

Analysis of the standing age distribution and age-specific recruitment rate of the George River and Beverly barren-ground caribou populations.

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Abstract: The primary advantage of the standing age distribution of a population is that it can be sampled. Analysis of the age frequencies for estimates of survival rates and determinations of population status by life table construction depend heavily on assumption that require additional data to evaluate. The analysis of age structures for the George River (Messier *et al.* 1988) and Beverly (Thomas and Barry 1990a,b) caribou herd was reviewed. An alternative method of estimating age specific survival rates was explored. The dependence of the life tables produced by the analysis of Messier *et al.* (1988) and Thomas and Barry (1990a, b) on tenuous and untestable assumptions regarding population growth rate over the life span of the oldest animals, stability of the standing age distribution, and constancy of life table parameters was emphasized. Although the life tables produced by Messier *et al.* (1988) for the George River herd and Thomas and Barry (1990a,b) for the Beverly herd are probably the best available for barren-ground caribou, they should be used with caution, particularly for management decisions.

Key words: age distribution, caribou, life table, mortality, *Rangifer*, recruitment, population dynamics.

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Introduction

The distribution of animals by age class (Standing Age Distribution) is one of the most common types of data available from harvested wildlife. The standing age distribution may be from a population that is stationary (i.e., neither increasing or declining), increasing, or declining. The standing age distribution may be stable (which occurs when the rates of recruitment and death have remained unchanged for a sufficient period) or unstable. For a given life table (i.e., a given set of age specific rates of recruitment and death) a single stable age distribution is defined.

Life tables are usually given for females only. Age specific recruitment (m_x) is only the number of females of age 0 produced per female of age x counted at the time of census. The time of census is not critical to defining the life table, however the time of census must be the same for the estimate of survival rate. The stab-

le standing age distribution is defined for that time of census only. These rules are required to maintain an internally consistent life table.

The recruitment schedule and standing age distribution can be estimated from field data that is easily obtained. When the standing age distribution is both stationary and stable, the age specific annual survival rates can be estimated directly as the geometric mean rate of decline for age constant survival. Age specific survival (p_x) for the stable and stationary case is just N_{x+1}/N_x . When the population is stable, but increasing or declining, the estimate of survival rate must be corrected by the rate of population growth (λ):

$$p_x = \frac{N_{x+1}}{N_x \lambda}$$

If the survival rate is known from cohort estimates (eg., radio telemetry) the standing age distribution may be compared to the expected

stable age distribution calculated from the survival and recruitment schedules. The population growth rate at stable age distribution, and the population growth rate from the observed standing age distribution may be calculated. If the population growth rate is known from census estimates, and the population growth rate has remained constant, the age specific survival schedule may be calculated.

Caughley (1977) notes the futility of recalculating the population growth rate from the recruitment and «corrected» survival schedule. No matter what the recruitment schedule, and even if the standing age distribution is *not* stable, the assumed population growth rate correction will be recovered. Analysis of the standing age distribution for estimates of survival rates requires that the age distribution is stable, (i.e., the population growth rate known from census has been constant for the period of time specified by the maximum age).

The age distributions described in Messier *et al.* (1988) and Thomas and Barry (1990a,b) have been used to develop life tables for the George River and Beverly caribou herds. The resulting life tables depend heavily on untested assumptions regarding the stability of age distributions, and the constancy and value of the populations growth rate.

Methods

The terminology used is taken from Caughley (1977) and Taylor and Carley (1988). At stable age distribution the relationship between the recruitment schedule (m_x), the survivorship schedule (l_x), and population growth rate (λ) is given by the discrete form of the life table equation (Cole 1954):

$$1 = \sum_{x=0}^{\omega} l_x m_x \lambda^x \quad (2)$$

The relationship of the survivorship schedule to the survival rate schedule is:

$$l_{x+1} = \prod_{j=0}^{j=x} p_j \quad (3)$$

where l_0 is defined as 0. The relationship of the survivorship schedule (l_x) to the standing age distribution (S_x) is:

$$l_x = S_x \lambda^x \quad (4)$$

where:

$$S_x = \frac{N_x}{N_0} \quad (5)$$

Rewriting equation 2 using the relationship in equation 4 yields:

$$1 = \sum_{x=0}^{\omega} S_x m_x \lambda^x \lambda^x \quad (6)$$

which reduces to:

$$1 = \sum_{x=0}^{\omega} S_x m_x \quad (7)$$

Caughley (1977) warns against analysis for standing age distributions that begin with the assumption that they are stable. Using the definitions of S_x and m_x , equation 7 may be rewritten as:

$$\begin{aligned} 1 &= \sum_{x=0}^{\omega} \left(\frac{N_x}{N_0} \right) \times \left(\frac{N_{0,x}}{N_x} \right) \\ &= \sum_{x=0}^{\omega} \frac{N_{0,x}}{N_0} \end{aligned} \quad (8)$$

where $N_{0,x}$ is the number of age 0 females produced by females of age x . Equation 7 will always be true for any age distribution and any m_x schedule, stable or unstable, biased or unbiased.

