

Using survivorship curves to estimate age of first reproduction in moose *Alces alces*

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Age-specific mortality of large mammals follows a general pattern of high juvenile mortality followed by low adult mortality. I outline a method which models this change in mortality rate to estimate age of maturity in hunted moose *Alces alces* populations. Kill data indicate that first time reproducers suffer the highest mortality during the hunting season. Cohort analysis of hunter kill data was used to estimate age-specific female moose numbers and annual survival of cohorts over 18-26 years. Age at maturity was defined as age at the inflection point (highest mortality rate) of a third-order log-polynomial of annual survivorship curves. The inflection point demarcates the change in mortality rate between juvenile and adult life stages. Thus, the inflection point represents the greatest moose mortality rate during the hunting season and is likely associated with hunting mortality of inexperienced females accompanied by 6-month-old calves. I tested this method by estimating age of first reproduction (inflection point - 0.5 years) and juvenile mortality for 15 Canadian moose populations. Results indicate a wide range of age at maturity (1.7-3.0 years) and percent of juveniles that survive to this age (29-70%). Estimating age at maturity from survivorship curves provides the opportunity to test life-history theory.

Key words: age at maturity, cohort analysis, demography, juvenile mortality, life history, recruitment, survivorship

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Life history theory predicts trade-offs based on growth, mortality, density and reproduction (reviewed in Roff 1992, Stearns 1992, Charnov 1993). Intraspecific comparisons have been used to describe trade-offs between timing of maturation, growth rate and juvenile mortality (e.g. Sæther & Haagenrud 1985, Elowe & Dodge 1989, Gaillard, Sempéré, Boutin, Van Laere & Boisauvert 1992, Hewison 1997). One such trade-off is the change in mortality associated with age at maturity (Cole 1954, Stearns 1992). In large mammals, age-specific mortality follows a general pattern (Siler 1979, Eberhardt 1985, Sibly, Collett, Promislow, Peacock & Harvey 1997). Typically, high juvenile mortality is fol-

lowed by low adult mortality (Linnell, Aanes & Andersen 1995, Gaillard, Festa-Bianchet & Yoccoz 1998).

I propose the following method for estimating age at maturity and juvenile mortality for hunted moose *Alces alces* populations. Using survivorship curves estimated from cohort analysis, I calculate the point of change from an increasing to a decreasing rate of mortality. From the survivorship curve, the x-value (age in years) at this point indicates age at maturity. The y-value (% survival) at this point indicates juvenile mortality. I use cohort data from 15 hunted moose populations in Ontario and Newfoundland, Canada, to test this technique. Moose have evolved flexible reproduction as an adaptation to

highly variable environments (e.g. seral stages associated with disturbances such as fire; Geist 1974, 1987). Thus, this technique will allow intraspecific comparisons of moose mortality patterns. Contrasting this change from juvenile to adult mortality among populations over time will assist in comparing life-history trade-offs.

Methods

Study area

Study areas included four moose management populations in Ontario and 11 moose management populations in Newfoundland (Ferguson & Messier 1996, Ferguson, Bisset & Messier 2000). Both study areas lie within the boreal forest region (Rowe 1972). Newfoundland moose density ranged within 0.5–4.0 moose/km² during 1969–1991 (Ferguson 1993). Harvest of moose accounted for the majority of annual mortality (Ferguson & Messier 1996) although black bear *Ursus americanus* predation of neonates occurs (Albright & Keith 1987). No wolves *Canis lupus* exist in Newfoundland and the recent arrival of coyotes *Canis latrans* did not affect moose population dynamics during the period of this study (Larivière & Crête 1993). The Ontario moose populations were located >1,000 km to the west of Newfoundland and average moose density ranged within 0.08–0.5/km² during 1971–1993 (Timmermann & Whitlaw 1992). Ontario moose experience high juvenile predation due to wolves and black bears (Krefting 1975).

Cohort analysis

I used the Deriso, Quinn & Neal (1985) cohort analysis model (CAGEAN) to estimate age-specific moose numbers and annual survival of female cohorts (Ferguson 1993). The minimum number of individuals alive each year can be reconstructed provided that catch-at-age data are provided from a long enough time series to allow several newborn cohorts to live out their lives (Gulland 1983). Moose demography can be modelled using cohort analyses as moose show synchronized spring parturition and time series data on age-specific kills (i.e. catch-at-age data) are available for hunted moose populations (Solberg, Sæther, Strand & Loison 1999). To reconstruct population size from cohorts with surviving members requires estimates of the number of individuals killed in recent years. I obtained such estimates by calculating age-specific hunting vulnerability per unit effort from completed cohorts and using hunting effort (total number of hunter days) from recent years.

