statistic for many research and management purposes. Natural mortality is the residual if hunting mortality can be measured accurately. The annual kill of caribou in the Beverly herd by hunters, mostly natives seeking meat only, is in the order of 5000 to 10 000, however, reliable estimates are not available. This annual kill is believed to constitute about 2 - 5% of the herd.

A third requirement, which is seldom satisfied, is an adequate sample size. Caughley (1977) suggested that 150 was the minimum number, though many factors (e.g., homogeneity and longevity) are involved. At one extreme,

sample sizes as small as 16-40 males (ages 1 - 3 years) and 24 - 51 females (ages 1 - 5 years) were adequate to produce reliable time-specific life tables for short-lived Belding's ground squirrels *(Spermophilus beldingi)*, even when fecundity and mortality changed markedly because of changes in environmental conditions (Zammuto and Sherman, 1986).

An unbiased sample is a fourth requirement in life table analysis. A sample of female caribou older than 2 years should have no human biases because hunters are unable to distinguish among female cohorts after age 2. Sampling at the front or rear of a movement could create a biased sample and investigation is needed in this area. Most of our samples were obtained from central portions of the distribution or from a cross section as the herd moved past a campsite. Obtaining an unbiased sample of male caribou would be exceedingly difficult because of the habits of older males to segregate from other groups except during late summer and in the rut and in their propensity to segregate by age.

An assumption implicit in this type of analysis is that the mortality rate changes uniformly from cohort to cohort and also within years. In the Beverly herd, the majority of hunting mortality occurs from November through March. Annual rates of natural mortality are unknown and rates at which natural mortality occurs during a caribou year are even more elusive. Accurate data on hunting mortality specific to sex and broad age classes would have yielded good estimates of natural mortality in this study. It should be afforded high priority in the future.

Previous life tables for barren-ground caribou have suffered from a number of problems. Banfield (1955) grouped males and females, obtained samples from hunters $(l_x$ data) and skulls $(d_x$ data) found on the summer range, estimated ages from eruption schedules and degree of wear, and didn't account for biased sampling by hunters and biases caused by diffe-

rential survival and detection of skulls and mandibles. Miller's (1974) sample was afflicted with high (1958-60) and low (1961-63) waves of productivity; with low recruitment during the study (1966-68) and perhaps after 1961; with samples obtained throughout the annual cycle; and with atypical samples which he excluded. His survival value for calf caribou is much higher than indicated by the recruitment data. Martell and Russell (1983) had a large sample (535) of unsexed caribou (that should not be grouped) but only 76 males and 62 females over 2 years old. In spite of those problems, average weighted mortality values differ marginally for females >3 years: Miller (1974) 17%; Martell and Russell (1983) 20%; this study 17.2%. These equate with 19% for radio-collared caribou >2 years old in the Delta herd in Alaska (Davis *et al.*, 1988).

Messier *et al.* (1988) obtained a standing age structure from 875 females among about 10 000 woodland caribou *(R. t. caribou)* that drowned on 28 and 29 September 1984 in Quebec. They adjusted observed age cohort values by 11%, the calculated growth rate of the population after 1970. Their calculated mortality rates of 1 and 2% in 1 - 2 and 2 - 3 year age classes obviously are low in view of an estimate 5 - 7% harvest in the mid 1980s (Messier *et al.*, 1988). The George River herd may have peaked in 1984 (Couturier *et al.*, 1988) or earlier. We arbitrarily decided to consider the herd's growth inclusive of age cohorts representing 75% of females in our table, i. e., to 6 years. We only accepted the survey results of 1980 and 1982 after 1978. The 1984 estimate was photographic, which usually exceed visual estimates by factors of 1.6 to 2.5 and once by 4.5 (D. Heard, pers. comm.) to 52:100 in late October growth from 1978 through 1984, developed the quadratic equation: $y = 0.567x^2 - 20.237x + 176.731$ $(R^2 = 0.92)$ at ages x.31 (June 8 to September 28 is 0.31 of a caribou year) and then calculated values at the birth pulse. Mortality rates for 1 - 2, 2 - 3, ... 15 - 16 years were

