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The influences of density on growth and reproduction in moose *Alces alces*

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We test whether high moose density results in smaller moose, slower growth rates, lower reproductive rates, and more variable year-to-year population size by comparing demographic characteristics of 15 Canadian moose *Alces alces* populations that spanned a range of population density (0.08-4.5 moose/km^2). Density negatively affected growth rate, reproductive rates and recruitment. We argue that primary productivity, measured as percent forest cover, and natural predation link density to reproduction in moose. Populations that lived in greater forest cover and experienced greater natural predation were associated with more predictable year-to-year variation in population size. In contrast, moose populations living in areas of low forest cover and low natural predation experienced greater density independent food limitation and greater unpredictability in population size. Thus, moose populations living in areas of low primary productivity and low natural predation show less persistence and require greater conservation efforts.

Key words: conservation, demography, density-dependence, Hurst exponent, life-history, recruitment, reproduction, stochasticity, unpredictability

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Life history theory describes trade-offs among density, growth, mortality and reproduction (reviewed in Roff 1992, Stearns 1992, Charnov 1993). Lower growth and reproductive rates are predicted when density increases and food quality decreases (Gadgil & Bossert 1970, Stearns & Koella 1986, Abrams & Rowe 1996, Arendt 1997). We use moose *Alces alces* to test for density-related trade-offs. Moose populations living with wolf *Canis lupus* and bear *Ursus* predators generally exhibit densities below 0.5 animals/km^2 (Messier 1994) whereas moose populations without major predators may exceed 2.0 animals/km^2 (Cederlund & Sand 1991, Oosenbrug & Ferguson 1992).

Study areas included four populations in Ontario characterized by regulating wolf predation that targeted juveniles (Messier & Crête 1985, Gasaway, Boertje, Grangaard, Kelleyhouse, Stephenson & Larsen 1992) and 11 populations in Newfoundland characterized by non-selective hunting mortality with varying degrees of food limitation (Albright & Keith 1987, Ferguson & Messier 1996a). Newfoundland moose density varied from 0.5 to 4.0 moose/km^2

(Ferguson 1993) with a human harvest of approximately 20% of the moose population per year (Ferguson & Messier 1996a). Black bears *Ursus americanus* are their only natural predators. Moose were introduced to Newfoundland from Nova Scotia in 1878 and 1904 (Pimlott 1953). The moose from Nova Scotia had lived without wolf predation since permanent settlement by Europeans in the 1700s and low juvenile mortality has characterized their life history (Dodds 1975). The Ontario moose populations were located >1,000 km to the east of Newfoundland and average moose density varied from 0.08 to 0.5/km^2 (Timmermann & Whitlaw 1992, Table 1). Moose have lived in northern Ontario since at least the 1600s (Krefting 1975) and high juvenile predation due to wolves and black bears has dominated their life history (Frenzel 1975, van Ballenberghe & Ballard 1994). Studies of moose genetic diversity show that Newfoundland and maritime Canada moose are genetically distinct from western Canada moose (Broders, Mahoney, Montevecchi & Davidson 1999) suggesting that life history differences may have a genetic basis.

As with most temperate ungulates, moose have evolved flexible reproduction as an adaptation to the highly changeable environments that they exploit (Geist 1974, 1987). Variable yearling pregnancy rates, age at maturity, and twinning rates reflect phenotypic plasticity in moose reproductive biology (Boer 1992). Here, we describe the influences of density on reproduction, growth rate, and year-to-year variation in population size by comparing moose populations over a wide range of mean density. We predicted that good quality habitat would have greater forest cover, larger moose, faster moose growth rates, and greater reproductive rates. The result of the correlation analysis can be summarized as follows: density was related to body growth and reproduction in moose with populations at low density experiencing high predation (including hunting), large body weight, fast body growth, high reproductive rates, and less year-to-year variation in population size.

Methods

Study areas

Both the Newfoundland and the Ontario study areas lie within the boreal forest region (Rowe 1972; Fig. 1). The boreal zone varies considerably, ranging from an area of some southern influence to areas of thin glacial soils and exposed bedrock. The region is dominated by conifer species including *Picea mariana*, *P. glauca*, *Abies balsamea* and *Pinus banksiana*. Less abundant deciduous trees include *Populus tremuloides* and *Betula papyrifera*. For Newfoundland, moose populations located on the Northern Peninsula (MMU 3; A in Fig. 1) and the South Coast (MMU 18 & 19; B in Fig. 1) were located in areas with little forest cover and characterized by the greatest maritime influences that included heavy precipitation (1,200-1,700 mm), intermittent snow cover and frequent freezing rain in late winter (Banfield 1983). The moose population located on the Avalon Peninsula (MMU 36; D in Fig. 1) resided in areas of low forest cover but more mild winters. Moose populations located in the interior of Newfoundland were located in areas of high forest

Table 1. Demographic statistics for 15 Canadian moose populations.

