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MOOSE RECRUITMENT, ADULT MORTALITY AND RATE OF CHANGE

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ABSTRACT: Rates of change in moose (*Alces alces*) abundance are typically measured from 2 or more population estimates. However, λ, the finite annual rate of change, can also be calculated from annual recruitment (R) and adult mortality (M) rates by the equation: $\lambda = (1 - M)/(1 - R)$. Thus, rate of change can be assessed without population estimates; mortality rates can be estimated from R and λ; and λ measured from absolute density surveys can be cross-checked with estimates of R and M. Moose managers may also find the equation useful for interpolating moose numbers between periodic absolute density surveys. Several examples are provided to illustrate use of the equation.

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As moose management becomes more intensive, good estimates of moose population parameters are increasingly more important. The primary population parameters required to make timely and effective management decisions include abundance, sex and age composition, mortality rates, and rate of change in abundance (Gasaway and Dubois 1987).

Absolute density surveys employing stratified random sampling have become an effective method for estimating moose abundance and sex/age composition (Larsen 1982, Gasaway *et al.* 1986, Ballard *et al.* 1991). Herd composition surveys, which can be conducted at a fraction of the cost of density surveys, are useful for providing ratio estimates of bulls:100 cows:calves. Both absolute density and herd composition surveys may be used to estimate recruitment rates, which are the proportion of new recruits (calves) in the population at some specified time (Peterson 1977, Bergerud 1978). Adult moose mortality rates may be estimated from either radio-marked animals (Gasaway *et al.* 1983, Larsen *et al.* 1989, Ballard *et al.* 1991), or age structure analysis (Peterson 1977, Boer 1988). The rate of change is typically measured from 2 population estimates by assuming geometric growth (Caughley 1977, Van Ballenberghe 1983); i.e.,

$$\lambda = (N_t/N_0)^{(1/t)}$$

where λ is the finite annual rate of change, N_t is the population size during year t and N_0 is the population size during the initial year. Where more than two estimates are available, λ may be estimated by linear regression of $\log_e (N)$ against time in years (Van Ballenberghe 1983, Eberhardt 1987). The finite rate of change can also be measured from age-specific fecundity and survival rates, using the Lotka equation for 'birth-pulse' populations (Eberhardt 1988), i.e.

$$1 = \sum \lambda^{-x} l_x m_x$$

where l_x and m_x refer to survival to age x and the age-specific birth rate, respectively. However, the estimated rate of change will differ from the actual rate of change if the age distribution is not stable. For long lived species such as moose, age distributions may seldom be stable (Van Ballenberghe 1980).

The purpose of this paper is to provide an alternative method for estimating the rate of change and adult mortality rates from moose populations. The major advantage of the 'recruitment-mortality' method (hereafter referred to as the R/M equation) is that all of the required parameters can be measured from, or estimated by, population surveys. Some examples from the moose literature are provided to demonstrate several applications of the method.

THE R/M EQUATION

Before deriving the basic equation, it is necessary to define the following:

N_0 = the number of adults at the start of the initial measurement year
N_1 = the number of adults at the start of the next measurement year (i.e., the number of adults plus new recruits)
d = the number of adults that die during the measurement year
r = the number of new recruits at the start of the next measurement year

If the population is closed to migration then,

$M = d/N_0$, the finite annual adult mortality rate (1)

$R = r/N_1$, the finite annual recruitment rate (2)

We note that

$$N_1 = N_0 + r - d \tag{3}$$

The following definitions for rate of population change are of interest:

$\lambda = N_1/N_0$, the finite annual rate of change (4)

$\Delta = (N_1 - N_0)/N_0$, the finite annual growth rate (5)

and we note that $\lambda = 1 + \Delta$ (6)

It is desirable to calculate the two rates of increase, λ and Δ, using only M and R.

