FECUNDITY OF NORTH AMERICAN MOOSE (*Alces alces*): A REVIEW

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ABSTRACT: I reviewed the available literature relating moose fecundity to population density and range carrying capacity. Adult pregnancy rates were relatively constant ($\bar{x}$ = 84.2%, CV = 6.8%) over a broad range of geographic areas, population densities, and winter severities. Yearling pregnancy rates varied between 0 and 93% and twinning rates between 4 and 80%. Yearling pregnancy rates and twinning rates were directly related and changed at approximately the same rate. Both were highly variable and appeared to be sensitive indicators of moose population status relative to carrying capacity. Moose populations above, near, and below K carrying capacity were estimated to produce 0.88, 1.06, and 1.24 calves/adult female at parturition and 0.18, 0.41, and 0.65 calves/yearling female, respectively. Fetal sex ratio varied widely among studies but the direction of change was inconsistent with respect to population density.

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Widespread evolution of bearing young likely is evidence of a long history of density-dependent population regulation (Hairston et al. 1970), implying that fecundity changes with density. Most density-dependent change in large mammal populations occurs at population levels close to K carrying capacity (KCC) (Fowler 1981). Large mammals such as moose, that produce 1 - 3 calves and have a long life span, have relatively slow rates of population change. Consequently, populations often lag behind changes in vegetation and population overshoots of KCC are likely. Fecundity and subsequent survival of progeny are the two determinants of recruitment rate and, hence, are important factors shaping the trajectory of moose populations. Knowledge of both of these dynamic variables is necessary to understand population dynamics of a particular population.

Fecundity can be a sensitive indicator of a population's status with respect to available food resources: as populations become food limited, fecundity declines (Clutton-Brock *et al.* 1982, Verme 1969). Production of calves is the product of a complex chain of biological processes including estrous cycles, rutting behaviour and breeding, fertilization, prepartum events and parturition. Moose fecundity can be reduced by delaying the sexual maturation of yearlings, reducing the incidence of twins, reducing the pregnancy rate of adult females and altering fetal sex ratio.

If changes in the order and magnitude of these variables occur consistently, then attributes of fecundity may provide wildlife managers with a diagonistic tool to assess the relationship between population and available resources. For example, Franzmann and Schwartz (1985) suggested that the proportion of twins among moose calves at parturition could reflect habitat quality. In a review of white-tailed deer (*Odocoileus virginianus*) literature, Verme (1985) concluded fetal sex ratios shift toward males in nutritionally stressed populations.

The purpose of this paper is to review the pertinent literature relating moose fecundity in North America to population density and range carrying capacity and to identify diagnostic relationships useful to wildlife managers.

METHODS

I reviewed the literature on moose reproduction for data on pregnancy rates, twinning rates, and fetal sex ratios. Following

McCullough (1979), KCC was defined as the number of animals the vegetation of an area could support without being damaged or altered. KCC is usually expressed in terms of density of animals but reflects available food resouces. Most authors selected for this study did not quantify KCC or population densities for their study areas. I subjectively classified populations as below, near, or above KCC on the basis of authors' comments about available food supplies and general condition of vegetation in their respective study areas.

Measures of reproductive performance of populations varied among studies. A number of workers examined the ovarian and uterine tissue of moose killed during annual hunting seasons or from non-hunting mortalities during the autumn and winter. Ovarian tissue can provide information about ovulation rates but not pregnancy rates. Similarily, embryo counts from uteri examined during September and early October may underestimate pregnancy rates. Only pregnancy rates determined by rectal palpation in the last trimester and intrauterine counts during pregnancy were compared. The number of calves observed/100 cows was not used as a measure of reproductive performance since this statistic does not separate yearlings and adult cows and reflects subsequent survival. Twinning rates were determined from aerial counts at parturition and from intrauterine counts.

Associations among adult and yearling pregnancy rates and twinning rates were tested by Spearman rank correlation coefficients. Average adult and yearling pregnancy rates and twinning rates were determined for populations below, near, and above KCC.

A Leslie matrix (Leslie 1945) was used to demonstrate the effect of differing fecundity rates on population growth. Initial population size, age structure, and survival rates were derived from data in southeastern New Brunswick (Appendix I). Survival of 15-year-old moose was set at 0. The matrix model was run with mean yearling and adult fecundity rates reflecting moose populations below, near, and above KCC and with fetal sex ratios ranging from 40-60% female.

