

PROGRAM INBRED: MODEL STRUCTURE, ASSUMPTIONS AND SENSITIVITY

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ABSTRACT: We developed a stochastic, individual-based computer model that simulates the dynamics of an introduced moose (*Alces alces*) population, tracks pedigrees, and estimates genetic variables. The program language is Borland C++ and was compiled to run on IBM DOS compatibles with a 386 processor and 640 kilo-bytes (K) of random access memory (RAM). However, running time and RAM requirements increase exponentially with population size and most applications will need 16-32 mega-bytes (100K) of RAM, and a 486 or Pentium processor is recommended. Each time-step is one reproductive cycle, time-steps can be reiterated, and statistics are output for each time-step. Vital rates are fixed or density-dependent. A default file is used to specify vital rates, density-dependent functions, breeding behavior variables, inbreeding depression, number of iterations, and age- and sex-specific harvest rates. A data file defines the number of time-steps, age-sex harvest levels, and the characteristics of the base population. The major assumption of the model is the random mating of all sexually mature individuals. However, this assumption can be constrained by a number of breeding behavior variables. An inbreeding coefficient (F_p) is estimated for each individual and fetal death can occur based on the lethal equivalent function of Mills and Smouse (1994). A 2 allele, dominant-recessive function can be used to estimate founder effects. Model outputs include population size and F_p estimates by sex- and age-class, an index of effective population size (N_e) by sex, finite rate of increase (λ), percent twins, pregnancy rate, gene frequencies, and males/female. Sensitivity analyses indicated that variation in output was minimized with 400-700 iterations, density-dependent functions produced expected results, and that population and genetic variables were influenced most by calf and adult female mortality, adult female group size, calf sex ratio, and age to sexual maturity. The effects of translocations and harvesting moose on the adult sex ratio, population increase (λ), and inbreeding rates (F_p) are illustrated with data from the introduction of moose to the Copper River Delta, Alaska. The ratio of effective population to total population (N_e/N) averaged 0.361 (SE=0.004).

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The genetic structure of wildlife populations is currently receiving a great deal of attention by conservation biologists, agencies responsible for imperiled species, and land managers. Population viability is assumed to be affected by inbreeding (Soulé 1980, Shaffer 1981), but the relationship between population size, inbreeding levels, genetic diversity, and individual fitness is largely unknown. This uncertainty has generated conflicting opinions on the natural

history of inbreeding (Shields 1982, Ralls *et al.* 1986) and this topic was identified as a research priority during a 1988 workshop (Soulé and Kohm 1989).

Inbreeding can effect fecundity and survival by increasing the probability of a homozygous combination of deleterious recessive alleles. In small, isolated populations this could lead to extinction (Mills and Smouse 1994). In moose, inbreeding could reduce recruitment rates, population growth,

and the harvestable surplus. However, many highly inbred populations do not exhibit negative effects (Shields 1982). Population bottlenecks may rapidly purge lethal recessive alleles and strong selection for a trait may favor inbred individuals. Many ungulate populations in North America experienced significant population bottlenecks in the late-1800s, early-1900s due to subsistence and market hunting, and habitat loss associated with European settlement. Some populations passed through these bottlenecks without human intervention, some went extinct, and some required intensive management in order to persist (International Union for the Conservation of Nature 1978). Inbreeding may be most detrimental over evolutionary time scales as a lack of genetic diversity may preclude adaptation to changing environments (Soulé 1980).

Moose populations throughout the world are subject to a number of forces that could effect genetic diversity. Sex- and age-biased harvest strategies may reduce genetic variability (Ryman *et al.* 1981) and alter allele frequencies (Thelen 1991, Hundertmark *et al.* 1993) in ways that could be detrimental over long time periods. Calling and killing dominant bulls during the breeding season may disrupt breeding behavior, reduce pregnancy rates, and also alter gene pools (Wilton 1995). Habitat fragmentation can divide and isolate populations, increasing inbreeding. Translocations to restore moose to former ranges (Kufeld 1994, Olterman *et al.* 1994) augment declining populations (Pulsifer and Nette 1995), and introduce the species to previously unoccupied areas (Burris 1965, LeResche *et al.* 1974) may create population bottlenecks and undesirable founder effects (MacCracken 1992).