By definition,

$$\Delta = (N_1 - N_0)/N_0$$
$$\Delta = (r - d)/N_0 \qquad \text{by (3)}$$
$$\Delta = (r/N_0)(N_1/N_1) - d/N_0$$
$$\Delta = RN_1/N_0 - M \qquad \text{by (1) and (2)}$$
$$\Delta = R(1 + \Delta) - M \qquad \text{by (4) and (6)}$$

Rearranging,

$$\Delta - R(1 + \Delta) + M = 0$$
$$\Delta(1 - R) = R - M$$

Hence,

$$\Delta = (R - M)/(1 - R) \tag{7}$$

and,

$$\lambda = (1 - M)/(1 - R) \tag{8}$$

CALCULATING RECRUITMENT AND MORTALITY FROM MOOSE SURVEYS

Moose population surveys are conducted primarily during early winter (October to December), or late winter (January to April) (Gasaway *et al.* 1986). By definition, the start of the initial measurement year (N_0) coincides with the completion of the population survey, at which time calves are recruited into the moose population. Ideally, calves should only be considered recruits when the new cohort is exposed to mortality factors of similiar magnitude as those experienced by adults (Hickey 1955, cited by Bergerud and Elliott 1986). If calves have a higher overwinter mortality rate than adults, then late winter surveys are preferred. Alternatively, N_0 may be defined at some specified time after the population survey, such as during late-winter or early spring, providing the finite mortality rates are known for both the calf cohort and adults during the intervening period. If calf and adult mortality rates are not equal after recruitment age, the mortality rates estimated from the *R/M* equation will be a composite of adult and mid-to-late winter calf survivals.

Recruitment Rates

Annual recruitment rates may be estimated for males (R_m), females (R_f) and both (R). If it is assumed that the number of male calves equals the number of female calves, then:

$$R = CC/(100 + BC + CC) \tag{9}$$
$$R_m = (CC/2)/(BC + CC/2) \tag{10}$$
$$R_f = (CC/2)/(100 + CC/2) \tag{11}$$

where CC is the number of calves per 100 adult females and BC is the number of adult males per 100 adult females.

Mortality Rates

Annual Surveys.—Rearranging eqn (8), M can be estimated from λ and R; i.e.,

$$M = 1 - \lambda(1 - R) \tag{12}$$

For unhunted populations, $M = Mn$, the natural (nonhunting) mortality rate. For hunted populations, M is related to the isolated hunting (Mh) and natural (Mn) mortality rates by

$$M = 1 - (1 - Mh)(1 - Mn) \tag{13}$$

(Caughley 1977:98), where

$$Mh = K/(N_0 - d)$$

K is the adult harvest during the measurement year and d is now the number of deaths due to natural causes between the start of the measurement year and the hunting season. Hence Mn can be estimated from eqn's (12) and (13):

$$Mn = 1 - \lambda(1 - R)/(1 - Mh) \qquad (14)$$

(Bergerud and Elliott 1986:1518). As with recruitment rates, adult mortality rates may be estimated for males (M_m, Mh_m, Mn_m), females (M_f, Mh_f, Mn_f) or both (M, Mh, Mn).

Periodic Surveys.—Absolute density surveys are expensive and it is neither practical nor efficient to estimate population size (N_t) annually. Ideally, these surveys should be separated by sufficient time to allow a detectable change in numbers to occur (Gasaway *et al.* 1986). Mn can still be estimated from periodic absolute density surveys providing R_t and K_t are estimated during the intervening years, and the adult natural mortality rate remains constant over the period of interest.