RESULTS

Twelve studies reporting reproductive information on North American moose met the criteria selected for this study (Table 1). Adult pregnancy rates averaged 84.2% (CV = 6.8%) and were remarkably consistent (Table 2). Yearling pregnancy rates and twinning rates varied widely among populations (Table 1). Yearling and adult pregnancy rates were not significantly correlated ($r_s = 0.548$, $T = 1.603$, $P = 0.16$). Twinning rates also were independent of adult pregnancy rates ($r_s = 0.515$, $T = 1.900$, $P = 0.087$). However, yearling pregnancy rates were directly related to the percent twins reported in respective studies ($r_s = 0.786$, $T = 3.111$, $P = 0.021$). A regression ($r = 0.70$, $P = 0.05$) of yearling pregnancy rates on percentage twins among adults had a slope of 1.090, indicating that both variables change at approximately the same rate (Fig. 1).

Average fecundity rates for moose populations below, near, and above KCC were 124.1, 106.1, and 88.0 calves/100 adult females and 64.5, 41.1, and 17.7 calves/100 yearling females, respectively (Table 3). Assuming constant age specific survival, changes in fecundity rates can greatly alter the trajectory of a moose population (Table 4). A 50:50 fetal sex ratio combined with twinning and yearling pregnancy rates calculated for below, near, and above KCC resulted in an annual change in populations of 7%, 3%, and -2%, respectively (Table 4, Fig. 2). The difference in growth rates calculated with fecundity values associated with populations above and below K indicated a range of population change attributable solely to changes in fecundity of 9% annually.

Changing fetal sex ratios from 40% to 60% female resulted in a 6.8% difference in rate of change of the female population (r = -

Table 1. Fecundity of moose in relation to K carrying capacity (KCC) reported in North American studies.

Area	Relation to KCC	Year	% Pregnant Yrlg	n	Adult	n	% Twins	n	Reference
Alaska Peninsula	Below	1977-80	-	-	84	57	80	15	Faro and Franzmann 1978
South Central Alaska	Below	1977-80	-	-	88	59	41	64	Ballard and Taylor 1980
Interior Alaska	Below	1975-78	-	-	88	52	32	35	Gasaway *et al.* 1983
Southwest Yukon	Below	1983-85	-	-	84	43	28	58	Larsen *et al.* 1989
Pukaskwa Park, Ontario	Below	1975-79	57	7	97	37	54	37	Bergerud *et al.* 1983
Elk Island Park, Alberta	Below	1963-64	93	14	81	21	48	28	Blood 1973
Southeast New Brunswick	Below	1980-86	39	24	79	46	26	31	Boer 1987
British Columbia	Near	1952-56	0	15	76	80	25	61	Edwards and Ritcey 1958
Eastern Newfoundland	Near	1951-56	67	18	87	38	41	29	Pimlott 1959
Montana	Near	1963-71	32	22	86	73	16	80	Schladweiler and Stevens 1973
Elk Island Park, Alberta	Above	1968-69	15	26	83	126	4	216	Blood 1974
Central Newfoundland	Above	1951-56	38	45	77	132	5	99	Pimlott 1959

Table 2. Summary of pregnancy and twinning rates in North American moose.

	% Adult pregnancy	% Yearling pregnancy	% Twins
No. of studies	12	7	12
$\bar{x}$	84.2	48.7	33.3
SD	5.7	25.8	21.4
CV(%)	6.8	52.9	64.3

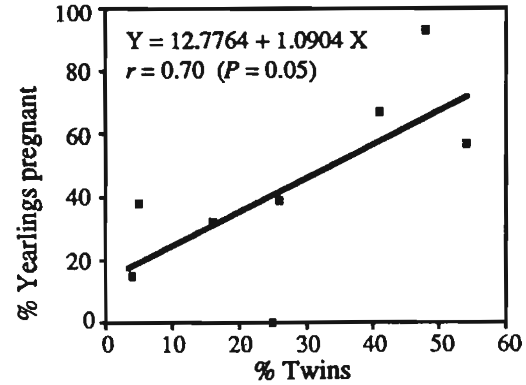

Fig. 1. Regression and correlation of yearling pregnancy rates on percent twins from moose populations in North America. Data from studies listed in Table 1.

