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A COMPUTER SIMULATION MODEL FOR THE STUDY OF DEER-ASPEN FOREST INTERACTIONS

presented by

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## A COMPUTER SIMULATION MODEL FOR THE STUDY OF DEER-ASPEN FOREST INTERACTIONS

By

Philip John Mello

### A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

## MASTER OF SCIENCE

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#### ABSTRACT

### A COLPUTER SIMULATION MODEL FOR THE STUDY OF DEER-ASPEN FOREST INTERACTION

By

#### Philip John Mello

A computer simulation model was developed which represents the interactions of white-tailed deer (<u>Odocoileus</u> <u>virginianus</u>) population with an aspen-type (<u>Populus</u> spp.) forest community. This model can be used by biologists as a simulation of deer responses to manipulations and as a teaching tool by instructors in wildlife and habitat management. It will aid students in the understanding of population dynamics and the effects of wildlife and habitat management policies on wildlife populations.

The aspen stand is described by such parameters as stand age, basal area, mean diameter breast height (dbh) and total tree numbers. Stand information is further broken down into dbh classes, height classes and the number of trees within each class. The dynamics of the stand are modeled with above ground biomass and tree numbers as a function of tree height, number of trees, and season of the year. Deer numbers within specified sex and age classes are used to describe the deer population. Deer population dynamics are modeled with age specific natality rates and 3 categories of mortality; miscellaneous mortality, harvest mortality, and starvation. Deer-aspen interactions are represented by algorithms which represent the effects of deer foraging on aspen growth and mortality, and the effects of food supply on deer mortality (starvation) and natality.

Management options for the user are deer harvest and tree harvest. The user is able to manipulate deer harvest by specifying the proportion of antlered and antlerless deer to be harvested for each year of the simulation. Logging operations can be simulated by specifying the size of the clearcut and the rotation period.

Several computer experiments were performed. Populations with high antlered harvest rates (50 to 70 percent) were able to reach higher peak densities than unexploited populations. Responses of populations to antlerless harvest were dependent on the rate of harvest and the response potential of the population. Logging intervals of 10 years caused significant declines in deer numbers while 5 year logging intervals showed no such declines. Low density populations, however, showed an immediate increase following a clearcut.

Sensitivity analyses were run on winter severity, vegetative energy content, and deer maintenance requirements. Sensitivity analysis of winter severity suggests that winter severity is a major limiting factor under conditions of abundant summer food supply. The model was highly sensitive to deviations in vegetative energy content and deer maintenance requirements. This suggests the need for more accurate and precise quantification of these variables.

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### INTRODUCTION

One of the major problems facing forest and wildlife management professionals today is evaluating the impact of forest management policies on wildlife populations. Modern foresters and wildlife managers realize that a more holistic view of the forest ecosystem must be taken to assure proper management of both forest and wildlife resources. Unfortunately, this approach involves a complex set of interactions which make it increasingly difficult to forecast the outcome of a set of management decisions.

One result of this new philosophy is the recent application of systems analysis and computer simulation modeling in forest and wildlife management. Jeffers (1978) listed 3 reasons for using systems analysis in ecological research. These were: 1) the inherent complexity of ecological relationships; 2) the characteristic variability of living organisms; and 3) the apparently unpredictable effects of deliberate modification of ecosystems by man. For these reasons, and the dynamic nature of the interactions which occur in a natural ecosystem, the conventional procedure of controlled laboratory or field experiments

often provides only fragmented information which, in many cases, is insufficient to develop a clear understanding of the interrelationships of an ecosystem.

Simulation models are tools which unify existing information and provide the user with a means to analyze the system under study and evaluate various management strategies while retaining to some degree the complexity and variability that is found in natural ecosystems.

Because of the greater ease of measurement, the use of modeling in forestry is both older and more sophisticated than modeling efforts in wildlife management (Bunnell 1974). Many models have been developed which simulate the growth of various types of forest stands and allow the user to examine the effects of various timber management strategies on the stand (Leuschner 1972, Fries 1974, Perala 1979, USDA 1979). The primary goal of these models was to predict the amount of merchantable timber produced under various timber management plans. In these models, forest growth is modeled as a function of some characteristic of the stand itself with no consideration of the effects of wildlife on forest growth. Other forest growth models have been developed which examine deer browse production in a stand, although again, the effects of wildlife on growth are not incorporated into the model (Myers 1977, Cooperrider and Behrend 1982).

This same approach has been taken in many models of ungulate populations (Lomnicki 1972, Walter and Gross 1972, Anderson et al. 1974, Fowler and Barmore 1976, Roelle and Bartholow, unpubl. rep. 1977, Short 1979). In these models, environmental factors are represented indirectly as density dependent natality and mortality rates. This type of model has been referred to as a complicated steadystate model (Watt 1968). Models of this type are the most commonly used type in wildlife management today. These models are considered appealing because fewer parameters, which can be measured and compared with simulation results, are dealt with, simplified assumptions are used, and many parameters which are difficult to measure are omitted. The results of these models are considered potentially less precise but more realistic than more complex and precise models (Pojar 1981). The major drawback of this type of model is the assumption that environmental conditions and the density dependent relationships within the system remain constant throughout the simulation. Therefore models such as these cannot be used for long range prediction. Also, since there are no environmental factors incorporated in the model, these models are obviously unable to evaluate the effects of habitat manipulations on wildlife populations.

Medin and Anderson (1979) developed a mule deer (<u>Odocoileus hemonius</u>) model that incorporated environmental influences on deer natality rates. This was done by a

3 step process which related forage nitrogen yield to precipitation, deer fat reserves to forage nitrogen yield and then modified the mean age-specific birth rate of deer as a function of fat reserves. This approach is useful in that it provides the user with more long range predictive power. However, it is limited by its inability to manipulate habitat and by the unreliability of many difficultto-measure parameters.

Still another approach has been introduced (Moen 1973, Mautz 1978) which calculates the carrying capacity of an area based on the nutritional requirements of an animal and the amount of energy or protein available in the area. Models of this type have been developed for deer (Wallmo et al. 1977, Spalinger 1980) and elk (<u>Cervus elaphus</u>) (Swift et al. 1976, Hobbs et al 1982). A more complex model developed by Bobek (1980) also incorporated this approach.

The value of these models is that they provide a link between range conditions and deer numbers. Therefore, as habitat conditions change, the maximum number of animals an area can support can be calculated and appropriate management strategies can be initiated depending on management goals. These models, however, are not dynamic and can only be used on a year to year basis.

The next step in model complexity is a model which links both habitat dynamics and populations dynamics. Such models

can help predict the long range effects of various wildlife and habitat strategies and also provide useful insights into the interrelations of the system under study. Very few models of this type relating ungulate populations and forest vegetation have been developed. Davis (1967) developed a model which allowed the user to make decisions on both wildlife and timber management strategies. Another model which combined vegetation dynamics and population dynamics was developed by Walters and Bunnell (1971). The primary purpose of this model was to devise a management game to be used as a teaching aid. Both of these models were very generalized and used simplified assumptions which made them difficult to apply to specific ecosystems.

Cooperrider (1974) developed a model which represented the interactions of a deer population with northern forest vegetation. This model was designed specifically for the Huntington Wildlife Forest in the central Adirondack region of New York, though the author suggested it may be applicable to other areas of similar vegetation composition. This model enabled the user to determine the effects of various habitat and wildlife management techniques and, through sensitivity analysis, identify inputs and parameters which have the greatest effect on the system. Additional models of this type dealing with different species or ecosystems are needed.

One such system involves white-tailed deer (<u>Odocoileus</u> <u>virginianus</u>) interactions with an aspen (<u>Populus</u> spp.) forest community. A close association exists between whitetailed deer and aspen in the Lake States region. Aspen has been found to be the preferred summer habitat of deer in Wisconsin (McCaffery and Creed 1969) and Minnesota (Kahn and Mooty 1971). Studies in Michigan have shown that a major proportion of deer harvested each year were taken in areas where aspen is the most frequently occurring forest type (Byelich et al. 1972). Aspen, in Michigan, is considered the most important deer producing cover type and maintaining and treating this type is given first priority in its deer habitat improvement program (Byelich et al. 1972, Bennett et al. 1980).

The purpose of this study was to create a computer simulation model which represents the interaction of a whitetailed deer population with an aspen-type forest community. The model can be used by biologists as a simulation of deer responses to manipulations and as a teaching tool by instructors of forestry and wildlife management courses. The value of computer modeling as a teaching aid has been discussed (Walters and Bunnell 1971, Zarnoch and Turner 1974) and is viewed as a tool which allows the user to develop an intuitive understanding of the ecosystem dynamics and provides simulated field experience in the application of management techniques. Paulik (1976) felt the use of

simulated resource management games provides students with the type of learning experience normally acquired through several years in a responsible management position. Such games allow students to "test their analytical skills as well as their decision-making abilities in realistic management situations." Therefore, by using this model, the user is expected to develop an understanding of the effects of manipulating various management options on deer-aspen interactions and devise a management plan which will meet previously specified management goals.