Empirical investigations of inbreeding in long-lived wild vertebrates are rare due to the difficulty of estimating pedigrees. Furthermore, molecular studies examine only a very small portion of loci and the sample of

individuals will contain an unknown proportion of inbred members with an unknown level of inbreeding, making cause and effect relationships difficult to elucidate (Soulé and Kohm 1989). Computer simulations can address some of these problems, but information on the starting or base population, vital rates (mortality, fecundity), breeding ecology, etc. is usually unavailable or inadequate.

Moose (*Alces alces gigas*) were introduced to the Copper River Delta (CRD) in southcentral Alaska with a series of calf-yearling translocations between 1949-1958 (MacCracken 1992). Reliable information on the sex, age, and time of release was available for each individual. Specifics on population growth and structure, distribution, and harvest rates were also available from 1960 to the present. In addition, recent studies on the CRD and other areas of Alaska provided estimates of vital rates and breeding behavior. This situation provided a unique opportunity to model a small, isolated population with the goal of examining hypotheses about inbreeding, founder effects, and fitness.

The purpose of this paper is to describe the structure and assumptions of the computer model (INBRED) we developed to study the CRD population, present the results of sensitivity analyses of the model, and illustrate model applications with data from the first 15 years of the CRD population.

MODEL STRUCTURE AND ASSUMPTIONS

Program INBRED simulates the dynamics of an introduced population. The program language is Borland C++ and was compiled to run on IBM DOS compatibles with a 386 processor and 640K (K = 1000 bytes) of random access memory (RAM), or better. A math co-processor, 720K 3.5" floppy disk drive, and EGA graphics are required.

The model is individual-based and pro-

ceeds as a series of discrete time-steps, which comprises a run. Each time-step represents a single reproductive cycle (Fig. 1). A basic assumption of the model is that the primary mortality events occur during a period bounded by successive birth pulses. The fate of an individual in each time-step depends on a number of randomized events, requiring several reiterations of a run to stabilize the

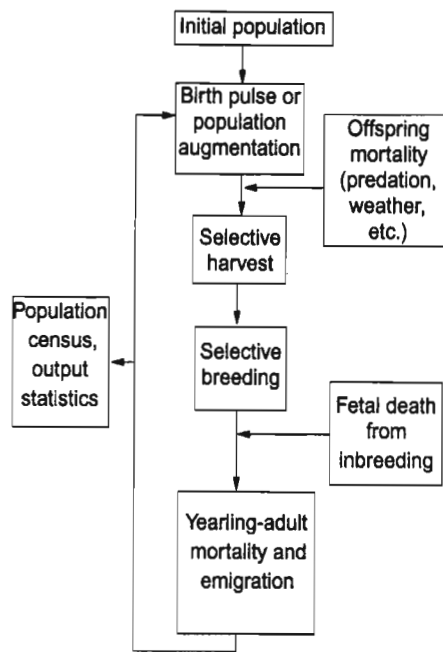


Fig. 1. Flowchart of the sequence of major events that occur during 1 time-step of Program INBRED.

output. Although it was developed for moose, we incorporated a number of options designed to increase its potential use for other species.

Model inputs can be entered interactively when prompted by the program or by editing 2 files. A default file initializes vital rates, activates density-dependent functions for vital rates, specifies breeding behavior, and sets harvest levels. These variables are sex- and age-specific. This file also specifies a population ceiling, habitat carrying capacity, the number of iterations of a run, and whether or not to invoke inbreeding depression.