0.055 to 0.013) if above KCC, a 7.9% difference near KCC, and a 8.9% change below KCC (Table 4). Magnitude of difference in rate of population change attributeable to altering fetal sex ratios between 40 and 60% was 8.9%: similiar to altering fecundity rates alone. Consequently, moose populations are equally sensitive to changes in fecundity and to fetal sex ratio.

Six studies reported fetal or neonate sex ratio and an estimate of density relative to KCC (Table 5). Fetal and neonate sex ratios among all studies approached unity (50.8% males overall, x^2 = 0.062, P = 0.578). Reported ratios for populations thought to be below KCC averaged 45.5% male. The average was not weighted, so a single area with a large data set could not disproportionately influence the outcome. One population, approaching KCC, had a neonate sex ratio of

Table 3. Number of calves produced by adults and yearlings from moose populations below, near, and above K carrying capacity (KCC). Yearling pregnancy rate and twinning rate for each level relative to KCC were averaged from Table 1.

Relation to KCC	% Adult pregnancy	% Adult twinning	Yearling pregnancy	Expected no. calves /100 adults	Expected no. calves /100 yearlings
Below	84.2	47.4	64.5	124.1	64.5
Near	84.2	26.0	41.1	106.1	41.1
Above	84.2	4.5	17.7	88.0	17.7

Table 4. Rates of population increase (*r*) calculated from a Leslie matrix model. Starting population size, age structure, and survival rates from Boer (1988).

	Fetal sex ratio % females				
Relation to K carrying capacity	40	45	50	55	60
Below[a]	0.022	0.046	0.069	0.090	0.111
Near[b]	-0.015	0.006	0.027	0.046	0.064
Above[c]	-0.055	-0.036	-0.019	-0.002	0.013

[a] Total calves produced: 0.645/yearling, 1.24/adult.

[b] Total calves produced: 0.411/yearling, 1.06/adult.

[c] Total calves produced: 0.177/yearling, 0.88/adult.

Table 5. Fetal and neonate sex ratios reported in North American moose populations.

Location	Relation to K carrying capacity	Years	% Male	n	Reference
New Brunswick	Below	1980-86	46.3	41	Boer 1987
Yukon	Below	1983-85	39.2	56	Larsen *et al.* 1989
Alaska	Below	1976-86	51	155	Ballard *et al.* 1991
Alaska	Near	1966-70	50.3	975	Gasaway (Unpubl. data)
Newfoundland	Above	1982-84	62.0	33	Albright and Keith (1987)
Newfoundland	Above	1973-75	56.0	90	Skinner (from Albright and Keith, 1987)
			50.8	1350	

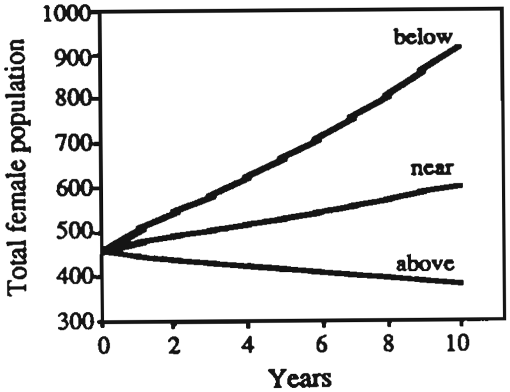

Fig. 2. Change in numbers of female moose calculated from Leslie matrices with fecundity rates associated with populations above, near, and below carrying capacity.

50.3% male, n = 975 (W. Gasaway, Alaska Dept. Fish and Game, unpubl. data). Over this 4 year study, ratios ranged from 45.6 to 56.3%; the population was declining following several severe winters. Two studies from southcentral Newfoundland reported ratios of 56 to 62% male where populations were above KCC.

DISCUSSION

Moose are a subclimax species adapted to exploit catastrophic events such as fire and wind that set back succession. Females are under selection pressure to produce more offspring, and hence, contribute more genetic material to a population at low densities. Since moose are slow dispersers (Cederlund and Okarma 1988, Gasaway *et al.* 1989), populations must have an intrisic ability to respond rapidly to local increases in carrying capacity. Geist (1974) theorized that twinning rates in moose evolved to facilitate exploitation of excellent range in a highly changeable environment. Variable yearling pregnancy rates may have evolved for similar reasons.

