

SENSITIVE POPULATION PARAMETERS IN MODELING LONG-LIVED
SPECIES SUCH AS MOOSE

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Abstract: The production of moose calves over a 20-year period is over 4 times greater if 75% of the yearlings breed compared to none of them breeding. The age at first breeding and the sex ratio of the breeding population are very important parameters when modeling populations of long-lived species. In addition, sex ratio at birth, sex-related mortality of suckling calves, and sex-related natural and hunting mortality of all age groups are important parameters when setting up proportion-based summation population models. Such models can provide accurate estimates of the population on an area if natality and mortality, including hunting mortality, are properly represented.

ALCES 23 (1987)

Biological productivity is the basis for renewable resource management. Management of big game, such as moose (Alces alces), has developed as a science and an art to the point where moose managers can, by regulating harvests in relation to natality and mortality, cause populations to go up, down, or stay about the same over a period of years.

If moose management is successful with present knowledge and understanding, why introduce computer modeling as a management tool? The reason is that moose management does not occur in a vacuum; other segments of society, ranging from antihunters to commercial exploiters, could keep the moose manager on the defensive. Computer models which are conceptually and biologically correct can make it possible for the moose manager to answer questions before they are asked by other segments of society.

This paper presents an argument for careful attention to some critical population parameters when modeling long-lived species such as moose. These critical parameters have a multiplicative effect on population growth, and must be biologically correct if a computer model is to represent population dynamics correctly over time.

MATHEMATICAL ANALYSES OF PRODUCTIVITY AND POPULATIONS

The simplest expression of productivity can be made with an interest rate calculation. If the \$ population is \$100 and the interest rate 6% compounded annually, there will be \$106.00 after one year, \$112.36 after two . . . and \$179.08 after 10 years. The calculations are simple because each dollar earns interest, and growth can be predicted to the penny for as long as the interest rate is known.

Growth of animal populations is more complicated than interest rate calculations because animal populations have variable sex and age structures. Males are added to a

population, and females are not only added but they also multiply. Hence the sex ratio and age structure of a breeding population are very important determinants of population productivity.

Population dynamics can be represented by mathematical procedures, such as regression models which calculate N in relation to time, and summation models of natality and mortality through the year. An exponential regression model is appropriate only when the sex ratio is 50:50 and young animals breed during the first breeding cycle after their birth. Neither are true of moose populations.

A summation model of calf production is illustrated in Table 1, beginning with an initial population of 2--one male calf and one female calf--in Year 0, and reaching 18.5 in the 10th year, assuming a 50:50 sex ratio throughout the population and no breeding yearling females.

Table 1. A calf production model illustrating summation calculations. Numbers have been rounded to 0.1.

Sex and Age Group	Year										
	0	1	2	3	4	5	6	7	8	9	10
ADMALE	0.0	0.0	1.0	1.0	1.0	1.5	2.0	2.5	3.3	4.3	5.5
ADFEML	0.0	0.0	1.0	1.0	1.0	1.5	2.0	2.5	3.3	4.3	5.5
YEMALE	0.0	1.0	0.0	0.0	0.5	0.5	0.5	0.8	1.0	1.3	1.6
YEFEML	0.0	1.0	0.0	0.0	0.5	0.5	0.5	0.8	1.0	1.3	1.6
CAMALE	1.0	0.0	0.0	0.5	0.5	0.5	0.8	1.0	1.3	1.6	2.1
CAFEML	1.0	0.0	0.0	0.5	0.5	0.5	0.8	1.0	1.3	1.6	2.1
TOTALS	2.0	2.0	2.0	3.0	4.0	5.0	6.5	8.5	11.0	14.3	18.5

Summation models may be set up for any sex ratio and age structure. They are calculation-intensive, however, and are best done by computer when several age classes are used. The Deer CAMP population programs (Moen et al. 1986) are complex proportion-based summation models.

SEX RATIO AND AGE EFFECTS IN POPULATION MODELS

Five factors affecting the sex ratio and age structure of a moose population need to be considered if a population model is to mimic population dynamics properly, without annual adjustment for error. These factors are discussed next.