Estimation of population size for cohort analysis depends on the following assumptions (Fryxell, Mercer & Gellately 1988, Solberg, Loison, Sæther & Strand 2000):

1. Hunters do not avoid animals older than the terminal age (12 years). A negligible number of female moose >12-years-old (<1%) was estimated from kill at age data.
2. Little annual variation in natural mortality. No estimate of age-specific natural mortality was available for Newfoundland and Ontario moose populations. I used annual survival rates of 0.99 and 0.95 for 0.5–1.5 and >1.5-year-old moose, respectively. Generally, adult's experience high and stable adult survival (Gaillard et al. 1998). Also, the largest mortality for moose was due to hunting accounting for 3–22% of the annual population size (Ferguson et al. 2000).
3. A closed population. I cannot evaluate this assumption although there is little evidence of large numbers of moose emigrating or immigrating.
4. No annual variation in age-specific harvest vulnerability due to a change in hunting methods. This effect is less important here, as I reconstructed later populations based on catch-at-effort data that will track changes in hunting methods over time.

I compared cohort analysis results with other population estimates. The most recent female population size based on percentage females classified from aerial surveys for each moose population (N = 15) was correlated (Pearson's product moment correlation) with estimates from cohort analysis to compare accuracy (closeness of measured value to its true value; Sokal & Rohlf 1981: 13). Aerial survey results were obtained for Newfoundland (Ferguson 1992) and for Ontario (Timmermann & Whitlaw 1992).

Data collection

Hunters provided the lower jawbone from harvested moose. Age of moose was estimated from tooth eruption pattern for juveniles and by counting incremental growth rings in the cementum layer on the first incisor from older animals (Sergeant & Pimlott 1959). During the study period, 311–2,780 female moose were harvested and age determined from each population (see Table 1). To correct for missing individuals (<23% of jawbones from hunter-killed moose were not collected), particularly calves, the annual number of moose within each sex and age group was multiplied by a correction factor (Ferguson 1993).

Age at maturity

In large mammals, age-specific mortality follows a general pattern (Siler 1979, Eberhardt 1985, Sibly et al. 1997). Typically, high initial mortality of newborns is followed by a less dramatic, but still high, mortality of juveniles that precedes a low adult mortality (Gaillard, Delorme, Boutin, Laere & Boisaubert 1993, Jorgenson, Festa-Bianchet, Gaillard & Wishart 1997, Gaillard, Festa-Bianchet, Yoccoz, Loison & Toigo 2000). For hunted moose, females with their first calves are highly vulnerable to hunting mortality, which is likely associated with the inexperience of new mothers during the hunting season (Ferguson 1993). Thus, I propose the following method for estimating age at first reproduction for hunted moose populations. I calculated the age of first reproduction as the inflection point of a third-order log-polynomial of survivorship curves (i.e. the point of greatest rate of mortality).

I decided on the following tests of the hypothesis that the point of greatest hunting mortality demarcates age at first reproduction in moose. First, I compare age of first reproduction for a Newfoundland (MMU 16) and two Ontario (District 15 & 21) populations that had data available to estimate age of first reproduction using survivorship curves and an independent method. Age at maturity (>50% of females; Sand & Cederlund 1996) was estimated using *corpora lutea* counts obtained from Newfoundland (Pimlott 1959) and Ontario moose ovaries (Cederwall & Ranta 1982, Bergerud & Snider 1988). I then calculated mortality rate of females using cohort analysis (see below) for the same population using catch-at-age data from Newfoundland (Bergerud & Manuel 1968) and Ontario (Timmermann & Whitlaw 1992). Second, for a hunted moose population in central British Columbia, examination of a sample of reproductive tracts estimated age at first reproduction that was compared with age-specific hunter-killed moose data to ascertain the female age class that experienced the greatest hunting mortality (Heard, Barry, Watts & Child 1997). Third, I compared estimates of age at first reproduction using cohort analysis from the 15 moose populations studied here to the range observed for 14 moose populations in Sweden (Sand & Cederlund 1996) estimated using examination of reproductive tracts. I recognize that these are necessary but not sufficient tests of the hypothesis that peak hunting mortality is correlated with age at first reproduction.

Estimating age at maturity

I fitted a third-order log-polynomial function to annual survivorship curves for each population (e.g. Caughley 1966, 1977, Messier, Huot, Le Hénaff & Luttich

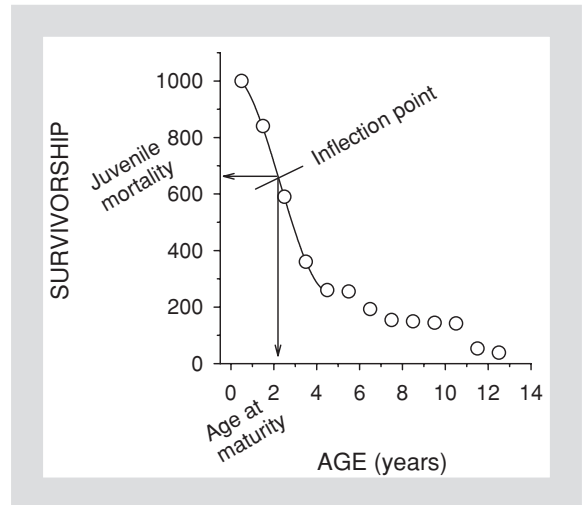


Figure 1. Survivorship versus age of female moose for a population in central Newfoundland. A third-order polynomial regression is fitted to data for ages 0.5 through 5.5 years, and the inflection point demarcates age at maturity and total juvenile mortality. The initial cohort was based on animals 0.5 years of age (i.e. first age class in hunter-kill samples).