The relationship in equation 4 is true only for stable age distributions. However, any age distribution (stable or unstable, biased or unbiased) can be corrected by some assumed population growth rate. Substitution for S_x from equation 4 in equation 7 gives equation 2, the life table equation. In other words the l_x schedule that results from the «correction» will, by definition, return the assumed population growth rate and initial standing age distribution as the stable age life table result (Caughley, 1977). This tautology does not test the stable age assumption or the accuracy of the «correction» term (λ).

The relationship between the standing age distribution (S_x) and age specific survival rate (p_x) can be developed from equations 3 and 4:

$$S_x = \prod_{j=0}^{x-1} \frac{p_j}{\lambda} \quad (9)$$

The value of Φ for the mature adult age strata is best determined by the Chapman-Robson truncated method (Chapman and Robson, 1960) when survival rates are age constant:

$$\Phi = \frac{N_{x+1}}{N_x} = \frac{p_x}{\lambda} \quad (10)$$

Table 1. The life table for the George River caribou herd as developed by Messier *et al.* (1988).

Age (x)	Frequency (N _x)	Recruitment rate (m _x)	Standing age distribution (S _x)	Corrected (λ=1.117) N _x ·λ ^x	Smoothed N _x	p _x	S _x ·m _x	
0	236.1	0	1.0	236.1	236.1	0.714	0	
1	138	0	.585	154.0	168.5	0.99	0	
2	156	0.06	.661	194.4	167.0	0.98	0.0397	
3	113	0.35	.478	157.2	163.0	0.96	0.1673	
4	94	0.40	.398	145.9	156.6	0.94	0.1592	
5	83	0.40	.352	143.9	147.9	0.93	0.1408	
6	65	0.40	.275	125.8	137.3	0.91	0.1100	
7	63	0.40	.267	136.1	125.0	0.89	0.1068	
8	57	0.40	.242	137.4	111.4	0.87	0.0986	
9	40	0.40	.169	107.6	96.6	0.84	0.0676	
10	24	0.40	.107	72.1	81.2	0.81	0.0428	
11	18	0.40	.076	60.4	65.4	0.76	0.0030	
12	12	0.40	.051	44.9	49.5	0.69	0.204	
13	7	0.40	.030	29.2	33.9	0.56	0.0120	
14	1	0.40	.004	4.7	18.8	0.24	0.0016	
15	4	0.40	.017	20.8	4.4	0.10	0.0680	
$\lambda = 1.117$							$\Sigma = 1.0$	

Results

The standing age distributions reported by Messier *et al.* (1988) and Thomas and Barry (1990a) were reported as stable age distributions with assumed population growth rates of 1.117 for the George River Herd and 1.0 for the Beverly Herd. Messier *et al.* (1988) used recruitment rates from other sources to develop a life table for the George River herd. The «natality» rates reported by Thomas and Barry (1990b) for the Beverly herd may be taken as recruitment rates by considering age 0 to be unborn calves.

The life Table for the George River herd is given in Table 1, and the life table for the Beverly herd is given in table 2. As described above, life tables developed in this manner always return the assumed population growth rate as the stable age growth rate, and the observed standing age distribution as the stable age distribution. The survival rate estimates are based on the assumption that the population growth rate has been constant over the time span embodied by the age distribution, that survival rates have not varied systematically, and that the age distribution was sampled without bias (Messier *et al.* 1988; Thomas and Barry 1990a,b). A George River life table was developed assuming the po-

pulation growth rate was 1.0 to illustrate Caughley's (1977) tautology of age distribution analysis (Table 3). Similarly, recruitment rates for the George River herd can be arbitrarily doubled and the «corrected» life table will still return the correction as the stable age population growth rate (Table 4).