A data file defines the number of time-steps in a run and the number of animals harvested, by sex, at each time-step. Characteristics of the base (initial) population are also specified for each individual including; age, inbreeding coefficient (F), sex, generation, entry time-step, and the structure of a 2-allele locus (i.e., AA, Aa, or aa). Population augmentation can be conducted by specifying the introduction of additional individuals at any time-step during a run.

Model outputs can be displayed on a monitor, printed, and saved to a file. Results are output for each time-step and include the number of individuals by sex- and age-class and the mean F for each age-class. Total population is displayed by sex as is the effec-

Table 1. Default equations for estimating finite rate of population increase, expression of inbreeding depression, and density-dependent vital rates in program INBRED.

Variable	Function ^a
Finite rate of increase	$(\lambda) = \sqrt[N_t/N_0]$, where N_0 = beginning population, and N_t = population at time t.
F_p -lethal equivalents	{P}Mortality = $(-\ln(S)-0.32)$, where $S = e^{-0.32((F/1-F)*1.57)}$
Density-dependent twinning rate	% twins = $90.53 + 102.81(\#/km^2) + 29.07(\#/km^2)^2$
Density-dependent mortality	base mortality $\pm N - 0.5K/0.5K$, where N = total population, K = ecological carrying capacity

^aThese expressions can be easily modified or replaced by editing the program code.

tive population size (N_e). The finite rate of population increase (λ) is also calculated (Table 1). Other demographic information presented includes percent twins, percent of breeding females pregnant, and the male/female ratio. In addition, the number of heterozygous and homozygous males, females, and totals for the population are shown.

Breeding Ecology And Vital Rates

Components of both fecundity and mortality can be deterministic or density-dependent. Density-dependent functions require the specification of the area (km^2) used by the population and the areas carrying-capacity.

Individuals are randomly assigned to the breeding pool subject to the following constraints. A maximum and minimum breeding age is set separately for males and females. Breeding of yearling females occurs when the proportion of that cohort eligible to breed is specified. Other adjustments to the size of the breeding population occur through the designation of female group size and the sequential allocation of the oldest males to female groups. For example, if female breeders were divided (randomly) into 5 separate groups (based on the specified group size and the number of females) and the male breeding pool consisted of 3 4-year olds, 3 3-year olds, and 8 2-year olds, then 3 female groups would receive 1 4-year old male each and 2 female groups would pair with a 3-year old male with all assignments made randomly. We used the number of individuals that breed as an index of effective population size (N_e). There are a number of equations used to estimate N_e depending on the process of interest, e.g., the number of heterozygous individuals, the genetic variance of a deme, the number of segregated loci, and within or among deme variation (see Gliddon and Goudet 1994). Program output provides the data necessary to calculate most estimates of N_e .

Fecundity is influenced by the above

breeding behavior specifications. In addition, a fetus can die in-utero based on the curvilinear relationship between F and the expression of lethal equivalents used by Mills and Smouse (1994) (Table 1). Fetal mortality makes the effects of inbreeding immediate and quantifiable through comparisons of pregnancy rates in runs with and without inbreeding depression. An individual's F is calculated from its pedigree using the additive relationship matrix method (Ballou 1983). It is the estimate of inbreeding due to shared ancestry or the probability of identity-by-descent, termed "pedigree inbreeding" (F_p) by Templeton and Read (1994). When averaged over individuals in a population, F_p is an estimate of inbreeding due to genetic drift (F_d) which may correlate with the loss of genetic variation (Templeton and Read 1994:97).

Twinning rates (twins/reproductive female) can be deterministic or allowed to fluctuate based on density. The twinning rate-density function used was curvilinear (Table 1) and estimated based on data from a number of studies of Alaskan moose (Schwartz and Franzmann 1989, Gasaway *et al.* 1992, Modafferi 1992, MacCracken 1992). Calf sex ratios are set by the user and the sex of calves is determined by random assignment.