1988) using SigmaStat's (Jandel Scientific Software, 1992, Chicago, Illinois) non-linear estimation procedure. Moose are considered sexually mature by at least four years of age (Sand & Cederlund 1996). Thus, I fit the following regression equation to the number of female moose survivors against age from 0.5 to 5.5 years (Fig. 1).

$$Y = b_0 + b_1 X + b_2 X^2 + b_3 X^3 \quad (1)$$

where Y is survivorship (number of female moose survivors out of an initial cohort of 1,000), X is age in years, b_0 is the intercept, and b_1 , b_2 , b_3 are the regression coefficients. In these survivorship curves, b_0 estimates the initial number in the cohort, $-1 < b_1 < 1$, and $b_2 < 0$. The inflection point (I) was calculated as the second derivative (Larson, Hostetler & Edwards 1990). Age at maturity was the x -value of the inflection point minus 0.5 years (birth occurred six months previously) estimated from the polynomial regression equation (1):

$$I = x_{\text{inflection}} = -b_2 / 3 b_3 \quad (2)$$

where b_3 is constrained to be positive and $b_2 < 0$.

First, I compare years within a population to describe the relationship between juvenile mortality and age at maturity. This relationship is constrained by the sampling correlation between the two parameters estimated from the same survivorship curves. Such sampling correlations may invalidate the relationship. Therefore, I compare population means (mean of years) to describe

Table 1. Demographic statistics for the 15 Canadian moose populations with data on age at maturity (in years), number of females and juvenile mortality (in %) given as mean \pm SE.

Population	Years	Sample size ^a	Area (km ²)	Location		Age at maturity (years) ^b	Number of females ^c	Juvenile mortality (%) ^d
				Latitude	Longitude			
Ontario								
WMU 13 ^c	1971-1991	2421	13325	48° 40'	89° 23'	2.04 \pm 0.24	2419 \pm 1153	60.2 \pm 5.4
Dist. 13	1975-1993	1952	9759	49° 40'	90° 21'	1.71 \pm 0.20	3691 \pm 825	70.0 \pm 5.1
Dist. 15	1975-1993	2284	57670	51° 31'	90° 50'	2.22 \pm 0.24	6635 \pm 1484	60.6 \pm 5.4
Dist. 16	1975-1993	2780	103023	51° 49'	93° 28'	2.07 \pm 0.12	2250 \pm 1071	58.0 \pm 5.4
Newfoundland								
MMU 3 ^c	1973-1991	299	3580	50° 25'	56° 44'	2.38 \pm 0.26	9652 \pm 4572	29.3 \pm 5.9
MMU 7	1973-1991	576	1720	49° 6'	57° 30'	2.44 \pm 0.27	2120 \pm 1004	40.5 \pm 5.8
MMU 9	1970-1991	496	809	48° 7'	58° 52'	2.82 \pm 0.31	4653 \pm 2221	39.9 \pm 5.8
MMU 11	1973-1991	502	2844	48° 10'	58° 8'	2.80 \pm 0.29	4864 \pm 2304	38.1 \pm 5.9
MMU 16	1966-1991	1007	1676	48° 39'	56° 4'	2.59 \pm 0.28	3167 \pm 1532	41.1 \pm 6.7
MMU 18	1973-1991	548	3871	48° 14'	56° 23'	2.50 \pm 0.27	2181 \pm 1023	35.9 \pm 6.3
MMU 19	1973-1991	327	2228	47° 53'	57° 48'	2.63 \pm 0.28	6038 \pm 2861	29.1 \pm 4.2
MMU 22	1975-1991	312	2015	49° 14'	54° 48'	2.64 \pm 0.28	1942 \pm 916	51.4 \pm 6.6
MMU 23	1973-1991	311	4302	49° 11'	53° 58'	2.99 \pm 0.29	2621 \pm 1242	46.3 \pm 6.8
MMU 24	1966-1991	1882	910	48° 49'	55° 3'	2.83 \pm 0.31	2569 \pm 1231	50.7 \pm 5.7
MMU 36	1973-1991	1210	3469	47° 2'	53° 15'	2.25 \pm 0.25	2184 \pm 1035	54.9 \pm 8.5

^a Number of aged female moose from hunter harvest.

^b Calculated as the x-value at the inflection point of survivorship data - 0.5 years (see Methods).

^c From cohort analysis (see Ferguson 1993).

^d Calculated as the y-value at the inflection point of survivorship data (see Methods).

