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A COMPUTER SIMULATION MODEL FOR THE STUDY OF WOLF-MOOSE POPULATION DYNAMICS

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ABSTRACT

A computer simulation model has been developed of a wolf-moose (*Canis lupus-Alces alces*) system. The program is formulated in APL (A Programming Language) which is an interactive language between user and computer. This language is ideal for use as a teaching aid because the student is continuously in contact with the simulation problem. Parameters in the program which may be externally manipulated by the user consist of initial age and sex distributions of the moose and wolf populations, vegetation supply (herbaceous and browse) available for the moose, moose hunting season, length of the simulation run, and output options. The other parameters in the model are reproductive rates (age specific) and mortality rates (age and sex specific) for moose and wolves, wolf predation rate upon moose (age specific), vegetation consumption by moose, and human hunting success on moose (age and sex specific). These can be altered by internal programming which may be performed with minimal computer training.

An ecological system can be regarded as an interacting mechanism of functionally dependent processes, none of which could be eliminated without exerting an effect on the whole. The components of an ecosystem are dependent on factors that have minimum and maximum constraints and each could be described by a function of one or more variables. Hence, whole systems may be broken down into various components, each of these modeled by separate but

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functionally dependent equations, and then the components combined to represent the real system. Once such a model is formulated, it can be incorporated into a computer program called a simulator, permitting the computer to solve the enormous number of equations in seconds. The purpose of this paper is to introduce a model of a hypothetical wolf-moose system which has been developed primarily as a teaching device for use in a wildlife management course [1]. With this model the instructor is able to set a number of ecological parameters at certain levels and ask the students to determine management strategies by manipulating the other parameters to achieve a particular goal. This should give the students a feeling for ecosystem dynamics that may not be achieved from texts and lectures on the subject.

Models of the wolf-moose system have been developed by Dixon and Cornwell [2], Jordan et al. [3], and Rykiel and Kuenzel [4]. A teaching model not specifically pertaining to either wolf or moose was developed in FORTRAN by Dean and Gallaway [5]. Their model contains a variety of input options and may be used to study population dynamics of a single species. In the present work, the wolf-moose system was stochastically modeled and formulated into an APL (A Programming Language) computer simulator. APL was utilized as the language because all inputs to and outputs from the computer are via a remote terminal, eliminating card punching and allowing the student to correspond directly with the computer. This is a very favorable characteristic for a language which is to be used in a teaching simulation model because the student is always in contact with the simulation problem.

Geographical Setting

The setting for this model is an imaginary island in an immense body of water located in the northern latitudes of North America. It is assumed that animal migrations to and from the island are nonexistent. Two seasons are recognized on the island; summer, which commences on June 1 and continues through September 30, and winter, which is the remainder of the year. The vegetation on the island consists of any combination of deciduous and gymnosperm species as well as any successional age desired. Composition is never explicitly stated in the model but may be imaginatively deduced from the food level assigned per acre. The animal life of the island always consists of moose and may also include wolves. Any other species may also be present provided it 1) does not serve as a food for wolves, 2) does not compete with the moose, and 3) does not prey on either moose or wolves.

Modeling Approach

The approach taken in modeling components of this system was to approximate known relationships between variables by known mathematical distributions. A frequently occurring relationship for example between density dependent factors and food supply was that the increase in the dependent variable (density dependent factor) was approximately proportional to the independent variable (food) until other factors in the environment reflected constraints on the dependent variable, causing a continuing decrease in the slope to the point where the curve became asymptotic to a constant value. A mathematical distribution which has these characteristics is the negative exponential.

The negative exponential curve is a two parameter family of curves (Figure 1). The general form of the equation is

$$y = a(1 - e^{-b.x})$$

where

a = an asymptote and
b = a constant.

In general, y will approach the asymptote a as x approaches infinity. With the correct selection of parameters, a and b, many biological relationships could be reasonably modeled. This family was found appropriate for many of the models in this work.

The parameters have been selected for the model with reference to previous work found in the literature. Many assumptions were utilized to achieve the final result: a simulation model that represents a realistic wolf-moose system. However, by no means is the model restricted to these selections and most parameters can easily be altered with minimal previous computer training. This leads to the development of many different systems each with slightly variable biological capabilities.

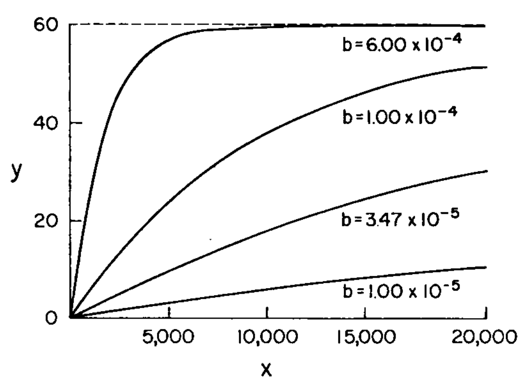

Figure 1. The negative exponential family of curves for a fixed *a* and various values of *b*.

