

RATE OF INCREASE IN MOOSE POPULATIONS

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Abstract: Rate of increase of an animal population may be expressed in either finite (λ) or exponential (r) terms; the former is the annual coefficient of population growth, the latter is its natural logarithm. Stationary populations have a λ of 1.0 and an r of zero. Rate of increase of a moose (*Alces alces*) population may be estimated in several ways including regressing \log_e numbers on time, subtracting \log_e of an initial population from \log_e of a final population and dividing the result by the number of years in the time interval, and by comparing survival and fecundity rates if these are known. Rate of increase cannot be calculated solely by determining the percent calves in a population. Rate of increase is a decreasing function of population density for moose and many other mammal species. If the necessary data are in hand, rate of increase statistics can be computed and used to estimate harvest rates required to hold a moose population stationary. This paper reviews the literature on rate of increase as applied to moose and discusses the ecological factors that affect this important population parameter.

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Observers of animal populations know that stationary populations are rare; animals typically increase or decrease in abundance over time. One of the first problems facing population ecologists was how to characterize these changes. Wildlife biologists have also been concerned with measuring numerical change in animal populations but they have been inclined to use indirect measures and to concentrate more on concepts such as age ratios, productivity, and turnover than on direct measures of numerical change. The moose literature still typically contains references to percent calves as indices to population trends despite Caughley's (1977a) warnings that such indices may be poor measures of population growth. Accordingly, the purpose of this paper is to review the literature on rate of increase, to illustrate techniques for its computation as applied to moose populations, to discuss certain ecological factors that affect this population parameter, and to illustrate certain management applications that are possible if rate of increase is known.

DEFINITIONS AND METHODS OF CALCULATION

Caughley (1977b) and Caughley and Birch (1971) discussed rate of increase, defined its various forms, and illustrated methods for its calculation. Rate of increase is the rate at which the number of animals in a population changes annually. The simplest measure of this is the ratio of numbers in two successive years, labelled the

coefficient of annual population growth, the growth multiplier, or the finite rate of increase, and taking the symbol lambda (λ).

Stationary populations have $\lambda = 1.0$; increasing populations have $\lambda > 1.0$ and decreasing populations have $\lambda < 1.0$.

For several reasons discussed by Caughley (1977b:52) population ecologists have preferred instantaneous or exponential expressions of rate of increase to finite expressions. Exponential rate of increase (r) is simply the natural logarithm (\ln) of λ . It is centered at zero, rather than unity, and its magnitude does not immediately reveal the magnitude of annual population change. For example, $\lambda = 1.25$ clearly indicates that a population of 200 animals will grow to 250 one year later, whereas the expression $r = 0.223$ ($\ln 1.25 = 0.223$) is more difficult to interpret. Thus, λ and r are related by the functions $r = \ln \lambda$, and $\lambda = e^r$ where e is the base of natural logarithms, taking the value 2.71828.

Wildlife biologists are often interested in computing rate of increase given a series of population estimates for a certain population over time. They may also wish to apply a given rate of increase to a population and compute population size several years hence. Table 1 contains equations for these procedures using either finite or exponential rates and assuming that rate of increase is constant over time. It should be noted that number of years of increase is a key component of these calculations; in any series of years the initial population is assigned to year zero rather than year one.

The equations in Table 1 for computing λ or r use only two population estimates, the initial number and the final number after t years of increase. If more than two estimates are available, the method of choice for computing r is to regress $\ln N$ for each estimate against time in years. The slope of the regression line is then r (Caughley and Birch 1971). This method can account for sampling error in each estimate and does not assume that r is constant. In effect it estimates an average r over the time interval. Care must be taken to use natural logarithms (not base 10 logs) for this method.

The above discussion deals with observed rate of increase and emphasizes a rate that is actually achieved by a population. This depends for accuracy on unbiased population estimates and does not assume that age structure of the population is stable or fixed. Caughley (1977b:53-56) defines several other measures of population growth including intrinsic, survival-fecundity, and potential rate of increase (Table 2). All are potentially valuable for the student of moose population dynamics.

Finally, a convenient measure of population growth is the time a population requires to double given a certain rate of increase. Table 3 lists selected finite rates of increase, their exponential equivalents, and the associated doubling time for a population exposed to these rates. Rate of growth can be negative as well as positive; a population with $r = -0.140$ (Table 3) would halve every 5 years.

RATE OF INCREASE DISPLAYED BY MOOSE

Keith (1983) reviewed the literature and listed observed finite rates of increase for moose populations in Alberta (Blood 1974), Alaska (Spencer and Hakala 1964), Newfoundland (Mercer and Manuel 1974), and Michigan (Krefting 1974). All populations had adequate food, large predators were scarce or absent, and hunting pressure was light. Values of λ for these increasing populations ranged from 1.15 to 1.30 with a mean of 1.23. To these can be added two additional recent examples. Moose on the Tanana Flats in interior Alaska increased at an observed finite rate of 1.23 between 1978 and 1982 following a wolf reduction program (Gasaway et al. 1983). Moose at Isle Royale Michigan increased at an observed finite rate of 1.23 from 1981 to 1982 following a wolf decline (R. Peterson 1983, personal communication). Both populations had adequate food and the Alaska population was lightly hunted for bulls only.