Both Messier *et al.* (1988) and Thomas and Barry (1990a) used a linear regression to fit the quadratic equation to the age distribution data. Linear alternatives that assume constant age specific survival rates within a given age stratum (Figures 1 and 2) gave an equally good fit to the data. The linear approach suggested 2 age strata of caribou could be identified: «mature» (age 2-10) and «senescent» (age 11-16). The Chapman-Robson estimates for the 2 strata are given for both George River and Beverly herds (Table 5). The recruitment rates for senescent age classes did not appear to decline (Thomas and Barry, 1990b).

Discussion

The standing age distribution is a history of the population dynamics over the period embodied by the number of age categories. It is information rich and easily measured. Age specific re-

cruitment is also relatively straight-forward to measure. However, the information contained in the standing age distribution is not accessible without other information. As seen from the examples: stable and unstable; and biased and unbiased age distribution all give estimates of survival rates that are indiscernible.

Constancy checks are possible when additional information is available. Caughley (1977) argues that survival and recruitment rates are age constant for adult females of most harvested species. The caribou age distribution data suggests that the survival rates of senescent adult females are about 74% of mature animals. When survival rates of age strata are age constant, the Chapman-Robson Φ (p_x/λ), estimated from a stable age distribution, gives the relationship between survival rates and population growth rate. When the survival rate of mature ($x > a$) females is age constant (Caughley 1977) equation 8 may be rewritten in a manner that is useful for testing the stable age assumption from available field data:

$$\begin{aligned}
 &a = \text{age for first reproduction,} \\
 &w = \text{final age class} \\
 &\Phi = p_x/\lambda \text{ (constant for mature adults);} \\
 &l = S_a x m_a + \sum_{x=a}^{\omega} S_a x \Phi^{x-a} x m_x \quad (11)
 \end{aligned}$$

A measure of deviation from stable age distribution (D) may be defined as:

$$D = 1 - S_a x m_a + \sum_{x=a+1}^{\omega} S_a x \Phi^{x-a} x m_x \quad (12)$$

This deviation from Stable Age Distribution (D) depends on the number of age 0 (N_0) and the number of N_x for $x \geq a$ (i.e., S_x); and the number of N_0 per N_x for $x \geq a$ (i.e., m_x). Age specific juvenile survival is not an issue. An estimate of the variance of D may be calculated using Monte Carlo methods from the variance of Φ calculated from the Chapman-Robson procedure, and the variance of m_x (pooled age classes or age specific as required).

The deviation from stable age distribution defined by equation 11 examines the consistency of the standing age distribution with the known underlying life history. A deviation from stable age distribution may be interpreted by examining the fit of the Chapman-Robson Φ to the adult strata of the standing age distribution (see Figures 1 and 2). If the residuals are symmetrical, the deviation is probably due to an incompatibility between the recruitment schedule and the standing age distribution. Asymmetrical residuals indicate that survival rates may not be age constant, survival rates may

Table 2. The life table for the Beverly caribou herd as developed by Thomas and Barry (1990a,b).

Age (x)	Frequency (N_x)	Recruitment rate (m_x)	Standing age distribution (S_x)	Corrected ($\lambda=1.007$) $N_x \cdot \lambda^x$	Smoothed N_x	p_x	$S_x \cdot m_x$
0	305	0	1.0	305	305	0.478	0
1	146	0	0.478	146	145.9	0.929	0
2	136	0.06	0.444	136	135.5	0.896	0.027
3	120	0.3585	0.398	120	121.4	0.889	0.142
4	109	0.4075	0.354	109	107.9	0.881	0.143
5	83	0.4275	0.312	83	95.2	0.872	0.132
6	101	0.4375	0.272	101	83.0	0.864	0.118
7	70	0.4375	0.235	70	71.6	0.847	0.102
8	59	0.4375	0.199	59	60.8	0.834	0.086
9	52	0.4375	0.166	52	50.6	0.813	0.072
10	45	0.4375	0.135	45	41.2	0.785	0.058
11	21	0.4375	0.106	21	32.3	0.745	0.045
12	31	0.4545	0.079	31	24.2	0.696	0.035
13	12	0.4545	0.055	12	16.7	0.582	0.024
14	9	0.4545	0.032	9	9.8	0.375	0.014
15	2	0.4545	0.012	2	3.7	0.000	0.005

$\lambda = 1.002$

$\Sigma = 1.0$

Table 3. A life table for the George River caribou herd based on the same information as given in Messier *et al.* (1988) but corrected for an assumed population growth rate of 1.00.