Ecological Components

The ecological components of the model are diagrammed in Figure 2. The parameters for these ecological components have been divided into two types, internal and external. Internal parameters are those that are built into the program and may be altered only by reprogramming. Parameters in this category include reproduction rates, mortality rates, and food consumption. External parameters are those which the user has the option of supplying to the program as input. These include vegetation supply, moose and wolf populations, and human predation on moose which could be realistically managed.

VEGETATION

The vegetation components consist of herbaceous (available only during summer) and browse (available all through the year) vegetation utilized by moose. Consumption of each type is assumed to be proportional to its availability in the habitat. All plant food enters the system on June 1, which is considered the first day of summer and starting point for the model. For each month of the simulation this resource is diminished by the amount of food consumed by the moose herd during that month. This continues until the following June 1 when the original supply is renewed in the system. This assumes that a fixed amount of herbaceous and browse foods will be produced each year regardless of the size of the moose herd, implying that destruction of the habitat by high moose densities is nonexistent in the model.

Two mathematical models had to be constructed to represent the amount of summer and winter food consumed by a moose under various levels of food availability. The negative exponential was selected to represent food consumption as a function of food availability. Available data on moose consumption were used to derive the parameters for the summer and winter food consumption models.

MOOSE REPRODUCTION

The moose reproduction components consist of ovulation, double ovulation, conception, and the sex ratio. Age specific probabilities of ovulation and double ovulation were formulated from past research on moose reproduction and the negative exponential family was again utilized. Since both of these factors are operating immediately after summer, they are represented as a function of summer food consumption because evidence suggests that the preceding food levels govern the capabilities of moose to ovulate. Age specific probabilities were also determined for conception but expressed as a function of the winter food consumption because fertilization occurs after the onset of winter. The sex ratio was considered to affect the conception rate only if the male-female ratio

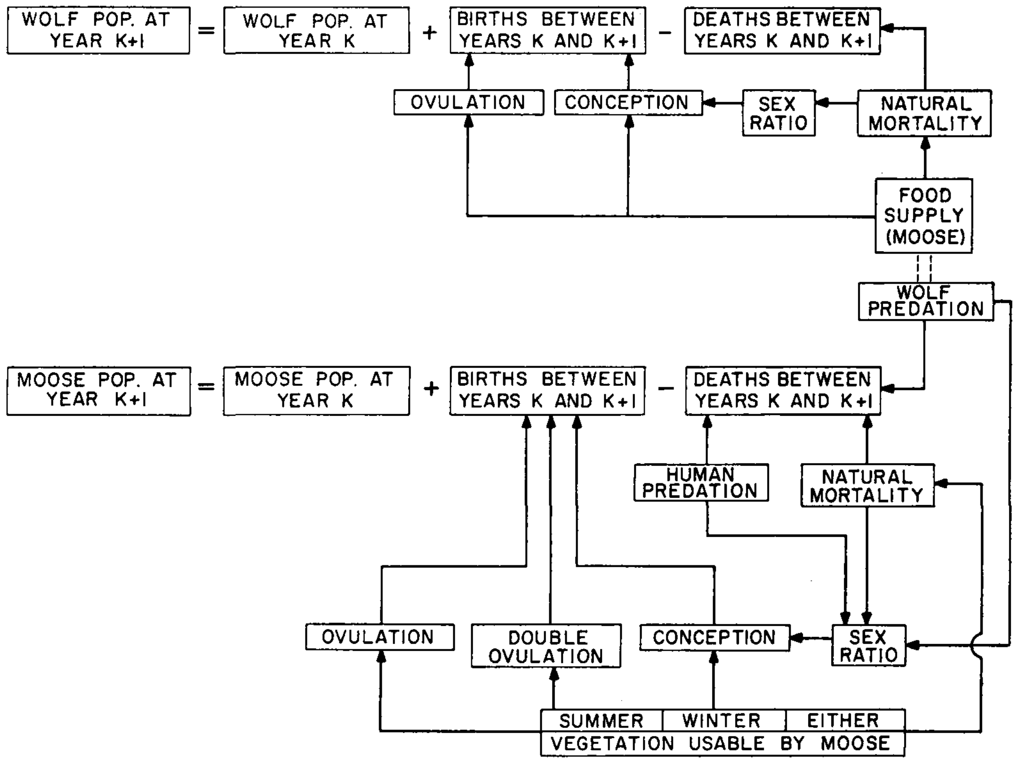

Figure 2. Diagrammatic model of the wolf-moose system. Arrows indicate the pathway for interdependence of various components while the dotted lines show the interface between the separate wolf and moose systems.

dropped below a specific level (assumed to be 1:10). Hence, with the reproductive model defined on an age-specific basis, each female moose was stochastically assigned to one of three reproduction classes (non-pregnant, pregnant with one calf, pregnant with two calves) and assumed to deliver her young into the population on June 1.

