A STOCHASTIC MODEL OF THE ISLE ROYALE BIOME*

W. A. BEYER, D. R. HARRIS, AND R. J. RYAN

ABSTRACT. A stochastic model employing an event-consequence technique is developed for a three-species interaction. If the system is in some state \mathbf{x}^1 at time t, the elapsed time to the next event is chosen by means of a Poisson distribution $\exp\left[-\tau \sum_{\mathbf{x}^2} g(\mathbf{x}^1, \mathbf{x}^2, t)\right]$. The type of event (birth, death, predation, etc.) is then chosen from the distribution: $g(\mathbf{x}^1, \mathbf{x}^2, t)/\sum_{\mathbf{x}^2} g(\mathbf{x}^1, \mathbf{x}^2, t)$ where g is some non-negative function. Thus the classical system of differential equations is replaced by a set of transition probabilities $P_{t,t+\delta t}(\mathbf{x}^1 \to \mathbf{x}^2) = g(\mathbf{x}^1, \mathbf{x}^2, t)\delta t + o(\delta t)$. The set of states and transition probabilities incorporates the age structure of the three species (17 for the moose, 9 for the wolf, 1 for the plant). This discrete space-continuous time model is applied to the data from the Isle Royale National Park studies of Allen, Mech, etc. An estimate of the predictive ability of this simulation is made after considering the statistical uncertainty of the model and the model's goodness of fit.

A code, called BIOTA1, exists in Fortran, which will process a general *n*-species stochastic model.

1. Introduction. The purpose is to develop a Monte Carlo simulation of population interactions in a biome to provide a close fit to existing real data, as well as provide a rational basis for quantitative predictions.

Hopefully with the development of better simulations the effects of human decision and reactions on the biome can be made more beneficial.

A realistic model leads to a better understanding and hence assessment of methods of chemical and biological manipulation of a biome.

A simulation of a 3-species interaction of the type where X preys on Y which feeds on Z with on further interaction is described. There are a total of 27 age groups. The introduction of further species into the simulation is possible. Perhaps, the introduction of additional parameters and species would be desirable. In the present paper as with the Dixon-Cornwell paper [4] the application is the 3-species system of Isle Royale, where moose are the only large herbivore, wolves the only large predator and birch, aspen, aquatic plants, etc., comprise the third category (plants).

The model developed in this paper is used to simulate the 3-species

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system over a 15 year period of time, providing a moderately long range predictive capability.

A code, called $\hat{B}IOTA1$, written in Fortran, exists which processes the general *n*-species stochastic model.

2. Literature Review. Volterra [21] developed a deterministic model based upon a system of coupled nonlinear differential equations

(1)
$$\frac{dx_i}{dt} = f_i(x_1, \cdots, x_n, t) \quad i = 1, \cdots, n, t > 0,$$

with the values $x_i(0)$ given.

Feller [7] later developed a stochastic model of population interactions via probability generating functions satisfying a linear partial differential equation. Analytic solution of the forward stochastic equation provided a relatively complete description of one or two species, one age group per species and one or two offspring per litter. This approach becomes intractable with the addition of complexities. Numerical solutions for the forward stochastic equation with population interaction are untried. The forward stochastic equation can be transformed to its moment equation form when moments exist. Without population interaction the moment equations for first moments are identical with the deterministic system. With population interactions the moment equations are in principle insoluble since each equation for a given moment involves higher moments. Approximations are available which ignore third and higher order moments, thus adding the problem of adequacy of the approximation to the already sufficient problems of analytic and numerical solution.

Engstrom-Heg [6] has described a model for population interactions which amounts to a time-difference numerical solution of the deterministic equations but with random coefficients to represent the effect of climatic fluctuations. This system also succumbs to the same problems of analytic and numerical solution as arose with the Volterra deterministic case. This time-difference schema does not include the other random effects contained in the forward stochastic equation or its moment equation representation.

Leslie and Gower [14] have described a computer technique in which time is advanced by steps, and with each step populations are altered randomly according to selected rules, one of which involves normality. In this technique both the choice of time step and the normality assumption provide problems.