Mean adult pregnancy rates were similar across a broad range of geographic areas, population densities, winter severities, and habitats. Adult pregnancy rates are apparently resilient to a wide variety of environmental conditions and reflect the species norm. The North American rate of 84.2 ± 5.2% was similar to adult pregnancy rates reported in Scandanavia (Haagenrud and Lordahl 1978) and the U.S.S.R. (Glushkov 1987). Adult pregnancy rates of moose were similiar to those for other large cervids. Flook (1970) found pregnancy rates of elk (*Cervus cervus*) to be a stable 94 ± 4%. Rates among caribou (*Rangifer tarandus*) populations were 78-90% (Bergerud 1978). In Nova Scotia, 85% of white-tailed deer were pregnant (Patton 1976).

Two things are of immediate interest about adult pregnancy rates: 1) the consistency of the rate over a wide variety of habitats and winter severities and 2) that the rate is not closer to 100%. Pregnancy rates less than 100% in adult females could result from a failure to conceive or from *in utero* loss of embryos. In cattle, an index of normal reproductive performance is 63 calves produced for every 100 inseminations (Davies *et al.* 1971). Consequently, 63% of cows are usually pregnant after a first insemination, 85% after a second, and 94% after a third. Early embryonic death is apparently normal and represents shedding of genetic "mistakes". Markgren (1969) found a 10-15% in utero loss of embryos in moose in Sweden. Most adult female red deer that failed to give birth failed to conceive; resorption and abortion were less likely causes (Clutton-Brock *et al.* 1982). Abortion in white-tailed deer was rare even during acute malnutrition (Verme 1969). Most of the loss of ova occurred prior to implantation. Indeed, Robinette *et al.* (1955) concluded that prenatal mortality between implantation and mid-pregnancy was approximately 3%.

Low numbers of adult males during the rutting period may result from sex selective hunting strategies and a likely consequence would be an increase in unbred females and late conceptions (Bishop and Rausch 1974, Crête *et al.* 1981). Cows with late-born calves may not breed during the subsequent rut because of the energetic costs associated with lactation. The cost of reproduction is evident in reduced fecundity of red deer hinds which raised a calf the previous year compared to hinds that had not raised a calf (Clutton-Brock *et al.* 1982).

With relatively constant pregnancy rates for adults, twinning rates among adults, and yearling pregnancy rates must be the variable components in fecundity. Twinning rate has been speculated to be an indicator of nutritional status of moose populations (Franzmann and Schwartz 1985). Twinning rates varied widely among moose populations in this review. Populations characterized as below KCC had twinning rates of 44.1% and were variable (CV = 42.9%). High variability is likely because twinning rates and densities relative to K form a continuum. Since relative densities were not known, all were lumped together and classed as below K.

The density of moose in an area can influence the share of resources available to young females providing an opportunity for density dependent feedback to regulate population. Production of young is tied to the quality of range and density dependent relationships centered on food limitation among adults (Saether and Haagenrud 1983); nutritionally stressed moose populations are expected to have reduced fecundity. The density of females is likely more important than density of the total population since daughters occupy portions of their mother's home range (Cederlund *et al.* 1987). There is an adaptive advantage for females to share range with a single daughter as food resources become limited on the premise that sharing diminishing resources with 1 will more quickly result in a reproducing offspring than if available resources are partitioned out to twins. Return on maternal investment is likely better from a strategy to maximize quality of young rather than quantity if food is limited.

Yearling pregnancy rate is predicted to be sensitive to habitat quality since puberty is dependent on physiological development and condition of females; both reflect nutritional history and, hence habitat quality (Mitchell and Brown 1974 in red deer, Saether and Haagenrud 1983 in moose, Verme 1969 in white-tailed deer). Winter severity may also influence yearling pregnancy rates by reducing growth and development of calves.

Changes in twinning rates in adults and pregnancy rates in yearlings act synergistically to alter the number of calves produced. Impact on population growth was similiar in magnitude to changes in either twinning rate or yearling pregnancy rate. The relationship appears intuitively correct since both are influenced directly by the same ultimate factor: available food per individual.

Shifts in fetal sex ratio can dramatically alter population growth rate of moose (Reuterwall 1981). Changes in fetal sex ratio from 40-60% male changed rate of population growth 8.9%; equal in magnitude to changes in fecundity alone. Trivers and Willard (1973) hypothesized a selective advantage in skewed fetal sex ratios. They predicted that since the maternal investment required to produce and raise males was greater than females, nutritionally stressed mothers should produce more daughters as maternal condition declines. Thomas *et al.* (1989) examined caribou fecundity in northern Canada and agreed with the model proposed by Trivers and Willard (1973). However, Skogland (1986) for reindeer and Verme (1985) for white- tailed deer presented evidence that fetal sex ratios favour males as maternal condition declined. Clutton-Brock *et al.* (1982) could not detect a unidirectional trend in fetal sex ratio with changing density of red deer relative to KCC. The moose literature does not clarify either concept.

