Send correspondence to: William C. Gasaway Alaska Department of Fish and Game Division of Game 1300 College Road Fairbanks, AK 99701 USA

ESTIMATING MOOSE POPULATION PARAMETERS: A REVIEW

By

William C. Gasaway

and

Stephen D. DuBois

•

Alaska Department of Fish and Game

1300 College Road

Fairbanks, Alaska USA 99701

Abstract

The purpose of this paper is to discuss the requirements of good estimators (mathematical formulae) of population parameters; to review methods of estimating moose (Alces alces) abundance, sex and age composition, rates of population growth and decline, mortality rate, and distribution and relative density; and to show how population data have or will improve moose management. Good estimators are precise, unbiased, and robust. Advances in the past decade have improved precision by incorporating estimates for most sources of variation and have decreased bias of estimators so that repeated estimates center near the true value. We discuss the effects of imprecision and bias on estimated population parameters and on conclusions drawn from them. The most important advances in estimating abundance and sex-age composition were development of sampling designs that correct for sightability bias and which incorporate the variance of the sightability correction factor in the precision estimate. The need for a measure of precision of estimated rate of population change is demonstrated; without which, random sampling error frequently causes erroneous conclusions on rates of change. Mortality rates of

-2-

'calf and adult moose are best estimated using mortality sensing devices in radio collars and estimators that minimize bias. Currently available estimators provide population data adequate to effectively manage most moose populations. However, cost of estimating population parameters is often too great for management agencies. Examples of the use of population data are given.

. Introduction

The primary moose population parameters required to make timely and effective management decisions are abundance, sex and age composition (including recruitment), rate of change in abundance, and mortality rates. Successful management can occur without estimates for all these population parameters. However, the faster populations change, and the more intensive and intricate the management, the more critical it becomes to have good estimates of major population parameters.

The purpose of this paper is to substantiate the need for better population data, to discuss the requirements of good estimators of population parameters, to review and evaluate methods of estimating some population parameters

c

Ľ

-3-

developed in the past decade, and to indicate ways currently available population data can improve moose management.

Need for population data

Management difficulties encountered by agencies during the past decade clearly demonstrate the need for better population data. For example, marked declines occurred in moose populations before the magnitude and rate of decline were recognized and before timely and effective solutions were implemented (British Columbia, Bergerud 1978; Manitoba, V. Crichton pers. commun.; Yukon Territory, D. Larsen unpubl. data; Saskatchewan, R. Stewart pers. commun.; Alaska, Gasaway et al. 1983). As an example, numbers of moose in Interior Alaska declined sharply during the early 1970's, reaching a low density by the time biologists were convinced that the decline was rapid and not self-reversing (Gasaway et al. 1983). Drastic reductions in man's harvest of moose and in wolf numbers were required to begin the population recovery. Recovery could have been initiated sooner with less severe restrictions on man and wolves had better data on population size, rate of change, and mortality been available and applied.

-4-

Improved population data are also needed for complex, new management programs designed to alter moose sociobiology, increase populations, and alter sex-age composition (Stewart 1978, Bubenik 1981, Macgregor and Child 1981, Child 1983, Euler 1983, Gollat and Timmermann 1983). Equally good population data are required for research that elucidates ecological principles on the control and regulation of populations (Keith 1974, 1983; Caughley 1976, 1977<u>a</u>; Peterson 1977; McCullough 1979; Bergerud 1980; Bergerud et al. 1983; Gasaway et al. 1983; Peek and Eastman 1983; Peterson and Page 1983) and that assesses man's impact on wildlife populations, e.g., industrial development (Cameron and Whitten 1980, Whitten and Cameron 1983) and hunting (Crichton 1981; Crête 1985).

Qualities of Estimators

A population parameter is calculated from an estimator, which is a mathematical expression that indicates how to calculate an estimate of a parameter from sample data (White et al. 1982). A good estimator is (1) precise, i.e., minimizes variance; (2) unbiased or virtually unbiased, i.e., the mean

-5-

of a large number of estimates will equal the actual value (μ) ; (3) robust, i.e., estimates are not influenced much if important assumptions are violated; and (4) one that calculates normally distributed estimates for sample sizes usually encountered; if not normally distributed, then the approximate distribution should be known (White et al., op. cit.). For a readable and lucid discussion of statistical concepts related to estimation procedures, we recommend White et al. (op. cit.).

Recent efforts to improve estimators of population parameters have focused on precision and bias. Precision and bias must be understood before discussing specific estimators of parameters. An example by White et al. (op. cit.) of a rifleman shooting at a target clarified precision and bias. The size of the group of bullets on the target is a measure of the shooter's precision, and the location of the group's center with respect to the bull's-eye is a measure of bias resulting from sight alignment. Ideally, the rifleman shoots a small group centered on the bull's-eye, i.e., precise and unbiased. Similarly, estimators of population parameters should be precise and unbiased, i.e., repeated estimates

ł

-6-

 \cdot repeated estimates should virtually equal μ . However, most population estimators are biased and are commonly imprecise, or have no measures of precision.