In addition to the above examples, Rolley and Keith (1980) reported that λ for a moose population near Rochester, Alberta declined from 1.24 to 1.03 during a 6-year interval partly as a result of attainment of a stable age distribution and partly due to a shift from net ingress to net egress. The survival and fecundity data of Mytton and Keith (1981) for this same area allow computation of an r_s (Table 2) estimate for this population. With the age distribution stable at 32:22:47 (yearlings, 2-year-olds, and older animals, respectively) $r_s = 0.157$ and $\lambda = 1.17$.

The above estimated rates are necessarily crude estimates of true rate of increase parameters for these several moose populations. The problems in obtaining accurate census data for moose are well known. They are overshadowed only by the difficulty of obtaining unbiased data on survival and fecundity. Nevertheless, it is noteworthy that λ values exceeding 1.30 have not been reported for moose populations in North America.

Intrinsic rate of increase

To Caughley's (1977b) definition of r_m (Table 2) one might append the phrase, "...and predators are absent." This is essential when comparing moose population growth in several areas of North America. Also, it must be stressed that Caughley's (1977b) concept of r_m involves a stable age distribution. This constraint would lower r_m for a population below the level of population growth achieved in the absence of a fixed age distribution. Thus, r_m does not necessarily represent maximum rate of population growth; this may be represented by the symbol r_{max} .

No good estimates of r_m for moose are evident in the literature. Population estimates during the early stages of an eruption have seldom been available; the stable age distribution assumption has not been met in field studies in any event. Values of r_m must therefore be estimated from maximum reported values of

survival and fecundity. Values of r_m for North American moose populations would fall along a gradient from the approximate center of distribution of the species ($r_m \approx 0.30$) to areas in the far north ($r_m \approx 0.25$). The claim by Bergerud (1981) that r_m for moose in Ontario was at least 0.35 appears too optimistic.

Maximum exponential rate of increase for moose could approach 0.35 ($\lambda = 1.49$) for populations where age distributions were not stable, dispersal was prevented, adult annual survival was about 0.95, calf survival approached 0.8, and fecundity was maximum for the species. For feral horses (*Equus caballus*) with a lifespan equivalent to moose but having a much lower fecundity, r_m is apparently about 0.19 ($\lambda = 1.21$) (Eberhardt et al. 1982). Similarly, Murphy (1963) estimated r_{max} for elk (*Cervus canadensis*) at 0.27 ($\lambda = 1.31$).

FACTORS AFFECTING RATE OF INCREASE

Mammal populations typically display a sigmoid growth curve produced by a rate of increase that is a continuously declining function of density. As asymptotic population densities are reached, rate of increase approaches zero. Tanner (1966) examined these relationships and the data supporting them for a variety of different species. Thus, relative density of a population acting on the survival and fecundity of individuals is perhaps the most important determinant of rate of increase in moose and other mammal populations.

Changes in the relative density of ungulate populations can influence several demographic variables that profoundly affect rate of increase. These include age at first reproduction, litter size, first year survival, adult survival, and sex ratios of young and adults (Caughley 1976). Nelson and Peek (1982) modeled the effects of varying survival and fecundity on rate of increase of elk. They concluded that within a narrow range of fecundity rates adult survival showed the greatest relative order of magnitude of effect on rate of increase. They stressed that adult parameters involve 12 or 13 cohorts in contrast to subadult parameters that affect only one or two. Eberhardt et al. (1982) modeled feral horse population dynamics and found adult survival to be the key parameter in determining rate of increase. Both studies found that annual adult survival of 0.95 or higher was required to produce maximum λ values. Survival rates this high could not persist after the age distribution of the populations became stable.

Few adult survival rate estimates for moose exist in the literature. Mytton and Keith (1981) reported mean annual survival of radiocollared yearlings and adults was 0.84 in Alberta in an unhunted, predator-free population. Hauge and Keith (1981) reported a similarly obtained statistic of 0.75 for adults and yearlings hunted and preyed upon by wolves in northeastern Alberta. Gasaway et al. (1983) reported mean annual survival rates of 1.0, 0.67, and 0.59 for radiocollared moose aged 1-5, 6-10, and ≥ 11 years, respectively, in Alaska during a period when wolf predation was intense. Survival rates improved to 1.0, 0.93, and 0.79, respectively, for these cohort groups after wolf numbers were reduced.