For unhunted populations, Mn is estimated from the following model equation:

$$N_t = N_{t-1}Sn/(1 - R_t) \qquad (15)$$

where Sn is $1 - Mn$, or the adult natural survival rate. For hunted populations, Mn is estimated from one of the following harvest removal models, depending upon the most appropriate time to measure R_t:

$$N_t = (N_{t-1}Sn - K_{t-1})/(1 - R_t) \qquad (16)$$

$$N_t = (N_{t-1}Sn_1 - K_{t-1})Sn_2/(1 - R_t) \qquad (17)$$

$$N_t = (N_{t-1} - K_{t-1})Sn/(1 - R_t) \qquad (18)$$

Eqn (16) assumes calves are recruited at the end of the hunting season and N_t is the postseason population size. Eqn (17) assumes the calf cohort is recruited during mid-to-late winter and N_t is the population size at this time. Since N_t does not coincide with either the start or end of the hunting season, two estimates of Sn are required. Sn_1 is the survival rate from the start of the initial measurement year to the start of the hunting season, i.e. late winter/summer adult survival, and Sn_2 is the survival rate from the end of the hunting season to the start of the next measurement year, i.e. early winter adult survival. Eqn (18) assumes the calf cohort is recruited during spring, adult summer mortality is negligable, and N_t is the preseason population size. Eqn's (16), (17) and (18) also assume no natural adult mortality during the hunting season.

Mn is estimated from the model equations (eqn 15, 16, 17 or 18) by iteration. This is easily achieved by writing a simple computer program that contains the model and the annual parameter estimates (N_t, R_t and K_t). For two population estimates, trial values of Sn (in increments of 0.01) are substituted into the appropriate equation along with the initial estimate (N_0) and annual estimates of R_t and K_t until the right hand side of the equation equals the second estimate (N_t). For 3 or more population estimates, a χ^2 criteria ((observed - expected)^2 /expected) must also be included where the 'observed' is the empirical estimate of N_t and the 'expected' value is the model estimate (Eberhardt 1987). The best estimate of Mn is obtained by fitting the models with combinations of N_0 (in increments of 1 individual) and Sn until a minimum sum of χ^2 values is achieved.

SOME EXAMPLES

The following examples are provided to illustrate various uses of the R/M equation for estimating λ, M, or Mn. Each example is provided only to explore the basic approach and may require further study.

Northeastern Alberta

A study of the population dynamics of moose in northeastern Alberta by Hauge and Keith (1981) provides estimates of both recruitment and adult mortality, which may be used to estimate rate of change. R was measured from the proportion of calves observed during surveys conducted from December through March, and varied from R = 0.30 in 1975-76, to 0.18 in 1976-77 and 0.20 in 1977-78. M (including both hunting and non-hunting mortality) was measured from radio-collared yearling and adult moose and averaged 0.25 over the three years.

Using eqn (8) and assuming calves had a

similiar mortality rate as adults after March, λ ranged from 1 - 0.25)/(1 - 0.18)= 0.91 to (1 - 0.25)/(1 - 0.30)= 1.07 and averaged 0.97. This rate of change is consistent with moose density estimates that suggested a stationary or slowly declining population from 1973-78.

Southwestern Yukon

A study of the causes and rates of moose mortality in southwestern Yukon (Larsen *et al.* 1989) may be used to estimate rate of change from both natural and hunting mortality rates, and recruitment. The annual natural adult female mortality rate, as estimated from radio-telemetry, was 12% (Mn_f=0.12) in 1983. The moose population, as estimated from an absolute density survey in November 1983, was 651 ± 143 (90% CI) and included 153 2^+ year-old males, 371 2^+ year-old females, 16 yearlings and 111 calves. Overwinter (November through May) mortality rates were 33% for calves and 0% for older moose. It was assumed that the yearling sex ratio was equal. Thus, the 1984 pre-calving population estimate was 161 adult males, 379 adult females, and 74 calves. Hunting losses occurred between August to November, 1983 and comprised 43 adult males and and 4 adult females.

For males, $R_m = (9.76/52.24) = 0.187$ (eqn 10) and $Mh_m = (43/[43 + 153 + 8]) = 0.211$. Assuming equal natural mortality rates between adult males and females, and incorporating eqn (13) into eqn (8):

$\lambda_m = (1 - 0.120)(1 - 0.211)/(1 - 0.187) = 0.854$

For females, $R_f = (9.76/109.76) = 0.089$ (eqn 11), $Mh_f = [4/(371 + 8 + 4)] = 0.010$, and $\lambda_f = 0.956$.