Sex Ratio at Birth

The sex ratio at birth is a difficult and costly parameter to determine, especially when factors which might affect this sex ratio are considered. In white-tailed deer (*Odocoileus virginianus*), for example, both age and nutritional status of dams affect the sex ratio of fawns produced; relatively more males are born to younger dams than older dams, and relatively more males are born to poorly-nourished dams than well-nourished ones. It has been suggested by Verme (1985) that male fawns predominate among malnourished mothers but well-fed does produce an even sex ratio or have more females.

The Deer CAMP population models (Moen et al. 1986), which consider both the numbers of breeders in each age class and the nutritional quality of the range show,

however, that on good range the sex ratio of the neonate fawn population is more in favor of males. This is so because females living on good range breed at a younger age, and because there are more fawn and yearling breeders than any single adult age-class of adult breeders, the neonate cohort from the does bred as fawns and yearlings, which has a relatively higher M:F ratio, shifts the male component of the entire fawn population upward. The use of such a dynamic sex ratio at birth, adjusted for both primary sex ratio and the age structure of the breeding female population, was necessary when reconstructing deer populations for 25 years of harvest data in New York State.

Moose biologists tend to assume that the sex ratio of moose at birth is about 50:50. This appears to be due in some cases to small sample sizes which do not show definite trends toward a preponderance of either males or females. Serafinski (1969), for example, reported that among 51 newborn calves, the M:F sex ratio was 27:24.

Fetuses showed a ratio 55 (N = 220) males to 45 females, and the M:F sex ratio of calves harvested in Newfoundland was 60:40 (N = 284) (Pimlott 1959a). The author also states that hunter bias should not have influenced the calf sex ratio of the harvest. Markgren (1971) found a slight preponderance of males in the secondary sex ratio. Analyses of large samples suggest that the sex ratio at birth favors males over females; this is discussed in the next section.

Sex-related Mortality of Calves

Factors affecting sex-related mortality of calves are difficult to determine because moose calves are not abundant, they are hard to locate due to habitat conditions, and sex cannot always be determined from field observations. Therefore, little is known about sex-related survival differences during the suckling period.

Sex-related mortality of suckling calves is of interest because so much more sex data can be obtained from calves in the harvest than from neonates in the field, and if sex-related mortality were known, then harvest data could be used to estimate sex ratio at birth.

Sex distribution among 160,911 moose calves in 22 Swedish counties from 1970-1978 was analyzed by Reuterwall (1981), based on data obtained from hunting statistics of the National Swedish Environmental Protection Board. The calf sex ratio varied in different areas from 51% to 69% males, with an overall weighted mean M to F ratio of 57.4 to 42.6 in harvested calves. Reuterwall did not know if the observed sex ratios among harvested calves indicated variations in the secondary sex ratio, or if they reflected sex-related differences in natural and hunting mortality.

In Northwestern Ontario, 117 of 220 calves (53%) harvested were males (Simkin 1963). If these kills were not influenced by hunter bias, then the sex ratio of 53:47 would correspond to the sex ratio of the calf population during harvest, and if there was no difference in summer mortality

between male and female calves, then the M:F ratio in the harvest would reflect sex ratio at birth.

As the evidence accumulates for a preponderance of male calves, conclusions such as that reported by Simkin (1965): "The sex ratio of 220 calves examined at the checking station was 117[M]:103[F] and did not differ significantly from 100[M]:100[F]" need to be reevaluated. The very large data set from Sweden (Reuterwall 1981) and several smaller sets from North America indicate that the male component of the calf cohort is greater than 50% of the total.

How important is the sex ratio at birth and sex-related mortality rates from birth to breeding age? Summations of calves produced and animals accumulating for three populations with M:F sex ratios of 0.6:0.4, 0.5:0.5, and 0.4:0.6 are illustrated in Figure 1. Each population began with two calves, and the numbers diverged from the 10th through the 20th year (the longevity of moose). Less than 140 were born with a M:F sex ratio of 0.6:0.4, about 250 with a sex ratio of 0.5:0.5, and over 430 with a sex ratio of 0.4:0.6. No yearlings were bred in this summation model, and each adult produced one calf. The results illustrate the relative importance of the sex ratio to population growth.