As discussed above, changes in age distribution have strong effects on rate of increase. Highest r values can be expected when most adults are in the "prime" age classes where fecundity and survival are both maximal. Data on fecundity rates of moose (Saether and Haagenrud 1983) and information on mortality from life tables (Peterson 1977) suggest that these cohorts span the approximate interval of 5 to 10 years of age.

Fecundity rates of moose vary widely throughout North America as do calf survival rates. Both parameters interact to produce calf:cow ratios in fall and winter that can vary more than 5-fold (Rolley and Keith 1980:13). VanBallenberghe and Dart (1982) reported that decreasing calf survival from 0.5 to 0.25 during the first six months of life decreased λ of a model moose population from 1.14 to 1.05. The corresponding calf:cow ratios produced by this change were 0.42 and 0.24, respectively. Early calf survival rates as low as 0.25 that result in fall calf:cow ratios approaching 0.20 are not unusual in northern areas where wolves (Canis lupus) and bears (Ursus spp.) are abundant.

The effects of skewed adult sex ratios on λ can be illustrated with a simple example wherein two populations with identical fecundity, calf survival and adult survival are compared. Assume that annual adult survival is 1.0 and fall calf:cow ratios are 0.6. For one such population with 1:1 adult sex ratio, λ is 1.30 compared to 1.53 for a second population having a 1:7 adult sex ratio favoring females. Clearly, higher λ values are potentially possible in moose populations with an excess of adult females.

Calf sex ratios at birth can similarly influence rate of increase. For two model populations with identical fecundity (1.0 female calves per 2+ female adult), first year survival (0.8), and adult survival (1.0), the population with a 50:50 ($\sigma^{\circ} \sigma^{\circ} : \text{♀} \text{♀}$) calf sex ratio had $\lambda = 1.58$ vs. $\lambda = 1.43$ in a population with a 65:35 calf sex ratio at birth. This seemingly small difference becomes more dramatic when comparing population size after 10 years of increase starting with 2 adults in each population. For $\lambda = 1.43$, 125 moose result compared to 358 for $\lambda = 1.58$. Distorted calf sex ratios at birth are known to occur in a variety of mammalian species including moose, and result from a complex set of factors involving maternal age and condition as well as time of conception.

Finally, a cautionary note concerning dispersal and its effects on rate of increase. Rolley and Keith (1980) reported that a moose population near Rochester, Alberta had the highest reported productivity in North America; calves averaged 44% of the population in winter and winter calf:cow ratios ranged from 0.78 to 1.46. Despite this, λ was relatively low (1.12 to 1.03) during a 3-year period of net egress. The tendency of moose to disperse under certain ecological conditions is well known but the effect of dispersal on their rate of increase has rarely been evaluated.

RATE OF INCREASE: MANAGEMENT IMPLICATIONS

Wildlife managers have long been interested in monitoring the trends of the populations they manage. As management has become more intense and as population assessment techniques have improved, it has been necessary and possible to quantify such trends and to accurately predict the future status of a population. The techniques of the population ecologist have become increasingly important to the managers of moose populations in North America; computation of rate of increase and the information it generates about a population have important management implications.

One important value of rate of increase estimates is their relationship to sustained yield. For a population that obeys logistic growth rules, maximum sustained yield (MSY) occurs at a population size of $N = K/2$ where K is the carrying capacity. Furthermore, for such populations instantaneous rate of harvest (H) = $r_m/2$ (Caughley 1977b:179). Cervid populations do not grow according to the logistic model (McCullough 1979); their yield curves are skewed to the right and they tend to overshoot K . Nevertheless, yield and MSY density can be crudely estimated for a population if K and r_m are known. Harvests can then be conservatively applied as density trends are carefully monitored.

Managers often have no good estimate of K , nor do they clearly know the relationship between natural mortality and that due to hunting. However, they may have good information on fecundity and they can perhaps estimate λ from monitoring population trends under

varying harvest rates. If λ and fecundity are known for a population not subject to harvest, or if r_p (Table 2) can be estimated for a harvested population, then sustained yield (SY) can be estimated by the methods of Caughley (1977b:172-174). An example for a moose population is provided (Table 4) where $\lambda = 1.20$, and fecundity (m_x) = 0.75. After 12 months, an unharvested population of 1000 yearlings, adults and newborn calves is reduced to 685 by natural mortality. A total of 514 newborns then results in a λ of 1.20, the specified rate. The same population if harvested likewise begins in May with 1000 animals and declines to 882 in September when the harvest is taken. The isolated rate of harvest (h) required to keep the population stationary results in a total harvest of 147 moose. This population then declines to 571 by the following May when the specified m_x brings the total population back to 1000. Hidden in these calculations are several important assumptions, not the least of which is that SY must be correctly and consistently apportioned into the proper sex and age classes. However, the example can at least conceptually portray relationships between λ , m_x , N , and SY. Note that the harvest here is 16.7 percent (147/882) of the population in September with $\lambda = 1.20$ and a relatively high fecundity rate. Substantial reductions in either λ or m_x or both would reduce SY accordingly.