Isle Royale, Michigan

Ongoing studies of wolf (*Canis lupus*) ecology and prey relationships on Isle Royale (Peterson 1977, Page 1989) provide a unique opportunity for estimating adult natural mortality rates in an unhunted moose population. Absolute density surveys were conducted each year during February to estimate moose abundance and recruitment. From 1984 to 1990, the moose population displayed three growth periods: stable (1984-86: $\lambda = 0.992$); increasing (1986-88: $\lambda = 1.276$); and declining (1988-90: $\lambda = 0.854$).

Direct fitting with eqn (12), using annual estimates of $\lambda = N_t/N_{t-1}$ and R_t provided unreliable estimates of ***Mn***, presumably because of errors associated with annual measurements of moose abundance and/or recruitment. For example, estimates of *Mn* for 1987 and 1988 were -0.117 and -0.003 respectively. The alternative 'model-fitting' approach (eqn 15) was therefore used to estimate *Mn* for each growth period. This yielded a minimum χ^2 of 11.19 with $N_0 = 1021$ and survival (mortality) rates of 0.91 (0.09), 1.00 (0.00), and 0.76 (0.24) for the 3 growth periods repsectively (Fig. 1). The average annual mortality rate for the entire period was approximately 11%, which is similiar to Peterson's (1977) earlier life table estimate of 12.8%.

Northeastern British Columbia

Wolf-ungulate investigations in northeastern British Columbia (Elliott 1989) provide an example for calculating *Mn* in a hunted moose population from periodic absolute density surveys. These surveys have been used to assess the impact of wolf reductions on moose rate of change (Hatter 1990). Wolf numbers were reduced during 1983-84, 1984-85 and 1986-87. Absolute density surveys for moose were conducted during late February and early March in 1982, 1985 and 1989. Herd composition surveys were conducted during the intervening years to measure fluctuations in R_t. It was assumed that early winter and late winter adult natural mortality rates were equal (eqn 17), i.e.

$$N_t = (N_{t-1}Sn^{0.5} - K_{t-1})Sn^{0.5}/(1 - R_t)$$

Moose densities in 1982 (0.98 moose/km^2 ± 33.0%, 90% CI) and 1985 (0.77 moose/km^2 ± 33.2%) on a 1352 km^2 survey area indicated an annual rate of decline of 8% ($\lambda = 0.920$). Moose densities in 1985 (0.98 moose/km^2 ± 25.7%) and 1989 (1.62 moose/km^2 ± 16.1%)