Population	Area (km^2)	Location		% hunter harvest	Moose density[1]	% forest	Unpredictability of population size[2]	Coefficient of variation
		Latitude	Longitude					
WMU 13[3]	13325	48° 40'	89° 23'	20.4	0.36	75.9	0.75	19.9
Dist. 13	9759	49° 40'	90° 21'	20.8	0.25	83.5	0.89	21.3
Dist. 15	57670	51° 31'	90° 50'	17.2	0.28	89.8	0.81	15.1
Dist. 16	103023	51° 49'	93° 28'	22.2	0.08	89.1	0.80	41.6
MMU 3	3580	50° 25'	56° 44'	3.4	2.35	25.8	0.47	5.2
MMU 7	1720	49° 6'	57° 30'	11.2	1.37	57.0	0.62	7.2
MMU 9	809	48° 7'	58° 52'	6.7	4.54	59.0	0.43	8.7
MMU 11	2844	48° 10'	58° 8'	7.4	1.21	26.9	0.71	9.9
MMU 16	1676	48° 39'	56° 4'	7.0	1.93	51.8	0.97	47.9
MMU 18	3871	48° 14'	56° 23'	10.2	1.12	13.5	0.46	8.1
MMU 19	2228	47° 53'	57° 48'	3.9	1.24	6.2	0.42	11.3
MMU 22	2015	49° 14'	54° 48'	8.6	3.77	65.5	0.66	25.9
MMU 23	4302	49° 11'	53° 58'	9.1	2.21	54.4	0.66	12.0
MMU 24	910	48° 49'	55° 3'	16.1	2.57	64.1	0.63	26.5
MMU 36	3469	47° 2'	53° 15'	21.7	1.94	20.2	0.85	15.2

[1] Moose/km^2 from Ferguson (1992) and Whitlaw et al. (1993)
[2] Hurst exponent measures unpredictability of total population size (see Methods)
[3] WMU & Dist. for Ontario and MMU for Newfoundland

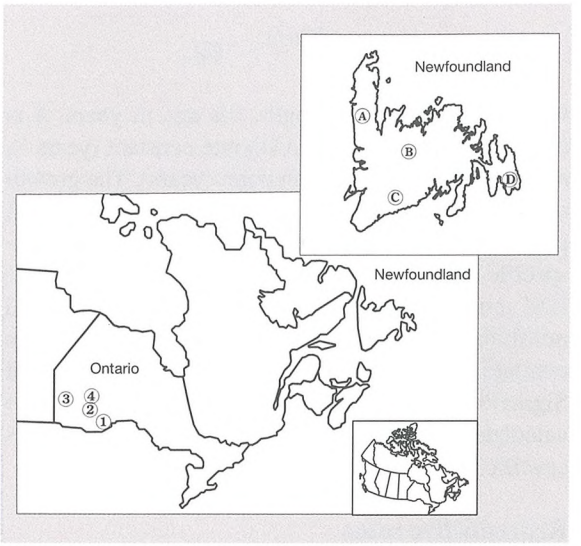

Figure 1. Location of 15 moose populations in Ontario (1-4) and Newfoundland & Labrador (A-D), Canada. For Ontario populations, 1 refers to WMU 13; 2 to Dist. 13; 3 to Dist. 15; and 4 to Dist. 16 (see Table 1). For Newfoundland populations, A refers to MMU 3; B to MMU 7, 9, 11, 16, 22, 23 and 24; C to MMU 18 & 19; and D to MMU 36.