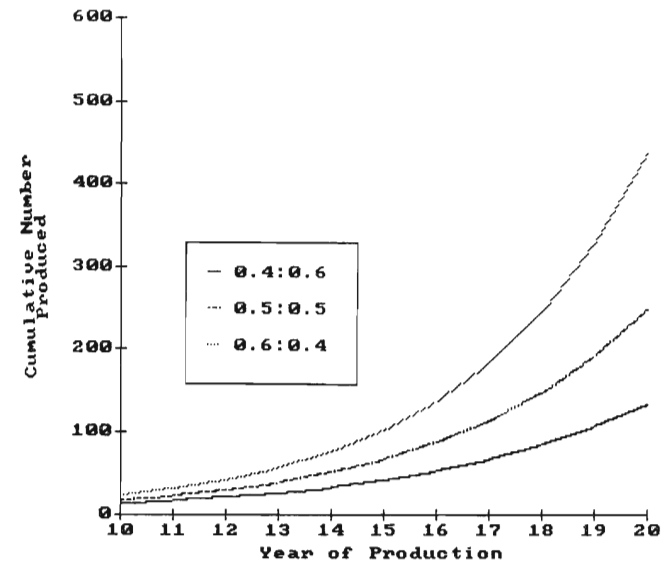


Figure 1. The M:F sex ratio in a population has an important effect on the number of calves produced over a 20-year period.

Age at First Breeding

"One of the most important factors determining the productivity of a big game herd is the proportion of the youngest age group which is sexually mature" (Simkin 1965). If moose cows breed as yearlings rather than as two-year-olds, they not only give birth one year earlier, but the first offspring will be present in the population for one extra year, and they and their offspring will breed to cause a multiplicative effect.

Initial breeding age was considered by Pimlott (1959b) who noted that yearling females are sometimes bred, and variations in the age at which cows are successfully bred for the first time can be attributed to differences in range quality. A yearling ovulation rate of 0.51 was reported in the more productive coastal region of Sweden, and only 0.08 in the less productive inland region (Markgren 1969).

How important is the age at first breeding, i.e. the fraction of yearling cows bred? Results of a 20-year summation model based on a M:F sex ratio of 0.5:0.5, one calf per adult cow, and four fractions of yearling breeders are illustrated in Figure 2. Note that about 250 calves were produced after 20 years with no yearling breeders, 330 with 0.25 yearling breeders, 450 with 0.50, and almost 600 with 0.75 yearling breeders. The production potential is greater as a result of a 0.50 or higher fraction of yearling breeders than a M:F sex ratio of 0.4:0.6.

Data on the fractions of yearling breeders in different areas are summarized in Table 2. Note that the reported variations in North America fall within the range used in calculating the results in Figure 2; the highest fraction we found in the literature was the 0.80 in Finland. The combination of sex ratio and age-at-first-breeding can have a marked effect on the potential for growth of moose populations.

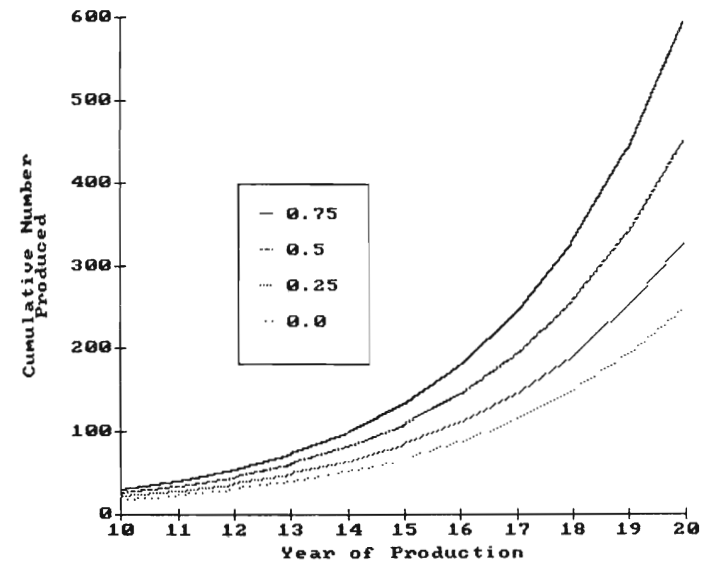


Figure 2. The fraction of yearlings which breed has an important effect on the number of calves produced over a 20-year period.

