# POSIM-A GENERAL WILDLIFE POPULATION SIMULATOR

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## ABSTRACT

Theoreticians have been interested for some time in constructing mathematical models of biological population dynamics. More recently, with the advent of powerful digital computers, modeling has taken a more practical turn. A case in point is given in this paper. In 1975, the Montana Department of Fish and Game initiated work, through a research contract, on a computer program to aid in development of simulation models for wildlife game populations. The resulting program, POSIM, allows interactive development and verification of models for virtually all game species in Montana. These models may be formulated as simple accounting, discrete time models, or more complex models operating in continuous time and comprised primarily of differential equations. This paper documents the development of POSIM, describes its design, and illustrates its operation with an example showing the development of a simulation model of a Montana deer population.

## INTRODUCTION

Since the time of Lotka and Volterra scientists have been concerned with expressing the growth of populations mathematically. Pielou (6) has identified two reasons for modeling population dynamics: (i) to explain or describe population behavior and (ii) to predict future behavior. Descriptive models have typically been formulated as sets of differential equations relating growth and decline to environmental, ecological, and population factors. Models used for prediction have, on the other hand, involved methods ranging from simply extrapolating previous birth/death rates to relying on descriptive models. Simulation has been used extensively for both purposes. For example, the dynamics of, among others, insects, timber and wildlife species have been successfully modeled (1, 2, 3, 5).

The Montana Department of Fish and Game is responsible for management of a myriad of wildlife species and numbers that range over virtually all of the 147,138 square miles of Montana. The department also has the responsibility for investigating and understanding the population dynamics of all wildlife species within the framework of its management goals and objectives. Management can be significantly improved if reliable forecasts of animal numbers are available for a given management strategy. Similarly, meaningful synthesis of research results concerning population growth requires a means for testing and communicating hypotheses.

In 1975 the Wildlife Division initiated work on a population modeling program which would be useful in satisfying both of these stated objectives. The resulting simulation program, POSIM, is general enough to accomodate population models for a wide variety of game species in the discrete time mode of operation. In this mode mortalities and birth rates can be specified for each year of the simulation if necessary. In addition, wildlife managers may experiment with harvesting strategies, obtaining desired population performance while documenting assumptions made in arriving at the resulting predictions.

Models may also be implemented using POSIM in a continuous time mode. In this mode, relationships are included in the model which determine instantaneous conception, fetal mortality (resorption) and other mortality rates. Harvest strategies may also be specified endogenously. Furthermore, the two basic modes may be easily combined for operation in a mixed mode. POSIM was developed using a modified version of GASP IV (7).

In the discrete time mode POSIM is a next event simulator with population updates occurring at times corresponding to field observations, the end of the biological year, and the beginning and ending of each hunting season. In either the mixed or continuous time modes, however, POSIM becomes a combined simulation.

## DESIGN CONSIDERATIONS

The simulator described here may be used to model a wide variety of game populations in the discrete time mode. This is possible largely due to the similarity, from a population dynamics perspective of different game species. Naturally, during the development of POSIM, the first step was to identify the features of game species important to their growth. As a result of this activity, it became apparent that a number of critical factors exist for virtually all game animal populations.

Probably the most important of these factors is the age/sex structure of the population. That is, most of the species of interest to the Department of Fish and Game exhibit highly age and sex dependent mortality and, for females, fertility rates. Hence if a simulator is to be general enough to allow prediction for these species, it must allow for the representation of age and sex dependent mortality and birth rates. A second very important factor in the management of game animal populations is the representation of harvest. Again, hunting losses must be incorporated in the simulator so that specification by sex/age class is allowed. This is necessary since harvest is presently the primary management tool used by the Department of Fish and Game, and a principal use for models developed using POSIM is experimentation with alternative harvesting strategies.

In addition to the age and sex dependencies exhibited by game species, the timing of events affecting growth is important. One such event is birth. Virtually all of these species bear young only once a year. This fact defines the beginning of the biological year as the time of birth. Also when modeling these populations the birth of young can, without loss of generality, be represented as an instantaneous event. The relatively short life span of most game species - on the order of 10 years for most - is also significant from the modeling perspective.