MOOSE MORTALITY

The moose mortality components consist of natural mortality, wolf predation, and human predation. Natural mortality is defined as deaths due to causes other than wolf or human predation. A negative exponential model was derived for survival on an age and sex specific basis. Survival was considered either a function of the summer or winter food supply depending on which month was under consideration.

The wolf predation model is dependent on four criteria: 1) moose population, 2) moose age structure, 3) wolf population, and 4) maximum predation rate of a wolf. The general model, developed from Dixon and Cornwell [2] is

$$N_a^k = P^k \cdot Q(1 - e^{-a(N_o{}^k)^2} \cdot (P^k)^{(1-c)})$$

where

N_a^k = number of moose killed by wolves in month k,

N_o^k = initial population of moose in month k,

P^k = population of wolf predators (at least one year old) in month k,

Q = maximum number of moose kills that could be made per wolf per month,

a = a constant, and

c = a constant

In the Dixon-Cornwell model no consideration was given to the differential killing of various ages of moose. It has been verified [6] that wolves tend to concentrate their kill on the young and old. Therefore, a vulnerability vector was added to quantify the age classes of moose according to their relative vulnerability with regard to wolf predation. Hence, the simulation model considers the moose age structure as a vital factor in the abundance and distribution of kills.

Moose hunting on the island consists of six options: 1) male only with no calf hunting, 2) female only with no calf hunting, 3) male only including calf hunting, 4) female only including calf hunting, 5) male and female with no calf hunting, 6) male and female including calf hunting. The hunting season may be during any month, consist of one to thirty days, and involve as many hunters as desired. Hunter success probabilities were formulated on an age and sex basis and the kills assigned stochastically to the various age-sex groups.

WOLF REPRODUCTION

The wolf reproduction components consist of ovulation, conception, sex ratio, and litter size. Ovulation and conception were considered a function of food supply; however, no distinction was made with regard to summer and winter because the moose levels do not fluctuate drastically between the seasons. The wolf sex ratio is considered to exert an effect on reproduction if the male-female ratio is below a specific level (assumed to be 1:10). Female wolves are then assigned on February 1 as being either pregnant or non-pregnant and assumed to produce pups on April 1. The litter size for wolves range from one to ten, and a discrete probability density function was formulated to stochastically assign a litter size to each pregnant female.

WOLF MORTALITY

The only component of wolf mortality is natural mortality since no form of predation is present on the wolf population. Age and sex specific models for survival of wolves were based on food consumption and formulated from the negative exponential family.

Results

Experimentation was performed on the model under a variety of biological conditions to determine how it would represent reality. A sample simulation run showing the input format is presented in Figure 3.

TWENTY YEAR MOOSE SIMULATION

A simulation of a moose population free from wolf predation was performed for five twenty year periods and illustrated in Figure 4. The initial moose age and sex distributions and food level were derived from the literature. The average moose population for each twenty year simulation could be considered the carrying capacity of the range. Thus, the average carrying capacity for the five simulations was 690, illustrating the adjustment of the carrying capacity from an initial population of 726 animals. These simulations also indicate that the moose population is neither exploding nor dying out over an extended time period.

This simulation also illustrates the differential mortality among the age classes of the moose population. Table 1 shows the percentage age distribution in the first year on June 1 immediately after calving and then on May 1 just prior to the next calving. The parameters in the model were set to clearly demonstrate

POPULATION

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DATA CONTROL (0,1)

□: 0

INITIAL MALE WOLF AGE DISTRIBUTION
  (0-9+)

□: 2 1 1 1 1 1 1 1 1 1

INITIAL FEMALE WOLF AGE DISTRIBUTION
  (0-9+)

□: 2 1 1 1 1 1 1 1 1 1

INITIAL MALE MOOSE AGE DISTRIBUTION
  (0-9+)

□: 110 40 39 38 36 33 28 22 12 5

INITIAL FEMALE MOOSE AGE DISTRIBUTION
  (0-9+)

□: 110 40 39 38 36 33 28 22 12 5

HERBACEOUS FOOD PRODUCTION
  (LBS./ACRE)