Dixon and Cornwell [4] have provided a set of difference equations, one for the predator population and the second for the prey population. Various components are included; namely, reproduction, mortality due to predation, natural mortality, and immigration. The Dixon-Cornwell model utilizes the concept of limited attack rate and competition between predators as advanced by Watt [22]. Their particular model for the Isle Royale system consists of the following:

$$N_0(t + 1) = N_0(t) + bN_0(t) - N_a(t)$$

$$P(t + 1) = P(t) + P_b(t) - dP(t)$$

where

 $N_0(t) =$ prey population at time t,

b = prey birth rate,

$$\begin{split} N_a(t) &= P(t) K_1 [1 - e^{-a N_0(t)^2 P(t)^{1-c}}] \\ &= \text{limited attack and competition rate,} \end{split}$$

P(t) = predator population at time t,

d = death rate of predators,

 $P_b(t)$ = threshold birth response

$$= P(t)K_{2}[1 - e^{-fN_{0}(t)^{2}P(t)^{1-\sigma}}],$$

where a, c, f, g, K_1 , and K_2 are certain constants.

This approach fails to incorporate random fluctuations. In this respect it is subject to the same criticism as is Engstrom-Heg. Also as Dixon-Cornwell point out, "... inputs into the system in the form of changes in the prey food supply would cause fluctuations...". The plant life of Isle Royale plays an integral part in the wolf-moose cycle. Although it is possible in a deterministic system, no accounting of different age groups within species was made.

Bartlett's approach [2] is to enhance the value of the deterministic model of population dynamics within a more comprehensive stochastic model.

In separate papers both Bailey [1] and Kendall [12] provide discussions of the stochastic processes involved in population dynamics.

For an interesting discussion of the meaning of the term "model" in the physical and biological sciences, see Suppes [20].

Volterra's system (1) becomes increasingly difficult to solve as n becomes large and the nonlinear functions f_i become more complex. Numerical solutions via difference techniques encounter problems of instability and an inability to measure the degree of inaccuracy.

To facilitate ease of solvability in the deterministic model, the nonlinear functions f_i normally do not incorporate age structure or reproductive and predator abilities of the animals. 3. Stochastic Model. In a stochastic model of population interactions, the Volterra system (1) is replaced by a set of transition probabilities for each pair of state vectors $\mathbf{x}^1 = (x_1^1, x_2^1, \dots, x_n^1)$ and $\mathbf{x}^2 = (x_2^2, x_2^2, \dots, x_n^2)$. These transition probabilities denote the probability of transition from state \mathbf{x}^1 to state \mathbf{x}^2 in the time interval t to $t + \delta t$:

(2)
$$P_{t,t+\delta t} \{ \mathbf{x}^1 \to \mathbf{x}^2 \} = g(\mathbf{x}^1 \to \mathbf{x}^2; t) \delta t + \mathbf{o}(\delta t).$$

Consider the special case that $g(\mathbf{x}^1 \rightarrow \mathbf{x}^2; t) = 0$ unless \mathbf{x}^2 differs from \mathbf{x}^1 by 1 unit in the *i*th coordinate. Put

$$\begin{aligned} P_{t,t+\delta t}[(x_1\cdots x_n) &\to (x_1, \cdots, x_{i-1}, x_i \pm 1, x_{i+1}, \cdots, x_n)] \\ &= g_i^{(\pm)}(x_1, \cdots, x_n; t)\delta t + o(\delta t). \end{aligned}$$

The stochastic model (2) is sometimes said to be analogous to the deterministic model (1) if

(3)
$$g_i^+ - g_i^- = f_{i'}$$

However, (3) does not define the g_i^{\pm} uniquely in terms of the f_i 's.

Suppose in (2) that g does not depend on t. Put $\tau = n\delta t$. Then the probability that the first transition $\mathbf{x}^1 \rightarrow \mathbf{x}^2$ after t takes place after $t + \tau$ is given by

$$1 - P_{t,t+\tau} \{ \mathbf{x}^1 \to \mathbf{x}^2 \}$$

= $[1 - g(\mathbf{x}^1 \to \mathbf{x}^2) \delta t + o(\delta t)]^n$
= $\left[1 - g(\mathbf{x}^1 \to \mathbf{x}^2) \frac{\tau}{n} + o\left(\frac{\tau}{n}\right) \right]^n$.