Also related to the program design is the type of data generally available for input to game population models. Typically, data regarding game species such as accurate census figures at regular intervals and mortality and birth rates is either nonexistent or extremely sparse. This is due largely to the nature of the animals; their mobility, and the size of their range. A second problem with data concerns the time periods that are typically needed to characterize a given population's performance. Naturally over short periods relative stability may be observed, but extremes of environmental conditions and population behavior will occur over periods measured in decades. Finally, man himself is continually affecting game populations both directly and indirectly, possibly in nonrepeatable ways.

## POSIM OPERATION

The characteristics of wildlife populations and the available data concerning their dynamics place some very explicit requirements on the design of a useful simulator. In this section the way these requirements were translated into an interactive simulation program will be described. First, the means for representing the age/sex structure of the population will be given, followed by a description of the timing mechanisms used in the model to update the population status.

### AGE/SEX STRUCTURE REPRESENTATION

POSIM provides a compartmental framework for the representation of age/sex structure. That is, counters are maintained in the program for each of a variable number of population age classes. This situation is depicted in Figure 1. Also, different counters are maintained for males and females, since rates affecting the growth of each age class are also highly variable by sex.

In the simulator, an age class compartment is defined by the number of years an animal belongs to it. But, since the age structure of the population depends on the aging process itself, a method must be employed to insure that the proper number of animals make the transition from each age class to the next each year. There is more than one way to model this process. The method employed in POSIM is to utilize counters for the number of animals of each age within an age group. At any point in

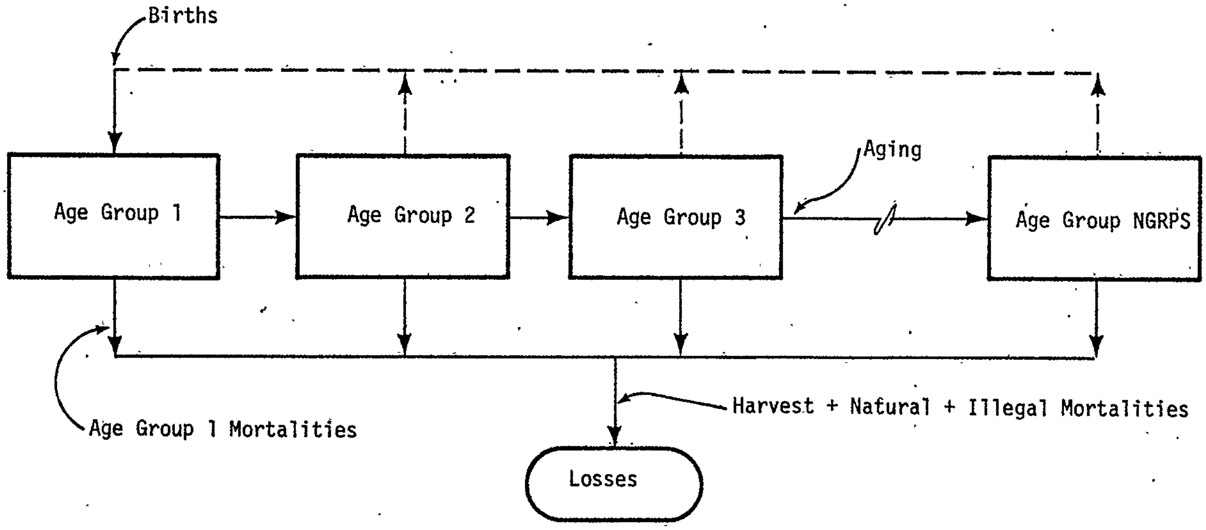

Figure 1 - POSIM Age Class Compartments

time, then, the age group count must be the sum of the appropriate "year group" counts, as indicated by equations 1 and 2.

$$M_i(t) = \sum_j M_{ij}(t) \qquad (1)$$

$$F_j(t) = \sum_j F_{ij}(t) \qquad (2)$$

Where:

$M_i(t), F_i(t)$ = males, females in age group i at time t.

$M_{ij}(t), F_{ij}(t)$ = males, females age group i, year group i at time t.

Notice that the relatively short longevity of most game species suggests this approach for representation of aging effects. Species which endure longer and for which detailed data concerning individuals of all ages is available would suggest a different scheme.