Precision

Fig. 1

A measure of precision is required to evaluate the goodness of an estimate. Precision is measured by the sampling variance, which is a function of random sampling error. Sampling error results when the parameter value in individual sample units (SU's) differs from µ. The estimated value is a function of the parameter values in the specific SU's selected. Gasaway et al. (in review <u>b</u>) illustrate this by drawing 10 replicate random samples of 32 SU's each from a hypothetical moose population, referred to as the Square Mountain population (Fig. 1). The actual number of moose is 763, whereas the 10 estimates range from 624-879 and none equal µ. In real life, one will make 1 population estimate and not know µ; therefore, it is impossible to know if the single estimate is close to or distant from the true population. By calculating a confidence interval (CI), you can predict, with a specified

probability, a range in which μ will likely lie. For example,

-7-

90% CI's for 10 replicate estimates of the Square Mountain population show that μ is included in the CI 9 of 10 times (Fig. 2A). But in real life, there is no way to predict where μ is within a specific CI or even to be positive it is in the CI.

Bias

Fig. 2

ł

Many factors bias estimators of population parameters. For example, overlooking animals results in an underestimate of animal abundance (Caughley 1974), and differential behavior of sex-age classes results in over- and underestimates of relative abundance for specific sex-age classes (Thompson 1979; VanBallenberghe 1979; Novak 1981; Gasaway et al. 1981; Gasaway et al., in review <u>a</u>, <u>b</u>). Also, estimators of sampling variance may be biased, causing precision to be over- or underestimated.

Some biases can be estimated and corrected for. For example, several methods of estimating sightability bias have been used (Novak and Gardner 1975; Floyd et al. 1977; Cook and Jacobson 1979; Crête and St-Hilaire 1979; Crête et al., in review; Gasaway et al., in review <u>b</u>); however, correction

-8-

factors for composition have rarely been estimated (VanBallenberghe 1979, Gasaway et al. 1981). Computer simulation models have been used to identify biased estimators of sampling variance and to alter estimators and minimize bias (Gasaway et al., in review \underline{b}).

Unrealistic confidence intervals--a common problem

Calculating CI's that include µ with the specified probability is a major problem throughout the science of population biology. Because of bias, reported CI's commonly do not include µ the specified percentage of the time and therefore are unrealistic. We will show the effects of 2 common biases on CI's. First, a CI will have a lower than specified probability of containing µ when calculated from an estimator that underestimates µ. The problem can be illustrated with the Square Mountain example. The unbiased estimator of moose abundance was: area X estimated density. All moose in selected SU's were seen. Now assume 20% of the moose were missed during 10 replicate surveys and no correction factor for bias was available. Only 5 of the CI's for the 10 estimates from the biased estimator include µ (Fig. 2B).

-9-

Therefore, the CI is closer to a 50% CI rather than the stated 90%.

Secondly, unrealistic CI's result when variance is not estimated for all sources of sampling error. This problem is nearly universal among the estimators of moose abundance used today. To illustrate this, we use the following estimator of moose abundance: area X observed moose density X SCF, where SCF is the sightability correction factor that estimates and corrects for bias.

Each component in the formula is estimated. Commonly, only the sampling variance for observed moose density is used to calculate the CI. The result is an underestimate of total sampling variance and an underestimate of CI width for a specified probability. In other words, more confidence is put in the estimate than it deserves.

2

Required precision

The degree of precision needed varies with the questions asked and consequences of an error. If consequences of a mistake are severe, then precision must be higher than if the consequences are minor. Timely, effective management decisions require reasonably precise estimates that are corrected for most biases. This translates into realistic 90% CI's that are less than $\pm 20\%$ of the estimate. If estimators account for only a portion of the variance, CI's must be smaller. How much smaller depends on the size of the missing variance component. With CI's of $\pm 20\%$, a population must increase or decline about 20% to detect a significant ($\underline{P} < 0.05$) change in abundance and to calculate a significant rate of change (Gasaway et al., in review <u>b</u>). From a manager's perspective, that can be a large change; however, it is necessary if a high probability of making the correct decision is desired. The only recourse is to increase the level of precision.

Methods of estimating population parameters

Moose abundance

Aerial survey methods

Timmermann's (1974) conclusion that aerial surveys were the only feasible means of estimating moose abundance still

applies today. The 2 approaches currently used are searching an entire area or sampling. Sampling techniques are used most commonly because estimates can be made for larger areas. Sampling schemes usually involve stratifying the survey area into 2-4 strata of varying moose density and randomly selecting SU's within each strata.

SU's take 2 general forms--transects and plots. Transects are long, narrow belts varying in length and width, whereas plots refer to a general category of SU's that are square (Evans et al. 1966) or rectangular and uniform in size (Crête and St-Hilaire 1979) or irregular in shape and area (Norton-Griffiths 1978; Gasaway et al., in review b).