If $\delta t \to 0$, then $n \to \infty$ and

$$1 - P_{t,t+\tau}(\mathbf{x}^1 \longrightarrow \mathbf{x}^2) \longrightarrow e^{-g(\mathbf{x}^1 \rightarrow \mathbf{x}^2)\tau},$$

which is a Poisson distribution. See Feller [8, page 158].

Suppose a set of possible events is given with transition probabilities described in (2). Suppose the system is in state \mathbf{x}^1 at time t. The probability that no transition takes place in t to $t + \tau$ is given by $\exp\left[-\tau \sum_{\mathbf{x}^2} g(\mathbf{x}^1 \to \mathbf{x}^2)\right]$. In our program, the time of the first transition after t is determined from this distribution. Having determined the time of the first transition, one then determines \mathbf{x}^2 from the distribution

$$h(\mathbf{x}^2) = g(\mathbf{x}^1 \rightarrow \mathbf{x}^2) / \sum_{\mathbf{x}^2} g(\mathbf{x}^1 \rightarrow \mathbf{x}^2).$$

In an experimental situation the value of $g(\mathbf{x}^1 \rightarrow \mathbf{x}^2)$ can be determined by noting that the expected waiting time is $1/g(\mathbf{x}^1 \rightarrow \mathbf{x}^2)$, given that the system is in \mathbf{x}^1 and that the next event is $\mathbf{x}^1 \rightarrow \mathbf{x}^2$.

4. The Monte Carlo Method. The (analog) Monte Carlo method as applied to random walk problems, of which our Isle Royale model is an example, consists in generating realizations of the walk on a computer equipped with a random number generator.

Let Ω be the set of all random walks of a certain given type which are terminated after a definite period of time, say T. Let ξ be a real valued function defined on Ω . Define the distribution of ξ by

$$F(t) = P[\xi(\omega) \leq t]$$

where P is the probability function induced by the random walk model. Define the mean and variance of ξ by

$$m = E(\xi) = \int_{-\infty}^{\infty} t dF(t)$$

and

$$\sigma^2 = E[(\xi - m)^2] = \int_{-\infty}^{\infty} (t - m)^2 dF(t).$$

The central limit theorem (see Spanier and Gelbard [19, page 14]) then asserts that if ξ_1, ξ_2, \cdots is a sequence of independent and identically distributed random variables with common mean, m, and standard deviation, σ , then the average

$$\overline{\xi}_N = \frac{1}{N} \sum_{i=1}^N \xi_i$$

is asymptotically normal; i.e.,

$$\lim_{N\to\infty} P \left\{ \frac{\overline{\xi}_N - m}{\sigma/\sqrt{N}} \leq x \right\} = (2\pi)^{-1/2} \int_{-\infty}^x e^{-t^2/2} dt.$$

This is the result which justifies our computations as a suitable method of simulation of the stochastic model with the following caveats. (1) The finiteness of the mean and standard deviation needs to be discussed. (2) The computer has a finite word length. (3) The random number generator used is actually deterministic and should be called a pseudo-random number generator.

Caveats (2) and (3) need not be discussed further here. With respect to caveat (1), we have not provided a proof of the finiteness of any means and standard deviations used here. However, we believe a proof could be provided in the following way. The walks in the model can be projected onto any axis, say the axis of the number of moose of a certain age. The projection is itself a random walk. The walk is dominated by a pure birth walk in the sense that the probability of the transition $x \rightarrow x + 1$ is greater for the pure birth process than for the projected walk. Since the pure birth process has finite mean and variance after a fixed time *T*, it may be possible to prove the same for the projected walk and thus for the original walk.

5. Differences between Deterministic and Stochastic Models. The essential differences between the two models in dealing with biologically interacting populations fall into three categories:

- (1) recognition of stochastic fluctuations,
- (2) recognition of discrete character of events and populations,
- (3) notion of efficiency upon introduction of complexity.

For example, in (1) one could mention that the deterministic model does not differentiate between the intrinsic rate of growth where purely reproductive, and the reproductive balance between birth and death process, whereas the stochastic model does.

In (3) the point is that in complex situations Monte Carlo simulation seems to become very efficient compared to other methods of solution.