POPULATION UPDATE MECHANISMS

To allow for adequate modeling of game populations, POSIM must be capable of simulating in both discrete time and continuous time modes. As indicated the use of GASP IV greatly facilitates this. However, as with any digital computer simulation, update of the status of the system, in this case the population count, actually occurs at discrete points in time. Equations (3) and (4) which are the general equations used to update population counts in POSIM illustrate this. These equations neglect births which are added instantaneously at the start of each biological year.

$$M_{ij}(t_k) = M_{ij}(t_{k-1}) + M'_{ij}(t_{k-1})\Delta t_k \qquad (3)$$

$$F_{ij}(t_k) = F_{ij}(t_{k-1}) + F'_{ij}(t_{k-1})\Delta t_k \qquad (4)$$

Where:

$M'_{ij}(t_{k-1}), F'_{ij}(t_{k-1})$ = The sum of hunting, natural and illegal loss rates in effect at time $t_{k-1}$.

$t_k$ = The $k^{th}$ update time.

$\Delta t_k = t_k - t_{k-1}$

Equations 3 and 4 show difference equations. Continuous time can be closely approximated by making $\Delta t$ small enough. Similarly, if $t_{k-1}$ is an event time such as the start of the biological year, discrete time models can be accommodated, with the $\Delta t_k$ being unequal time intervals. Note that in the latter case, $M'_{ij}(t_k)$ and $F'_{ij}(t_k)$ may actually be constant for several values of k (i.e. events), being changed only at particular event times.

Timing in the simulator is related to what we have defined as the biological year. During the year time is advanced in months, with a time of 1 corresponding to the beginning of month 1, or the time when the young are born for the species being simulated. The end of the year is defined as the point in time just before births occur. Hence, for each year this represents the lowest population count, assuming no immigration, and corresponds to month 12.99.

In other words, the beginning of year count is simply the end of year count adjusted for births and aging. Both counts are of interest, but it should be kept in mind that in the model they are obtained an instant of simulated time apart. Simulated time is set back to 1 following births, and another biological year begins. This is only an approximation to the real world situation, but appears to be an acceptable one. Figure 2 illustrates the situation for a typical year. Since the simulation begins at time 1.0 (not 12.9999) the initial population count must include the young of year and must reflect the age structure after aging.

While Figure 2 shows a smooth transition throughout the year, this would not likely be the case. In addition to the start of year and end of year events, other points in time are identified by the user where, while the population itself isn't changed, rates affecting the population (hunting, illegal and natural mortalities) may be altered.

For this purpose mortality periods and hunting seasons have been incorporated in the model. A mortality period is defined as a time interval during which natural and illegal mortality rates or parameters used to determine instantaneous mortality rates remain constant. The beginning time during the biological year of each mortality period is specified by the POSIM user. There may be up to 12

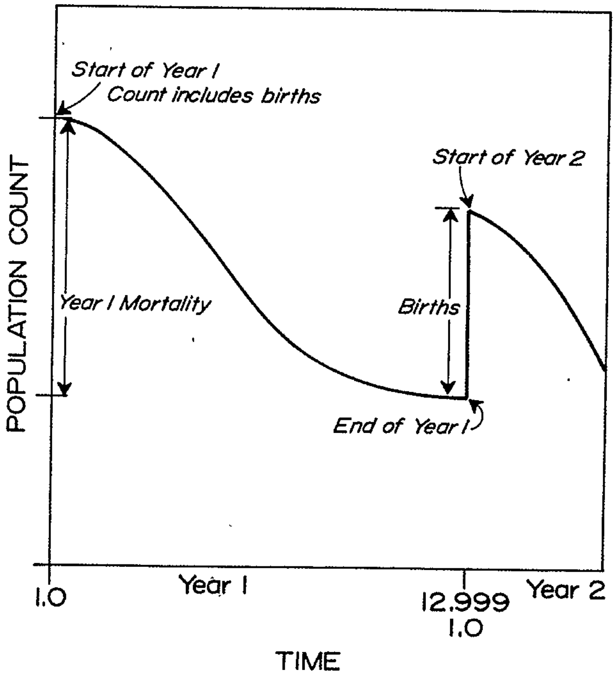

Figure 2 - Biological Year

separate mortality periods and there must be at least one. Figure 3 illustrates the behavior of a hypothetical population with three mortality periods specified for a year of simulated time. Note that the rates specified for a year of simulated time are not expressed as fractions per month, but they are values for mortality in fraction (percentage) or actual number of individuals per mortality period. Therefore, the population appears to decline evenly throughout each mortality period assuming relationships to calculate instantaneous rates are not included in the model.