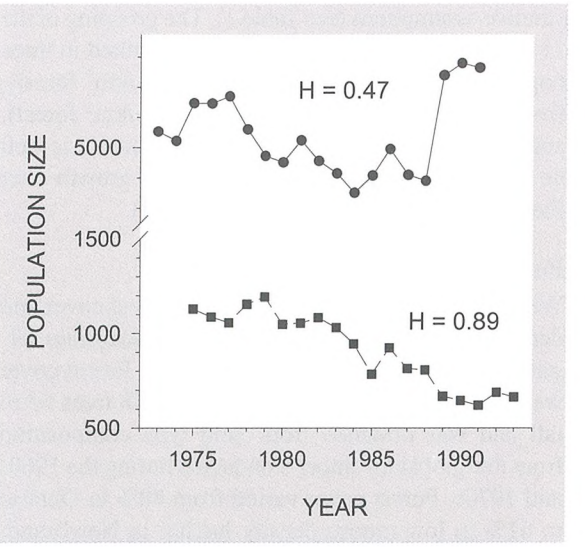

Figure 2. Contrasting two moose populations showing dissimilar patterns in year-to-year fluctuations in population size. The Hurst exponent (H) measured predictability of population size. Line at top shows a near random series of population sizes (H = 0.5) for a moose population not exposed to wolf predation (MMU 3; see Table 1). Line at bottom shows a trend-reinforcing or highly correlated time series of population sizes (H = 0.9) for a population exposed to wolf predation (Dist. 13; see Table 1).

cover characterized by colder and drier winters (75% of winter precipitation falls as snow and snow cover remains more continuous) and warmer and moderately sunny summers (Banfield 1983).

Variation and unpredictability of population size

We used coefficient of variation and Hurst exponent to evaluate year-to-year variability in total population size. Coefficient of variation (CV) measured temporal variability of moose abundance (Gaston & McArdle 1994). Year-to-year variability was estimated from ca 20 year time series data obtained from cohort analysis of hunter statistics (see Ferguson 1993, Ferguson 1996a). We used the last 19 years of data to compare CV among populations to avoid bias due to differences in sample sizes.

In contrast, Hurst exponent (H) evaluated unpredictability of total population size for each moose population, a different quality than parametric measures of dispersion (Peters 1991, Cox & Wang 1993, Arino & Pimm 1995, Ferguson & Messier 1996b). H close to 0.5 describes a close to random series of events that are uncorrelated, whereas H approaching 1.0 indicates a persistent, or trend-reinforcing, series (Fig. 2). We used the Hurst growth of range correlation estimated using a Turbo Pascal program written by Hastings & Sugihara (1993: 57-61) that follows a general power law relationship characteristic of fractal patterns:

$$\log(\text{range}) = \text{constant} + H^*\log(\Delta t) \qquad (1).$$

Density

Moose density estimates came from Ferguson (1992) for Newfoundland populations and Whitlaw, Timmermann, Pernsky & Bisset (1993) for Ontario populations and both are based on aerial surveys (Bergerud & Manuel 1969, Oosenbrug & Ferguson 1992, Timmermann & Whitlaw 1992). For Newfoundland, aerial survey density estimates were mostly done by helicopter in winter by counting moose on 4-km^2 quadrats whereas Ontario aerial surveys were mostly conducted using strip transect censusing.

Newfoundland moose populations were grouped using cluster analysis according to habitat quality defined according to habitat characteristics, hunter statistics, and demographic parameters (Ferguson, Mercer & Oosenbrug 1989). This classification was used in moose growth and reproductive tests to maximize the number of populations (20 populations; see Appendix I) whereas cohort analysis was performed on only 11 Newfoundland moose populations due to more re-

strictive assumptions (see Table 1). The grouping of the 11 Newfoundland moose populations resulted in three populations in good habitat (<5 moose/km^2 forest), five in intermediate habitat (5-9 moose/km^2 forest), and two in poor habitat (>9 moose/km^2 forest), as well as a recent population that experienced growth over the study period (MMU 36; see Table 1).

Forest cover

We predicted a relationship between forest cover and density as found for white-tailed deer *Odocoileus virginianus* by Roseberry & Woolf (1998). Forest cover was estimated as the percentage area with trees >3 m tall and was obtained from land type composition from the 'global inventory' conducted during the 1960s and 1970s. Forest cover varied from 88% in Ontario to 61% in low moose density habitat in Newfoundland to 42% in medium moose density habitat and 16% in high moose density habitat.

Growth rates

Weights of moose by age, sex and location were obtained from a butchering facility in Manuels, Newfoundland (Murrays Meats Inc.) for the years 1990 and 1991 (N = 261; Mercer, Porter, Ferguson & Oosenbrug 1988). Total weights of carcasses with skin and viscera removed were obtained by summing the weights of quarters (N = 14 Newfoundland moose populations).

Lower mandibles were collected from hunters (samples ranged from 299 to 1,752 females per MMU) and covered 19-23 continuous years (see Ferguson 1992 and Appendix I). Each mandible was cleaned and total jaw length was measured to the nearest 1.0 mm. Mandible length was the distance between the point where the first incisor enters the gum at the anterior end and the tip of the angular process at the posterior (cranial) end (Lowe 1972).