### METHODS

### Model Structure

The sequence of events for a simulated year is diagrammed in Figure 1. More detailed flow diagrams of the main program and subroutines are shown in Appendix A. The model was written in FORTRAN IV computer language for a CDC 170 Model 750 computer. System dynamics were modeled using a set of difference equations. This type of model has been classified as a finite difference model (Lassiter and Hayne 1971).

Data for this model were obtained from a literature review of past studies in aspen and deer research. Thus no field work was performed for this study. Data were gathered primarily from published studies from Michigan and other areas of the Lake States region. Therefore, this model is considered a generalized model of deer-aspen interactions in the Lake States region and does not simulate the interactions of any 1 aspen stand in particular.

Simulation begins in November of the first year. This was done because the information used to derive the age structure of the deer population was obtained from the deer harvest. There are 3 main components of the program:



Figure 1. Sequence of computations in 1 year of a simulation run of the model.

- 1) forest dynamics; 2) deer population dynamics; and
- 3) deer and forest management options.

## Initial Inputs

The initial deer population is created by the user by assigning values for the total number of deer in the population, the mean age of males and females, and the proportion of males in the population. The total number of males and females is calculated by multiplying the total number of deer by the appropriate proportion. The age distribution for each sex is then computed using a negative exponential distribution with the appropriate mean age (Cooperrider 1974).

All information on an individual deer is stored in a 600 by 5 matrix. Therefore, the model is unable to handle more than 600 deer in a population. The statistics which are kept on a deer include sex, age, weight, critical weight, and the number of fawns dropped.

Initial weights for males less than 8 years old and females less than 5 years old were obtained from Moen's (1978) sine wave curve (Table 1). It is assumed that male deer reach their maximum weight at 7 years of age and female deer at 4, as has been reported for mule deer (Bandy et al. 1970). Therefore, initial weights for male deer older than 7 years of age were set equal to the initial weight of a 7 year old buck. Similarly, initial weights of older females were set equal to the initial weight of a 4 year old doe.

					Age				
Sex	Fawn	±	2+	3+	<b>+</b> +	5+	+9	+2	8+
Male	3.20	77.78	94.04	106.26	116.26	124.83	132.41	139.23	139.23
Female	3.04	56.76	68.31	77.39	85.02	85.02	85.02	85.02	85.02

Initial weights (kg) of deer for different age and sex classes.\* Table 1.

\*Data for males up to seven years old, and females up to 4 years old obtained from Moen (1978).

The critical weight is used to compute the probability of death due to starvation for a deer and the number of fawns a doe will bear. This is set equal to the initial weight at the beginning of the program. The number of fawns dropped is set equal to 0 for all deer at the beginning of the program. The program ignores this value in the winter months for female deer (and all year round for male deer) since the number of fawns a doe is carrying has little significant effect on a doe's metabolism at this time of year (Moen 1973). Since the program begins in November, any arbitrary value could have been chosen for this parameter.

After the initial deer population has been established, the deer matrix is sorted by age and sex. First, deer are sorted by age with the oldest deer occurring in the first position in the matrix and the youngest occurring in the n<sup>th</sup> position for a population of n deer. Deer of the same age are sorted according to sex with males occurring before females. The matrix is sorted in this manner to represent deer social organization with older males having greater access to browse than older females and both having greater access to browse than fawns (Ozoga 1972, Townsend and Bailey 1981).

The initial aspen forest is created simply by assigning the proportion of the total area for a specific aged stand. A maximum of 7 age classes can be assigned with initial ages ranging from 1 to 61 at 10 year intervals: Values for

mean diameter breast height (dbh), total number of trees/ ha, and standard deviations for each stand are specified within the program (Table 2). Values for total number of trees/ha in a stand greater than or equal to 20 years of age were obtained from Perala (1977). The value for the number of suckers/ha in a new stand was obtained from Graham et al (1963). Scant information on 10 year old aspen stands could be found in the literature. Therefore, the initial number of trees/ha was estimated from the program by running the forest submodel separately for a period of 10 years.

Diameter breast height distributions for aspen stands of various mean dbh's have been reported by the Lake States Forest Experiment Station (1933). Chi-square goodness of fit tests performed on these distributions showed all stands, with the exception of the 7.62 cm stand, were normally distributed. To be consistent, all stands greater than or equal to 11 years of age (mean dbh  $\geq$  5 cm) were assumed to be normally distributed. These mean dbh's and standard deviations were then assigned to different stands such that the mean dbh was approximately equal to reported mean dbh's for stands of different ages in the Lake States region (Perala 1977).

The youngest dbh distribution which could be found in the literature was for a 4 year old stand (Pollard 1971). The distribution of a 4 year old aspen stand (Figure 2)

ages.
different
of
stands
aspen
describing
parameters
Initial
Table 2.

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		dbh (cm)	
Age	Trees/ha	Ϋ́	SD
1	4010	0	0
11	1043	4.80	1.93
21	729	7.18	2.76
31	431	12.22	3.83
41	308	14.64	4.26
51	200	17.30	4.50
61	134	22.28	4.62



Figure 2. dbh distribution of a 4 year old aspen stand (Pollard 1971).

contained a greater proportion of trees in the smaller dbh classes. As the stand ages, many of the smaller trees will die due to competition for sunlight with larger overstory trees and the distribution will approach normality.

Initial information on a tree stand included dbh, number of trees within a dbh class, and tree height. The interval for the initial dbh classes is 0.25 cm. The midpoint of these intervals is designated as the initial dbh of the tree. The number of trees within a dbh class is calculated by multiplying the initial total number of trees within a stand by the probability that a tree will occur in that dbh class. This probability is computed by a function subprogram listed in Kossack and Henschke (1975) which calculates the area of an interval under a specified curve. The initial height of a tree is then computed as a function of its dbh.

Values for tree height, dbh, and number of trees within a dbh class are stored in 3 respective 120 by 7 matrices. Each column of the matrix represents a stand (the 1 year old stand in column 1 and the 61 year old stand in column 7) while each row represents a dbh class. This allows for a maximum of 120 dbh classes within a stand.

All values for the 1 year old stand are set equal to 0 since trees in this stand are not distributed to dbh classes until the fourth year of the simulation. When a stand reaches 4 years of age, the process described above

for assigning dbh and height values, and calculating the number of trees within a dbh class is used. In this case, however, the curve shown in Figure 2 is used rather than the normal curve.

In addition to these parameters, the user must specify the size of the area to be modeled, choose from 3 levels of winter severity (mild, normal, and severe) and designate various deer and habitat management plans. The method for implementing these plans will be discussed in the section titled management options.

### Forest Dynamics

There are 3 food sources available to deer in the model: aspen browse, cedar browse, and herbaceous vegetation. Neither cedar browse nor herbaceous vegetation are modeled dynamically in the program. A fixed amount of herbaceous material and cedar browse is supplied to the deer at the appropriate times of the year for each year of the simulation. This assumes that deer browsing has no effect on cedar or herbaceous production and that a fixed amount of cedar and herbaceous vegetation will be produced each year regardless of the intensity of browsing in the previous years.

Aspen growth is modeled as a dynamic process using a simplified version of a model developed by the North Central Forest Experimental Station (USDA 1979).

Growth and mortality coefficients have been developed for various pure and mixed stand forest ecosystems of the Great Lakes region. Yearly forest growth is summarized in the following equations (Leary 1979):

۸V

$$\frac{\Delta I}{\Delta t} = F_1(D, CR, SI) * NT * F_2(Y, NT)$$
where
$$\Delta Y = \text{change in the sum of tree diameters in a year}$$

$$F_1 = \text{the potential growth function}$$

$$F_2 = \text{the modifier function of potential}$$

$$\overline{D} = \text{mean dbh}$$

$$\overline{CR} = \text{mean crown ratio}$$

$$SI = \text{site index}$$

$$Y = \text{sum of the tree diameters}$$

$$NT = \text{number of trees}$$

The potential growth function is designed to estimate how rapidly the mean tree would be growing in dbh if it were not interacting with any other trees (Hahn and Leary 1979). This number is then multiplied by the number of trees in the stand to give the potential change in the sum of tree diameters in the stand. The modifier function reduces the potential change to what has been observed from permanent growth plots (Leary and Holdaway 1979). The equations used and the coefficients for aspen are listed in Appendix B, Table 10. Change in dbh for an individual tree is then calculated using what is termed the "allocation rule" (Leary et al. 1979). This rule calculates change in dbh as a function of its proportion to the total growing stock in the stand. Change in height growth is then calculated using the regression equation which relates the tree height to tree dbh. This value is then modified (Figure 3) to represent the effect of deer browsing on aspen growth. This modified change in height growth is then converted back to a modified change in dbh. If height growth is negative or, in other words, if a tree is shorter than it was the previous year, diameter growth is set equal to 0. The probability of a tree dying is then computed as a function of its diameter growth (Buchman 1979).

Since there is no distribution for a stand younger than 4 years old in the literature, stands of these ages are described in the model simply by mean height, mean dbh and total numbers of trees. Due to a lack of data on average tree heights of a young aspen stand, site index curves for the Lake States region were used to estimate this value (Lundgren and Dolid 1970). This method will most likely result in an overestimation of mean stand height. This value is then modified to show the effects of deer browsing in the same manner as an older stand. Tree mortality, however, is computed as a function of stand age and the number of trees in the stand (Perala 1973).