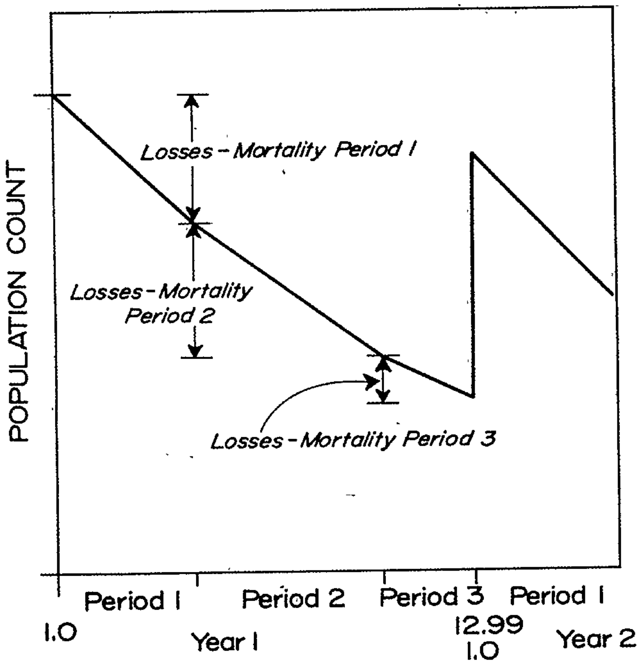

Figure 3 - Mortality Periods

The timing within POSIM is complicated slightly by hunting seasons, which may be scheduled throughout the year. Up to 5 hunting seasons may be accommodated by POSIM with the user specifying the starting time and the length of each. Figure 4 illustrates the case where 1 hunting season is specified and starts and ends during the second mortality period. The effect as shown is to accelerate population decline during the hunting season. Both Figures 3 and 4 show typical results using the model in the pure discrete time mode, but both hunting and natural mortalities may be calculated at fixed time intervals. When this is the case simulated population behavior depends on the difference equations being approximated.

## POSIM PROGRAM DESCRIPTION

POSIM was implemented as a combined GASP IV simulation. The original GASP executive was modified for this application, however. As can be seen in Figure 5, the basic logic is unchanged. However, since only difference equations were used, the executive was shortened to exclude Runga Kutta