□: 75

BROWSE FOOD PRODUCTION (LBS./ACRE)

□: 75

YEARS TO RUN SIMULATION

□: 20

YEARLY OUTPUT OPTION (0,1)

□: 1

ADDITIONAL YEAR OPTION (0,1)

□: 0

MOOSE HUNTING SEASON (0,1)

□: 1

MOOSE HUNTING SEASON MONTH (JUNE=1)

□: 5

BULL HUNTING (0,1)

□: 1

COW HUNTING (0,1)

□: 1

CALF HUNTING (0,1)

□: 0

NUMBER OF MOOSE HUNTERS

□: 100

DAYS OF MOOSE HUNTING

□: 14
```

Figure 3. Input of a sample simulation. The statements above are a series of questions asked by the computer with the answers supplied by the user adjacent to the quad symbol (□:). No-yes options utilize the 0-1 method where 0 indicates no and 1 indicates yes. The input for the various age distributions is in vector form with the first element being the number of animals in the youngest age class and the last element the number in the oldest age class.

that calves and animals seven years or older are more vulnerable than those in the prime age classes, a trend suggested by Mech's work on the Isle Royale moose herd [6, 7].

MANIPULATION OF VEGETATION

The controlling effect of the food supply on the moose herd was illustrated by comparing two simulations which were identical (726 animals initially)

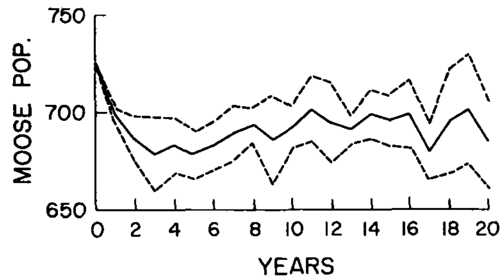

Figure 4. Yearly means with one standard deviation for the five simulations of the moose population for a twenty year period.

except for the food supply. One simulation had twice the amount of vegetation of the other and, hence, the resulting populations the following year were 712 and 403 respectively. This emphasizes the effect of vegetation on moose survival and reproduction.

The distribution of food over the year is also a vital determinant of the moose population. If there is a large supply of both summer and winter foods, mortality of moose should be low and fairly constant throughout the year. However, if summer food is abundant while winter food is scarce, large mortality will result during the winter. Three one-year simulations were performed with varying food supplies (Figure 5). Simulations A and C have high summer food levels when compared with B and, consequently, have a lower summer mortality rate. However, with the initiation of winter and loss of all herbaceous foods, the moose population in Simulation C undergoes a drastic decline due to a very low winter food supply. This indicates the effect that a low winter food supply could have on a moose herd. Therefore, a moose hunting season would have been advisable management practice during October if it was known that the moose herd would exceed the winter carrying capacity. This suggests the possibility that such a model may prove useful in helping wildlife managers regulate the hunting season to maximize resource utilization.

Table 1. Percentage Age Distribution of the Moose Population

Ages (years)	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9+*
Percent of population at June 1 after calving	30.3	11.0	10.7	10.5	9.9	9.1	7.7	6.1	3.3	1.4
Percent of population the following May 1	21.1	14.1	13.3	12.6	11.8	10.3	8.3	4.3	2.6	0.9

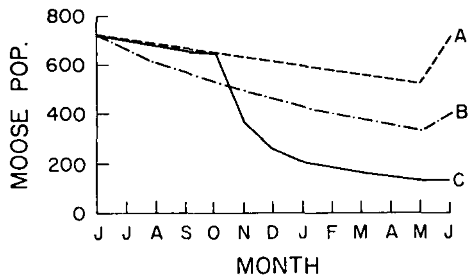

Figure 5. Moose populations on a monthly basis under various food levels. The respective summer and winter food levels (pounds per acre) for simulation A is 75 and 75, simulation B is 37.5 and 37.5, and simulation C is 140 and 10.

HUNTER KILLS AND AGE DISTRIBUTIONS

To determine the age distributions of moose populations, a sample of the hunter kill is often examined. This estimate of the age distribution will be biased if an age class is not harvested in proportion to its availability. Data from a bull-cow hunting simulation indicates that of 642 animals killed in thirty years, 136 of them were yearlings. This implies that yearlings make up 21.2 per cent of the true population. Upon examination of the yearly population on June 1, it was found that yearlings comprise only 15.0 per cent of the population, revealing that a sample of the hunter kill is not always a reliable estimate of the true population. This illustrates that the moose internal parameters were set so that yearlings are more vulnerable to hunting than the other age classes, a situation found to exist in reality [8].

INCREASED VULNERABILITY OF A MOOSE SEX-AGE CLASS