^e Wildlife Management Unit (WMU) and District (Dist.) for Ontario, and Moose Management Unit (MMU) for Newfoundland.

the relationship between age at mortality and juvenile mortality. I test among different models to find the best regression that describes this relationship. Comparing populations avoids the problem of the sampling artefact.

Estimating juvenile mortality

I calculated juvenile mortality (%) using the survivorship (y-value) at the inflection point ((1,000-survivorship)/10). The values for juvenile mortality given in Table 1 are percent of total population mortality that occurred before maturity (i.e. the inflection point). The form of the relationship between juvenile mortality and age at maturity was investigated by comparing R² values derived from fitting logarithmic ($y = y_0 + \ln x$), power ($y = ax^b$), exponential ($y = e^{ax}$), and polynomial ($y = y_0 + ax + bx^2$) models.

Results

The following tests evaluated the hypothesis that the point of greatest hunting mortality demarcates age at first reproduction in moose. First, a study area in Newfoundland (MMU 16 located near MMU 24; see Table 1) estimated age at maturity (>50% of females; Sand & Cederlund 1996) as 3.5 years using Pimlott's (1959) data of *corpora lutea* counts obtained from moose ovaries (N = 347). I then calculated mortality rate of females using cohort analysis for the same population over the

subsequent years (1960-1966; Bergerud & Manuel 1968). Using the inflection point method I estimated age of maturity at 3.3 years, which compares with 3.5 years estimated independently from inspection of ovaries. For two northern Ontario populations 66 ovaries were examined for *corpora lutea* and more than 50% (6 of 11) of moose aged at 1.5 years in the autumn were pregnant for the first time (Cederwall & Ranta 1982, Bergerud & Snider 1988). These estimates (i.e. first reproduction at two years of age) agree with my independent estimates of age at first reproduction of 2.5 years of age using cohort analysis data to calculate the inflection point in survivorship. Second, for a hunted moose population in central British Columbia, a sample of 1,198 reproductive tracts estimated age at first reproduction at age 2.0, which was the same female age class that experienced the greatest hunting mortality (Heard et al. 1997; Fig. 2). Further evidence supporting the hypothesis that age at inflection in survivorship curves represents age at maturity is that the range in age at maturity between the 15 moose populations studied here (1.7-3.0 years) is similar to the range observed for 14 moose populations in Sweden (2.1-3.2 years; Sand & Cederlund 1996).

I tested the accuracy of cohort analysis to provide reasonable estimates of the number of female moose. The estimated number of females in each population from cohort analysis was correlated with aerial survey estimates ($r = 0.73$, $P = 0.002$, $N = 15$; Fig. 3).

Age at maturity was positively correlated with juve-

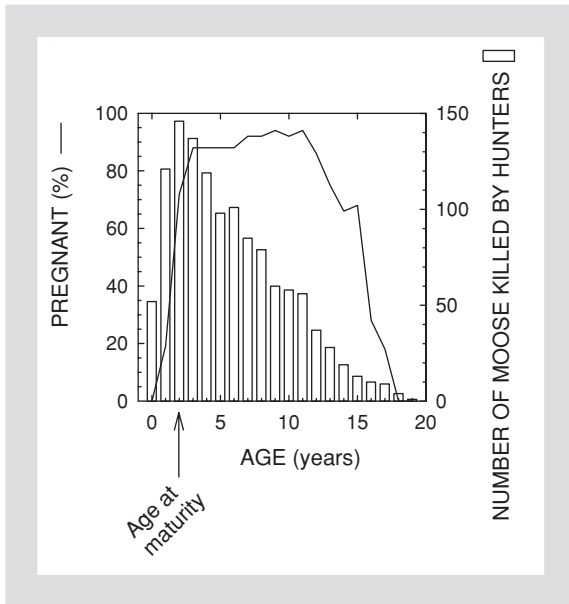


Figure 2. Age-specific mortality and pregnancy for central British Columbia moose (Heard et al. 1997). Age of the greatest number of moose shot by hunters (2.5 - 0.5 = 2.0 years; horizontal bars) agrees with age at first reproduction (2.0 years; line) defined as >50% of age class pregnant.

nile mortality within populations ($0.46 < r > 0.91$, $P < 0.01$, $N = 18-26$ years). Modelling population means for age at maturity and juvenile mortality indicated a curvilinear relationship (Fig. 4) that was best fit by a polynomial model ($y = y_0 + ax + bx^2$; logarithmic model $r^2 = 0.32$; power model $r^2 = 0.30$; and exponential model $r^2 = 0.23$). Among populations, age at maturity was negatively correlated with juvenile mortality ($r = -0.64$, $P = 0.01$, $N = 15$). Mean age at maturity among popu-