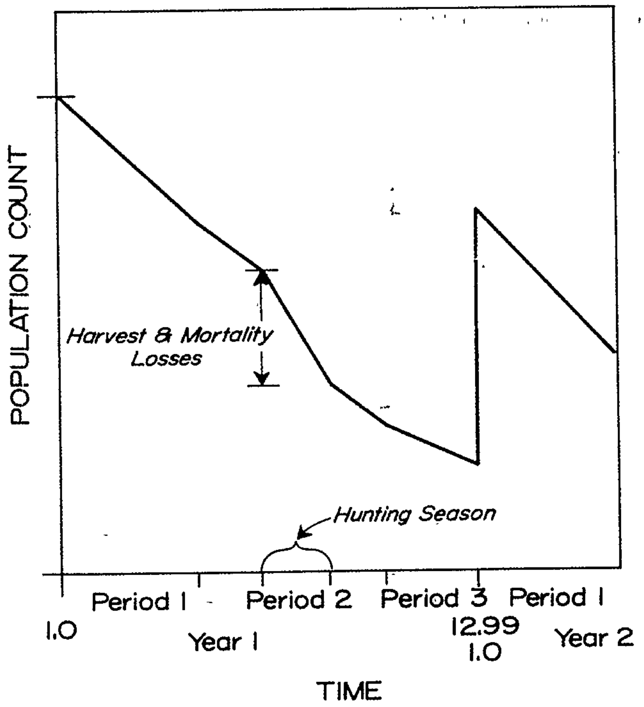

Figure 4 - Effect of Hunting Seasons

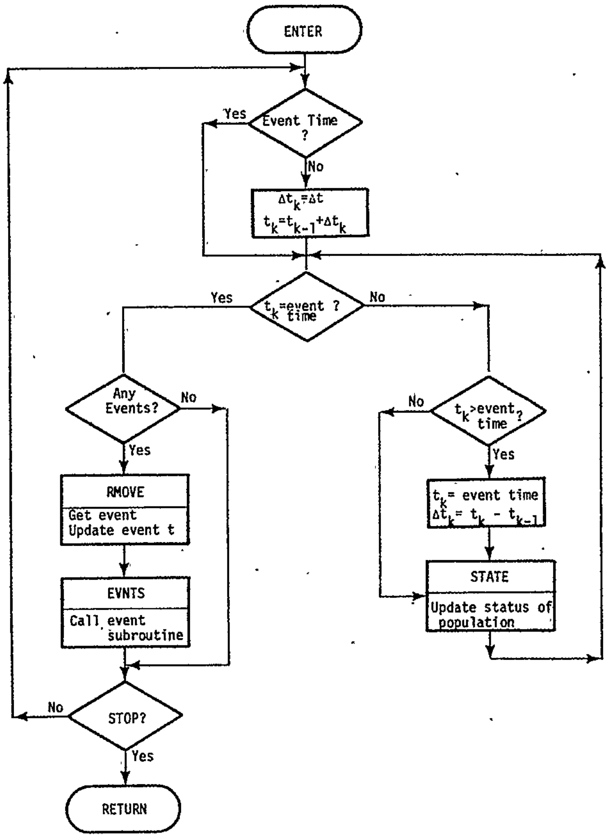

Figure 5 - POSIM Executive Flow Chart

integration logic. In addition to decreasing the program size from some 350 to 80 lines of FORTRAN, the resulting executive is more efficient. Also, the initializing routine, DATIN, was eliminated entirely, with the necessary GASP variables set in a separate routine transparent to the POSIM user. Other GASP utilities such as the file management programs were used without change.

As shown in Figure 5, when an event occurs, the subroutine EVNTS is called. At event times STATE is also called with the result that the population is updated prior to processing an event. EVNTS provides necessary branching to subroutines which modify the system's status, usually by changing rates affecting the population. There are six events in POSIM. Figure 6 provides a brief description of each of them.

| Event Subroutine | Description |
|---|---|
| START | This event occurs at the start of the year. The subroutine is responsible for obtaining the necessary input for the next year of simulated time, setting the time to 1, the start of the biological year, and updating the population to reflect births and aging effects. |
| MPER | This event is triggered at the start of a mortality period. At this time mortality rates are set to the values for the ensuing period. |
| CNCPT | When CNCPT is called conception occurs. That is, a number of potential births are entered into the population status, and are depleted as the result of resorption (fetal mortality) until the start of the year when they are handled as births. |
| HNTG | This routine is called at both the beginning and ending of hunting seasons to process the respective events. At these times the hunting rates are set, interactively if indicated, and reset to zero, respectively. Harvest totals are also maintained here. |
| EOY | EOY is called by EVNTS at the end of the biological year. At this time the status of the population is saved and final totals are calculated. A rerun of the year just completed is executed if elected by an on-line user. |
| DMP | DMP provides all of the output from the simulator, with the exception of the final reports. It is also called by EVNTS at status event times; i.e., times specified by the user for population status report generation. |

Figure 6 - Event Routine Descriptions

## INTERACTIVE FEATURES

In POSIM, the use of continuous-discrete simulation logic provides a great deal of flexibility in terms of the types of population models which can be accommodated. Additional power is provided to the user of POSIM by allowing operation in an on-line, interactive environment. By running interactively, the user has the ability to recursively verify input data. Once this is done, he may interactively "game" with the resulting model, experimenting with harvest strategies, testing sensitivity to assumed rates, and so on.

In order to facilitate the use of the simulator in the on-line mode, special options were incorporated into POSIM and are available only to the interactive user. First among these is a rerun capability which allows the user to specify, at the end of each year whether to proceed to the next year or reinitialize the population to the start of the year just completed. If rerun is selected, all input options are available and he may specify whether he does or does not want to change hunting timing and/or harvest numbers, birth rates, or other mortality rates. This done, the model will proceed through the year again. This process may be repeated until a satisfactory population performance is obtained at which time POSIM allows time to advance to the next year.