Mortality rates are based on sex and age and can also be constant or density-dependent. Separate mortality probabilities are specified for calves, yearling females, yearling males, and adults. In addition a maximum age is set at which death occurs automatically. A different adult mortality rate can be used if hunting occurs to simulate a compensatory effect. Density-dependent mortality rates are determined based on the total population at each time-step in relation to K using the approach of Thelen (1991). The absolute value of the ratio of the population to the carrying capacity is used to adjust mortality rates up or down if the population is above or

below the carrying capacity, respectively (Table 1).

The harvest of individuals in 34 sex- and age-classes (ages 1-17) at each time-step, as specified in the data file, is randomly allocated among individuals based on the percentages specified in the default file. For example, if a population contained 100 males, 10 of which were harvested and 50% were to be yearlings and 50% 2 year-olds, 5 members of each of those 2 age-classes would be randomly chosen for harvest. If an age-class did not contain 5 individuals, "leftovers" are taken randomly without regard to age-class.

Translocations and other population bottlenecks can result in a founder effect, i.e., the establishment of a new population from a relatively few founders representing only a small subset of the gene pool of the original population (Cook 1991). A small founder event could effect population dynamics if inbreeding depression reduces fecundity and survival (Antonovics *et al.* 1994). In addition, phenotypes that were rare in the source population may come to dominate the new population. Program INBRED assigns a simple 2-allele, dominant-recessive gene to each individual to estimate the founder effect through changes in allele frequencies of the population over successive time-steps.

SENSITIVITY ANALYSES

The effects of various starting conditions were assessed by adjusting most proportional variables by approximate 10% increments. Adjustments to variables such as female group size, calf sex ratio, minimum and maximum breeding ages etc. were bounded by realistic scenarios. Adjustments were initially made to a single variable while all others were held constant. Variable interactions were estimated by running all possible combinations of the variables that responded the most to the individual changes. A data file representing the first 15 years of the CRD translocation (1948-1963), with 100 iterations, was used

for these analyses.

The effects of the number of iterations of a run was examined using the same data file and setting vital rates to reach a population of about 350. Reiterations began with 1, then 10, then 10% increases up to 100, then doubling until a 32M RAM capacity was reached. Each adjustment was replicated 10 times and the mean, standard deviation (SD), standard error, and coefficient of variation ($CV = SD/\text{mean}$) was estimated based on the 10 replicates.

Changes in calf mortality rates, adult mortality rates, female breeding group size, minimum age of breeding females and percent of calves that were male had the greatest effects on the total population, males/female, twinning rates, calves/female, and F_d (Table 2).

Based on these results, we examined the effects of female group size (5, 15, and 30), minimum age of breeding females (1-3), and calf sex ratio (45, 50, 55% male) using all possible combinations. These were independent variables in multiple regressions with total population, effective population, lambda, males/female, twinning rate, pregnancy rate, calves/female, or F_d as the dependent variable.

All equations were significant ($P \leq 0.001$), and explained > 70% of the variation, except for calves/female or F_d (Table 3). In addition, most relationships were negative. The minimum age of breeding females, followed by percentage of male calves had the greatest effects on all dependent variables.

Variation in model outputs was minimized ($CV \leq 1\%$) and appeared stable at 400-700 iterations (Fig. 2). Even with no reiteration CV estimates were < 20% for any variable. Estimates of lambda, twinning rate, pregnancy rate, and calves/female were the least variable and stabilized with relatively few iterations. Total population, effective population, and F_d were the most variable and least stable of the parameters estimated.

Table 2. Results of sensitivity analyses of response variables (demographic and genetic estimates) to changes in input variables (vital rates, breeding system, etc.) in program INBRED.