Figure 3. The effect of deer browsing on aspen growth.

For a stand less than 4 years old, available browse for deer is calculated simply as a function of mean stand height and total number of trees (Westell 1954). First the total biomass of aspen in a stand is computed. This value includes leaves in the spring, summer and early fall months (April to October) but only woody vegetation in the late fall and winter. The percent of the total biomass available to deer as browse in the appropriate season is then calculated as a function of mean stand height.

For an older stand, the process of computing available browse is much the same with slight modifications. The total above ground biomass of an individual tree is estimated using equations developed by Young and Carpenter (1967). Again, this includes or excludes leaves depending on the season. Available browse per tree is then computed by multiplying the percent of woody material available as browse (computed as a function of individual tree height (Westell 1954)) by the total biomass and then adding the total biomass of leaves per tree. This value is then multiplied by the number of trees of equal dbh and height to give the total available browse per dbh class. This process is repeated for each dbh class. The sum of these values equals the total aspen browse available within a stand. The equations and coefficients used for estimating browse availability are listed in Appendix B, Tables 11-12.

For both young and old stands, 2 values for browse availability are calculated. One value assumes deer will browse aspen stems and twigs to the 0.64 cm diameter as is the case under light browsing conditions, while the other assumes deer will browse to the 1.27 cm diameter. Heavy browsing to the 1.27 cm diameter usually occurs when deer populations are large and food is scarce (Westell 1954).

The model assumes that a tree greater than 3.34 meters in height will provide no woody browse to an adult buck. Trees out of reach of adult does are assumed to be those which are greater than 3.1 meters, while trees greater than 2.7 meters are assumed out of reach of fawns. However, the leaves on these trees were provided to deer under the assumption that they will fall in early autumn and become available to deer.

Prior to calculating yearly growth of aspen, the total amount of aspen consumed in each stand in the previous year is allocated to the tree height classes. Three possibilities exist when comparing the amount of aspen consumed to the amount available: 1) the browse consumed is less than the browse available to the 0.64 cm diameter; 2) all available browse is consumed; 3) the browse consumed is greater than the browse available to the 0.64 cm diameter but not all available browse is consumed. If the first possibility exists, the amount of browse consumed is proportionally
allocated to each height class. That is, if height class X makes up Y percent of the total browse available, then Y percent of the total browse consumed is allocated to height class X. If all available browse is consumed, the amount of browse consumed in each height class is set equal to the amount available.

In the case of the third possibility, the following equation illustrates how browse is allocated to each height class:

 $BC = BA6 + ((BA - BA6) \times \frac{(TBC - TB6)}{(TBA - TBA6)})$ 

where,

BC = browse consumed per height class BA = browse available per height class BA6 = browse available to the 0.64 cm diameter per height class TBC = total browse consumed TBA = total browse available TBA6 = total browse available to the .064 cm diameter

First, the proportion of browse greater than 0.64 cm in diameter that was consumed is calculated. This value is then multiplied by the amount of available browse greater than 0.64 cm in diameter in a height class to give the amount of consumed browse greater than 0.64 cm in diameter. The total amount of browse consumed in a height class is then calculated by adding the amount of available browse less than 0.64 cm in diameter to this value. This process is repeated for each height class.

#### Deer Dynamics

The major food source for deer in this model is aspen browse. In the summer and fall from June to November, herbaceous vegetation is provided to supplement the deer's diet. For 3 months during winter, no aspen browsing takes place and deer are provided with a specified quantity of cedar browse. This represents the behavioral adaptation of northern deer to gather in coniferous swamps which provide maximum thermal protection during winter months. Winter severity is represented by the quantity of cedar supplied to deer during the winter with higher amounts supplied during mild winters and smaller amounts in severe winters.

In the model, deer yarding season occurs during a 3 month period from January to March. A deer yard is assumed to provide 184 kg/ha of browse on the average (Ryel 1953). The size of the deer yard in the model is equal to one-tenth of the total aspen area. The size of the area in which a deer herd will cover is then further reduced for each month of the yarding season to represent the reduction of deer mobility due to severe winter conditions. The magnitude of this reduction is dependent on the severity of the winter. Each stand is assigned 2100 kg/ha of herbaceous material in the month of June (Stormer and Bauer 1980). This is assumed to be the total amount of herbaecous material available to deer during the summer and early fall. If there is not enough aspen available to meet a deer's monthly demand, its diet is then supplemented with herbaceous material. The amount consumed is then subtracted from the amount available and the process is repeated for each deer.

Many herbaceous species are preferred by deer over aspen (Graham et al. 1963, Stormer and Bauer 1980). However, it has been found, that a majority of the herbaceous vegetation in an aspen stand consists of bracken fern (<u>Pteridium aquilinum</u>) and grasses (<u>Gramineae</u>) which are of low preference to deer (Stormer and Bauer 1980). For this reason, the composite category of herbaceous material in the model was given lower preference than aspen.

The amount of food consumed by a deer is computed as a function of deer weight, the metabolizable energy of the food, and the metabolic rate of a deer. The following equation was used to compute the amount of forage a deer will consume (Moen 1978):

$$DWFK = \frac{(MBLM) (70 IFWK^{0.75})}{(GEFO) (PDEC) (MECO)}$$

where,

MBLM	-	metabolic rate expressed as a multiple of baseline metabolism
IFWK	=	<pre>ingesta-free weight (= .9*live weight)</pre>
GEFO	=	gross energy in forage
PDEC	=	digestible energy coefficient
MECO	=	metabolizable energy coefficient

Deer show a cyclic pattern of food consumption throughout the year due to changes in metabolic rates (Figure 4). The values for MBLM shown in this curve are the same for adult deer of different ages since metabolic rate and baseline metabolism increase by the same factor (Weight $^{0.75}$ ) as the animal grows older and gains weight. The greatest amount of food is consumed in the late summer and early fall and the lowest in the winter months (French et al. 1955, Long et al. 1965, Moen 1978). This reflects the deer's need to build up fat reserves to help survive the approaching winter and their behavioral adaptation of restricting activity and conserving energy during the winter months (Ozoga and Verme 1970). The model also incorporates a decrease in food consumption by male deer in the month of July (French et al. 1955, Long et al. 1965). A possible explanation for this is deer decrease their activity at this time due to the warm summer temperatures (Short 1969).

Female deer not bearing fawns show a pattern similar to male deer for metabolic rate with peak and minimum rates occurring at the same time of year. However, the amplitude





of this change is smaller for female deer (Moen 1978). Pregnant females, on the other hand, show a sharp increase in metabolic rate in the spring, reaching a peak in July. This is due to the increased energy requirements of a female deer during the latter third of gestation and the lactation period (Moen 1973).

Metabolic rates expressed as a multiple of baseline metabolism were calculated separately for young fawns. Examination of growth patterns of deer fed <u>ad libitum</u> indicate that young fawns do not exhibit the yearly cyclic weight gain and weight loss of adult deer (Figure 5). Rather, female fawns show a linear increase in growth during the first 3 months of life before exhibiting adult growth patterns. Male fawns show the same linear increase for the first 3 months and then show an exponential relationship between age and growth during the first winter of life. This, combined with the fact that the metabolic efficiency of a small animal is less than that of a large animal, suggests that the metabolic rate of a fawn in relation to baseline metabolism may be greater than adult deer.

This idea is supported in the literature. Robbins and Moen (1975) reported newborn fawns consumed 369.48 Kcal/ day/Wkg of digestible energy as milk. This is equal to 302.93 Kcal/day/Wkg of metabolizable energy (digestible energy x 0.82) which is 4.81 times baseline metabolism,



a value higher than any value reported for adult deer. In addition, a t-test performed on data from Holter et al. (1977) showed a significant difference (P < .05) in metabolizable energy intake (Kcal/kg<sup>0.75</sup>) during the fall months in the first and second years of a deer's life.

Average monthly metabolizable energy requirements expressed as a multiple of baseline metabolism for fawns were estimated in the following manner: For female fawns, a linear relationship was assumed, with metabolizable energy set equal to 4.81 in the first month and equal to the adult female value in the fourth month. Adult values were used when fawns reached the age of 4 months. For male fawns, a linear relationship was established between fawn age and metabolic rate using data from Holter et al. (1977). This line was used for male fawns aged 4 to 10 months. For young fawns another line was established which connected the value for a 4 month old fawn and the value 4.81 for a 1 month old fawn. Adult values for male deer were used when the deer reached 11 months of age.

The choice of stand in which feeding occurs is based upon the total amount of energy available to the deer in the stands. In each month, the model calculates the total amount of energy in each stand. These values are then compared to each other and the stand with the highest energy content is selected as the stand in which feeding will occur for that month. This assumes that deer choose

feeding areas and select foods which maximize their energy intake.

Once a stand has been chosen for feeding, it is assumed all deer will feed in that stand for the entire month. This is a simplistic assumption, as the possibility exists that after a few days of feeding another stand might have more available energy than the stand chosen at the beginning of the month. However, because the program is constructed in monthly time steps, the program is unable to deal with any switching of feeding areas which might occur in a shorter time interval.