Within any population it is conceivable that a specific sex-age class may be more susceptible to an environmental factor than the others. This is especially true with regard to hunting as was previously indicated, but may also apply to a disease epidemic or parasite infestation. To illustrate this effect on the moose population, the summer survival parameters of two year old males were altered so they would be more susceptible to mortality. The results of that simulation are compared to one under default conditions. With default parameters, this sex-age class decreased slightly from 5.4 initially to 5.2 per cent of the total population in the following year. However, in the modified simulation the decrease was from 5.4 to 3.5. This reflects the sensitivity of the model to changes in mortality rates in selected sex-age classes.

TWENTY YEAR WOLF-MOOSE SIMULATION

A twenty year simulation was performed on the wolf-moose system to determine the behavior of the model when wolves are incorporated into the system. The results of the run indicate that both populations do not increase or decrease continuously but exhibit natural fluctuations around specific carrying capacities (Figure 6). The carrying capacities of wolves and moose were determined and found to be 47 and 724 respectively.

It is interesting to compare the moose population under wolf pressure to the simulation when wolves were absent (Figure 4). Generally, both populations oscillate around a carrying capacity of 700 animals with the former actually higher, implying that wolves do not adversely affect the moose herd. It may be hypothesized that wolves mainly consume the moose that would have died naturally.

WOLF-MOOSE-HUNTER SIMULATION

A moose simulation was performed utilizing wolves and hunters to demonstrate their simultaneous effect on the moose population. The moose food supply in this test was a high summer and low winter food level identical to Simulation C of Figure 5. With the initial moose population at 726 and wolves at a density of 66, the summer moose population underwent a fairly rapid decline due exclusively to wolf predation. The advent of winter and a shortage of the food supply for the moose resulted in a sharp decline of the herd similar to that occurring in Simulation C. However, in the present simulation (Figure 7) the moose were exposed to 200 hunters and the wolf population during October. Since both simulations have comparable deductions, it appears wolves and hunters are harvesting moose that would have died due to natural causes. In effect, they help reduce the moose population to its winter carrying capacity.

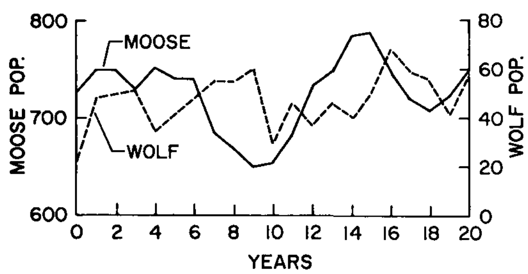

Figure 6. Simulation of a wolf-moose population for a period of twenty years.

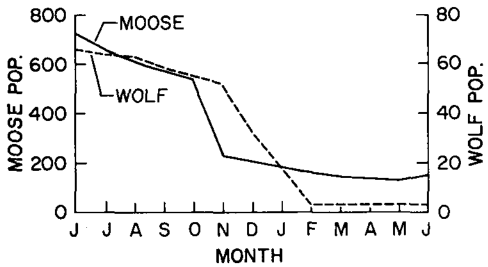

Figure 7. Wolf-Moose-Hunter simulation.

As winter proceeds, the moose population is eventually adjusted to a winter carrying capacity of 127 at May 1. During this period the wolf population has declined to a low of three. Note that no wolf reproduction has occurred under this food shortage, a hypothesis believed to be true by Mech [7]. The reproductive response of the moose is also low and practically identical to that of Simulation C.

This simulation demonstrates the control of vegetation on the moose population, which in turn manifests constraints on the wolf population. It has illustrated many of the basic biological properties of predatory and hunted systems and, in particular, the fact that under appropriate conditions, predators and hunters do not damage the moose population but only harvest the excess animals that are already doomed to death.

Conclusion

The manipulation of parameters presented above serves to illustrate the high degree of flexibility which is incorporated within the model. With this model it is easy to visualize the enormous number of systems that could be simulated. These simulations should prove useful in teaching aspects of population dynamics in wildlife courses. In large classes the most efficient method for utilizing this teaching aid would be for the instructor to use the internal parameters developed here and ask the students to manipulate the external parameters to achieve a particular goal. In small classes the instructor may be able to alter the internal parameters to better meet course objectives or, if time permits, various moose herds may be developed by altering the internal parameters. Hence, different programs could be given to groups of students who could compare their data from the individual moose herds by various mathematical and statistical tests. Students may be introduced to mathematical and statistical analysis by this unconventional approach, possibly overcoming their aversion to these valuable tools for the wildlife biologist.

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