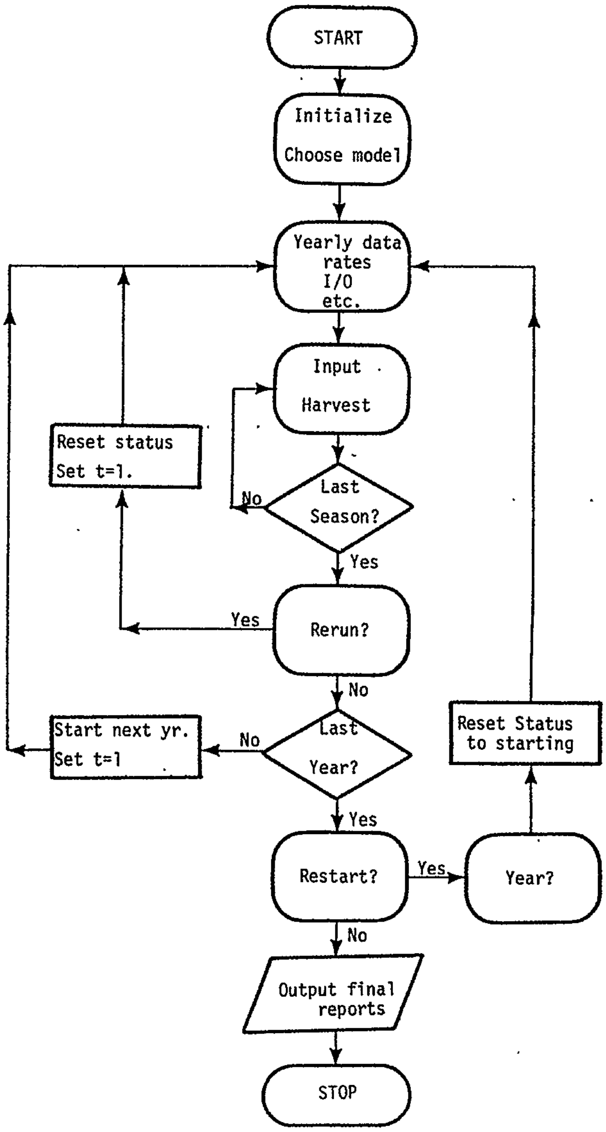

Figure 7 - POSIM Interaction Logic

Two other features, similar in operation to the rerun option are the restart and continue options. That is, while the end of the simulation is generally specified explicitly by input, the on-line user may elect to either restart at the beginning of any year, or alternatively, continue the simulation any number of years when the original time limit has been reached. Figure 7 illustrates the logical progression of the simulator as seen by the interactive user. Control provided in "real" simulated time by the user is shown with display symbols. Other program processes are shown with the usual flow chart symbols.

Additional control over the program is provided for on-line users of POSIM. First, input to the program may be from a file. In addition, if the first part of the input is generally fixed, a file may be used to specify input to the point in time where interaction is desired. When POSIM runs out of input, if appropriate options have been selected, further input requests will be directed to the user's terminal. Also, exacting control is provided over the type of output and input from one year to the next. While some of the features described are dependent on implementation on the Xerox Sigma 7 system currently in use at Montana State University, in most cases conversion to other systems with interactive FORTRAN capabilities would be straight forward.

## EXAMPLE

In the example which follows a simulation model is developed using the POSIM program to aid both preliminary data verification and testing of relationships which are subsequently proposed to describe the population dynamics. The data used in the development was collected by Mackie (4) and others during a continuing study of mule deer in the Missouri River Breaks of North-Central Montana.

For this example a ten-year study period, from 1961 to 1971, was chosen. Values for input to the program were derived using data from the first five years. This data is summarized in Table 1. Population counts were made primarily by air from late December to early January with counts available for 1/2 year olds (fawns), 1 1/2 year olds (yearlings), and adult animals. Since births occur in late spring, beginning with the first part of June, for mule deer the observation times did not correspond to the biological year of the species. One of the objectives of the study was to model the population on a biological year basis.

The first step in the modeling process was to determine estimates of natural mortality for each age class. As seen in Table 1, estimates existed for beginning and ending population counts as well as harvest mortalities for each of the observed years. By inputing these known values to the program as whole numbers and iterating with POSIM until each of the first five years' counts were matched, natural mortalities were determined. The corresponding rates were automatically calculated and output by the program, for the first five years to be simulated.

Initially then, POSIM was used as a powerful calculator to interactively allocate mortalities in a way which was consistent with the original data. From a game management perspective, this may well be one of the primary uses of the model. That is, where data is generally sparse, but where estimates are made on a regular basis using that data, by experimenting with assumed values for population counts, harvest, and mortality losses as well as birth rates in many cases the consistency of the various assumptions can be tested from a purely arithmetic standpoint.

Once estimates were available for annual mortalities, development of a simulation based on the biological year was begun. To do this, the year was broken into two mortality periods. The first began at June 1, the start of the biological year, and ran to January 1, the assumed observation time.