Linear measurements of the mandible are commonly used as indices of skeletal development (Mitchell et al. 1976, Nugent & Frampton 1994, Hewison, Vincent, Bideau, Angibault & Putman 1996). The mandible has a high growth priority over other bones shortly after birth while reduction of mandible growth occurs sometime during the second year of life (Huot 1988). Length of mandibles for yearlings is likely a sensitive indicator of individual growth rate in a population (Sand & Cederlund 1996).

We calculated growth of female mandible length by applying the Gompertz sigmoidal growth equation (Zullinger, Ricklefs, Redford & Mace 1984) to data on Newfoundland moose populations:

$$L_t = A \cdot e^{-e^{-K(t-I)}} \quad (2),$$

where L_t is mandible length, t is age in years, A is asymptotic length, K is growth rate constant (years^{-1}), and I is age at the inflection point (years). The growth model was fitted to mandible length data for each population to provide growth parameters for intraspecific (populations) comparisons (N = 9 Newfoundland moose populations). Some population data did not fit the model and results were not included in the comparisons. The non-linear estimation procedure of SigmaPlot (Jandel Scientific Software) was used to calculate estimates for the parameters of the size-specific Gompertz model.

Reproductive rates

Reproductive rates (% yearlings pregnant, % adults pregnant, and % twins) were obtained from published reports of *corpora lutea* counts (Pimlott 1959, Simkin 1965, Bergerud et al. 1983, Cederwall & Ranta 1982, Albright & Keith 1987) whereas recruitment (calf survival to 0.5 years of age) was estimated from hunter harvest information as the proportion of total harvest consisting of calves (Ferguson et al. 1989, Timmermann & Whitlaw 1992).

Statistical analyses

Statistical tests included log-linear models for binomial data (% pregnant) and ANOVA for continuous data. Significant log-linear differences were followed by multi-comparison tests according to Siegel & Castellan (1988: 195-197). Significant ANOVA tests were followed by Tukey's multiple comparison test. All data were log transformed to ensure normality. Analyses were done using SAS (SAS Institute Inc. 1987) statistical software for microcomputers.

Results

Density was related to body growth and reproduction in moose. Populations at high densities experienced: a) low predation (including hunting), b) small body weight, c) slow body growth, d) low reproductive rates, e) low recruitment, and f) greater year-to-year variation in population size. In Newfoundland, the amount of forested area negatively correlated with moose density (r = 0.65, P = 0.03, N = 11; see Table 1). Therefore, we used moose/km^2 forest as a measure of density.

Table 2. Moose growth statistics for Newfoundland populations.

Variable	Population density[1] Low	Medium	High	F	P
Body size from carcass weights (kg):					
Female 1-year	a[2]132 (4)	a 118 (9)	a 111 (2)	2.99	0.07
Male 1-year	a 144 (7)	b 112(12)	c 99 (3)	8.61	<0.01
Female >4-years	a 171 (5)	a 163 (9)	a 161 (1)	0.25	0.78
Male >5-years	a 258 (6)	b 145 (6)	b 140 (2)	9.43	<0.01
Gompertz growth formula for female mandible length (mm):					
Growth constant	a 15.6(3)	a 18.2(4)	b 2.4 (2)	10.51	0.01
Asymptote	a 444 (3)	a 449 (4)	a 436 (2)	1.70	0.26

[1] Population density (Low = 4.6, medium = 4.9, high = 9.4 moose/km^2 forest) within population boundaries (Ferguson et al. 1989)
[2] Means with the same letters within a row are not significantly different according to Tukey's test

a) Percent human harvest was negatively correlated with moose density (moose/km^2 forest) with high density areas in Newfoundland experiencing the lowest harvest ($r = -0.71$, $P = 0.003$, $N = 15$; see Table 1). We tested for a geographic effect using partial correlation analysis and found that province ($F_{1,12} = 0.00$, $P = 0.98$) did not have a significant effect on the percent harvest*density relationship.
b) Adult and yearling male moose were larger in low density areas whereas female moose weight did not differ with density. Yearling males (1.5 years old) differed in body weight for populations living in high (99 kg), medium (112 kg), and low (144 kg) densities (Table 2). Similarly, adult males (>5 years old) differed in body weight for populations living in high (140 kg), medium (145 kg), and low (258 kg) densities (see Table 2). In contrast, adult female (>4 years old) and yearling female body weights did not vary with density.
c) In Newfoundland, female moose from low and medium density populations had higher body growth rates than high density populations as measured by mandible growth constant (15.6 vs 2.4; see Table 2). Asymptotes (maximum body size) did not differ for female moose from different density populations. Sample sizes for male moose were not sufficient to calculate growth rates.
d) Moose reproduction also varied with density (Table 3). Pregnancy rates decreased from 97% in Ontario to 87% in low density areas to 77% in medium density areas in Newfoundland, respectively. Percent twins decreased from 49% in Ontario to 41% in low density areas to 5% in medium density areas to 1% in high density areas in Newfoundland, respectively. Pregnant yearlings increased from 54% in Ontario to 64% in low density areas to 38% in high density areas in Newfoundland, respectively.
e) Low moose density populations had greater recruitment than medium or high density populations (8.8 calves vs 3.1 calves per 100 females in hunter harvest; see Table 2).
f) Population density (moose/km^2 forest) did not correlate with year-to-year variation in population size (coefficient of variation; $r = -0.44$, $P = 0.09$, $N = 15$;