calculated as: 11.8, 12.6, 13.4, 14.4, 15.6, 17.0, 18.7, 20.7, 23.4, 26.8, 31.7, 39.0, 52.0, 83.5, and 100.0%. The mortality rate from 0 to 4.5 months was calculated as 28% based on a calf:cow ratio change of 72:100 at calving (Parker, 1972; Thomas and Barry, this issue; D. Heard, pers. comm.) to 52:100 in late October (Messier *et al*., 1988). Assuming that mortality after 4.5 months equals that of yearlings (11.8%), (Davis *et al*., 1988), the calculated mortality rate in the first year was 37%, which completes the life table. We acknowledge that the herd was growing before 1978 but did not adjust 1978 and earlier cohorts. Smoothed cohort frequencies could be adjusted by a sliding rate of growth if accurate herd numbers could be obtained. The mortality rates probably lie somewhere between those calculated by us and by Messier *et al*., 1988.

Weak and strong cohorts relate to fluctuations in fecundity and early mortality. Where these can be related to environmental fluctuations we can begin to gain insights into caribou ecology. The relatively strong cohort in 1982 may be related to large fat reserves and high fecundity in breeding-age females in March 1982; the weak 1980 cohort to moderate pregnancy rates and low fat reserves in March 1980 (Thomas and Kiliaan, 1990). D. Heard (pers. comm.) observed an unusually large number of dead calves on the calving ground of the Beverly herd in June 1978. Causes of death were not determined.

The weakest link in the life table for all ages of caribou is the mortality rate for caribou 1 to 2 years old. We initially selected 20% because by late winter of most years some yearlings are thin and marginally heavier than large calves (Thomas and Kiliaan, 1990). They likely are more susceptible to predation than older caribou. The mortality rate of yearlings will vary considerably among and within herds depending on their nutritional state and the prevalence of predators. Fortunately, manipulating mortality rates in the first two age classes does not affect the rates in older classes in the life table.

The strongest support for this cohort specific analysis comes from the work of Zammuto and Sherman (1986) on ground squirrels. A cohort-specific life table using combined data from 8 years was statistically indistinguishable from time- specific tables generated from six

Conclusions

1. A pooling and smoothing of age distributions of female caribou $\geqslant$ 2.5 years old obtained each winter from 1979-80 through 1986-87 yielded a cohort-specific life table containing average long-term mortality and survival rates for those age classes.

2. The frequency of females (*y*) in cohorts 2.71, 3.71, ... 14.71 years old at February 21 was described by the quadratic equation: $y = 0.330x^2 - 15.558x + 161.113$ where *x* was age.

3. We used the regression equation to calculate birth pulse life tables: mortality rates gradually and progressively increased from 11.3% from 3 to 4 years of age to 22.4% from 10 to 11 years and accelerated therafter to 100% from 15 to 16 years.

4. The long-term average mortality rate of females 2 to 3 years old was calculated at 10.6% after extrapolating the survival curve to age 2 using the regression equation for older caribou.

5. Variation among years in age class structures was caused by differences in productivity and by sampling errors, attributed to sample size (chance) and non-randomness of age classes in samples.

6. The statistics produced by this analysis are believed to be the best obtained for a population of barren-ground caribou in Canada; previous attempts suffered from various problems.

7. The results are useful in studies on populations with similar habits, habitats, and mortality factors (predators, hunting etc.). Such comparative data are useful where the mor-

tality rate is measured by use of radio collars, particularly where the environment (e.g. wolves) is manipulated.

8. Life table analysis combined with good data on hunting mortality will yield the rate of natural mortality, which is needed to effectively manage caribou and to understand their ecology.

Acknowledgments

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