6. Isle Royale Background and Statistics. The Isle Royale National Park provides a very suitable closed biological world. There are three dominant populations: moose, wolf, and plant with the moose consuming the plants while wolves prey upon the moose. This park is a 210-square mile island in northwestern Lake Superior. The topography consists of a series of ridges and valleys, narrow lowlands and lakes. The climate is akin to the upper Great Lakes region with daily lows in winter not as low as the mainland and highs in summer not quite as high. The cooler-damper regions of the island have balsam fir and white spruce, as well as some white birch. In the southwestern part of the island sugar maple and yellow birch are predominant. The swamps and lower regions have black spruce, white cedar and balsam fir. Fires touched approximately half of the island in 1870–1900 and in 1936. The subclimax cover in the area of these fires is aspen, shrubs, lesser trees, ferns, and herbs.

The present moose population established itself in the early 1900's. Prior to the appearance of wolves about 1950, two factors influenced the behavior of the moose population: overbrowsing and the 1936 fire.

Overbrowsing caused a severe dip in the moose population about 1930. Recovery came after the 1936 burn with the re-emergence of browse. In the late 1940's and early 1950's, the wolf was introduced upon the scene; numbers at that time ranged between 15 and 25. Throughout the 1960's the wolf population has varied from 18 to 25 with the predominant social structure being a large pack varying between 12–16, a triplet pack and a few lone stragglers. The wolves tend ISLE ROYALE BROME

to be territorial and range over the entire island with some areas less visited than others. Since the wolves test about 12 moose on the average before a kill, they tend to travel extensively. Wolves do not breed until between 2 and 3 years. Reproductive capabilities do not seem to be shared by all the females, but perhaps by a dominant few. Pup mortality due to lack of food, competition, and adverse winter conditions is high. The wolves appear to exhibit a threshold reproductive response. Wolves, being a big prey animal, tend to feed upon the moose population. An average of 10–12 pounds of meat per day per animal seems to be consumed.

Since the introduction of the wolves, the wolf population has been fairly steady; the moose population still experiences crashes, though not of the proportion of the 1929–1930 period.

The moose population without a wolf population succumbs to a variety of factors: old age, malnutrition, disease; however, with the wolves present natural mortality is insignificant. Immigration and emigration of both the moose and wolf is relatively insignificant; we ignore it in our simulation. An estimated rate of predation is 227 moose killed annually, one every 1.6 days or .62 moose per day. The reproductive rate of the wolves appears to be 1.6 young per wolf per year. The reproductive rate of the moose is 227/600 = .38 calves per moose per year. The estimated wolf mortality rate is 1/22 = .045 animals per animal per year.

Figure 1 shows the known history of moose and wolf populations on Isle Royale. The pre-1957 data for moose are from Mech [16, page 22]; the data for moose from 1964 to 1970 are from Johnson et al. [9]; the figure of 600 moose in 1960 is in Mech [17, page 273]. The data for wolves for 1952 to 1966 are from Mech [17, page 65]; the data for 1968, 1969 are from Johnson et al. [9].

Several warnings and observations concerning this graph should be made. (1) The data before 1960 are not very reliable; in particular, the peak size for moose in 1929–1930 is estimated at anywhere between 1000 and 5000. (2) The change in moose population from 530 in 1967 to 1015 in 1968 seems unreal. An estimated reliability for post-1960 moose population figures is 10–25 percent. (3) In the years 1933–34 and 1945–50 the moose exhibited signs of starvation. (4) The 1936 forest fire in Isle Royale probably created the conditions needed for the post-1960 increase in moose population. (5) The decrease in wolf population of 23 in 1967 to 17 in 1968 seems to be due to emigration of six wolves.

7. Stochastic Model for Isle Royale: set of states and transition probabilities for the plant-moose-wolf predation of Isle Royale. The vector **x** is assigned 27 components: $\mathbf{x} = (z, x_1, \dots, x_{17}, y_1, \dots, y_9)$ where z



Figure 1. History of the moose and wolf populations on Isle Royale from 1900-1970.

denotes the 1 age group for the plants; x_1, \dots, x_{17} denote the 17 age groups for the moose and y_1, \dots, y_9 denote the 9 age groups for the wolves. x_i and y_i are the number of animals in age (i - 1) to *i* years. *z* denotes tons of plant material. Time *t* is measured in days modulo 365.

The following is a list of events which are permitted in our model and their corresponding coefficients. Only the components of the state vector which change are listed.