Table 3. Moose reproduction statistics for 15 Canadian populations.

Variable	Ontario	Newfoundland Population density[1] Low	Medium	High	Statistical test F df	X	P
Reproductive rates:							
Yearling % pregnant	a[2]54(80)	a 67 (18)	b 38 (45)	NA[3]	2	5.13	0.02
Adult % pregnant	a 97(244)	b 87 (38)	c 77 (132)	NA	2	37.5	<0.001
% Twins	a 49(214)	a 41 (29)	b 5 (99)	c 1 (107)	3	183.9	<0.001
Recruitment:							
% Calves (hunter kill)	a 18.5(5)	b 8.8 (4)	bc 6.0 (5)	c 3.1 (2)	3,14	8.58	0.01

[1] Population density (Low = 4.6, medium = 4.9, high = 9.4 moose/km^{-2} forest) within population boundaries (Ferguson et al. 1989).
[2] Means with the same letters within a row are not significantly different according to Tukey's test (F) or Chi-square multi-comparison test (X).
[3] Data not available.

see Table 1). In contrast, population density was negatively correlated with year-to-year changes in population size (Hurst exponent: r = -0.59, P = 0.02, N = 15; see Table 1). Thus, moose populations in Ontario were characterized by more predictable year-to-year changes in population size and greater persistence, whereas Newfoundland population size was characterized by more random, uncorrelated year-to-year changes.

Discussion

Density was the major factor associated with variation in growth and reproduction in moose. Under most natural conditions, predation regulates prey (Arditi & Berryman 1991) and density dependent effects will predominate (Putman, Langbein, Hewison & Sharma 1996). This is the case for moose, where predation effects generally exceed food effects (Messier 1994, 1995). Natural predators of moose reduce prey density resulting in an adequate food supply for the prey. As a result, high predation by wolves and black bears on juveniles (Pimlott 1967, Keith 1974, 1983, Gasaway et al. 1992) has led to high growth rate of moose, high reproductive rates, and early age at maturity (Geist 1987, Boer 1992).

In the absence of high predation on juveniles, moose populations increase density resulting in reduced habitat quality. In Newfoundland, population responses to high density relative to low primary productivity (% forest cover) were decreased body growth rate, decreased reproduction, and decreased recruitment. Newfoundland populations were not limited by natural predators but instead by a combination of hunter predation and food limitation (Albright & Keith 1987, Ferguson & Messier 1996a). Apparently, the selective phenotypic response of moose populations in Newfoundland was for a shift to smaller body size and reduced reproductive rates. Females of temperate ungulates vary offspring size and quality (Sadleir 1969, Clutton-Brock, Guinness & Albon 1982, Bronson 1989, Verme 1989, McNamara & Houston 1992) and age and size at maturity with habitat quality (White 1983, Albon, Clutton-Brock & Guinness 1987, Reimers 1983, Sæther & Heim 1993, Festa-Bianchet, Jorgenson, Lucherini & Wishart 1995, Sand & Cederlund 1996). Thus, the pattern of density-dependent predation and density-independent food limitation selecting for different growth and reproductive rates in moose may also occur in other ungulates. For example, North American woodland caribou *Rangifer tarandus caribou* experience greater juvenile mortality and earlier age at maturity relative to barren ground caribou *R.t. groenlandicus* and wild reindeer *R.t. tarandus* (Dauphine 1976, Bergerud 1980, Leader-Williams & Ricketts 1982, Skogland 1989).