After the feeding area has been chosen, the number of deer-days in which the area can support the deer herd is calculated by dividing the total supply of forage available by the daily demand of the deer herd. If this value is greater than the number of days in the month, it is set equal to the number of days in the month. The amount of food consumed by each deer per month is then computed by multiplying the daily demand of the individual deer by the number of days in the month.

If the number of deer days the area can support is less than the number of days in the month, this number is truncated and then multiplied by the daily demand of the deer. This value will be referred to as X. The extra fraction of a deer day is then converted to available browse. This is then compared to the daily demand of the deer. The smaller value is added to X to give the amount of food

consumed by the deer in that month. The extra available browse is then reduced and the process is then repeated for each deer in the population.

This process was used because it is assumed that all deer will meet their daily demand for at least X days. For example, if the number of deer days equalled 20.5 then all deer will feed for 20 days. On the 21st day only half the herd will meet its daily demand. Since the deer matrix is sorted first by age, only the older deer will feed on this day.

Growth of adult and yearling deer in terms of weight change is computed by the following equation:

$$\frac{\Delta W}{\Delta t} = 0.005357 (C - M)N$$

where,

۵W	= body weight change in kilograms
С	<pre>= mean metabolizable energy consumed in a month</pre>
М	<pre>= mean energy requirements for maintenance in a month</pre>
N	= the number of days in a month

The slope of this line was derived from Moen (1973). Growth of fawns was computed using the same form of the equation shown above. However, the slope was equal to 0.002349. This slope was derived from data reported in Holter et al. (1979). Estimates of mean monthly energy requirements for maintenance were derived graphically (see Figure 4). A linear relationship was assumed between maintenance requirements and time of year with peak requirements occurring during breeding and minimum requirements occurring in mid-winter. For pregnant females, peak maintenance requirements occurred during the lactation period (Moen 1973). A line was drawn which intersected the metabolic rate curve at points where deer fed <u>ad libitum</u> began to gain weight in the spring and lose weight in the fall (French et al. 1955, Magruder et al. 1957, Long et al. 1965). A second line was drawn which connected peak and minimum requirements.

There are 3 types of mortality which occur in this model: 1) starvation; 2) miscellaneous mortality; and 3) harvest. The probability of starvation is computed as a function of percent weight loss (Figure 6). Miscellaneous mortality is defined as all mortality which is not starvation or harvest mortality (road kills, poaching, disease). This rate is a constant throughout the simulation for each sex and age class. This assumed density independence, though in reality, all 3 are most likely density dependent. Deer harvest is controlled by the user and will be discussed further in the management options section.

The probability of a doe producing 0, 1 or 2 fawns is a function of age (fawn, yearling or adult) and winter weight loss (Figure 7). The nutritional condition of a doe is a



Figure 6. The probability of a deer dying as a function of percent weight loss.



Figure 7. Fawn/doe ratio as a function of female winter weight loss.

major factor affecting productivity (Cheatum and Severinghaus 1950, Whelan and Riffe 1966). Does which enter the spring in poor physical condition, due to low nutritional diets during the winter yarding season, will produce weaker fawns with a low probability of surviving past the first few days of life (Verme 1962, 1977).

The model computes the average fawn/doe ratio for specific age classes and weight loss levels, and then calculates the probability of each doe bearing 0, 1 or 2 fawns with the following functions:

f(0)	=	1 - r 0	r < 1 r <u>&gt;</u> 1
f(1)	=	r 2 - r	r < 1 r > 1
f(2)	=	r - 1 0	r <u>&gt;</u> 1 r < 1

where,

r = fawn/doe ratio (0 < r < 2)

For example, if the average fawn/doe ratio is 1.4 for a doe, then the probability of that doe bearing 1 fawn (assuming a doe will produce only 0, 1 or 2 fawns) is 2 - 1.4 = 0.6. The probability of bearing 2 fawns is 1.4 - 1 = 0.4 and the probability of not bearing fawns is 0. The total number of fawns produced is then tallied and added to the population in the month of June. This number reflects the number of fawns which survive to at least 1 month of age.

### Management Options

Management options for the user include deer harvest and tree harvest. At the beginning of the program, the user is able to assign a proportion of antlered and antlerless deer to be harvested for each year of the simulation. Antlered deer are defined as yearling and adult bucks while antlerless deer include all does plus buck fawns.

The probability of a deer in a particular category (antlered or antlerless) being harvested is set equal to the proportion assigned by the user. This assumes that all deer in a category have an equal probability of being harvested and that hunters show no preference for a particular age class within a category. This is, most likely, a simplistic assumption, as studies have indicated hunter preference and greater vulnerability in certain age classes (Maguire and Severinghaus 1954, Van Etten et al. 1965, Roseberry and Klimstra 1974). However, this relationship is extremely difficult to quantify, and disagreement exists as to which age classes are harvested at higher rates (Coe et al. 1980). Harvest mortality is calculated in November and the number of deer harvested are removed at this time.

The only silvicultural treatment allowed in this model is clearcutting. The user is able to specify the size of the clearcut in acres and the stand age when the cut is to occur. When a stand reaches this age, the number of acres

specified by the user is removed from that stand and added to the 1 year old stand. The total number of suckers per acre in the 1 year old stand is a function of the basal area of the cut stand (Graham et al. 1963).

### Computer Experiments and Sensitivity Analyses

Several computer runs were performed under various biological conditions. Due to the stochastic make-up of the model, a total of 3 runs were made for each condition. Computer experiments were performed to investigate the effects of varying antlered and antlerless harvest rates on deer populations. Clearcut intervals were also varied.

In addition, sensitivity analyses were performed on such variables as winter severity (mild, normal and severe), vegetation energy content (cedar and aspen), and maintenance energy requirements. For the sensitivity analysis of vegetation energy content, reported values of metabolizable energy of cedar and aspen were used (Ullrey et al. 1964, 1967, 1972) along with values computed as a function of the proximate composition of the species using equations derived by Mautz et al. (1974). Mean monthly maintenance energy requirements were changed by adding or subtracting a factor of 0.1 or 0.2 to the multiple of baseline metabolism. Each deviation of 0.1 from the multiple of baseline metabolism was equivalent to a change in daily maintenance energy requirements of 6.3 times the metabolic weight of the animal.

#### RESULTS

## Winter Severity

Initial conditions for these simulations included a deer population of 8.4 deer/km<sup>2</sup> consisting of 38 percent males and 62 percent females. The average age of the male segment of the population was 1.5 years of age while the average age of females was 2.42 years old. The total forest area simulated was 2.59 km<sup>2</sup> consisting totally of an aspen clearcut. No clearcuts were performed on these runs.

Peak deer densities in severe winter conditions were approximately 7 deer/km<sup>2</sup> while densities in normal conditions were twice this amount (Figure 8). Densities in mild conditions, however, were able to increase to  $40 \text{ deer/km}^2$ , an extremely rare occurrence in Michigan. All populations showed a decline and eventual die out following year 10 of the simulation. This is a result of the aspen forest growing out of reach of deer.

# Pattern Responses

The initial conditions for all the following runs (unless stated otherwise) included a deer population of



Figure 8. Simulated response of deer densities to varying winter severity.

9.39 deer/km<sup>2</sup> with average ages and proportions of males and females equal to these in the previous runs. The aspen stand consisted of 5 age classes ranging from 1 to 41 with each class comprising 20 percent of the total area. The total area simulated was 25.89 km<sup>2</sup>. Normal winter conditions were selected. In year 10 of the simulation, a clearcut was performed on the 51 year old stand. Each simulation was run for a period of 20 years.

Examination of yearly deer numbers revealed 3 distinct patterns of deer response over a 20 year period (Figures 9-11). This variability in deer response is due, not only to changes in some parameter of interest (as in the sensitivity analyses) or management plans, but also, to the stochastic nature of the model. This is reflected by the fact that some runs under identical initial conditions and management options showed different response patterns.

The pattern 1 response shows a deer population, at first, oscillating at peak densities, followed by a sharp decline in numbers due to the aspen vegetation growing out of reach of deer. This is followed by a rapid increase to peak densities after the clearcut, before a second decline takes place. The pattern 2 response showed an initial population decline of a lesser magnitude followed by a slight increase or leveling off in numbers the next year and then the eventual dying out of the population. The pattern 3 response is similar to the pattern 1 response



Figure 9. Pattern 1 response. Population decline followed by an increase to original peak densities.



Figure 10. Pattern 2 response. Population decline followed by the eventual dying out of the population.



Figure 11. Pattern 3 response. Population decline followed by a slow increase in numbers. The population is unable to reach peak densities.

except the magnitude of the decline is greater, the rate of increase in the second half of the simulation is slower, and the population is unable to restore itself to peak density.

#### Harvest Experiments

Deer numbers were examined under buck harvest intensities of 70 percent, 50 percent and no buck harvest. The 3 runs with a 70 percent buck harvest were the most variable with all 3 pattern responses displayed. All runs with a 50 percent buck harvest exhibited a pattern 1 response. Two runs exhibited a pattern 3 response while a third showed a pattern 2 response for runs in which no buck harvesting occurred.