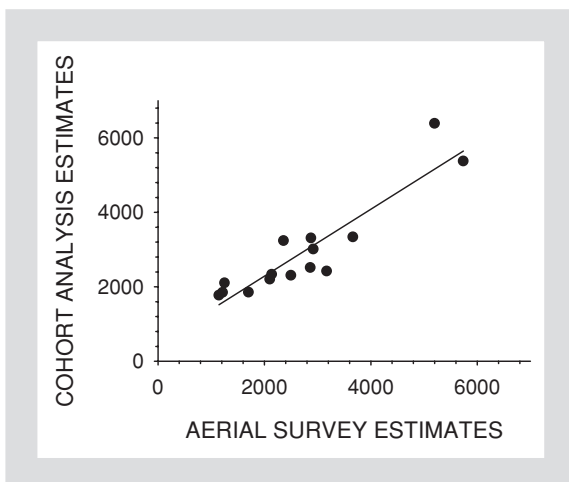


Figure 3. Comparison of number of moose estimated from cohort analysis and number of moose estimated from aerial surveys for the same year.

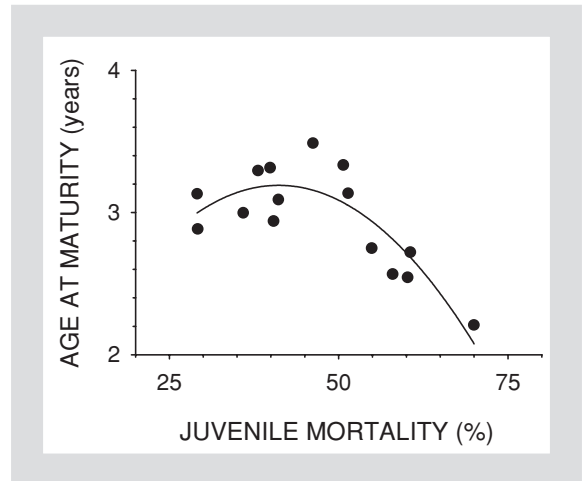


Figure 4. Plot of age of first reproduction against juvenile mortality for 15 Canadian moose populations. Model: $y = 0.925 + 0.110x - 0.00134x^2$, where y = age in years at maturity and x = % juvenile mortality; $r^2 = 0.72$, $F_{1,13} = 18.3$, $P = 0.001$.

lations ranged within 1.7-3.0 years and juvenile mortality varied from 29 to 70% of the total mortality (see Table 1). Ontario populations experienced the greatest juvenile mortality (mean = 64%) and had the earliest age at maturity (mean = 2.0 years), whereas the Newfoundland populations with low juvenile mortality (mean = 40%) had later age at maturity (mean = 2.7 years; see Table 1).

Discussion

Estimating age at maturity using survivorship curves provides the opportunity to test life-history theory. For example, is greater juvenile mortality among populations associated with earlier or later age at maturity (Cole 1954, Law 1979, Reznick & Endler 1982), or is recruitment and juvenile mortality related to density (Abrams & Rowe 1996, Sæther 1997)? The age-specific mortality hypothesis predicts that maturation should be attained at an earlier age if adult mortality increases relative to juvenile mortality, and the converse if adult mortality decreases (Gadgil & Bossert 1970, Charlesworth 1994, Abrams & Rowe 1996). Hunted populations have considerable demographic data available over long time periods and this method would allow for testing ecological theory. Moose are an appropriate species to test life-history predictions as females of temperate ungulates vary offspring size with habitat quality (Sadleir 1969, Clutton-Brock, Guinness & Albon 1982, McNamara & Houston 1992). Additionally, age and size at maturity vary with habitat quality (Albon, Clutton-Brock &

Guinness 1987, Sæther & Heim 1993, Festa-Bianchet, Jorgenson, Lucherini & Wishart 1995). If the age at inflection in the survivorship curve approximates age at maturity, researchers could measure age of first reproduction maturity determined from time series data.

Does the inflection point of survivorship curves approximate age at maturity? Theoretical models show that mortality influences both shape and position of maturation reaction norms (Stearns & Koella 1986, Perrin & Rubin 1990). Differential mortality between juvenile and adult stages in fish has often been shown to produce good predictions of maturation age (Hutchings 1993, Reznick, Butler, Rodd & Ross 1996). The mortality pattern of female moose in a Norwegian population was U-shaped with highest harvest mortality of less fecund young (1-3 years) age classes (Solberg et al. 2000). Testing this method requires estimated age at maturity from independent data such as *corpora lutea* counts of moose ovaries. Accuracy of the survivorship method of estimating age at maturity depends on the quality of data used in cohort analysis, particularly the sample size of female moose from hunter kills.