Variation and unpredictability of environmental variables may be as important as their means in selecting for optimal life history traits (Schaffer 1974, Tuljapurkar 1982, Bulmer 1985, Boyce & Perrins 1987, Benton, Grant & Clutton-Brock 1995). For example, stochastic effects of climate on population viability has been demonstrated in Scandinavian moose (Sæther, Andersen & Hjeljord 1996, Solberg, Sæther & Strand 1999). We found more persistent, or trend-reinforcing behaviour (i.e. high Hurst exponent), for moose populations occurring at low density in areas of high primary productivity. Ontario moose populations are regulated at low densities by wolf predation (Bergerud et al. 1983) and live in more stable forested environments. Possibly as a result, Ontario moose populations showed more predictable year-to-year changes in density. In contrast, for Newfoundland moose populations living in poor quality habitats (low forest cover), density independent food limitation due to winter severity strongly influenced population demography (Albright & Keith 1987). As a result, Newfoundland moose populations experienced unpredictable year-to-year variations in population size (i.e. low Hurst exponent), relatively high densities, and variable food availability due to climatic effects. A possible life-history response to environmental stochasticity is a spreading out of the risk of reproductive failure by delaying maturation, extending interbirth interval and living longer (i.e. bet hedging; Murphy 1968, Schaffer 1974, Ferguson, Virgl & Larivière 1996, Simons & Johnston 1997). Future investigations can test for these life-history effects by using the intraspecific comparative method.

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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.

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.

Arditi, R. & Berryman, A.A. 1991: The biological control paradox. - Trends in Ecology & Evolution 6: 32.

Arendt, J.D. 1997: Adaptive intrinsic growth rates: an integration across taxa. - Quarterly Review of Biology 72: 149-177.

Arino, A. & Pimm, S.L. 1995: On the nature of population extremes. - Evolutionary Ecology 9: 429-443.

Banfield, C.E. 1983: Climate. - In: South, G.R. (Ed.); Biogeography and ecology of the island of Newfoundland. Dr. W. Junk Publishers, Hague, pp. 37-106.

Benton, T.G., Grant. A. & Clutton-Brock, T.H. 1995: Does environmental stochasticity matter? Analysis of red deer life-histories on Rhum. - Evolutionary Ecology 9: 559-574.

Bergerud, A.T. 1980: A review of the population dynamics of caribou and wild reindeer in North America. - In: Reimers, E., Gaare, E. & Skjenneberg, S. (Eds.); International Reindeer/Caribou Symposium 2: 556-581.

Bergerud, A.T., Wyett, W. & Snider, B. 1983: The role of wolf predation on limiting a moose population. - Journal of Wildlife Management 47: 977-988.

Bergerud, A.T. & Manuel, F. 1969: Aerial census of moose in central Newfoundland. - Journal of Wildlife Management 33: 910-916.

Boer, A.H. 1992: Fecundity of North American moose (Alces alces): a review. - Alces Supplement 1: 1-10.

Boyce, M.S. & Perrins, C.M. 1987: Optimizing Great Tit clutch size in a fluctuating environment. - Ecology 68: 142-153.

Broders, H.G., Mahoney, S.P., Montevecchi, W.A. & Davidson, W.S. 1999: Population genetic structure and the effect of founder events on the genetic variability of moose Alces alces in Canada. - Molecular Ecology 8: 1309-1315.

Bronson, F.H. 1989: Mammalian reproductive biology. - University of Chicago Press, Chicago, 325 pp.

Bulmer, M.G. 1985: Selection for iteroparity in a variable environment. - American Naturalist 126: 3-71.

Cederlund, G. & Sand, H.K.G. 1991: Population dynamics and yield of a moose population without predators. - Alces 27: 31-40.

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, 31 pp.

Charnov, E.L. 1993: Life history invariants. - Oxford University Press, Oxford, 167 pp.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982: Red deer: behaviour and ecology of two sexes. - University of Chicago Press, Chicago, 378 pp.

Cox, L.B. & Wang, J.S.Y. 1993: Fractal surfaces: measurement and applications in earth sciences. - Fractals 1: 87-117.

Dauphine, T.C. 1976: Biology of the Kaminuriak population of barren ground caribou, Part 4. Growth, reproduction and energy reserves. - Canadian Wildlife Service Report Series 38: 1-69.

Dodds, D.G. 1975: Distribution, habitat and status of moose in the Atlantic provinces of Canada and northeastern USA. - Naturaliste canadien 101: 51-65.

Ferguson, S.H. 1992: Newfoundland moose model I: harvest management based on relationship between productivity and vegetation. - Unpublished Internal Report for Newfoundland & Labrador Wildlife Division, 36 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., Mercer, W.E. & Oosenbrug, S.M. 1989: The relationship between hunter accessibility and moose condition in Newfoundland. - Alces 25: 36-47.