While a general trend to favour males in populations near and above KCC was apparent (Table 5), 4 of 6 studies had small sample sizes. Also, wide fluctuations in fetal and neonate sex ratios between years in some localities preclude a definitive trend. Gasaway (W. Gasaway, Alaska Dept. Fish and Game, unpubl. data) found variable proportions of male calves (45.6-56.3%) among neonates captured. In 1974-88 harvest data from New Brunswick, sex ratio of calves averaged 45.4% male (n = 1,909) and ranged from 32.1 to 61.6 (A. Boer, N. B. Dept. Nat. Res., unpubl. data). Survivability of both sexes is assumed equal up to the first 6 months of life (Ballard *et al.* 1991). In Sweden, Reuterwall (1981) examined harvest data over 22 counties from 1970-78: a period of rapid growth of moose populations and presumably adequate nutrition (Cederlund and Markgren 1987). The weighted average of 160911 calves was 57.4% male with significant temporal and spatial differences. Males made up from 51 to 69% within single combinations of year and county. Hence, there was no evidence in the literature consistent with the premise that fetal sex ratio changes with population density relative to KCC. Highly variable sex ratios introduce a stochastic element to the productivity side of a population dynamics equation because changes in fetal sex ratio can greatly alter the growth profile of a moose population.

Confounding the relationship between range quality and selective shifts in sex ratio are the influence of female age, time of conception and twinning rate. Among caribou and white-tailed deer, young and old females tend to produce more males and prime-aged breeding females produce more females (Thomas *et al.* 1989, Ozoga and Verme 1982, Verme 1983). Mule deer (*Odocoileus hemionus*) does which conceive late in the rutting period and have a longer time to build fat reserves tend to produce proportionally more females (Robinette *et al.* 1977). White-tailed deer twins contain more females than males (Verme 1983).

Many of the factors affecting sex ratio of progeny operate concomitantly; at the population level, the effect may be augmented or cancelled. For example, on good range following a mild winter a high proportion of yearling moose are likely to breed and the majority are expected to produce male singletons. Twinning rates are also expected to be high in this population. Twins are produced by prime-aged cows and these tend to produce sex ratios favouring females. Depending on relative proportion of each age cohort in the population, fetal sex ratio may shift from 50:50. Population and time specific factors such as inherent variability in sampling, small sample sizes, population level responses to changes in age composition and to density-independent factors such as severe winters, and nutritional condition of females related to food availability make interpretation of trends difficult. With survival rates held constant, changing fecundity rates alone could increase or decrease a moose population. Of course, in natural populations survival rates change in concert with fecundity rates. Hanks (1981) suggested a generalized model for cervids in which juvenile mortality was most sensitive, followed by yearling pregnancy rate and then total fecundity: implying no linkage between twinning and yearling pregnancy rates. However, Schwartz and Franzmann (1989) found no difference in neonatal survival rates on "good" vs "poor" range. Those 2 populations did differ significantly in twinning rates and in the number of cows observed without calves. Presumably, most of the barren females would have been yearlings since adult pregnancy rates are relatively constant (this study). This suggests that fecundity is a more sensitive indicator of habitat quality than is survival rate. Hence, sequential changes of population processes in nutritionally stressed moose populations would be: reduced fecundity (twinning and yearling pregnancy rates decline concomitantly), followed by reduced survival of neonates and finally, reduced adult survival.

ACKNOWLEDGEMENTS

I thank S.A. Boer for programming the Leslie matrix model. W.C. Gasaway and 3 anonymous reviewers provided critical reviews of the manuscript.

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Appendix I. Initial population size, age structure, and survival rates of female moose in southeastern New Brunswick (from Boer 1988) used in the Leslie matrix.

Age class	No.	Survival rate
0	128.8	0.68
1	87.1	0.70
2	60.7	0.71
3	43.2	0.73
4	31.4	0.75
5	23.4	0.77
6	18.1	0.78
7	14.0	0.80
8	11.3	0.83
9	9.2	0.83
10	7.8	0.88
11	6.8	0.88
12	5.9	0.89
13	5.3	0.93
14	4.9	0.00