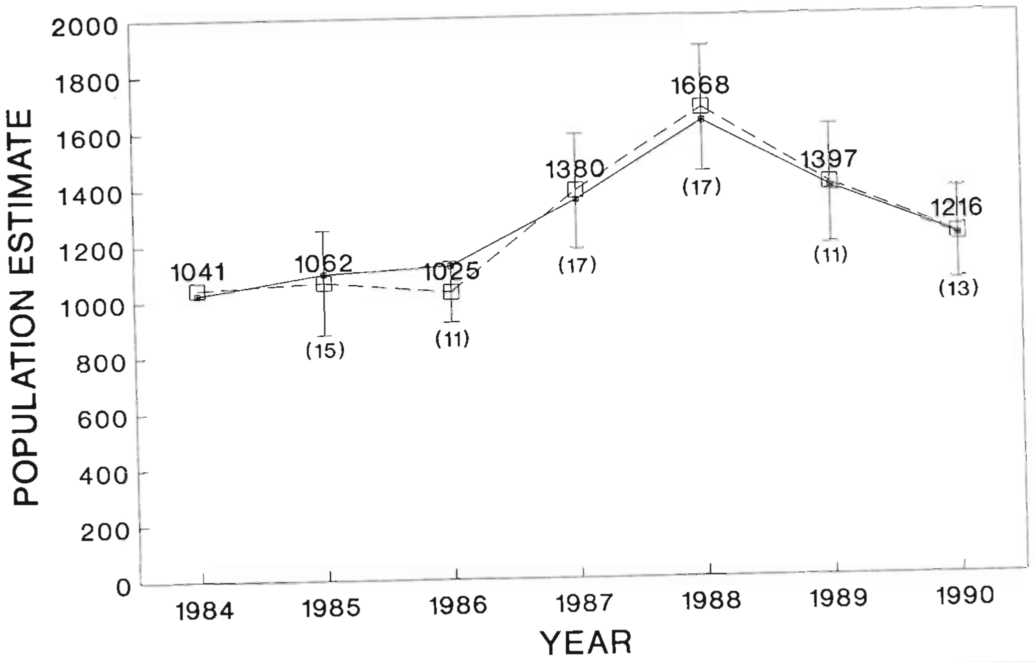

Fig. 1. Isle Royale moose population estimates and recruitment rates from 1984 to 1990. Open squares with vertical bars are population estimates with 95% CI. The numbers in brackets are recruitment rates (% calves in winter). The solid line is the fitted model estimates of population size. Data provided courtesy of R. Page.

on a 1759 km^2 survey area indicated an annual rate of increase of 13% ($\lambda = 1.134$). Additional survey coverage in 1989 yielded a population density of 1.44 moose/km^2 ± 15.7% over a 3025 km^2 survey area. This density, when extrapolated to a larger 6057 km^2 area where annual harvest estimates were available, suggested a population of about 6000 moose in 1982, 3600 in 1985 and 4700 in 1989.

Direct fitting of the model equation to the expanded population estimates indicated $Sn = 0.85$ ($Mn = 0.15$) for the 1982-85 period and $Sn = 1.01$ ($Mn < 0.00$) for the 1985-89 period. Thus, either the recruitment and/or abundance estimates were in error during the latter period. Assuming the error was associated with the population estimates and that Mn was constant throughout the 1982-89 period, the minimum χ^2 (232.8) estimate of Sn was 0.94 ($Mn = 0.06$) at an initial population of 4261 (Fig. 2). This scenario suggests a slight decline in moose numbers from 1982-84 ($\lambda = 0.97$) prior to wolf removal, a moderate increase from 1984-86 ($\lambda = 1.10$) following 2 years of wolf removals, and a reduced rate of increase from 1986 to 1989 ($\lambda = 1.05$) with only one year of wolf removal. The actual rates of change, however, were likely much greater since Mn probably exceeded 6% prior to wolf removal and decreased following the wolf reductions.

Interior Alaska

A wolf-ungulate study in interior Alaska (Gasaway *et al.* 1983) provides an example for comparing the rate of change estimated from a moose population index with an expected rate based on annual estimates of recruitment, natural mortality, hunter harvest and a single statistically based population estimate. Rates of change were estimated for two growth periods, the first corresponding to a period before wolf removal (1973 - 75) and the latter (1976 -78) during wolf removal.

Mn was estimated from radio-collared moose older than 1 year of age, and averaged 0.20 before wolf removal and 0.06 after wolf