Input variable (10% change)	Response variable (% change)						
	N	λ	$\frac{\sigma}{\Omega}$	% twins	% pregnant	calf/ Ω	F_d
Mortality rates							
calf	12	1	4	1	1	10	3
Adult	10	1	3	4	1	16	7
yearling σ	1	1	1	1	1	2	2
yearling Ω	1	0	1	0	1	2	2
Breeding structure							
Ω group size	4	0	1	2	4	1	8
minimum σ breeding age	1	<1	<1	<1	<1	<1	4
minimum Ω breeding age	1	<1	<1	<1	<1	<1	18
maximum σ breeding age	<1	<1	<1	<1	<1	<1	<1
maximum Ω breeding age	<1	<1	<1	<1	<1	<1	<1
Calf ratio	10	1	43	1	1	11	5

N = total population, λ = finite rate of population increase, % twins = females producing twins/females producing a calf, % pregnant = females pregnant/mature females, F_d = inbreeding due to genetic drift

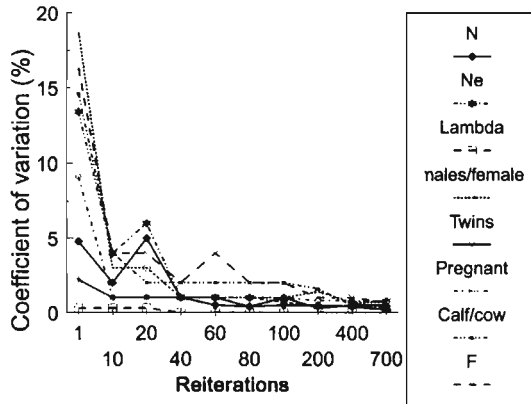


Fig. 2. The coefficient of variation (mean/standard deviation) in 8 output variables as a function of the number of iterations of a run of Program INBRED.

AN EXAMPLE

Program output and utility were briefly illustrated using the same data as for the sensitivity analyses. During the first 10 years, 22 calves (8 males, 14 females) and 1 yearling female were released on the CRD and

hunting occurred in years 12 (25 males), 14 (25 males), and 15 (15 males, 2 females). Twinning rates and adult mortality were density-dependent. Mortality was set at 70% for calves, 90% for yearling males, and 40% for yearling females. Minimum breeding age was set at 2 for males and females, maximum breeding age was 7 for males and 14 for females, and maximum age for all individuals was 15. Female breeding group size was 5 and the run consisted of 10 iterations.

In 15 years the population grew to 198 resulting in $\lambda = 1.46$; an extremely high value attributable to the translocation of calves during years 1-10. The rate of increase for years 10-15 was 1.09 (Table 4). Breeding did not occur until year 3 and N_t/N averaged 0.360 (SE = 0.004), within the range estimated by Ryman *et al.* (1981). The population sex structure was initially biased toward males with a gradual dominance by females. Twinning rates were greatest at the lowest population levels and pregnancy rates increased

Table 3. Results of regression analyses on changes in response (dependent) variables due to simultaneous changes in 3 input (independent) variables in program INBRED.

Dependent variable	intercept	Regression coefficient			r ²	P
		♀ group size	♀ breeding age	calf ratio		
Total population (N)	514	-0.99	-72.61	-2.47	0.98	0.001
Effective population (N _e)	419	-0.12	-65.28	-3.07	0.73	0.001
Population increase (λ)	1.60	-0.00	-0.04	-0.00	0.95	0.001
Males/female	0.34	-0.00	-0.12	0.02	0.91	0.001
Percent twins	99	-0.27	-6.67	-0.13	0.75	0.001
Percent pregnant	88	-0.33	-17.28	0.24	0.97	0.001
Calves/female	0.35	0.00	-0.04	0.01	0.12	0.12
Inbreeding coefficient (F _d)	0.07	0.00	-0.01	-0.01	0.39	0.001

with time, but would be considered low relative to other moose populations in Alaska. Estimates of F_d increased with time. The effect of hunting was most pronounced on , males/female, and the percent change in F_d (Table 4).

DISCUSSION AND CONCLUSIONS

Three other simulation models have been developed that estimate the genetic structure of wild ungulate populations. The question that all three addressed was the effects of various harvest strategies. Ryman *et al.*

Table 4. Output from Program INBRED for the initial 15 years of population growth of moose on the Copper River Delta, Alaska.