Deer populations with buck harvests ranging from 50 to 70 percent were able to reach densities of approximately 4 more deer/km<sup>2</sup> in the first half of the simulation than unexploited populations (Figure 12, Table 3). These populations were also able to maintain a larger number of deer immediately following the decline period allowing them to increase in the second half of the simulations at a faster rate than those populations with no buck harvest.

The response of a deer population to antlerless harvest levels of 0, 25 and 50 percent (with a 70 percent antlered harvest) was also examined. Two runs in which there was a 25 percent harvest displayed a pattern 3 response



Figure 12. Simulated effects of different antlered harvest levels on deer densities (antlerless harvest equal to 0).

Table 3.	Yearly deer numbe (antlerless harve	rrs (deer/km <sup>2</sup> ) under sst equal to 0).	r varying antlered har	vest levels
Year	70	)% Harvest	50% Harvest	No Harvest
20876543210987654321 2111111110987654321		1.110.3	9.4+ 14.2 $\mp$ 0.2 13.4 $\mp$ 0.2 15.0 $\mp$ 0.4 15.0 $\mp$ 0.4 15.1 $\mp$ 0.5 14.1 $\mp$ 0.5 14.1 $\mp$ 0.5 14.1 $\mp$ 0.6 2.4 $\mp$ 0.1 2.4 $\mp$ 0.1 2.4 $\mp$ 0.6 3.9 $\mp$ 0.8 3.9 $\mp$ 0.6 3.9 $\mp$ 0.6 11.3 $\mp$ 2.1 12.7 $\mp$ 1.1 14.7 $\mp$ 0.6 4.4 $\mp$ 1.6	$\begin{array}{c} 9.44\\ 12.970.1\\ 12.970.1\\ 12.970.1\\ 12.370.1\\ 11.570.1\\ 12.370.2\\ 11.570.3\\ 11.570.3\\ 0.270.0\\ 0.370.1\\ 0.370.1\\ 0.470.2\\ 0.970.0\\ 0.710.0\\ 0.710.0\\ 0.710.0\\ 0.1\\ 1.9710.0\\ 0.1\\ 0.1\\ 0.1\\ 0.1\\ 0.1\\ 0.1\\ 0.1\\$

while the third run showed a pattern 2 response. All runs in which a 50 percent harvest occurred showed a steady decline in numbers with little variability among runs. Runs in which no antlerless harvest occurred were used previously to compare the effects of antlered harvests on deer numbers and were discussed earlier.

Under initial conditions a population with a 25 percent antlerless harvest was able to reach the same population level as a population with no antlerless harvest, although more time was needed to reach that level (Figure 13, Table 4). This is further substantiated in runs where clearcuts were performed in 5 year intervals to prevent any substantial declines in deer numbers (Figure 14). In these runs, the population with an antlerless harvest was able to consistently maintain numbers comparable to the population with no antlerless harvest, once this level was attained.

In none of the runs in which a 25 percent antlerless harvest occurred were the populations able to rebound after the decline and restore themselves to their original numbers. This occurred regardless of the antlered harvest rate (Figure 15). A series of runs were then made to see if peak densities could be reached when more time was allowed. Twenty year simulations were run with an initial population of 1.08 deer/km<sup>2</sup>. In addition, clearcuts were performed in 5 year intervals to insure that browse



Figure 13. Simulated effects of different antlerless harvest levels on deer densities (antlered harvest equal to 70 percent).

Yearly deer numbers (deer/km <sup>2</sup> ) under varying antlerless harvest levels (antlered harvest equal to 70 percent).	No Harvest 25% Harvest 50% Harvest	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Table 4. Year] (ant]	Year	219876551120987655221 2198765551212



Figure 14. Simulated effects of different antlerless harvest levels with clearcuts performed in 5 year intervals.



Figure 15. Simulated effects of different antlered harvest levels with a 25 percent antlerless harvest on deer densities.

availability would not be a limiting factor. None of the populations were able to increase to substantial numbers in the time allowed (Table 5).

# Vegetative Energy Content

Several runs were made to investigate the effects of varying metabolizable energy content for cedar and aspen browse on deer numbers. Harvest rates were set at 70 percent for antlered harvest and 0 for antlerless harvest. All runs using a value of 1.88 Kcal/g for cedar metabolizable energy content exhibited a pattern 3 response although the rate of increase in the second half varied considerably. Two runs using a value of 2.11 Kcal/g showed a pattern 1 response, although, again, the rate of increase varied in the second half of the runs. The third run showed a pattern 3 response, although the population was able to reach a peak of  $11.12 \text{ deer/km}^2$ . The runs in which the value 2.47 Kcal/g was used are the same runs that were used in the antlered harvest experiments.

At peak densities, a difference of about 0.3 Kcal/g resulted in an average difference of approximately 1 deer/km<sup>2</sup> (Figure 16, Table 6). In addition, the overall magnitude of the population decline increased as the energy content of cedar decreased, although the opposite is true when looking at the initial decrease in year 9 of

Year	Number of deer
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20	1.1 $1.2+0.2$ $1.3+0.2$ $1.2+0.4$ $1.0+0.2$ $0.9+0.2$ $0.9+0.1$ $0.8+0.1$ $0.9+0.2$ $0.9+0.2$ $0.9+0.2$ $0.9+0.2$ $0.9+0.2$ $1.2+0.0$ $1.4+0.1$ $1.3+0.1$ $1.5+0.1$ $1.5+0.1$ $1.5+0.5$ $1.8+0.4$

Table 5.	Yearly numbers (deer/km2) of a low density deer
	population subjected to a 25 percent antlerless
	harvest.



Figure 16. Simulated effects of varying metabolizable energy content of cedar browse on deer densities.

le 6. Yearly energy r	deer numbers (deer/km <sup>2</sup> ) under conditions of varying metabolizable content of cedar browse.	Metabolizable Energy (Kcal/g)2.472.111.88	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
α   ¤  -υναγονασο-1004ηδ-2000	able 6. Yearly deer numbers (deer/l energy content of cedar bro	ear 2.47	0 0 0 0 0 0 0 0 0 0 0 0 0 0

the simulation. Here, the runs with the highest energy content showed the greatest decrease. The decrease the following year, however, was slight where runs with a lesser energy content showed a second substantial drop in numbers.

The metabolizable energy content of cedar browse did not affect the rate of increase of a deer population at low densities, however (Figure 17). No change in the rate of increase was seen until year 6, when each population was approaching its peak densities.

Runs in which the aspen metabolizable content was set equal to 1.47 Kcal/g showed little variation in deer numbers up to year 17 of the simulation. The runs in which the value 1.57 Kcal/g was used were, again, the same runs used in the antlered harvest experiments.

The model showed no sensitivity to different values of aspen metabolizable energy for the first 8 years of the simulation (Figure 18, Table 7). When aspen metabolizable energy was set at 1.47 Kcal/g, the simulation showed a greater decline in deer numbers than when the value 1.57 Kcal/g was used.

## Maintenance Energy Requirements

All populations in runs where the multiple of baseline metabolism was increased by 0.2 showed a continual decline in numbers. For only 1 run, in which the multiple of baseline metabolism was increased by 0.1, was the


Figure 17. Simulated effects of varying metabolizable energy content of cedar browse on mitially low density deer populations. Clearcuts were performed in 5 year intervals.



Figure 18. Simulated effects of varying metabolizable energy content of aspen browse on deer densities.

Table 7.	Yearly deer numbers (deer/km <sup>2</sup> ) under conditions o energy content of aspen browse.	: varying metabolizable
	Metabolizable Energy	(Kcal/g)
Year	1.57	1.47
00876543210987654321	$\begin{array}{c} 9.4\\ 14.1+0.3\\ 15.2+0.5\\ 14.7+0.4\\ 14.7+0.6\\ 14.7+0.6\\ 14.7+0.6\\ 15.3+0.2\\ 3.2+0.2\\ 1.2+0.8\\ 3.12+1.7\\ 3.12+1.7\\ 1.2+10.8\\ 3.12+1.7\\ 1.2+10.8\\ 3.12+1.7\\ 1.2+10.8\\ 3.12+1.7\\ 1.2+10.8\\ 3.12+1.7\\ 1.2+10.8\\ 1.2+10.5\\ 1.2+10$	9.4 14.1+0.3 14.1+0.3 15.2+10.3 15.2+10.3 3.2+10.4 11.1+10.1 0.7+10.4 11.1+10.1 11.1+10.1 11.1+10.1 11.1+10.3 11.1+1

population able to restore itself to peak densities. When the multiple of baseline metabolism was decreased by 0.1, the deer populations were able to restore their numbers in 2 of the 3 simulations. The same situation occurred when the multiple of baseline metabolism was reduced by 0.2.

The expected results of decreasing maintenance requirements would be an increase in summer weight and a decrease in winter weight loss with the opposite expected from an increase in maintenance requirements. This would be reflected by larger deer in simulations where maintenance requirements were reduced and smaller deer where requirements were increased. Such was the case with deer showing considerably different weights for each maintenance requirement level (Table 3).