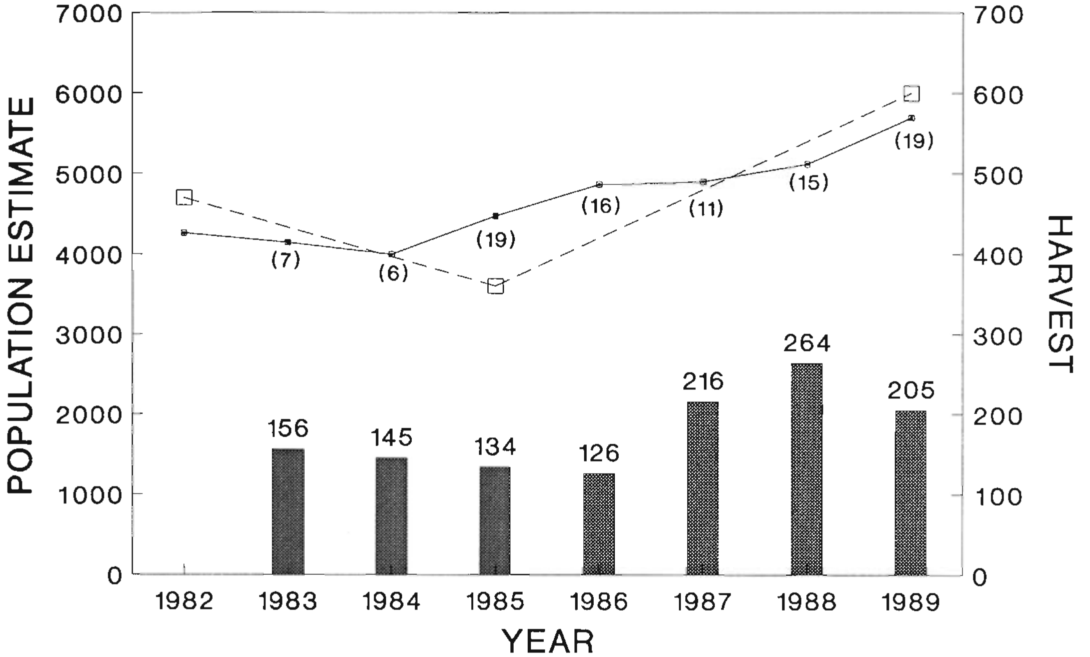

Fig. 2. Moose population estimates, recruitment rates and harvests within the Muskwa area of Northeastern British Columbia from 1982 to 1989. Open squares are population estimates. The numbers in brackets are recruitment rates (% calves in mid-winter). The solid line is the fitted model estimates of population size assuming constant mortality ($Sn = 0.94$). The vertical bars are the adult harvest estimates.

removal. With one exception, all of the radio-collared adult mortality occurred during the winter (October-April) period. Herd composition surveys for moose were conducted in both November and May. Changes in calves:100 cows during the two time periods, when adjusted for adult natural mortality, indicated that overwinter calf mortality rates were approximately 50% (1972 - 74) and 30% (1976 - 1978). These winter calf and adult mortality rates were then applied to the November calf:adult ratios to estimate R_t at the start of the next hunting season.

The annual number of moose from 1973 to 1978 was estimated from eqn (18) by selecting an initial prehunt estimate for moose (excluding calves) in 1973 (4367) that predicted 3500 moose postseason in 1978 (Fig. 3). The postseason population estimates (including calves) were estimated from the preseason population estimates by subtracting the adult harvest and dividing by the proportion of adults in the November surveys. The estimated rate of change was $\lambda = 0.79$ before wolf removal and $\lambda = 1.11$ during wolf removal. This compares favourably with estimates from the moose population index ($\lambda = 0.82$ before wolf removal and $\lambda = 1.08$ after wolf removal).

DISCUSSION

Birth, death, immigration, and emigration are the four fundamental demographic parameters in any study of population dynamics. Assuming immigration and emigration are negligible or counterbalanced, the rate of change is determined by one addition (natality) and two reductions (calf mortality and adult mortality) to the population each year (Sinclair 1973). Estimates of natality are difficult to obtain, as are estimates of calf mortality. Recruitment integrates both natality and calf