Ferguson, S.H. & Messier, F. 1996a: Can human predation cause stable limit cycles in a moose population? - Alces 32: 149-161.

Ferguson, S.H. & Messier, F. 1996b: Ecological implications of a latitudinal gradient in inter-annual climatic variability: a test using fractal and chaos theories. - Ecography 19: 382-392.

Ferguson, S.H., Virgl, J.A. & Larivière, S. 1996: Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. - Écoscience 3: 7-17.

Festa-Bianchet, M., Jorgenson, J.T., Lucherini, M. & Wishart, W.D. 1995: Live history consequences of variation in age of primiparity in bighorn ewes. - Ecology 76: 871-881.

Frenzel, L.D. 1975: Occurrence of moose in food of wolves as revealed by scat analyses: a review of North American studies. - Naturaliste canadien 101: 467-479.

Gadgil, M. & Bossert, W.H. 1970: Life historical consequences of natural selection. - American Naturalist 104: 1-24.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, R.O. & Larsen, D.G. 1992: The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. - Wildlife Monographs 120: 1-59.

Gaston, K.J. & McArdle, B.H. 1994: The temporal variability of animal abundances: measures, methods and patterns. - Philosophical Transactions of the Royal Society of London, Series B 345: 335-358.

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.

Hastings, H.M. & Sugihara, G. 1993: Fractals: a user's guide for the natural sciences. - Oxford University Press, Oxford, 235 pp.

Hewison, A.J.M., Vincent, J.P., Bideau, E., Angibault, J.M. & Putman, R.J. 1996: Variation in cohort mandible size as an index of roe deer (Capreolus capreolus) densities and population trends. - Journal of Zoology, London, 239: 573-581.

Huot, J. 1988: Review of methods for evaluating the physical condition of wild ungulates in northern environments. - Centre d'Etudes Nordiques, University of Laval, Québec, 164 pp.

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.

Leader-Williams, N. & Ricketts, C. 1982: Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. - Oikos 38: 27-39.

Lowe, V.P.W. 1972: Variation in mandible length and body weight of red deer (Cervus elaphus). - Journal of Zoology, London 166: 303-311.

McNamara, J.M. & Houston, A.I. 1992: State-dependent life-history theory and its implications for optimal clutch size. - Evolutionary Ecology 6: 170-185.

Mercer, W.E., Porter, R.M., Ferguson, S.H. & Oosenbrug, S. 1988: Moose management Newfoundland island. - Unpublished Report to Resource Policy Commission Newfoundland & Labrador Wildlife Division, Research & Management Section, 78 pp.

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. & Crête, M. 1985: Moose-wolf dynamics and the natural regulation of moose populations. - Oecologia 65: 503-512.

Mitchell, B., McCowan, D. & Nicholson, I.A. 1976: Annual cycles of body weight and condition in Scottish red deer. - Journal of Zoology 180: 107-127.

Murphy, G.I. 1968: Pattern in life history and the environment. - American Naturalist 102: 391-403.

Nugent, G. & Frampton, C. 1994: Microgeographic and temporal variation in mandible size within a New Zealand fallow deer (Dama dama) population. - Journal of Applied Ecology 31: 253-262.

Oosenbrug, S.M. & Ferguson, S.H. 1992: Moose mark-recapture survey in Newfoundland. - Alces 28: 21-30.

Peters, E.E. 1991: Chaos and order in the capital markets. - John Wiley & Sons, New York, 240 pp.

Pimlott, D.H. 1953: Newfoundland moose. - Transactions of the North American Wildlife Conference 18: 2.

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.

Putman, R.J., Langbein, J., Hewison, A.J.M. & Sharma, S.K. 1996: Relative roles of density-dependent and density-independent factors in population dynamics of British deer. - Mammal Review 26: 81-101.

Reimers, E. 1983: Reproduction in wild reindeer in Norway. - Canadian Journal of Zoology 61: 211-217.

Roff, D.A. 1992: The evolution of life histories: theories and analysis. - Chapman & Hall, New York, 243 pp.

Roseberry, J.L. & Woolf, A. 1998: Habitat-population density relationships for white-tailed deer in Illinois. - Wildlife Society Bulletin 26: 252-258.

Rowe, J.S. 1972: Forest regions of Canada. - Canadian Forestry Service, Publication No. 1300, 171 pp.

Sadleir, R.M.F.S. 1969: The ecology of reproduction in wild and domestic animals. - Methuen, London, 321 pp.

Sæther, B-E. & Heim, M. 1993: Ecological correlates of individual variation in age at maturity in female moose (Alces alces): the effects of environmental variability. - Journal of Animal Ecology 62: 482-489.