Table 1 - Missouri Breaks Deer Population Data, 1961-66

| Sex | Age Group | Count | 1961 | 1962 | 1963 | 1964 | 1965 | 1966 |
|---|---|---|---|---|---|---|---|---|
| Male | 1 | Census | 232 | 108 | 128 | 192 | 148 | 72 |
| | | Harvest | 94 | 40 | 33 | 30 | 6 | |
| | 2 | Census | 47 | 65 | 60 | 75 | 107 | 50 |
| | | Harvest | 26 | 46 | 13 | 11 | 9 | |
| | 3 | Census | 55 | 73 | 115 | 85 | 120 | 100 |
| | | Harvest | 48 | 9 | 21 | 25 | 24 | |
| Female | 1 | Census | 231 | 108 | 128 | 192 | 147 | 71 |
| | | Harvest | 38 | 13 | 4 | 10 | 8 | |
| | 2 | Census | 135 | 144 | 60 | 101 | 128 | 91 |
| | | Harvest | 14 | 36 | 8 | 7 | 3 | |
| | 3 | Census | 400 | 402 | 409 | 355 | 350 | 316 |
| | | Harvest | 124 | 64 | 30 | 15 | 14 | |

Table 2 - Regression Results

Net Change Rate = $b_0 + b_1 X$ Population X $10^{-3}$

| Sex | Age Group | $b_0$ | $b_1$ | $R^2$ |
|---|---|---|---|---|
| Male | 1 | -.13 | .21 | .78 |
| | 2 | -.078 | .13 | .66 |
| | 3 | -.018 | .058 | .303 |
| Female | 1 | -.135 | .212 | .798 |
| | 2 | -.024 | .052 | .757 |
| | 3 | -.007 | .030 | .753 |

The second was defined to be from the end of the first to the end of the biological year, May 30. Mortality rates were then converted from annual to periodic rates, and an estimate for the birth rate was established at 1.5 births per adult female.

Following initial analyses to determine density dependent relationships for natural mortality rates independent of hunting losses, the relationship between total mortality and density was examined. A strong linear relationship was found between total mortality and population size for all age classes. Table 2 summarizes the regression equations incorporated into the model. Actually, since total mortalities can take on negative values as was determined during the available data verification, the rates predicted by these equations actually represent net change rates. The rates, prior to regression, were converted continuous rates. Hence, the resulting simulation model must operate in a continuous/discrete mode.

As with most wild populations, density is only one component of the mortality equation. An equally important variable, from the standpoint of population regulation, is the environment. The environment includes weather, forage availability, competing species, etc. The effect of environment on the rates affecting the population was incorporated into the relationship by multiplying equations shown in Table 2 by an environmental index. Hence, external effects are modeled as a time varying forcing function. Initial estimates were made for these indexes based on available weather data and expert opinion for the 10 year period of interest. POSIM was then used, again in the interactive mode, to refine these estimates until total population performance was acceptably close to the observed. At this point the model was believed to be calibrated for the population and the time period of interest.

Figure 8 shows the result of the final calibration run, where the simulated total population is