Age (x)	Frequency (N _x)	Recruitment rate (m _x)	Standing age distribution (S _x)	Corrected (λ=1.001) N _x •λ ^x	Smoothed N _x	p _x	S _x •m _x
0	236.1	0	1.0	236.1	236.1	0.6567	0
1	138	0	.585	138	155.0	0.8622	0
2	156	0.06	.661	156	133.7	0.8584	0.0397
3	113	0.35	.478	113	114.8	0.8536	0.1673
4	94	0.40	.398	94	97.9	0.8474	0.1592
5	83	0.40	.352	83	83.0	0.8397	0.1408
6	65	0.40	.275	65	69.7	0.8298	0.1100
7	63	0.40	.267	63	57.8	0.8168	0.1068
8	57	0.40	.242	57	47.2	0.7995	0.0968
9	40	0.40	.169	40	37.8	0.7757	0.0676
10	24	0.40	.107	24	29.3	0.7406	0.0428
11	18	0.40	.076	18	21.7	0.6868	0.0030
12	12	0.40	.051	12	14.9	0.5914	0.0204
13	7	0.40	.030	7	8.8	0.3807	0.0120
14	1	0.40	.004	1	3.4	0.2310	0.0016
15	4	0.40	.017	4	0.8	0.0	0.0680

λ = 1.001 Σ = 1.0

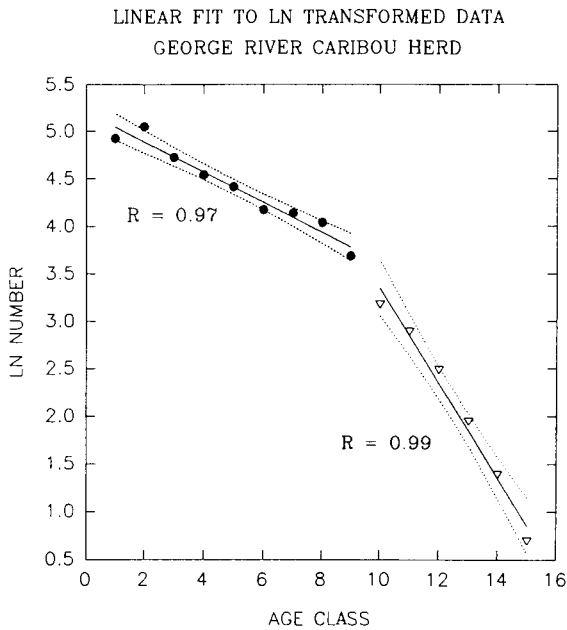


Fig. 1. The standing age distribution of the George River caribou herd (Messier *et al.* 1988) may be divided into «mature» (age 2-9) and senescent (age 10-15) age strata that have age constant rates of decline (Φ).

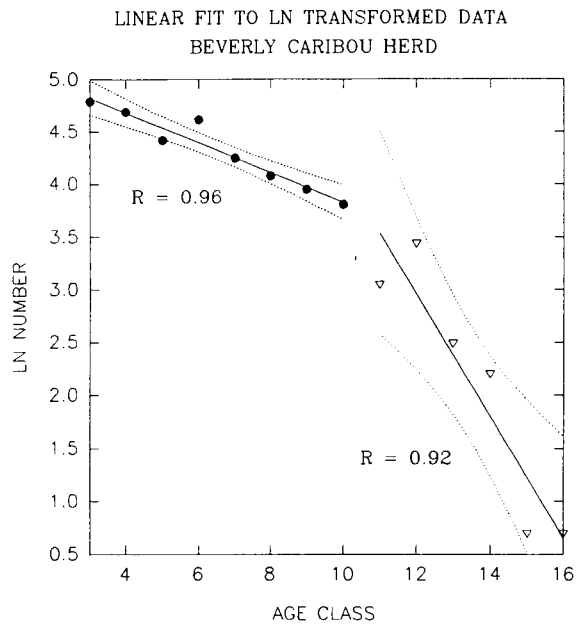


Fig. 2. The standing age distribution of the Beverly caribou herd (Thomas and Barry 1990a) may be divided into «mature» (age 2-10) and senescent (age 11-15) age strata that have age constant rates of decline (Φ).

have increased or decline, or population growth rate may have increased or declined.