Sæther, B-E., Andersen, R. & Hjeljord, O. 1996: Ecological correlates of regional variation in life history of the moose Alces alces. - Ecology 77: 1493-1500.

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.

Schaffer, W.M. 1974: Optimal reproductive effort in fluctuating environments. - American Naturalist 108: 783-790.

Siegel, S. & Castellan, N.J., Jr. 1988: Nonparametric statistics for the behavioral sciences. - McGraw-Hill Inc., New York, 399 pp.

Simkin, D.W. 1965: Reproduction and productivity of moose in northwestern Ontario. - Journal of Wildlife Management 29: 740-750.

Simons, A.M. & Johnston, M.O. 1997: Developmental instability as a bet-hedging strategy. - Oikos 80: 401-406.

Skogland, T. 1989: Natural selection of wild reindeer life history traits by food limitation and predation. - Oikos 55: 101-110.

Solberg, E.J., Sæther, B-E. & Strand, O. 1999: Dynamics of a harvested moose population in a variable environment. - Journal of Animal Ecology 68: 186-204.

Stearns, S.C. 1992: The evolution of life histories. - Oxford University Press, New York, 249 pp.

Stearns, S.C. & Koella, J.C. 1986: The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size of maturity. - Evolution 40: 893-914.

Timmermann, H.R. & Whitlaw, H.A. 1992: Selective moose

harvest in North Central Ontario - a progress report. - Alces 28: 1-7.

Tuljapurkar, S.D. 1982: Population dynamics in variable environments III. Evolutionary dynamics of r-selection. - Theoretical Population Biology 21: 141-165.

van Ballenberghe, V. & Ballard, W.B. 1994: Limitation and regulation of moose populations: the role of predation. - Canadian Journal of Zoology 72: 2071-2077.

Verme, L.J. 1989: Maternal investment in white-tailed deer. - Journal of Mammalogy 70: 438-442.

White, R.G. 1983: Foraging patterns and their multiplier effects on productivity of northern ungulates. - Oikos 40: 377-384.

Whitlaw, H.A., Timmermann, H.R., Pernsky, P. & Bisset, A.R. 1993: Northwest region moose population and harvest profile. - Ontario Ministry of Natural Resources, Internal Publication No. 50449, 129 pp.

Zullinger, E.M., Ricklefs, R.E., Redford, K.H. & Mace, G.M. 1984: Fitting sigmoidal equations to mammalian growth curves. - Journal of Mammalogy 65: 607-636.

Appendix I. Population statistics for Newfoundland moose populations.

Population	Habitat quality[1]	Census estimate (year)	% calves harvested	Mean body weight (kg)	Mandible growth		
					Growth constant	Asymptote	
MMU 3	P	6306 (1981)	2.2	266 (1)[2]	438.3	2.52	(489)[2]
MMU 4	M	-	-	282 (9)	-	-	-
MMU 7	M	1164 (1981)	5.1	278 (1)	448.9	23.8	(727)
MMU 9	M	2946 (1982)	8.2	-	454.4	17.5	(459)
MMU 11	M	2343 (1983)	5.6	277 (4)	437.8	12.4	(819)
MMU 12	M	-	-	339 (1)	-	-	-
MMU 13	M	-	-	386 (3)	-	-	-
MMU 16	M	1758 (1978)	6.4	255 (4)	452.8	19.1	(461)
MMU 17	M	-	-	304 (14)	-	-	-
MMU 18	M	2200 (1973)	4.5	366 (5)	-	-	(679)
MMU 19	P	2500 (1973)	3.9	243 (6)	433.7	2.35	(347)
MMU 20	M	-	-	287 (4)	-	-	-
MMU 21	M	-	-	323 (4)	-	-	-
MMU 22	G	6270 (1989)	10.3	-	433.6	12.7	(549)
MMU 23	G	9156 (1991)	7.6	332 (2)	452.3	14	(453)
MMU 24	G	1600 (1985)	6.6	398 (17)	-	-	(1198)
MMU 27	M	-	-	323 (5)	-	-	-
MMU 28	M	-	-	378 (4)	-	-	-
MMU 31-35	M	-	-	341 (55)	-	-	-
MMU 36	M	5700 (1986)	10.6	299 (21)	447.2	20.2	(1752)

[1] Habitat quality (G = good, M = medium, P = poor) is defined according to Ferguson et al. (1989) and correlates with moose/km^2 forest within population boundaries (see text).

[2] Sample size is given in parenthesis.