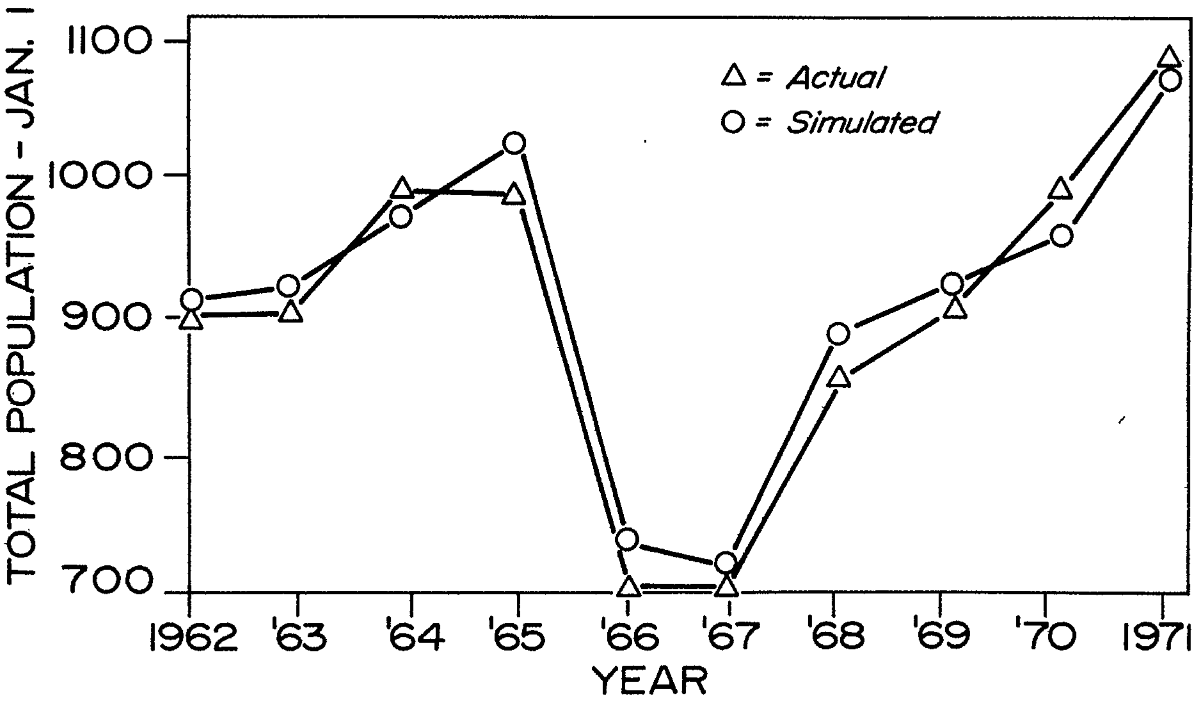

Figure 8 - Final Calibration Results

Table 3 - Missouri Breaks Deer Population
Model Validation Results

| Group | Value | 1962 | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | $r^2$ | F(1,18) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adults | Actual | 684 | 644 | 616 | 704 | 556 | 490 | 486 | 600 | 610 | 738 | | |
| | Simulated | 701 | 622 | 665 | 691 | 560 | 498 | 571 | 639 | 658 | 713 | .830 | .30 |
| Females | Actual | 654 | 597 | 648 | 626 | 479 | 473 | 547 | 584 | 646 | 709 | | |
| | Simulated | 650 | 635 | 649 | 666 | 501 | 475 | 552 | 572 | 596 | 653 | .827 | .01 |
| Males | Actual | 246 | 303 | 352 | 375 | 222 | 226 | 302 | 316 | 361 | 379 | | |
| | Simulated | 251 | 293 | 332 | 369 | 233 | 239 | 331 | 347 | 370 | 422 | .903 | .15 |
| Young | Actual | 216 | 256 | 384 | 296 | 144 | 210 | 364 | 300 | 390 | 362 | | |
| | Simulated | 200 | 306 | 317 | 345 | 174 | 228 | 313 | 281 | 309 | 363 | .702 | .07 |

compared with the observed at the beginning of the second mortality period. A sample correlation coefficient between observed and simulated total counts of .98 was obtained. Information concerning the validity of the model is gained by comparing various age class counts with observed values. That is, if relationships used in the model are valid, and the model is calibrated to total population counts, the age structure for those counts should be acceptably close to the observed. Table 3 summarizes the results of validation. In addition to the correlation coefficients shown in Table 2, any number of validation plots, complete with detailed statistics are optionally available with POSIM. This output can aid in calibration and validation, as well as reaching targeted behavior patterns by providing graphical and statistical output to the user.

This example has shown the power of the POSIM program as a tool for use in the development of wildlife population models. Beginning with 5 years of data, the program was used first to verify observed counts and to estimate annual mortality or turnover rates between observation times. Next, with the annual rates converted to continuous rates and the relationships derived to determine continuous mortalities included in the model, a combined simulation was run for the entire 10 year period. Finally, with the model parameters calibrated to total population counts, validation of the internal age structure indicated that an acceptable model had been developed. At each stage of the model development, features of the POSIM program aided the analyst. Specifically, the interactive use of the rerun and restart dramatically reduced the verification and calibration phases of the model development.

## SUMMARY

POSIM is finding application in several areas of game management and research. For field personnel, the modeling activity itself is a valuable source of insight concerning past population performance The availability and ease of use of POSIM greatly encourages this type of work. Furthermore, as demonstrated in the example, the program can be a powerful aid in the development and implementation of descriptive population models. Work is now proceeding which will make it easier to use in either the on-line or batch modes. Also, research is underway using POSIM in the development of models of specific populations in Montana for management use.

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