Data collected in long-term studies have provided evidence for demographic patterns throughout life that include the apparent inferiority of first-time breeders (i.e. breeding probability, reproductive success and survival). Bird and mammal studies have found evidence of 1) an increase in probability of breeding after the first reproduction (Wooller & Coulson 1977, Weimerskirch 1992, Boyd, Croxall, Lunn & Reid 1995, Cézilly, Viallefont, Boy & Johnson 1996), 2) an increase in breeding success after first reproduction (Nelson 1988, Gailard, Allainé, Pontier, Yoccoz & Promislow 1994, Lunn, Boyd & Croxall 1994, Forslund & Pärt 1995, Clutton-Brock, Stevenson, Marrow, MacColl, Houston & McNamara 1996, Cam & Monnat 2000), and 3) increased survival or return rate after initial reproduction (Wooller, Bradley, Skira & Serventy 1990, Promislow 1991, Chastel, Weimerskirch & Jouventin 1995, Clutton-Brock et al. 1996, Cam & Monnat 2000). Inferiority of first-time breeders (e.g. survival) may be due to inexperience in survival requirements (Newton 1985) that include behavioural mechanisms that minimize hunting mortality or greater proportional energy investment in reproduction relative to stored somatic energy (Ainley & DeMaster 1980, Promislow 1991, Künkele 2000) that may predispose low quality individuals to mortality.

For moose, predation effects generally exceed food effects (Messier 1994, 1995) and populations generally experience high predation by wolves on juveniles (Pimlott 1967, Keith 1974, 1983). In Ontario moose populations that live with wolf predation as the major mor-

tality factor age at maturity was earlier than in Newfoundland populations which live without wolf predation and with human hunting as the major mortality factor. Previous research found that low predation on juvenile moose in Newfoundland has led to decreased growth rate and fecundity (Ferguson et al. 2000), and now, later age at maturity relative to Ontario moose. Natural predators did not limit Newfoundland moose populations but instead limitation occurred by a combination of hunter predation and food limitation (Ferguson & Messier 1996). Apparently, the selective phenotypic response of moose populations in Newfoundland in the absence of significant natural predation on juveniles was for a shift to smaller body size, reduced fecundity, and later ages of first reproduction.

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References

- Abrams, P.A. & Rowe, L. 1996: The effects of predation on the age and size of maturity of prey. - *Evolution* 50: 1052-1061.
- Ainley, D.G. & DeMaster, D.P. 1980: Survival and mortality in a population of Adélie penguins. - *Ecology* 61: 522-530.
- Albon, S.D., Clutton-Brock, T.H. & Guinness, F.E. 1987: Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. - *Journal of Animal Ecology* 56: 69-81.
- Albright, C.A. & Keith, L.B. 1987: Population dynamics of moose, *Alces alces*, on the south-coast barrens of Newfoundland. - *Canadian Field-Naturalist* 101: 373-387.
- Bergerud, A.T. & Manuel, F. 1968: Moose damage to balsam fir-white birch forests in central Newfoundland. - *Journal of Wildlife Management* 32: 729-746.
- Bergerud, A.T. & Snider, B. 1988: Predation in the dynamics of moose populations: a reply. - *Journal of Wildlife Management* 47: 977-988.
- Boyd, I.L., Croxall, J.P., Lunn, N.J. & Reid, K. 1995: Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. - *Journal of Animal Ecology* 64: 505-518.
- Cam, E. & Monnat J-Y. 2000: Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. - *Journal of Animal Ecology* 69: 380-394.
- Caughey, G. 1966: Mortality patterns in mammals. - *Ecology* 47: 906-918.