Rate of increase estimates are useful not only to estimate harvests of moose by humans but also can be useful in determining the impact of predation on moose numbers. Keith (1983) illustrated a valuable method of relating wolf:moose ratios to λ , human harvests, and predator kill rates. The number of moose per wolf required to maintain stationary moose numbers was estimated by:

$$N = \frac{K}{(\lambda - 1)(1-H)}$$

where: N = moose per wolf in
spring before births
 λ = potential finite rate of
increase of moose
H = proportion of annual
increment of moose removed
by hunting
K = moose per wolf killed
annually

This assumes that predation and hunting mortality are additive. This relationship is valuable as a conceptual model because it relates parameters that are often available from field data and because it integrates many other variables (such as functional and numerical response of wolves) that are not clearly related to changes in moose numbers. Keith (1983) illustrated use of this relationship with a moose/wolf example from Alberta where moose demography was documented by Hauge and Keith (1981). Figure 5 in Keith's (1983:77) paper illustrates well how seemingly small changes in λ can have large effects on population dynamics. For example, reducing λ from 1.10 to 1.05 with hunters taking half the annual increment of moose required twice the number of moose per wolf to keep the moose population stationary.

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Table 1. Equations used to compute finite (λ) and exponential (r) rates of increase and to compute population size if r , λ , initial population size, and number of years of increase are known.

$$\text{I. } \lambda = \left(\frac{N_t}{N_0} \right)^{\frac{1}{t}}$$

$$\text{II. } r = \frac{\ln N_t - \ln N_0}{t}$$

$$\text{III. } N_t = N_0 \lambda^t$$

$$\text{IV. } N_t = N_0 e^{rt}$$

$$\text{V. } r = \ln \lambda$$

$$\text{VI. } \lambda = e^{\frac{r}{t}}$$

where: λ = finite rate of increase

r = exponential rate of increase

N_t = number of individuals in year t

N_0 = number of individuals in initial year, or year zero

\ln = natural logarithm

e = base of natural logarithms = 2.71828

Table 2. Definitions of different kinds of rate of increase, after Caughley (1977b:53-55).

I. Intrinsic rate of increase (r_m): the exponential rate at which a population with a stable age distribution grows when no resource is in short supply.

II. Survival - fecundity rate of increase (r_s): the exponential rate at which a population would increase if it had a stable age distribution appropriate to its current schedules of age-specific survival and fecundity.

III. Observed rate of increase (r): the exponential rate at which a population increases over a period of time.

IV. Potential rate of increase (r_p): the exponential rate at which a population initially increases after one agent of mortality is eliminated.

Table 3. Selected finite rates of increase, their corresponding exponential equivalents, and the time in years that a population displaying these rates requires to double in size.

λ	\underline{r}	Doubling time ^{1/}
1.05	0.049	14.2
1.10	0.095	7.3
1.15	0.140	5.0
1.20	0.182	3.8
1.25	0.223	3.1
1.30	0.262	2.6
1.35	0.300	2.3
1.40	0.337	2.1

^{1/} Doubling time = $\frac{0.6931}{\underline{r}}$

Table 4. Sample calculation of sustained yield from a moose population with known rate of increase and fecundity. Harvest taken during the month of September.

- 1) $\lambda = 1.20$ ($\underline{r} = 0.182$)
- 2) fecundity rate (\underline{m}_x) = 0.75 calves born per adult and yearling of both sexes.
- 3) mean annual survival (P_a) = 0.685

$$P_a = \frac{\lambda}{1 + \underline{m}_x}$$
- 4) mean monthly survival (P_m) = 0.969

$$P_m = P_a^{\frac{1}{12}}$$

Month	Unharvested population N	Harvested population N	Harvest ^{1/}
May	1000	1000	
June	969	969	
July	939	939	
August	910	910	
September	882	735	147 ^{2/}
October	854	712 ^{3/}	
November	828	690	
December	802	669	
January	777	648	
February	753	628	
March	730	608	
April	707	590	
May	685	571	
	$685 \times \underline{m}_x = 514$ calves born	$571 \times \underline{m}_x = 428$	
	$685 + 514 = 1199$	$571 + 428 = 999$	
	$\lambda = \frac{1199}{1000} = 1.20$	$\lambda = 1.0$	

^{1/}If $\underline{r} = 0.182$, instantaneous rate of harvest needed to produce a stationary population (H) = 0.182

Isolated rate of harvest taken during one month (h) = $1 - e^{-H}$
 (Caughley 1977:172). $h = 0.167$

^{2/} $882 \times 0.167 = 147$; $882 - 147 = 735$

^{3/} $735 \times P_m = 712$