The model was quite sensitive to changes in maintenance requirements (Figure 19, Table 9). Peak densities ranged as high as 21 deer per square kilometer in populations where the multiple of baseline metabolism was decreased by 0.2 while populations showed a continual decline to 0 in runs where the multiple was increased by 0.2. A decrease of 0.1 resulted in peak densities of approximately 2 more deer per square kilometer, while an increase of 0.1 resulted in approximately 3.5 fewer deer per square kilometer at peak densities.

							Age			
Deviation	Sex	Fawn	4	2+	3+	<del>4</del> +	5+	6+	7+	8+
-2	Male	42.13	82.49	105.38	126.00	149.39	NA*	NA	NA	NA
	Female	45.19	75.01	98.67	123.20	149.43	155.90	164.28	176.28	175.98
-1	Male	35.02	74.82	90.53	104.40	122.11	NA	NA	NA	NA
	Female	38.49	65.12	80.16	95.58	107.53	120.86	131.42	135.51	143.14
0	Male	34.11	67.45	77.03	85.58	NA	NA	NA	NA	NA
	Female	36.43	55.71	62.65	70.78	69.57	88.09	98.84	105.31	107.86
<b>1</b> +	Male	33.21	61.05	70.16	103.48	NA	NA	NA	NA.	NA
	Female	34.37	47.76	54.76	NA	47.21	62.82	71.31	82.34	82.73
+2	Male	NA	53.76	55.61	57.10	60.51	NA	NA	NA	NA
	Female	32.31	NA	NA	NA	NA	NA	NA	NA	NA

Some typical simulated deer weights (kg) in year 5 of the simulation under condition of varving maintenance energy requirements. Table 8.

\*No deer available in this age class



Figure 19. Simulated effects of changes in maintenance energy requirements on deer densities. Changes are reflected by deviations of the multiple of baseline metabolism.

Table 9.	Yearly deer numt energy requireme multiple of base	oers (deer/km <sup>2</sup> ) ents. Changes eline metabolis	under conditic are reflected b m. Deviation	ns of varying y deviations o	f the
Year	-2		0	+1	+2
219876543210987654321 219876543210987654321	$\begin{array}{c} 9 & 4 \\ 14 & 64 & 64 \\ 17 & 97 & 64 & 64 \\ 19 & 17 & 97 & 64 & 64 \\ 10 & 17 & 07 & 0.6 & 64 \\ 20 & 37 & 0.7 & 0.7 & 0.7 \\ 20 & 37 & 0.7 & 0.7 & 0.7 \\ 10 & 37 & 0.7 & 0.7 & 0.7 \\ 10 & 87 & 1.7 & 0.7 & 0.7 \\ 10 & 87 & 1.7 & 0.7 & 0.7 \\ 10 & 87 & 1.7 & 0.7 & 0.7 \\ 10 & 87 & 1.7 & 0.7 & 0.7 \\ 11 & 10 & 10 & 0.7 & 0.7 \\ 11 & 10 & 10 & 0.7 & 0.7 \\ 12 & 10 & 10 & 0.7 & $	9.4 15.970.3 15.970.3 15.970.3 16.670.6 16.770.3 16.770.3 16.770.3 16.770.3 16.770.3 16.770.3 16.770.3 16.770.3 16.770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.3770.3 10.27700.3 10.2770.3 10.2770.3 10.2	9 146 157 157 157 157 157 157 157 157 157 157	9.4 13.240 13.240 13.070 13.070 13.070 11.171 11.17	9.4 7.7+0.5 0.0700.0 0700.0 0700.0 0700.0 0700.0 0700.0 0700.0 0700.0 0700.0 0700.0 0 00 00 00 00 00 00 00 00 00 00 00

The population decline period also differed as maintenance requirements were changed. The population decline appeared 1 year earlier in runs where the multiple of baseline metabolism was decreased by 0.2 as compared to unaltered runs. Deer numbers in all of these runs showed significant declines over a 3 year period with the extent of the second and third declines dependent on the magnitude of the preceding decline. The reverse occurred in runs where the multiple of baseline metabolism was increased by 0.1. Here, the population decline appeared 1 year later than runs where the maintenance requirements were not altered. A decrease of 0.1 resulted in a population decline the same year as runs where maintenance requirements were not altered, however the magnitude of the decline was greater.

### DISCUSSION

### Winter Severity

The importance of winter severity to deer numbers in the model is reflected by deer densities ranging from 7 deer/km<sup>2</sup> in severe conditions to 40 deer/km<sup>2</sup> in mild conditions. This would indicate that winter severity is a major factor in controlling deer numbers under conditions of abundant summer food supply, although other factors such as social stress cannot be discounted.

It was also shown that a young 2.59 km<sup>2</sup> aspen stand can support a substantial deer population for a period of 10 years. This conflicts with claims that deer densities in excess of 17.5 deer per square kilometer will cause extensive damage to an aspen stand (Graham et al. 1963). However, Graham simply compared deer census data and the degree of damage to an aspen sucker stand. He did not consider the size of the stand or the concentration of deer within the aspen stand. Therefore, the density of deer feeding in the young aspen stand examined by Graham may have greatly exceeded 17.5 deer per square kilometer.

Another explanation for this conflict is that estimates of aspen browse may have been too high. However, since

other deer foods such as grasses and forbs were not allocated to deer in this model until aspen browse had been consumed, it is unlikely that the influence of deer on aspen was underemphasized.

### Pattern Responses

There are 4 main factors that determine which pattern a deer population will follow: 1) the number and biomass of deer in the year preceding the population decline; 2) the amount of browse available in the year preceding the population decline; 3) the proportion of female fawns in the fawn crop of the year preceding the population decline; and 4) the proportion of females in the population in the year preceding the population decline.

The magnitude of the population decline depended, largely, on the degree in which the population demand exceeded the amount of available browse in the years of scarce food supply. Populations in which the demand greatly exceeded the supply showed a large initial decline. Because of this, however, the ratio of demand/supply was quite small the following years and no further significant losses were seen. Populations in which the demand exceeded the supply to a lesser degree showed a smaller decline. In most cases the demand/supply ratio would still be large the following year and a second and sometimes third substantial decline in numbers would result. In some cases, however, the decline was large enough to allow a leveling off or increase in number the following year. This resulted in a large third year demand/supply ratio and a subsequent catastrophic decline in numbers. In populations that showed this response, the percent of females in the population and the percent of female fawns in the fawn crop were higher in the year preceding the decline than in the previous case. As a result, more does were able to survive and reproduce during the initial decline creating a fawn crop that was large enough to increase or level off the population the following year.

The rate at which the population recovered from the decline was dependent mainly on the magnitude of the decline. Populations which declined to smaller numbers generally took longer or were unable to reach peak densities than populations which showed a lesser decline. However, populations which declined to similar numbers also showed different rates of increase. Here, populations with a larger percent of females in the population in the year preceding the crash showed the greatest rate of increase following the clearcut. The reason for this was that, even though total numbers were similar, more females were able to survive and produce larger fawn crops.

### Harvest Experiments

Populations with a 50 percent or 70 percent buck harvest were able to maintain higher peak densities than

unexploited populations because less winter mortality occurred in these populations, particularly in the female segment. The harvest of a large number of bucks meant less competition for females for what little winter food was available. Thus, they were able to consume a larger proportion of their demand. This is important since the loss of a doe represents not only the loss of 1 deer, but also the loss of fawns she would potentially bear in future years. Also, the does that do survive the winter are in better physical condition than does in an unexploited population and a higher fawn/doe ratio will result (Verme 1969).

Unexploited populations were also unable to restore their numbers following the population decline. Although initial declines were smaller than exploited populations due to smaller demand/supply ratios, all populations showed extremely low numbers in the year preceding the clearcut.

The high degree of variation in runs where a 70 percent harvest occurred was due to a combination of factors. The population with the smallest demand/supply ratio also had the largest percent of female fawns and total females in the year preceding the population decline. Thus a small decline occurred the first year with many females surviving. This led to a large fawn crop and an increase in numbers the following year and then a catastrophic decline in numbers the year after. Conversely, the

population with the highest demand/supply ratio had the smallest percent of female fawns and total females in the year preceding the decline. This led to a large initial decline which nearly decimated the female segment of the population and the population was unable to recover from this. The third population was an intermediate between the two and showed a pattern 1 response.

The percent of females and female fawns in the year preceding the decline was the main factor causing a pattern 2 response in 1 population where no harvesting occurred. Demand/supply ratios were similar for all 3 populations. However, the percent of females in the population was much higher (50.0% compared to 43.4% and 41.0%) as was the percent of female fawns (62.4% compared to 42.6% and 50.6%) in the population which showed the pattern 2 response.

There was less variation in pattern responses in populations where an antlerless harvest occurred. The population that displayed a pattern 2 response showed the same characteristics as the population that displayed a pattern 2 response when no antlerless harvest took place. These were a lower demand/supply ratio, and higher percentages of females and female fawns in the year preceding the population decline.

A great deal of controversy exists concerning the feasibility of an antlerless deer harvest and its effects on deer numbers. The modeled populations exhibited

different responses to a 25 percent antlerless harvest, depending on the conditions in which they existed. At peak densities, the population showed little response to the antlerless harvest, except for smaller year to year fluctuations in numbers. Moderate density populations were able to withstand this harvesting pressure and increase to peak densities, although at a noticeably slower rate. None of the populations were able to increase after the population decline, however.