The survey options have their strengths and weaknesses (Norton-Griffiths 1978, Caughley 1977<u>b</u>, and Thompson 1979). Summarizing these: total area searches are most precise because there is no sampling variance among SU's, high initial sightability is achievable, and there are several options for estimating a SCF; however, total area searches are restricted to small areas because of high cost/km². Transect sampling is the least fatiguing, can provide precise estimates of observable moose density, SCF's can be estimated, locating SU's in areas with few landmarks is

-12-

easier than when using plots, and $cost/km^2$ is lowest. The major weaknesses are the method is restricted to relatively flat terrain, high resolution aerial photo maps are required for the line transect SCF to be most successful for estimating moose abundance (see line transect estimator below), and sightability of moose tends to be low, causing the SCF and its sampling variance to be large. Lastly, bias and precision of SCF estimators (Thompson 1979, Cook and Jacobson 1979) for moose surveys have not been adequately evaluated. Plot sampling can be used in all terrains except areas with few natural landmarks, high sightability can be attained and a SCF can be estimated. Drawbacks are that a portion of the SCF must be subjectively applied based on sightability estimates from radio-collared animals (Floyd et al. 1977; Rolley and Keith 1980; Crête et al., in review; Gasaway et al., in review b) or experiments with penned moose (LeResche and Rausch 1974) and that plot sampling is more expensive than transect sampling.

Correcting for sightability bias

The estimated observable number of moose is of limited value unless it can be corrected for moose not seen. Therefore, the quality of a specific method depends largely on the precision, bias, and robustness of the SCF estimator. Estimating the SCF, its variance, and merging these with the estimate of observed moose density and its variance has been the major area of research and advancement in estimation procedures during the past decade.

<u>Resurvey estimator</u>:-This is the most commonly used correction technique in North America. It is a 2- or 3-stage sampling technique (Novak and Gardner 1975; Gasaway et al., in review <u>b</u>); the estimator is SCF = SCF_o X SCF_c, where subscripts o and c stand for observed and constant. The SCF_o is estimated from 2-stage sampling; a SU is searched with a standard search and then a randomly selected portion is resurveyed with a higher search intensity that results in most moose being seen. The estimator is SCF_o = number moose seen on intensive search + number moose seen on standard search. Clearly, SCF_o underestimates SCF, except when no moose are missed on the intensive search. SCF_c is independently estimated using radio-collared animals missed during simulated intensive searches (Floyd et al. 1977; Rolley and Keith 1980; Gasaway et al. 1979; Crête et al., in review). When standard

-14-

search effort is high, in effect an intensive search, the $S\check{C}F_{c}$ has been applied directly to the estimated number of observable animals (Floyd et al. 1977; Crête et al., in review, Gasaway et al., in review <u>b</u>).

The resurvey estimator has 2 flaws. First, the SCF_c varies with sightability, thus several SCF_c are needed and must be applied subjectively. As with any application of a constant to estimate a variable, there is an unknown bias and loss of precision. Second, no variance estimate for SCF_c has been used, except for Crête et al. (in review).

The resurvey estimator can be used with any survey method if discrete areas can be defined for the intensive search. For example, Novak and Gardner (1975) used it with transects whose boundaries were identified on aerial photos. Gasaway et al. (in review <u>b</u>) used it with stratified, random sampling and irregular-shaped plots. Gasaway et al. (op. cit.) also optimally allocated sampling effort between standard searches and intensive searches to achieve the most precision for dollars spent. Confidence intervals (90%) were generally \pm 10-30% of the estimated number of moose.

<u>Multiple regression estimator</u>:-Crête and St-Hilaire (1979) proposed a model that used data collected from a fixed-wing aircraft to predict the observed density when searched from a helicopter. Recently, Crête et al. (in review) concluded this estimator was too imprecise for management purposes. They now estimate observed density directly from a helicopter and estimated the SCF_c as discussed above.

Line transect estimator:-This estimator is widely used in wildlife work (Eberhardt 1978, Burnham et al. 1980, Seber 1982) and was applied to estimation of moose abundance by Thompson (1979). The assumption is that 100% of the animals are seen in a strip along the center of the transect and sightability declines as distance from center increases. Estimation of the SCF can be visualized as follows. A histogram depicting number of animals seen in strips of increasing distance from the transect's center is plotted (Fig. 3A), and a curve is fitted to the frequency values (Fig. 3B). The estimator of SCF is the area of the rectangle surrounding the curve (F') divided by the area under the curve (F) (Fig. 3C) (Anderson and Pospahala 1970). Thompson (1979) does not give variance estimators for the SCF, but estimators can be obtained from Burnham et al. (1980). At

Fig. 3

-16-

'this point, we cannot determine the level of precision expected from this method when used to estimate moose abundance.

This correction estimator is inexpensive to apply, if the requirements can be met. Application of this estimator is a major improvement over uncorrected population estimates calculated from transect data. The weaknesses for widespread use of this correction method, as applied by Thompson (1979), are (1) high resolution photos are needed to define transects, plot moose locations, and estimate distances; (2) moose abundance is probably underestimated because the assumption that 100% of the moose are seen in the strip adjacent to the transect center is violated as a result of a blind spot under the plane and because more moose were missed on one side of the plane; (3) the assumption that searching is done from the center of the transect is violated if the plane deviates from the center transect line to collect sex and age data (this becomes increasingly serious as density increases); and (4) bias in the SCF estimator varies with the method of curve fitting for the frequency distribution.