- Caughley, G. 1977: Analysis of vertebrate populations. - Wiley, New York, New York, USA, pp. 584.
- Cederwall, K.E. & Ranta, W.B. 1982: Analysis of deer and moose ovaries in the Kenora District, 1976 to 1979. - Internal Report for Ontario Ministry of Natural Resources, pp. 31.
- Cézilly, F., Viallefont, A., Boy, V. & Johnson, A.R. 1996: Annual variation in survival and breeding probability in greater flamingos. - *Ecology* 77: 1143-1150.
- Charlesworth, B. 1994: Evolution in age-structured populations. 2nd edition. - Cambridge University Press, Cambridge, UK, 320 pp.
- Charnov, E.L. 1993: Life history invariants. - Oxford University Press, Oxford, United Kingdom, 167 pp.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1995: Influence of body condition on reproductive decision and reproductive success in the blue petrel. - *Auk* 112: 964-972.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: behavior and ecology of two sexes. - University of Chicago Press, Chicago, Illinois, USA, 378 pp.
- Clutton-Brock, T.H., Stevenson, I.R., Marrow, P., MacColl, A.D., Houston, A.I. & McNamara, J.M. 1996: Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. - *Journal of Animal Ecology* 65: 675-689.
- Cole, L.C. 1954: The population consequences of life history phenomena. - *Quarterly Review of Biology* 29: 103-137.
- Deriso, R.B., Quinn, T.J., II. & Neal, P.R. 1985: Catch-age analysis with auxiliary information. - *Canadian Journal of Fisheries and Aquatic Science* 42: 815-824.
- Eberhardt, L.L. 1985: Assessing the dynamics of wild populations. - *Journal of Wildlife Management* 49: 997-1012.
- Elowe, K.D. & Dodge, W.E. 1989: Factors affecting black bear reproductive success and cub survival. - *Journal of Wildlife Management* 53: 962-968.
- Ferguson, S.H. 1992: Newfoundland moose model I: harvest management based on relationship between productivity and vegetation. - Unpublished Internal Report Newfoundland & Labrador Wildlife Division. St. John's, NF, Canada, 23 pp.
- Ferguson, S.H. 1993: Use of cohort analysis to estimate abundance, recruitment and survivorship for Newfoundland moose. - *Alces* 29: 99-113.
- Ferguson, S.H. & Messier, F. 1996: Can human predation cause stable limit cycles in a moose population? - *Alces* 32: 149-161.
- Ferguson, S.H., Bisset, A.R. & Messier, F. 2000: The influences of density on growth and reproduction in moose *Alces alces*. - *Wildlife Biology* 6: 31-39.
- Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M. & Wishart, W.D. 1995: Life history consequences of variation in age of primiparity in bighorn ewes. - *Ecology* 76: 871-881.
- Forslund, P. & Pärt, T. 1995: Age and reproduction in birds-hypotheses and tests. - *Trends in Ecology and Evolution* 10: 374-378.
- Fryxell, J.M., Mercer, W.E. & Gellately, R.B. 1988: Population dynamics of Newfoundland moose using cohort analysis. - *Journal of Wildlife Management* 52: 14-21.
- Gadgil, M. & Bossert, W.H. 1970: Life historical consequences of natural selection. - *American Naturalist* 104: 1-24.
- Gaillard, J-M., Allainé, D., Pontier, D., Yoccoz, N.G. & Promislow, D.E.L. 1994: Senescence in natural populations of mammals: a reanalysis. - *Evolution* 48: 509-516.
- Gaillard, J-M., Delorme, D., Boutin, J.M., Laere, G.V. & Boisaubert, B. 1993: Roe deer survival patterns: a comparative analysis of contrasting populations. - *Journal of Animal Ecology* 62: 778-791.
- Gaillard, J-M., Festa-Bianchet, M. & Yoccoz, N.G. 1998: Population dynamics of large herbivores: variable recruitment with constant adult survival. - *Trends in Ecology and Evolution* 13: 58-63.
- Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000: Temporal variation in fitness components and population dynamics of large herbivores. - *Annual Review of Ecology and Systematics* 31: 367-393.
- Gaillard, J-M., Sempéré, A.J., Boutin, J.-M., Van Laere, G. & Boisaubert, B. 1992: Effects of age and body weight on the proportion of females breeding in a population of roe deer *Capreolus capreolus*. - *Canadian Journal of Zoology* 70: 1541-1545.
- Geist, V. 1974: On the evolution of reproductive potential in moose. - *Naturaliste canadien* 101: 527-537.
- Geist, V. 1987: On the evolution and adaptations of *Alces*. - *Swedish Wildlife Research Supplement* 1: 11-23.
- Gulland, J.A. 1983: Fish stock assessment: a manual of basic methods. - Wiley-Interscience Publications, John Wiley & Sons, New York, New York, USA, 223 pp.
- Heard, D., Barry, S., Watts, G. & Child, K. 1997: Fertility of female moose *Alces alces* in relation to age and body composition. - *Alces* 33: 165-176.
- Hewison, A.J.M. 1997: Evidence for a genetic component of female fecundity in British Roe Deer from studies of cranial morphometrics. - *Functional Ecology* 11: 508-517.
- Hutchings, J.A. 1993: Adaptive life histories effected by age-specific survival and growth rate. - *Ecology* 74: 673-684.
- Jorgenson, J.T., Festa-Bianchet, M., Gaillard, J-M. & Wishart W.D. 1997: Effects of age, sex, disease and density on survival of bighorn sheep. - *Ecology* 78: 1019-1032.
- Keith, L.B. 1974: Some features of population dynamics in mammals. - *Transactions of the International Congress of Game Biologists* 11: 17-58.
- Keith, L.B. 1983: Population dynamics of wolves. - In: Carbyn, L.N. (Ed.); *Wolves in Canada and Alaska: their status, biology and management*. Canadian Wildlife Service Report Series, No. 45, Ottawa, pp. 66-77.
- Krefting, L.W. 1975: Moose distribution and habitat selection in north central North America. - *Naturaliste canadien* 101: 81-100.
- Künkele, J. 2000: Does primiparity affect the efficiency of converting energy to offspring production in the guinea-pig? - *Canadian Journal of Zoology* 78: 300-306.
- Larivière, S. & Crête, M. 1993: The size of eastern coyotes