Year ^a	N	N _e	λ	♂/♀	Percent twins	Percent pregnant	F _d Percent	change in F _d
1	1	0	n.a.	n.a.	n.a.	n.a.	0	0
2	3	0	3.00	2.00	n.a.	n.a.	0	0
3	8	2	2.83	3.00	66.7	30.0	0	0
4	13	2	2.35	1.20	84.8	38.7	0	0
5	22	5	2.17	0.83	87.5	61.0	0.009	0
6	33	8	2.01	0.83	74.2	52.7	0.011	+18
7	52	15	1.93	0.86	63.2	74.2	0.014	+23
8	72	22	1.84	0.89	63.1	50.0	0.012	-17
9	97	34	1.77	0.94	42.5	69.8	0.016	+25
10	126	42	1.71	0.85	36.9	69.9	0.027	+41
11	148	61	1.65	0.87	34.1	60.9	0.050	+46
12	150	78	1.58	0.65	32.0	71.6	0.062	+19
13	174	89	1.54	0.67	29.8	70.0	0.073	+15
14	184	99	1.49	0.56	28.0	70.2	0.080	+9
15	198	110	1.46	0.56	26.7	72.2	0.086	+7

n.a. = not applicable

^a25 males were harvested in year 12, no harvest occurred in year 13, 25 males were harvested in year 14, and 15 males and 2 females were harvested in year 15.

(1981) modeled moose and white-tailed deer (*Odocoileus virginianus*) populations, focusing on females and estimating N_e , generation interval, and loss of heterozygosity. Thelen (1991) modeled a wapiti (*Cervus elaphus*) population and focused on changes in antler characteristics, and Hundertmark *et al.* (1993), using a modification of Thelen's model simulated changes in antler characteristics and harvest rates of moose.

All three models are complex, handle similar technical computing problems in different ways, and incorporate unique variations in reproductive or mortality functions. A detailed comparison of these models is beyond the scope of this paper, but should be made by those developing a new model or interested in using an existing model. However, the major differences include fixed reproductive rates, stable age structure, constant population size, and the harvest of calves-fawns by Ryman *et al.* (1981); and constant age structure and calf mortality, the incorporation of heritability functions, age-based reproductive rates, and density dependent mortality by Thelen (1991) and Hundertmark *et al.* (1993).

The structure of program INBRED should allow for use with other species that experience major mortality events between successive birth pulses. In addition to estimating the effects of inbreeding, INBRED can be used solely to model the dynamics of a population. Population losses are achieved by adjusting mortality rates. Emigration can be modeled with further adjustments to mortality, especially for yearlings, if it is assumed to be an additive loss. Population gains are made through the translocation of individuals and reproduction. Immigration could be incorporated in the same manner as translocations, but could be difficult with high immigration rates.

INBRED was developed to provide insights on the effects of inbreeding, at the population level, on a small moose popula-

tion that originated with a translocation program. It can be used to generate hypotheses about mating systems, harvest strategies, emigration, population fitness, etc. and genetic heterozygosity, assuming that heterozygosity and inbreeding are correlated. The model could also be used to design future translocation projects and estimate optimal rates of population augmentation for genetic and demographic purposes.

Since the model is individual-based, computer memory demands and execution times are high. Memory requirements are a function of population size, time-steps required, and the number of iterations desired. Preliminary calculations indicated that a population of 200 required about 1M of RAM, 400 2M, 600 4M, 1200 16M, and 1600 32M with 10 iterations. With 2 iterations, a population of >2500 was accommodated with 32M of RAM, but with 1000 iterations the population was limited to about 500 individuals. Running time may also be extensive; e.g., using a 486/66 processor it took approximately 84 hours to complete a run of 44 time-steps with 1000 iterations. Our results indicate that 500 iterations are adequate to stabilize model outputs. Modeling populations ≥ 500 individuals for ≥ 40 time-steps will require between 16-32M of RAM. In addition, a 486 or Pentium processor is recommended.

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