<u>Cook-Jacobson visibility bias estimator</u>:-This model estimates the probability of sighting groups of varying size (Cook and Jacobson 1979). It assumes the probability of sighting a group increases with group size, and that all group members are seen in each group located. The number of groups of each size is estimated for the survey area and the total number of moose calculated. The variance estimate for total moose includes the variance of the SCF. This estimator of sightability bias can be used with all survey methods.

The accuracy and precision of the predicted correction factor, to the authors' knowledge, has not been verified in field tests. Cook and Jacobson (1978), in an unpublished report that used the same data base as in Cook and Jacobson (1979), estimated that only about 10% of the deer were missed in the stratum with the densest forest canopy. In contrast, Floyd et al. (1977) in Minnesota missed approximately 50% of radio-collared deer in plots that received about twice the search effort (6.6 min/km²) as plots in Cook and Jacobson's study. This large discrepancy may be due to real differences in sightability, but it also indicates the need to rigorously field test the Cook-Jacobson estimator.

The precision of the estimator is greatest when the survey area is stratified by habitat type (Cook and Jacobson 1979). This presents problems in areas containing a diverse

-18-

mosaic of habitat types because SU's will generally contain several habitat types. Also, stratification by habitat is not the optimal strategy where moose density varies widely within a habitat type. The aircraft and manpower costs of applying this correction method are high because the entire survey must be flown in a 4-place plane with 2 observers viewing only half the potential area, i.e., 1 side of the aircraft.

Summarizing methods of estimating moose abundance, the single most important advance since Timmermann's (1974) review has been the development of sampling designs that correct for all or part of sightability bias and which incorporate the variance of the SCF estimate in the precision estimate (Cook and Jacobson 1979; Thompson 1979; Rolley and Keith 1980; Crête et al., in review; Gasaway et al., in review <u>b</u>). The SCF estimators are not perfect; all estimators are best when sightability is high and decline in quality as sightability declines. Other advances such as the use of high resolution aerial photos (Novak and Gardner 1975) and natural boundaries (Gasaway et al., in review <u>b</u>) for SU identification have increased sampling efficiency. Precision has also improved by optimally allocating search effort using

-19-

variance estimates made during the survey (Gasaway et al., in review b).

Despite these advances, the major problems still remain correcting for sightability bias and estimating precision. The available SCF estimators generally become more biased as sightability declines. Some variance estimators are still incomplete and some estimators produce approximations of variance that may be biased. Computer simulation experiments can assist in developing unbiased estimators or verifying currently used estimators.

Sex-age composition

Two approaches are used to estimate the sex-age composition of moose populations. The most common is to sample an unknown percentage of the population and calculate the percentage of moose in sex-age classes or calculate a ratio of 1 class to another. This is the limit of the use of the data if population size is unknown. The second approach is to estimate numbers in sex-age classes from population estimation data; 2 options exist. First, the proportion of each sex-age class in the sample of observed moose is calculated and the number of moose in a specific sex-age class is estimated by multiplying its proportion times the population estimate. No estimate of precision accompanies these proportions or estimated numbers in sex-age classes. The second option is to estimate numbers of moose in sex-age classes with estimators similar to those used to estimate moose abundance (Thompson 1979; Gasaway et al., in review <u>b</u>). With this procedure, estimates of precision can be calculated for numbers in sex-age classes, percentage in the population, and sex-age ratios. The precision estimates accompanying this latter method give it a clear advantage over other methods.

Estimators of sex-age composition are sometimes biased because estimators do not account for differing sightability among sex-age classes (Gasaway et al. 1981; Gasaway et al., in review <u>a</u>; Linkswiler 1982) and the nonuniform spatial distribution of sex-age classes (Fig. 4). Therefore, sex-age can vary with survey search intensity and sampling design, i.e., where you search. Search intensity that yields high sightability will lower the potential bias. Random sampling designs that estimate composition by strata also minimize bias compared to subjectively selected areas surveyed primarily for composition data.

Fig. 4

-21-

Rate of change

Rate of population change (increase or decline) is one of the more useful parameters. It is estimated from 2 or more population estimates over time (Caughley 1977a). The rate estimator depends on the trajectory of the population curve, e.g., exponential or linear growth are 2 possibilities (Gasaway et al., in review b). Caughley (1977a) gives formulae for calculating exponential rates of change, and Gasaway et al. (in review b) give formulae for linear rate of change and provide estimators of variances and CI for both exponential and linear rates. A measure of precision is necessary to evaluate the quality of the rate estimates, yet we know of no measure of precision accompanying rate of change estimates in the literature on ungulate population dynamics. Hopefully, wildlife biologists soon will recognize the value of precision estimates for rates of change and will begin calculating them when appropriate.