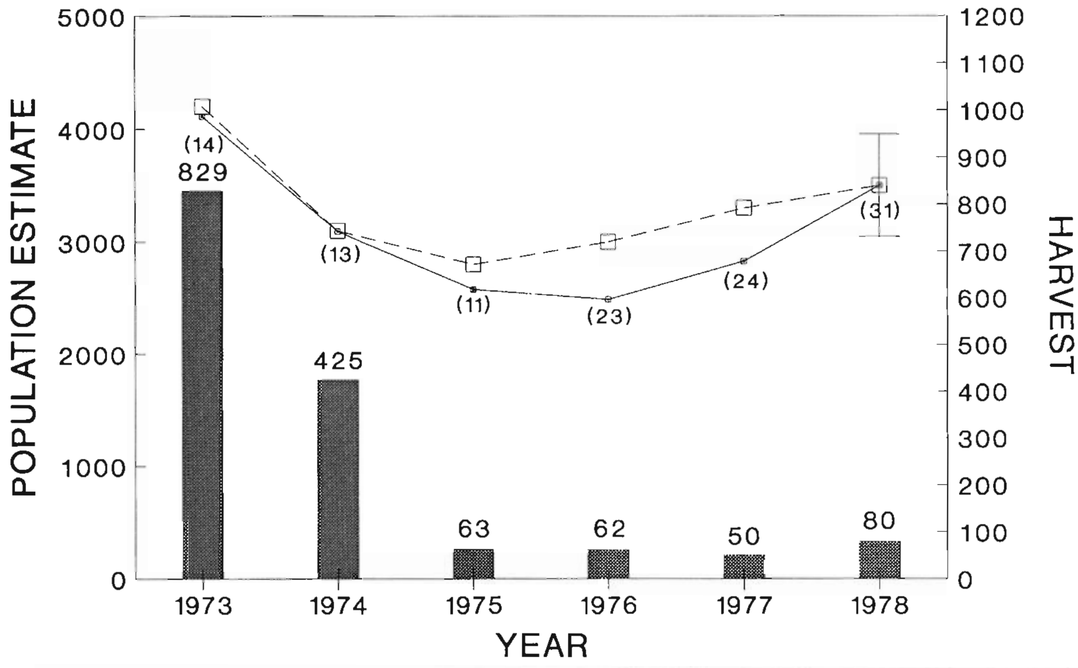

Fig. 3. Interior Alaska moose population estimates, recruitment rates, and harvests from 1973 to 1978. Open squares are posthunt population estimates based on the moose index of abundance. The numbers in brackets are recruitment rates (% calves in the posthunt population). The solid line is the fitted model estimates of population size. The vertical bars are the adult harvest estimates (adult harvests in 1973 and 1974 were estimated from total harvests assuming calves were harvested relative to their abundance).

mortality, is readily measured from composition surveys, and is an important parameter in assessing population growth. The *R/M* equation described here [$\lambda = (1 - M)/(1 - R)$] provides a convenient means for integrating R, M, and λ to calculate the adult mortality rate or rate of change.

The *R/M* equation is sensitive to estimates of R and M. For example, if $R = 0.15$ and $M = 0.05$, but R was incorrectly estimated to be 0.20, then λ would be estimated to be 1.188, rather than 1.118. If M was actually 0.10, the error would be substantial ($\lambda = 1.188$ rather than 1.059). Unfortunately, herd composition surveys may produce biased estimates of recruitment (Van Ballenberghe 1979) and absolute density surveys for moose are often imprecise (Gasaway *et. al.* 1983, Crete *et al.* 1986). Careful planning to reduce bias and increase precision in population surveys would help to improve the equation's utility. The equation would also be more useful if confidence intervals were associated with each estimated parameter.

It is recommended that the *R/M* equation be used primarily for the following: (1) to estimate λ or Mn from statistically precise and unbiased estimates of λ, R, M, Mh (or K); (2) to cross-check estimates of λ measured from 2 or more absolute density surveys with annual estimates of M and R; and (3) to interpolate moose numbers between periodic absolute density surveys. The latter should be particularly useful to moose managers. Providing annual estimates of R, K, and Mn are available, managers can monitor yearly changes in moose numbers and determine the most appropriate time to repeat absolute density surveys in order to detect significant changes in moose abundance.

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