A. Events involving moose.

1.
$$g(x_1 \rightarrow x_1 - 1) = x_1(\sum_{i=2}^8 y_i)/7800$$

Comment: For 20 predator wolves and 30 moose calves, the expected waiting time between calf kills is 13 days.

2. $g(x_1 \rightarrow x_1 + 1) = \sum_{i=4}^{10} x_i / 50, \ 140 < t < 165$ = 0 otherwise.

Comment: For 450 moose in the age group 4 to 10 (which became pregnant in the previous year) the expected number of calves is 225 in the 25 day period of moose natality on Isle Royale.

3.
$$g(x_i \rightarrow x_i - 1) = x_i (\sum_{i=2}^8 y_i) / 8,606,$$

 $i = 8, 9, \dots, 17, z \ge 7,500$

Comment: This event is the death of older moose due to wolf predation, assuming an adequate food supply for the moose.

4.
$$g(x_i \rightarrow x_i - 1) = x_i (\sum_{i=2}^{8} y_i) / 8,606 + (7500 - z) x_i / 7500,$$

 $i = 8, 9, \dots, 17, z < 7500.$

Comment: This is effect of wolf predation and starvation on older moose.

5.
$$g(x_i \rightarrow x_i - 1) = (7500 - z)x_i/7500, \quad z < 7500$$

= 0, $z \ge 7500,$
 $i = 1, 2, \dots, 7.$

Comment: This is a threshold food response on moose population.

6.
$$g[(x_1, x_2, \cdots, x_{17}) \rightarrow (0, x_1, x_2, \cdots, x_{16})]$$

= ∞ , $t = 140$.

Comment: Increase in moose age.

B. Events involving wolves.

1.
$$g(y_1 \rightarrow y_1 - 1) = y_1(1 - 33/365).$$

Comment: Wolf pup mortality.

2.
$$g(y_1 \rightarrow y_1 + 1) = \sum_{i=4}^{8} y_i / 14, 52 < t < 59$$

= 0 otherwise.

Comment: Pups are born in the last week of February on Isle Royale.

3. $g(y_i \rightarrow y_i - 1) = y_i(.33/365), \ i = 6, 7, 8, 9.$

Comment: Natural death of older wolves.

4.
$$g(y_j \rightarrow y_j - 1) = y_j(400 - \sum_{i=1}^{17} x_i)/4000,$$

 $j = 1, 2, \dots, 9, \sum_{i=1}^{17} x_i < 400$
 $= 0$ otherwise.

Comment: Starvation of wolves due to lack of moose.

5.
$$g[(y_1, y_2, \dots, y_9) \to (0, y_1, y_2, \dots, y_8)]$$

= ∞ , $t = 52$.

Comment: Increase in wolf age.

C. Events involving plants.

1.
$$g(z \to z + 1) = z/1000, \ 105 < t < 255$$

= 0 otherwise.

Comment: Plant growth in growing season, the third week of April to second week in September.

2.
$$g(z \rightarrow z - 1) = \epsilon z/400$$

+ $(\sum_{i=1}^{17} x_1) \min(15000, z)/15000$
where $\epsilon = 1, t < 105$, or $t > 255$
= 0 otherwise.

Comment: The first term represents plant death in the dormant season. The second term corresponds to plant consumption of about 25 pounds of browse per moose per day.



Figure 2. Example of 15 year simulation for plant, moose, and wolf populations on Isle Royale from 1960 to 1975. The circled curve represents the real data.

The computer, MANIAC, was encoded, using the BIOTA1 program, to simulate the above transition events. The simulation employed an event-consequence technique, the elapsed time τ to the next event and the event being chosen by the method given in § 3, where, however, g may be a function of time as well as of \mathbf{x}^1 and \mathbf{x}^2 .

This model is a denumerable state, continuous time Markov process. For a discussion of such processes, see Bharucha-Reid [3, chapter 2] or Doob [5, chapter 6].

The complexity of the simulation is such that the mean and variance has not been proved to be finite. However, if mean and variance were finite then the Central Limit Theorem could be applied to guarantee that the distribution is Gaussian. See Spanier and Gelbart [19, page 14].