- (*Canis latrans*): a comment. - *Journal of Mammalogy* 74: 1072-1074.
- Larson, R.E., Hostetler, R.P. & Edwards, B.H. 1990: Calculus of a single variable. 4th edition. - D.C. Heath, Lexington, Massachusetts, USA, 344 pp.
- Law, R. 1979: Optimal life histories under age-specific predation. - *American Naturalist* 114: 399-417.
- Linnell, J.D.C., Aanes, R. & Andersen, R. 1995: Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. - *Wildlife Biology* 1: 209-223.
- Lunn, N.J., Boyd, I.L. & Croxall, J.P. 1994: Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. - *Journal of Animal Ecology* 63: 827-840.
- McNamara, J.M. & Houston, A.I. 1992: State-dependent life-history theory and its implications for optimal clutch size. - *Evolutionary Ecology* 6: 170-185.
- Messier, F. 1994: Ungulate population models with predation: a case study with the North American moose. - *Ecology* 75: 478-488.
- Messier, F. 1995: Trophic interactions in two northern wolf-ungulate systems. - *Wildlife Research* 22: 131-146.
- Messier, F., Huot, J., Le Hénaff, D. & Luttich, S. 1988: Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. - *Arctic* 41: 279-287.
- Nelson, J.B. 1988: Age and breeding in seabirds. - *Proceedings of the International Ornithological Congress* 19: 1081-1097.
- Newton, I. 1985: Lifetime reproduction output of female sparrowhawks. - *Journal of Animal Ecology* 54: 241-253.
- Perrin, N. & J.F. Rubin. 1990: On dome-shaped norms of reaction for size-to-age at maturity in fishes. - *Functional Ecology* 4: 53-57.
- Pimlott, D.H. 1959: Reproduction and productivity of Newfoundland moose. - *Journal of Wildlife Management* 23: 381-401.
- Pimlott, D.H. 1967: Wolf predation and ungulate populations. - *American Zoologist* 7: 267-278.
- Promislow, D.E.L. 1991: Senescence in natural populations of mammals: a comparative study. - *Evolution* 45: 1869-1887.
- Reznick, D. & Endler, J.A. 1982: The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). - *Evolution* 36: 160-177.
- Reznick, D., Butler IV, M.J., Rodd, F.H. & Ross, P. 1996: Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. - *Evolution* 50: 1651-1660.
- Rowe, J.S. 1972: Forest regions of Canada. - Canadian Forestry Service, Publication No. 1300, 171 pp.
- Roff, D.A. 1992: The evolution of life histories: theories and analysis. - Chapman & Hall, New York, New York, USA, 243 pp.
- Sadleir, R.M.F.S. 1969: The ecology of reproduction in wild and domestic animals. - Methuen, London, United Kingdom, 321 pp.
- Sand, H. & Cederlund, G. 1996: Individual and geographical variation in age at maturity in female moose (*Alces alces*). - *Canadian Journal of Zoology* 74: 954-964.
- Sæther, B-E. 1997: Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. - *Trends in Ecology & Evolution* 12: 143-149.
- Sæther, B-E. & Haagenrud, H. 1985: Life history of the moose *Alces alces*: relationship between growth and reproduction. - *Holarctic Ecology* 8: 100-106.
- Sæther, B-E. & Heim, M. 1993: Ecological correlates of the moose (*Alces alces*): the effects of environmental variability. - *Journal of Animal Ecology* 62: 482-489.
- Sergeant, D.E. & Pimlott, D.H. 1959: Age determination in moose from sectioned incisor teeth. - *Journal of Wildlife Management* 23: 315-321.
- Sibly, R.M., Collett, D., Promislow, D.E.L., Peacock, D.J. & Harvey, P.H. 1997: Mortality rates of mammals. - *Journal of Zoology, London* 243: 1-12.
- Siler, W. 1979: A competing-risk model for animal mortality. - *Ecology* 60: 50-757.
- Sokal, R.R. & Rohlf, F.J. 1981: *Biometry*. - W.H. Freeman and Company, New York, New York, USA, 859 pp.
- Solberg, E.J., Sæther, B-E., Strand, O. & Loison, A. 1999: Dynamics of a harvested moose population in a variable environment. - *Journal of Animal Ecology* 68: 186-204.
- Solberg, E.J., Loison, A., Sæther, B-E. & Strand, O. 2000: Age-specific harvest mortality in a Norwegian moose (*Alces alces*) population. - *Wildlife Biology* 6: 41-52.
- Stearns, S.C. 1992: *The evolution of life histories*. - Oxford University Press, New York, New York, USA, 249 pp.
- Stearns, S.C. & Koella, J.C. 1986: The evolution of phenotypic plasticity in life-history traits: prediction of reaction norms forage and size at maturity. - *Evolution* 40: 893-913.
- Timmermann, H.R. & Whitlaw, H.A. 1992: Selective moose harvest in North Central Ontario - a progress report. - *Alces* 28: 1-7.
- Weimerskirch, H. 1992: Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. - *Oikos* 64: 464-473.
- Wooller, R.D. & Coulson, J.C. 1977: Factors affecting the age of first breeding of the kittiwake *Rissa tridactyla*. - *Ibis* 119: 339-349.
- Wooller, R.D., Bradley, J.S., Skira, I.J. & Serventy, D.L. 1990: Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. - *Journal of Animal Ecology* 59: 161-170.