Meaningful rates of change can best be estimated when a population makes a statistically significant change. Therefore, before estimating rates of change, determine if initial and final population estimates differ statistically with appropriate statistical tests (Gasaway et al., in review b).

-22-

Unbiased population and variance estimators must be available to make a valid statistical test. Even though estimators are commonly biased and generally underestimate true values, statistical tests still have merit. For example, population estimates that are not significantly different, based on underestimated variances, clearly are not significantly different with unbiased variances. Population estimates that are marginally statistically different with underestimated variances may be subjectively ruled not different if the size of the bias can be estimated.

Estimated rates of change based on nonsignificant population changes can be deceptively suggestive of change if the rate is viewed without its estimate of precision. For example, rates of increase or decrease can be calculated from any 2 or more estimates for the stable Square Mountain moose population (Fig. 1) by assuming a 2-year interval between replicate surveys. Random sampling error produced the variation among population estimates; that variation leads to estimated rates of changes as great as $\hat{r} = \pm 0.17$ when in fact no change was occurring (Fig. 5). Therefore, it is

Fig. 5

critical to use statistical procedures, when possible, to evaluate the precision of the data base and to minimize the probability of erroneous conclusions.

-23-

It is difficult to statistically detect a real change over a short period because of imprecision of moose population estimates, e.g., 1 or 2 years. Using the most precise population estimates in the literature (e.g., Peterson 1977; Bailey 1978; Gasaway et al., in review <u>b</u>), changes of about 20% or more are required for changes to be detected. Changes of that magnitude usually take several years with moderate rates of change or many years at low rates. Using imprecise estimates, populations may have to increase by 50-100% before a change can be detected. When no measure of precision is available, you cannot be statistically confident how much or how fast a population changed, although other data often support the conclusion that real changes occurred.

Distribution and relative abundance of moose

Little is known about distribution and relative density of moose in North America for 2 reasons. First, most fieldwork takes biologists repeatedly to a few sites; consequently, they often cannot accurately predict relative moose density in large areas where they are the primary moose manager. Second, it is difficult to record distribution and relative

-24-

density data in a form that is easily interpreted by other people.

Gasaway et al. (in review <u>b</u>) suggest a method for rapidly and inexpensively recording distribution and relative density data over large areas. This method is basically the application of the stratification procedure used in the population estimation method of Gasaway et al. (op. cit.) The end product is a map of relative densities that allows data to be easily transferred and interpreted by many people.

Mortality rates

The ability to estimate mortality rates and assess causes of death has improved with advances in biotelemetry. Previously, mortality rates of adult moose were estimated from life tables (Peterson 1977) or from yearlings recruited into a stable population (Bergerud 1978, 1980). Now, age- and sex-specific mortality rates can be estimated from radiocollared moose by using methods described by Trent and Rongstad (1974), Gasaway et al. (1983), and White and Bartman (1983). Despite the seeming simplicity of calculating mortality rates from radio-collared moose, there are biases that must be recognized and minimized (Gasaway et al. 1983).

-25-

Timing, causes, and rates of neonate moose mortality can be estimated using mortality sensing radio transmitters attached to expandable collars. The method has been used to identify the effect of specific predator species on calf moose survival in multipredator systems (Franzmann et al. 1980, Ballard et al. 1981; W. Gasaway, S. DuBois, and R. Boertje, unpubl. data; D. Larsen and R. Hayes, unpubl. data; R. Stewart, unpubl. data). The major limitation of this method is its great expense; radio collars cost about \$325 (US) in 1984 and helicopters and aircraft are generally needed in the capture and monitoring of calves and for retrieval of carcasses.

Calf mortality rates can also be estimated from unmarked calves of radio-collared cows (VanBallenberghe 1979, Hauge and Keith 1981, Gasaway et al. 1983). This method shows seasonal mortality rates, but provides no data on causes of death.

The least expensive and most commonly used method of estimating calf mortality rates is based on changes in calf/cow ratios. Ratios are estimated from aerial surveys or at parturition from natality data (VanBallenberghe 1979, Hauge and Keith 1981, Gasaway et al. 1983). Cause of death

-26-

cannot be determined with this method. As a cautionary note, mortality rates estimated by this method are subject to large errors because biased survey techniques can underestimate the calf/cow ratio during summer (Gasaway et al., in review <u>a</u>) and during winter (Gasaway et al. 1981; D. Larsen, unpubl. data) and because of wide variation in natality rates (Blood 1974, Franzmann and Schwartz 1984).

Management application

The 3 major shortcomings of population parameter estimators have been bias, imprecision, and high cost. Developments in the past decade have reduced biases and increased precision. Unfortunately, these improvements have brought higher costs that must be accepted when precise data are required.