The deviation from stable age distribution (D) calculated from the George River herd using mature (0.87) and senescent (0.64) values of Φ was -0.401 (SE = 0.100). The deviation from stable age distribution calculated for the Beverly herd using mature (0.86) and senescent (0.63) values of Φ was 0.251 (SE = 0.074). These deviations suggest some caution in interpreting the age distributions of these herds as stable, but do not demonstrate that the age distributions are not stable. A «D» value that is significantly different from 0 signifies inconsistent assumptions, but does not identify which assumptions are incorrect. As stated above, if the Φ values are calculated as age specific, D will equal zero. Using flexible equations (such as the quadratic) to fit observed age distributions offers limited opportunity to examine the underlying assumptions involved in analysis of standing age distributions.

An inconsistency in the life table developed by Thomas and Barry (1990a) was noted. Barry and Thomas (1990a) give survival rate estimates based on the assumption that the population growth rate is 1.0 (i.e., no correction term). They suggest the mortality rate for age 0 is 37% (Thomas and Barry 1990a, page 183), and the mortality rate of age class 1 is 10% (Thomas and Barry 1990a, page 179). This gives a survival rate of 0.567 for age 0 to age 2, the first age class they feel is reliably represented. However, the fecundity data given in Thomas and Barry (1990b) indicates that $N_0 = 305$ and $N_2 = 136$. This indicates a survival rate of 0.446 assuming the stable age $\lambda = 1.0$. This discrepancy is easily corrected by just accepting the age distribution estimate. A defensible argument for that approach would be that intra-uterine mortality was neglected in the lower calf mortality estimate.

Conclusion

Analysis of standing age distributions is an enigma. It appears that unless there is considerable additional information about population growth rate and age specific rates of survival, analysis of standing age distributions only returns the initial assumptions. Both Messier *et al.* (1988) and Thomas and Barry (1990a,b) were well aware of the assumptions they made in examining the George River and Beverly stan-

Table 4. An example taken from Messier *et al.* (1988) to illustrate that the sum of the standing age frequency (S_x) times the recruitment rate (m_x) does not depend on the values of m_x (i.e., it is always 1.0).

Age (x)	Frequency (N_x)	Recruitment rate (m_x)	Standing age distribution (S_x)	$S_x \cdot m_x$
0	472.2	0	1.0	0
1	138	0	0.292	0
2	156	0.12	0.330	0.0397
3	113	0.70	0.239	0.1673
4	94	0.80	0.199	0.1592
5	83	0.80	0.176	0.1408
6	65	0.80	0.138	0.1100
7	63	0.80	0.133	0.1068
8	57	0.80	0.121	0.0968
9	40	0.80	0.085	0.0676
10	24	0.80	0.051	0.0428
11	18	0.80	0.038	0.0030
12	12	0.80	0.025	0.0204
13	7	0.80	0.015	0.0120
14	1	0.80	0.002	0.0016
15	4	0.80	0.008	0.0680
Any m_x schedule \rightarrow stable age distribution				$\Sigma = 1.0$

ding age distributions. It did not appear that the data were sufficient to resolve whether survival rates were age specific or age constant for either age distribution. The data were also insufficient to determine whether the age distributions were unbiased or stable. Suspected changes in the population dynamics of both herds were mentioned by Messier *et al.* (1988) and Thomas and Barry (1990a,b) which would have caused deviation from stable age configuration.

The life tables developed for the George River and Beverly herd were consistent with the available data and the assumptions given. The recruitment rates given by Thomas and Barry (1990b) were measurements rather than interpretations. However, the other life table parameters for both the George River and Beverly herds are most correctly understood as hypotheses which currently depend on un-testable assumptions.

Life tables provide powerful tools for wildlife managers. However, it appears that the useful-

Table 5. The Chapman-Robson (Chapman and Robson 1960) truncated values of Φ for «mature» (age 2-10 and 2-9) and «senescent» (age 11-15 and 10-15) age strata are given for the Beverly (Thomas and Barry 1990a) and Georg River (Messier *et al.* 1988) caribou respectively.

Beverly herd		
Age Strata	C-R PHI (Φ)	SE of Φ
Mature (age 2-10)	0.87	0.02
Senescent (age 11-15)	0.64	0.06

George River herd		
Age Strata	C-R PHI (Φ)	SE of Φ
Mature (age 2-9)	0.86	0.02
Senescent (age 10-15)	0.64	0.06

ness of standing age distributions is limited unless there is precise and accurate population census data to accompany it. The ideal data set would include cohort estimates of age specific survival rates, age specific recruitment rates, and an independent census to confirm the population dynamics suggested by the resulting life table. Simulation studies might improve qualitative understanding of the value and dangers of simplifying assumptions to life table analysis of caribou.

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