Unlike populations with no antlerless harvest, this inability to increase was not due to high starvation losses or an insufficient number of remaining females following the decline period. Populations with no antlerless harvest which declined to comparable numbers were able to restore themselves to peak densities. Rather, it was the antlerless harvest rate which was preventing the populations from increasing to substantial numbers in a reasonable amount of time. In these populations, there were not enough does left after the harvest to allow for a substantial fawn crop the following year. The result was an extremely low rate of increase. Thus the model indicates that the response potential of the population should be a major consideration when evaluating the desirability of an antlerless harvest.

### Vegetative Energy Content

The variation in the magnitude of the decline, in runs where smaller energy values were used, appeared to be related mainly to the demand/supply ratio. However, since substantial declines in these runs appeared over a 2 year period, browse availability at both high and low extremes in the year preceding the population decline caused the same results, namely a greater overall decline in numbers. The demand/supply ratio is low when a large quantity of browse is available causing a relatively small decline in the first year. This creates a high ratio the following year and a major decline results. The converse occurs when browse availability is low with a major decline the first year and a smaller decline in the following year. Intermediate amounts of browse resulted in smaller overall declines. This suggests that under these conditions some optimum demand/supply ratio exists which will minimize deer losses during the period of population decline.

As the metabolizable energy content of cedar browse decreased, the amount of available aspen in year 8 of the simulation increased. There are 2 reasons for this. One reason is there were fewer deer in runs with lower energy values, but more significant was the fact that deer in these populations weighed less than deer in populations with higher energy values. This was due to the greater weight loss of deer in the winter months. These 2 factors

led to a smaller demand for aspen browse and subsequently, less was consumed.

Therefore, with a smaller demand and a greater supply of aspen these runs showed a smaller initial decline. Because of this, however, the demand of the herd the following year greatly exceeded the supply and a second substantial decrease occurred. In summary, the magnitude of the population decline was greatest when low cedar metabolizable energy values were used and smallest when using high energy values. However, this decline was extended over a 2 year period.

Another interesting result of these sensitivity analyses was the fact that the model showed no sensitivity to changes in aspen metabolizable energy content during the first 8 years of the simulation. This same lack of sensitivity to changes in cedar metabolizable energy content was exhibited by low density populations. In both of these cases, the browse supply was abundant in relation to the demand during this period. This indicates that the metabolizable energy content of browse is an important factor in influencing deer numbers only in times when the browse supply is limiting and has little, if any, influence when browse is more abundant.

## Maintenance Energy Requirements

As was the case when metabolizable energy contents of browse were altered, the variation in pattern responses

and magnitudes of decline appeared to be related primarily to the demand/supply ratio. In conditions where the decline was extended over a period of years, intermediate amounts of browse resulted in the smallest overall decline. In conditions where 1 major decline in numbers occurred, a positive relationship was seen between the demand/ supply ratio and the magnitude of the population decline.

Changes in maintenance requirements of deer affected the deer population in a manner similar to changes in energy values of browse, but to a much greater degree. The immediate effect was a change in deer weights. This increased or decreased the probability of a deer starving during the winter months with the result being considerable changes in peak densities of populations.

These weight changes and changes in peak densities also had a considerable effect on the decline period. Browse shortages occurred 1 year early when the multiple of baseline metabolism was decreased by 0.2 as a result of the excessive demand of a high number of extremely large deer. This caused a decline which continued over a 3 year period. Conversely, when the multiple of baseline metabolism was increased by 0.1, browse shortages did not occur until 1 or 2 years later than runs where maintenance requirements were not altered. Here, peak densities were lower and deer were smaller, resulting in a lower demand, and subsequently less consumption by the herd. The browse

shortage in runs where the multiple of baseline metabolism was decreased by 0.1 was not drastic enough to bring about an early population decline. However the magnitude of the decline was greater than runs where maintenance requirements were unaltered. Thus, changes in maintenance requirements had a considerable effect on peak density levels and the pattern, magnitude and timing of the population decline.

### Clearcuts

The frequency of clearcuts had a definite influence on the simulated deer populations. All but 2 populations in which clearcuts were performed on 10 year intervals showed an immediate increase the year following the clearcut. Populations which did not show an increase existed in conditions which were too harsh for a population to maintain itself, regardless of any habitat manipulation schedule. The response of the populations which showed an increase can be compared to Figure 8 where no clearcutting occurred and the populations died out in the fourteenth or fifteenth year. Additionally, populations, in runs where clearcuts were performed on 5 year intervals, continued to increase or maintain peak densities and showed no significant declines in numbers. Intervals of 5 to 10 years have been prescribed for aspen clearcuts when managing for white-tailed deer (Perala 1977). The model indicates

that this rate of manipulation should be followed, as longer intervals would result in an abrupt decline in deer numbers.

## Further Research

One school of thought views the objective of computer modeling as part of the accumulation of knowledge of the system under study (Hayne 1969). In this respect, an important aspect of modeling exercises such as these is to point out areas which are ill defined and require more investigation. As Hayne (1969) stated, "a successful model dictates the kind of data required in the future."

One such area which should be more precisely defined is the question of energy requirements of wild deer. Considerable research has been carried out in this area (Silver et al. 1969, Ullrey et al. 1970, Thompson et al. 1973, Moen 1973, 1978). However, results were often contradictory and lacked the precision which the model needed to accurately predict deer numbers

There is little information in the literature regarding deer growth as a function of energy consumption, particularly among adult deer. This is very important, as the most important factor affecting the amount of browse consumed is deer weight. This can be seen in Moen's (1978) equation for estimating browse consumption. Therefore a better understanding of the rate of increase of deer weight as a function of energy consumption will lead to better long range prediction of deer weights and ultimately, deer demands. More importantly, however, a better understanding of the rate at which a deer loses weight as a function of energy consumption will lead to better predictions of losses due to malnutrition in times of low food supplies.

The incorporation of other nutrients may be necessary, however, to develop better growth rate estimates. Although energy is considered the most critical factor in deer nutrition, other requirements, such as proteins and minerals, must also be met. It has been suggested that low protein contents in foods may account for low productivity and suboptimal growth (Murphy and Coates 1966). Holter et al. (1977) was unable to find a close correlation between body weight gain and energy deposition. In a further study (Holter et al. 1979), the use of multiple stepwise regression techniques showed growth to be a function of energy intake (digestible or metabolizable) and digestible nitrogen intake. Verme and Ozoga (1980) concluded that a protein rich diet was not vital, whereas small energy deficiencies could be detrimental. However when energy was not limited, the protein level became important for optimal development.

The model was also sensitive to small changes in the metabolizable energy content of both cedar and aspen

browse, particularly during the period of the population decline. One reason the results of different studies varied was that different parts of the plant were used. Some studies used only the tips of branches while others included more woody vegetation. A stratified sampling design could provide more precise estimates of the metabolizable energy content of aspen and cedar browse.

The conflict between the claims of Graham et al. (1963) and the results of the model raises questions about the accuracy of deer browse estimates in young aspen stands. Also, scant information exists concerning aspen growth response to deer browsing. High estimates of aspen response could be a factor contributing to this conflict. Further research is needed in both of these areas to help answer these questions.

One of the major assumptions of this model is that deer will feed in areas where the most energy is available. However, a study using tame deer showed that deer used a mature aspen forest and a clearcut equally in the month of June (Stormer and Bauer 1980). One could conclude from that that both stands had equal or adequate amounts of available energy or that other factors play a major role in selecting a feeding area. In either case, more information on deer behavior and their choice of feeding areas could have a significant impact on models such as these. A major limitation of this model is its lack of consideration of spatial distributions. This assumes that the energy cost of moving from 1 place to enother is negligible. Other models have shown, however, that the area a deer can forage in a day is quite critical in determining deer densities (Cooperrider 1974). Moen (1978) found that walking is one of the more costly activities for deer. This suggests that the consideration of spatial patterns could have a significant effect on these types of models. Before this can be realistically incorporated into a model, however, more research is needed regarding the energy costs of different activities and the behavior of wild free-ranging deer.

### Precautions

Some precautions should be taken when applying this model to specific situations. Although the model has been described as a generalized model for the Lake States region, not all aspen forest will behave as this model does. The site index for the model is set at 70 and the model does not allow for changes in soil characteristics, water levels or any other environmental factors which affect aspen growth. Therefore, one should be sure that stand characteristics are similar to those in the model.

Another characteristic of the model which one should take into account is that deer habitat is evaluated solely

on the basis of browse availability. Thus, the model would indicate that areas with greater proportions of clearcuts would support greater deer densities and that an optimum deer habitat would be one that is totally clearcut. In reality; however, optimum deer habitat requires a mix of clearings and forested areas which are used for hiding, thermal protection and fawning (Thomas et al. 1979). Studies in Michigan have shown that areas in which 25 percent was clearcut received greater overall use by deer than areas with more extensive treatments (Bennett et al. In addition, the size of a cleared area has a sig-1980). nificant bearing on its usage by deer. Studies have shown that the greatest amount of use by deer occurred in areas within 183 m of an edge (Reynolds 1962, 1966). Any use beyond this point was insignificant.