Table 2. Fractions of yearling breeders in different areas range from 0 to 0.8 (see effects in Figure 2).

<u>Area</u>	<u>Pregnancy Rate</u>	<u>Reference</u>
Finland	0.80	Rajakoski and Koivisto 1966
Montana	0.32	Schladweiler and Stevens 1973
Newfoundland	0.17-0.67	Pimlott 1959b
Ontario	0.17	Simkin 1965
Wyoming	0.06	Houston 1968*

*Cited by Schladweiler and Stevens 1973

Sex-related Natural Mortality

Mortality of moose calves during the winter is easier to determine than during the summer, but because of low population densities and difficult field conditions, little information is available on the sex and age distribution of winter moose. The sex ratio of twenty-five calves which died in northeastern Minnesota was about equal (Berg 1975). Moose mortality near Fairbanks, Alaska during the winter of 1970-1971 showed that for moose less than one year old, malnutrition caused the death of more males, but for moose greater than one year old, more females died of malnutrition (Bishop and Rausch 1974). Predation on yearling and adult moose in Alberta was slightly higher for males than females (Hauge and Keith 1981).

While data on sex-related winter mortality of moose is very limited, a proportion-based population model (Moen and Severinghaus 1985) enables one to calculate both summer mortality and winter mortality from harvest records. A proportion-based moose population model would track each sex and age group from year to year, and the sex and age fractions in the harvest would be used to calculate the numbers that died during the previous time periods. Calculations of summer and winter whitetail fawn mortality is described in the Deer CAMP manual (Moen et al. 1986); similar algorithms could be used to calculate summer and winter calf mortality in moose.

Sex-related Hunting Mortality

The sex-related harvest mortality of breeding-age animals is a part of just about every moose management plan. Moose hunters seek trophy animals--bulls with large horns, (Cumming 1974, Simkin 1965, Pimlott 1959b). Calves are always biased against, especially if they are in the presence of cows (Schladweiler and Stevens 1973, Simkin 1965). Areas with light hunting pressure and that are remote influence hunter selection toward trophy bulls as more time is spent looking for an adult moose that will make the hunting effort worthwhile (Simkin 1964). Nonresidents, especially, have been found to take a much higher proportion of bulls than residents (Cumming 1974).

The timing of the hunt can have marked effects on the sex ratio of the breeding animals in a moose. Behavioral differences based on sexual maturity make some sex and age groups more vulnerable to hunting at different times. Females and inquisitive male yearlings are most vulnerable in September before the rut, and bulls are more vulnerable in late September and early October during the rut when they come readily to many cow-type noises. These biases and proportional relationships need to be considered in a proportion-based population model.

THE PROPORTION-BASED POPULATION MODEL

The most biology-intensive population model is one which uses biological proportions to represent patterns of

natality and mortality in relation to population sex and age structure, not only on a yearly basis but for different time periods during the year.

Parturition is a logical time to begin the moose-year. The summer/fall, hunt, and winter/spring time periods are logical within-year periods for calculating mortality. The sex ratio at birth and sex-related mortality during the suckling (summer/fall) period are important biological parameters. A moose population model must include numbers of moose, by sex and age, which are harvested, and estimates of the numbers lost to crippling and killed by poachers. Differential sex and age mortality during the winter/spring period is another necessary parameter. These parameters need to be known for the calves, yearlings, and adult sex and age groups if a proportion-based population model is to be developed. If these are known, then the number of animals in a properly-proportioned population which will sustain a known legal harvest plus the mortality due to poaching, crippling, and natural causes will be a very good estimate of the actual moose population on an area.

ACKNOWLEDGEMENTS

The assistance of Susan M. Barrell, Kimberly A. Claypoole and Jennifer A. Sanchez is gratefully acknowledged.

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