Estimators currently available provide the wide range of data needed to interpret the dynamics of populations, which in turn is the basis for making meaningful and timely management actions. Meaningful actions solve problems. In contrast are the ineffective or cosmetic actions, done largely for appearance or to slow the rate of deterioration. For example, a moose population is declining because of mortality due to hunting

-27-

and predation, but only the hunting season is shortened. The population continues to decline because of losses to predators. This was not a meaningful action--it did not solve the problem of a declining population. Timely actions are critical to management success. If years of hindsight are required to make meaningful decisions, problems will be greater and actions may be more severe when solutions are implemented.

Currently available population data can assist in taking meaningful and timely management actions. For example, probable population status and rate of change at a point in time (rapid decline, rapid increase, nearly stable, etc.) can be quickly predicted using a simple population model (Bergerud 1978, 1983). Conceptually, the model is a balance sheet, weighing income (recruitment) against outflow (mortality) (Fig. 6). Required data are estimates of adult moose abundance, numbers recruited, and numbers dying. A single population estimation survey provides adult abundance and recruitment, whereas mortality estimates come from a variety of data sources and from rough estimates. For example, mortality from wolf predation can be estimated from the literature using a range of kill rates and the estimated number of wolves or packs (Gasaway et al. 1983, Keith 1983).

Fig. 6

-28-

Use of these simplistic models has allowed biologists to quickly predict the likely population trend with only a few months of fieldwork (e.g., Bergerud 1978). This is particularly important where data for many populations are being collected for the first time or is only intermittently collected. Judgments must be made quickly as to population status and their priority for management dollars and time. If, for example, the management objective is to maintain or increase moose abundance while the model predicts rapid decline, timely and meaningful actions are required. Several years of procrastination while confirming the decline and estimating the rate can leave a manager with a great strategy but few moose to manage.

Improved population data have enhanced our understanding and management of moose-predator systems. For example, a preliminary assessment of the effect of wolf predation on moose population dynamics can be predicted rapidly and inexpensively using moose/wolf ratios (Mech 1970, Peterson 1977, Gasaway et al. 1983, Keith 1983). Also, moose mortality studies using telemetry have helped identify the role of predators in multipredator systems, resulting in effective, predator-specific management (Franzmann et al. 1980; Fuller

-29-

and Keith 1980; Ballard et al. 1981; Gasaway et al. 1983; D. Larsen and R. Hayes, unpubl. data; R. Stewart, unpubl. data; Ballard and Larsen 1985, VanBallenberghe 1985).

A moose population estimate can calibrate an index of moose abundance which can be used to roughly predict past moose population levels (Gasaway et al. 1983). This procedure allows ecological insights to be drawn from historical population trend indexes. Implicit is the assumption that the index proportionately reflects a change in moose abundance.

Complex management programs designed to manipulate moose populations within specified bounds require precise population data. Managers must evaluate if progress is being made toward goals, when goals are achieved, and when populations significantly deviate from desired densities or composition. Today's techniques will accommodate most data needs. Thus, biologists are provided a reasonable probability of accomplishing relatively stable, long-term population management in many areas. In areas where data are less complete, large unexpected oscillations in population size will maintain our traditional crisis management policy.

Achieving goals and stability in management programs builds the public confidence in wildlife departments. That

-30-

confidence is necessary if departments are to be adequately funded and be given the opportunity to manage, as exemplified recently with the following controversial management programs. Wolf and/or bear management programs designed to increase ungulates were slowed, altered, and sometimes stopped by public opposition in Alaska, British Columbia, and the Yukon Territory. In British Columbia, Saskatchewan, Alaska, and Ontario, public acceptance was needed before testing sex- and age-specific harvest allocation schemes designed to alter the behavior and vigor of moose populations (Stewart 1978, Bubenik 1981, Macgregor and Child 1981, Child 1983, Euler 1983, Gollat and Timmermann 1983). Good population data demonstrating the biological effects and merits of programs such as these have satisfied many original critics of programs, leaving mainly philosophical differences to debate.

There are many other ways our understanding of moose population dynamics and management have been enhanced by improved population data during the past decade. For examples, see reviews in this symposium by Crête (1985), Page (1985), and VanBallenberghe (1985).

In conclusion, techniques are available that provide data acceptable for successfully managing many North American

-31-

moose populations. However, 2 factors often prevent successful management. First is the lack of funds. Shortages of funds can be partially compensated for by rigorous prioritization that ensures the most important data are collected. Second is the the lack of creativity by some biologists. We must strive for more innovative approaches. Let us ensure that technology and funding rather than biologists limit management success.

Acknowledgments

We thank Vince Crichton and Steve Peterson for suggestions that improved the manuscript.

References

- Anderson, D. R., and R. S. Pospahala. 1970. Correction of bias in belt transect studies of immobile objects. J. Wildl. Manage. 34:141-146.
- Bailey, T. N. 1978. Moose populations on the Kenai National Moose Range. Proc. North Amer. Moose Conf. Workshop 14:1-20.

Ballard, W. B., and D. G. Larsen. 1985. Implications of predator-prey relationships for moose management. Viltrevy. In press.

Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in southcentral Alaska. J. Wildl. Manage. 45:335-342.