The feeding habits of white-tailed deer have been greatly simplified in this model. At times when aspen browse was abundant, the diet of the simulated deer population would consist of 100 percent aspen browse. However, diversity is a very important aspect of a deer's diet (Rogers et al. 1981). Deer will prosper more with a variety of plants in their diet than with a diet of 1 preferred food (Dahlberg and Guettinger 1956, Halls 1978). In reality, a deer will maintain some degree of diversity in their diet, even when a preferred food is abundant.

The assumption that aspen is a preferred food throughout the non-yarding period also leads to an overemphasis of the importance of aspen in deer diets. In the spring, fresh green grasses and forbs are the most important deer foods while grasses, acorns (if available), asters, fruits and mushrooms equal or exceed aspen in importance during the fall months (McCaffery et al. 1974, Rogers et al. 1981). The primary effect of this simplification of deer food habits on the model is a high degree of sensitivity of deer numbers to aspen browse availability. This is reflected by the large variability seen among simulations where the initial conditions were identical.

The user should also be aware of the effect of short rotation intervals on aspen productivity. Harvest intervals of less than 10 years have been shown to have a deleterious effect on the ability of an aspen stand to sustain its production level (Berry and Stiell 1978). Since the model does not account for this, long range simulation, using intervals of less than 10 years, would result in overestimations of aspen browse availability in the latter years of the simulation.

In the model, there is an indirect relationship between tree height and stand density. Height is calculated as a function of dbh, which is affected by the density of trees in a stand. In nature, however, height appears to be related mainly to site index. Stand density has little

effect on tree height (Sorensen 1968). Therefore this relationship is 1 source of error in estimating the amount of aspen available to deer since browse availability is affected mainly by tree height.

Since the model does not consider spatial distributions it is unable to allow for the juxtaposition of clearcuts. This is a very important consideration, however, when managing for white-tailed deer. One must insure that all vegetation or habitat types are provided by juxtaposing clearcuts so that longer rotation periods are used, but new forage areas are created every 5 to 10 years. In this way, one can provide optimum deer habitat and sustain high aspen productivity.

These limitations and simplified assumptions must all be taken into account when evaluating the results of the model. Therefore, the user must possess sufficient knowledge to supply his/her own expertise in areas which the model is unable to address in order to devise a viable management plan.

# Validation

The subject of model validation has long been a problem area in system analysis and a subject of controversy which remains unresolved to this date (Naylor and Finger 1967, Van Horn 1971, Goodall 1972). Some argue that the validity of a model is determined by its purpose (Caswell 1976, VanKeulen 1976). That is, several models of a system may exist and all may be valid, but aiming at different goals.

This problem is further compounded, in this case, by the scarcity of sufficient deer data. Accurate censusing of large deer herds continues to be a difficult problem of deer research and management. Because of this, it may be of greater use to consider relative numbers of deer under different management conditions, rather than actual numbers, when evaluating model results.

Shannon (1975) stated, "by far the most important test for the validity of our model and the results obtained should be the answer to the question, 'Does the model make sense?'" In this case, the question is, 'Are there sound biological explanations for what is happening in the model?' Using this criterion and considering the purpose of the model and the current state of knowledge of deeraspen interactions, the model appears valid.

One should always keep in mind, however, the simplified assumptions and the limitations of the model and regard results tenatively until more data are gathered and a further understanding of deer and aspen ecology is developed. As more information becomes available, additional complexity can be incorporated into future simulation models of this type which will make them more realistic and add to their validity.

#### CONCLUSIONS

At this time, the primary benefit of computer models such as these is to synthesize existing information and point out gaps where existing knowledge of the ecosystem under study is lacking. This type of information is of great assistance to researchers in setting priorities and directions for future research. Currently, however, the limitations of existing data place severe restrictions on the use of models of this type in developing long range deer management policies. However, there remains great potential in this tool and modeling efforts should be continued.

The greatest practical use of this model in its current state is as a teaching aid. Although the accuracy of the estimations of peak densities and the magnitude of the population responses is questionable, the trends which the model exhibits appear realistic. Thus, the user will be able to see immediately the beneficial or detrimental effects of his/her management decisions. After repeated trials, the user then can develop an understanding of the effects of manipulating these options and devise a management plan which will meet previously specified management objectives.

APPENDIX A



Figure 20. The main program.



Figure 21. Subroutine ADVANC. Advances tree data to next age class.



Figure 22. Subroutine AGESEX. Initializes deer matrix.



Figure 23. Subroutine BROWSE. Computes amount of aspen consumed by individual deer per month. Allocates browse consumed to height classes.



Figure 24. Subroutine CHOOSE. Computes amount of aspen browse available in each stand and chooses feeding area.



Figure 25. Subroutine DIST. Initializes tree data for a 4 year old stand.



Figure 26. Subroutine FEED. Calculates individual deer demand, deer growth and probability of starvation.



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Figure 27. Subroutine MORTAL. Calculates miscellaneous and harvest mortality.


Figure 28. Subroutine NATAL. Calculate fawns per doe and adds fawns to the population.



Figure 29. Subroutine NORM. Initializes tree matrices.



Figure 30. Subroutine PRINT. Prints relevant deer data.



Figure 31. Subroutine SUM. Calculates monthly deer herd demand for aspen and cedar.



Figure 32. Subroutine TALLY. Tallies number of deer, harvest mortality, and starvation mortality per age/sex class. Removes dead deer from the population.



Figure 33. Subroutine TRECUT. Removes clearcut and adds area to 1 year old stand.

Figure 34. Subroutine TREGRO. Computes percent browse consumed in each height class. Calculates yearly tree growth. Prints relevant tree stand data.



Figure 34.



Figure 35. Subroutine YARD. Computes amount of cedar browse consumed by individual deer per month.

APPENDIX B

Table 10.	Some equations and coefficients used	in aspen	growth su	lbprogram	(USDA 19	. (6/
			CO	efficient		
Function	Equation	b <sub>1</sub>	b2	p <sup>3</sup>	₽¢	<sup>b</sup> 5
Potential growth	$\frac{\Delta \overline{D}}{\Delta t} = b_1 + b_2 * \overline{D}^{b3} + b_4 * SI * CR * \overline{D}$	.11789	00015	2.3618	.000042	I
Crown ratio	$CR = b_1 * AGE + (b_2 / (1 + b_3 / \overline{D} * BA))$	0070	4.298	.0230	ı	I
Modifier	$F = 1 - \exp(b_1(1 - \exp(b_2 + \overline{D})) / BA)$	-117	1366	ı	ı	ı
Mortality	$R = (1 + \exp(b_1 + b_2 * DGR^{b_3} + b_4 * \overline{D}))^{-1} + b_5$	0786	213.630	1.7126	.25812	.02276

BA = Basal area
F = Fraction of potential growth
R = Probability of a tree dying
DGR = Diameter growth rate

Table 11.	Equation and coefficients able as browse.	s used to estimate the propo	rtion of aspen avail-
		Coeff	icients**
Season	Diameter	τ	Ą
	1.27 cm	1.6465	0.2089
WINTEr	0.64 cm	1.3202	0.2022
c	1.27	1.4303	0.1393
Sumer	0.64 сш	1.4625	0.1984
*A the foi	rm of the equation is y	y = a + bH	
	where F	y = proportion of aspen avail H = mean height of stand (if H = height of individual tree	able as browse stand age < 4 years) e (if stand age <u>&gt;</u> 4 years
**The equation (1954).	ations were derived by leas	st squares curve fitting usi	ng datafrom Westell

Table 12.	Equations and coefficients used in es aspen sucker stand less than 4 years	stimating total old.	l biomass (kg) f	or an
			Coefficients	
Y	Equation	ល	þ	υ
Height	$\overline{H} = EXP(ln(\overline{dbh}) + a)/b)*$	4.1803	1.5919	I
Biomass (winter)	B = EXP(a+b*ln(H))*NT/1000*c**	4.7113	1.348	0.8
Biomass (summer)	$B = EXP(a + b*ln(\overline{H}))*NT/1000*c**$	5.1571	1.3709	0.8
*Derived **Derived	by least squares curve fitting using o by least squares curve fitting using o	data from Robir data from Weste	nove and Horton ell (1954).	(1929).
HmeanBBiomNTNumbé	height of the stand ass (kg) er of trees/ha			

Table 13.	Equation and coefficients used in est stand greater than 4 years old.	cimating total biomass (kg) fo	r an aspen
		Coefficients	
Y	Equation	5	Ą
Height	H = EXP(ln(dbh) + a)/b)*	4.1803	1.5919
Biomass of Leaves**	L = EXP(a*1n(H) - b)/1000***	2.328	0.228
Branch Biomass	B = EXP(a*1n(H) - b)/1000***	3.130	2.613
Stem Biomass	S = EXP(a*1n(H) - b)/1000***	3.364	1.482
*Derive **Leaf b:	1 by least squares curve fitting using lomass set equal to 0 in winter	data from Robinove and Horton	(1929).

\*\*\*Young and Carpenter (1967).

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