8. **Results.** Figures 2 and 3 are 15 year realizations beginning in 1960; the initial data (1960) are from the real history in Figure 1. In Figures 2 and 3 the sharp peaks and valleys for the plant population are a result of moose browsing and the plant growth pattern.

In Figure 2, it will be noticed that the envelope of oscillations for the plant population increases until 1967–68, at which time there begins a marked decrease in the envelope of oscillations. The pattern of



Figure 3. Another example of 15 year simulation for plant, moose, and wolf populations on Isle Royale from 1960 to 1975.

moose population is similar to the plants in the sense of having annual cycles. The moderately sharp annual increase in moose population corresponds to moose birth; the decrease is from the effect of predation.

The moose population shows a long range average increase before any significant dip is encountered between 10–12 years (1970–1972). The wolf population shows a long range decline; the pattern clarity is not as manifest as with the moose and plant population. Again as with moose-plant populations, the sharp, almost vertical, rises are due to pup birth; however, because of fewer wolves the decline is a sequence of decreasing plateaus as opposed to the steady decline for the moose population. The decline in the wolf population is seen primarily within the pup category, occasionally some litters surviving longer than others but rarely (1 out of 5) surviving till the second year; once past this critical first year the wolf is somewhat ensured of a full life.

Figures 4 and 5 are 15 year realizations beginning in 1970; the initial data (1970) for the realization were obtained from Figure 1. The pattern for both the moose and plant population is similar to the 15 year realization beginning in 1960. What is quite noticeable is the fact that the wolves under the given initial conditions went to extinction within



Figure 4. Example of 15 year simulation for plant, moose, and wolf population on Isle Royale from 1970 to 1985.

4 to 5 years. This result is tolerable within our 3-year predictive ability. However, it is felt that some of the wolf constants could be made better. (It may be that the wolf finds the moose too difficult a prey.)

For the 15 year realizations beginning in 1960 and in 1970, a modification of the plant growth-death interpretation is necessary. The present stochastic treatment of the plants views their cycle as a sharp dichotomy between growth and death. This dichotomy accounts for the sharp peaks and valleys; a more plateau-like peak and valley corresponding to a growth, dormant, death cycle would be better suited.

Some statistics will be viewed as a means for estimating the reliability of the predictive capabilities in the simulation. Statistics were accumulated in two areas, 3 year realizations and 10 year realizations. The analysis employed the calculation of mean $(\bar{\xi}_n = \sum_{i=1}^n \xi_i/n)$, the unbiased estimate of $\sigma_n^2 = (\bar{\xi}^2 - \bar{\xi}^2)/(n-1)$ where $\bar{\xi}^2 = \sum_{i=1}^n \xi_i^2/n$, and relative error $\pm (\sigma_n^2/n)^{1/2}/\bar{\xi}_n$. The results are listed in Tables 1 to 4. Values refer to total number of a population at the end of the stated period. As will be noticed, the relative error for the 3-year realization (1960 and 1970) is well within acceptable bounds. For the 10-year realization beginning 1960 (this is the first 10 years in a 15



Figure 5. Another example of 15 year simulation for plant, moose, and wolf populations on Isle Royale from 1970 to 1985.

year realization), the relative error was below 10%, except with the wolf population (11 percent). On this basis, a good reliability is attributed to predictions up to 10 years.

Another mathematical model of certain aspects of the Isle Royale biome is given by Jordan, Botkin, and Wolfe [10].

9. Conclusions. It is concluded that the event-consequence technique is an efficient and realistic method for simulating biological population interactions.

In the plant-moose-wolf model, probably the most unsatisfactory part is the treatment of plants. The incorporation of a wolf threshold birth response, sex, and multiple births should be improvements.

For future work, it is hoped that some of the parameters used in the model will be improved and that the model will be enlarged to include additional animals such as the beaver and fox.

This work (Tables 3 and 4) indicates that three-year realizations beginning in 1970 might be satisfactory, but ten-year realizations are not. This work was done in 1972 and has not been updated.

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Figure 6. Example of a 30 year simulation for the plant and moose population on Isle Royale from 1920-1950.