Bergerud, A. T. 1978. Caribou. pp. 83-101. Eds: Schmidt, J. L., and Gilbert, D. L. Big game of North America.

Bergerud, A. T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. pp. 556-581. Eds: Reimers, E., Gaare, E., and Skjenneberg, S. Proc. 2nd Int. Reindeer/Caribou Symp. Røros, Norway. Direktoratet for vilt og ferskvannsfisk, Trondheim.

Bergerud, A. T. 1983. The natural population control of caribou. pp. 14-61. Eds. Eastman, D. S., and Peek, J.
M. Symp. on Natural Regulation of Wildlife Populations.
For., Wildl., and Range Exp. Stn., Univ. Idaho.

Bergerud, A. T., W. Wyett, and B. Snider. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. 47:977-988.

-33-

Blood, D. A. 1974. Variation in reproduction and

productivity of an enclosed herd of moose (Alces alces). Trans. Int. Congr. Game Biol. 11:59-66.

Bubenik, A. B. 1981. Moose research and sociobiological management. Alces 17:78-94.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72. 202 pp.

Cameron, R. D., and K. R. Whitten. 1980. Influences of the Trans-Alaska Pipeline Corridor on the local distribution of caribou. pp. 475-484. Eds: Reimers, E., Gaare, E., and Skjenneberg, S. Proc. 2nd Int. Reindeer/Caribou Symp., Røros, Norway. Direktoratet for vilt og ferskvannsfisk, Trondheim.

Caughley, G. 1974. Bias in aerial survey. J. Wildl. Manage. 38:921-933.

1

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Adv. Appl. Biol. 1:183-247.

Caughley, G. 1977<u>a</u>. Analysis of vertebrate populations. John Wiley and Son, N.Y. 234 pp.

Caughley, G. 1977<u>b</u>. Sampling in aerial survey. J. Wildl. Manage. 41:605-615.

Child, K. 1983. Selective harvesting--some early experiences.

Cook, R., and J. O. Jacobson. 1978. A visibility biased model for aerial surveys of moose on the Aoserp study area. Alberta Oil Sands Environmental Research Program. unpubl. rep. 25 pp.

Cook, R., and J. O. Jacobson. 1979. A design for estimating visibility bias in aerial surveys. Biometrics 35:735-742.

moose. Viltrevy. In press.

Crête, M., and D. St-Hilaire. 1979. L'hélicoptère et

l'avion pour dénombres les orignaux dans le sud-ovest du quebec. Naturaliste Can. 106:487-495.

Crête, M., L. Rivest, H. Jolicoeur, J. Brassard, and F. Messier. Correcting visibility bias for moose aerial census over

mixed forests of Quebec. J. Wildl. Manage. In review. Crichton, V.F. J. 1981. The impact of treaty indian harvest

on a Manitoba moose herd. Alces 17:56-63.

Eberhardt, L. L. 1978. Transect methods for population studies. J. Wildl. Manage. 42:1-31.

Euler, D. 1983. Selective harvest, compensatory mortality, and moose in Ontario. Alces 19. In press.

- Evans, C. D., W. A. Troyer, and C. J. Lensink. 1966. Aerial census of moose by quadrat sampling units. J. Wildl. Manage. 30:767-776.
- Floyd, T. J., L. D. Mech, and M. E. Nelson. 1977. An improved method of censusing deer in deciduous-coniferous forests. J. Wildl. Manage. 43:258-261.
- Franzmann, A. W., and C. C. Schwartz. 1984. Moose twinning rates in recent vs. old burns. J. Wildl. Manage. In press.
- Franzmann, A. W., C. C. Schwartz, and R. O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. J. Wildl. Manage. 44:764-768.
- Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583-602.
- Gasaway, W. C., S. D. DuBois, and S. J. Harbo. 1981. Moose survey procedures development. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-11, W-21-1, and W-21-2. Juneau. 66 pp.
- Gasaway, W. C., S. D. DuBois, and S. J. Harbo. Biases in aerial transect surveys for moose during May and June. J. Wildl. Manage. In review <u>a</u>.

- Gasaway, W. C., S. J. Harbo, and S. D. DuBois. 1979. Moose survey procedures development. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-17-11. Juneau. 48 pp.
- Gasaway, W. C., S. D. Dubois, S. J. Harbo, and D. J. Reed. Estimating moose population parameters from aerial surveys. Biological Papers, Univ. of Alaska. In revíew <u>b</u>.
- Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84. 50 pp.
- Gollat, R., and H. Timmermann. 1983. Determining quotas for a selective moose harvest in northcentral Ontario. Alces 19. In press.
- Hauge, T. M., and L. B. Keith. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 45:573-597.
- Keith, L. B. 1974. Some features of population dynamics in mammals. Trans. Int. Congr. Game Biol. 11:17-58.