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TABLE 1

Mean, variance, and relative error for 27 3-year realizations of the Isle Royale biome beginning in 1960

	Mean	variance	Relative Error
Moose	637.9	5.6	.9%
Wolf	20.6	.66	3.2%
Plant	16,334	161	1%

TABLE 2

Mean, variance, and relative error for 17 10-year realizations beginning in 1960

	Mean	Variance	Relative Error
Moose	1,156	92	8%
Wolf	9	1	11.7%
Plant	12,281	1,032	8.4%

TABLE 3

Mean, variance, and relative error for 17 3-year realizations beginning in 1970

	Mean	Variance	Relative Error
Moose	1,123.5	25.6	2.3%
Wolf	14.6	.9	5.9%
Plant	7,879	96	1.2%

TABLE 4

Mean, variance, and relative error for 7 10-year realizations beginning in 1970

	Mean	Variance	Relative Error
Moose	757	100	13.3%
Wolf	3.6	2	56.6%
Plant	10,775	1,474	13.7%

BIBLIOGRAPHY

1. N. T. J. Bailey, Stochastic Birth, Death and Migration Processes for Spatially Distributed Populations, Biometrika 55 (1968), 189. 2. M. S. Bartlett, On Theoretical Models for Competitive and Predatory Biological System, Biometrika 44 (1957), 27.

3. A. T. Bharucha-Reid, *Elements of Theory of Markov Processes and their Appli*cations, McGraw-Hill Book Company, New York, 1960.

4. Kenneth R. Dixon and George W. Cornwall, A Mathematical Model for Predator and Prey Populations, Researches on Population Ecology 12 (1970), 127.

5. J. L. Doob, Stochastic Processes, John Wiley and Sons, New York, 1953.

6. V. L. Engstrom-Heg, Predation, Competition and Environmental Models, J. Theor. Biol. 27 (1970), 175.

7. W. Feller, Die Grundlagen der Volterraschen Theorie des Kampfes ums Dasein in wahrscheinlichkeitstheoretischer Behandlung, Acta Biotheor. 5 (1939), 11.

8. W. Feller, An Introduction to Probability Theory and its Applications, volume 1, 3rd edition, John Wiley and Sons, Inc., 1968.

9. Wendel L. Johnson, Michael L. Wolfe and Durward L. Allen, Community Relationships and Population Dynamics of Terrestrial Mammals of Isle Royale, Lake Superior, Fourth Annual Report, Purdue University, 1970.

10. P. A. Jordan, D. B. Botkin and M. L. Wolfe, Biomass Dynamics in a Moose Population, Ecology 52 (1971), 147.

11. P. A. Jordan, P. C. Shelton and Durward L. Allen, Numbers, Turnover, and Social Structure of the Isle Royale Wolf Population, Am. Zoologist 7 (1967), 233.

12. D. G. Kendall, Stochastic Processes and Population Growth, J. of Royal Statistical Society B, 11 (1949), 230.

13. P. H. Leslie, A Stochastic Model for Studying the Properties of Certain Biological Systems by Numerical Methods, Biometrika 45 (1958), 16.

14. P. H. Leslie and J. C. Gower, The Properties of a Stochastic Model for Two Competing Species, Biometrika 45 (1958), 316.

15. A. J. Lotka, *Elements of Mathematical Biology*, Dover Publishing Co., New York, 1956.

16. L. David Mech, *The Wolves of Isle Royale*, Fauna of the National Parks of the United States, Fauna Series 7, United States Government Printing Office, Washington, D.C., 1966.

17. ____, The Wolf, Natural History Press, Garden City, N.Y., 1970.

18. P. C. Shelton, Ecological Studies of Beavers, Wolves, and Moose in Isle Royale National Park, Michigan, Ph.D. thesis, Purdue University, 1966.

19. Jerome Spanier and Ely M. Gelbard, Monte Carlo Principles and Neutron Transport Problems, Addison-Wesley, London, England, 1969.

20. P. Suppes, *The Model in Mathematics*, D. Reidel Publishing Company, Dordrecht, Holland, 1961.

21. V. Volterra, Leçons sur la théorie mathématique de la lutte pour la vie, Gauthier-Villars, Paris, 1931.

22. K. E. F. Watt, A Mathematical Model for the Effect of Densities of Attacked and Attacking Species on the Number Attacked, Canadian Entomology 91 (1959), 129.

UNIVERSITY OF CALIFORNIA, LOS ALAMOS SCIENTIFIC LABORATORY,

Los Alamos, NM 87544