- Keith, L. B. 1983. Population dynamics of wolves. pp. 66-77. Ed: Carbyn, L. N. Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Rep. Ser. 45. Ottawa.
- LeResche, R. E., and R. A. Rausch. 1974. Accuracy and precision of aerial moose censusing. J. Wildl. Manage. 38:175-182.
- Linkswiler, C. 1982. Factors influencing behavior and sightability of moose in Denali National Park, Alaska. Unpubl. M.S. Thesis, Univ. Alaska. 84 pp.
- Macgregor, W. G., and K. Child. 1981. Changes in moose management in British Columbia. Alces 17:64-77.

- McCullough, D. R. 1979. The George Reserve deer herd. Univ. Michigan Press. Ann Arbor. 271 pp.
- Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, New York, N.Y. 384 pp.
- Norton-Griffiths, M. 1978. Counting animals. Handbook No. 1. African Wildl. Leadership Found., Nairobi, Kenya. 139 pp.
- Novak, M. 1981. The value of aerial inventories in managing moose populations. Alces 17:282-315.

-38-

- Novak, M., and J. Gardner. 1975. Accuracy of moose aerial surveys. Proc. N. Amer. Moose Conf. and Workshop 11:154-180.
- Page, R. 1985. Models for moose management. Viltrevy. In press.
- Peek, J. M., and D. S. Eastman. 1983. Factors which naturally control moose populations. pp. 175-193. Eds: Bunnell, F. L., Eastman, D. S., and Peek, J. M. Symp. on Nat. Regulation of Wildl. Populations. For., Wildl., and Range Exp. Stn., Univ. Idaho.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. 11. 210 pp.
- Peterson, R. O., and R. E. Page. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, USA. Acta Zool. Fennica 174:251-253.
- Rolley, R. E., and L. B. Keith. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta, 1965-1979. Can. Field-Naturalist 94:9-18.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Macmillan Pub. Co. Inc., N.Y. 654pp.

Stewart, R. R. 1978. Introduction of sex and age specific hunting licenses for the moose harvest in Saskatchewan. Proc. North Amer. Moose Conf. and Workshop 14:194-208.

Thompson, I. D. 1979. A method of correcting population and sex and age estimates from aerial transect surveys for moose. Proc. N. Amer. Moose Conf. and Workshop 15:148-168.
Timmermann, H. R. 1974. Moose inventory methods: a review.

Naturaliste Canadien 101:615-629.

- Trent, T. T., and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459-472.
- VanBallenberghe, V. 1979. Productivity estimates of moose populations: a review and reevaluation. Proc. N. Amer. Moose Conf. and Workshop 15:1-18.
- VanBallenberghe, V. 1985. Effect of predation on moose numbers: a review of recent North American studies. Viltrevy. In press.
- White, G. C., D. A. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos Nat. Lab., Los Alamos, N.M. 235 pp.

-40-

White, G. C., and R. M. Bartman. 1983. Estimation of survival rates from band recoveries of mule deer in Colorado. J. Wildl. Manage. 47:506-511.

Whitten, K. R., and R. D. Cameron. 1983. Population dynamics of the Central Arctic Herd, 1957-1981. Acta Zool. Fennica 175:159-161.

Τ

Τ

0	2 9	3 	⁴ 3	5 4	⁶ 4	7 4	MOOSE POPULATION ESTIMATES
ຶ9	์ 3		7	້2	ັ9	3	840 805
¹⁵ 3	¹⁶ 10	17 	18 12	¹⁹ 3	20 6	²¹ 12	742 788
²² 6	23	²⁴ 13	25 22	26 13	²⁷ 35	28 4	801 624
29 3	³⁰ 36	31 23	³² 67	³³ 24	³⁴ 15	35 4 1	714 677 733
³⁶ 12	37	38 7	³⁹ 57	40 49	4 4	42 3	879
43 13	⁴⁴ 19	45 20	⁴⁶ 32	47 2	48 3	49 2	μ=763
⁵⁰ 35	51 44	52 2	53 4	54 	55 2	56 - 3-	+SU number ← number of _ moose in SU

Figl



I.







F









Figure captions

Fig. 1. The fictitious Square Mountain survey area has 56 sample units (SU) of 12 mi² each and has 763 moose. Ten sets of 32 SU's each were randomly selected and used to calculate 10 population estimates.

Fig. 2. A) The actual number of moose, μ , with respect to confidence intervals around 10 estimates of the fictitious Square Mountain moose population (Fig. 1) calculated from an unbiased estimator. B) The effect of an uncorrected sightability bias on confidence intervals with respect to μ . In this example, 20% of the moose in SU's were not seen and no sightability correction factor was estimated.

A) Histogram of number of moose seen in distance Fig. 3. intervals measured perpendicular to the flight line. B) Curve fitted to the histogram. C) Area under the curve (F) and the area of the rectangle (F') surrounding F are used to calculate a correction factor for number of moose not seen, i.e., F'/F.

Fig. 4. Within survey areas, the ratio of calves/cow declined with increasing moose density (from Gasaway et al. 1981; D. Larsen, unpubl. data).

۰.

Fig. 5. Range of estimated exponential rates of change (f) calculated from population estimates of a stable moose population (Fig. 1).

Fig. 6. A simple population model used to assess moose population status.