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Age-specific, Deterministic Model of Predator-Prey Populations: Application to Isle Royale

Abstract: A deterministic model is proposed for the description of predator-prey systems in which the prey has an age-specific vulnerability to predation. The model is developed on the basis of observations of the moose and wolf populations of Isle Royale, Michigan. The moose are divided into three groups, the very young, the adults, and the very old or sick. The three groups have different vulnerability to predation by a single population of wolves. The model incorporates a saturation effect for the moose population and a satiation effect for the wolf population. It appears to reproduce quite well the almost monotonic trend toward equilibrium observed since the arrival of wolves on the island.

1. Introduction

Interest in mathematical models of populations of species, growing alone or in competition with other species, has been increasing as a result of growing concern for the preservation of an ecological balance. Among the most interesting population studies are those concerning a population of predators feeding on a population of prey. The first mathematical model for predator-prey interaction was proposed independently by A. J. Lotka [1] and Vito Volterra [2]. Although quite primitive, this model reproduced one observable feature of some predator-prey populations: the fact that cyclic variation of the number of predators is out of phase with a similar variation of the number of prey. Many improvements on the Lotka-Volterra model have been suggested for the purpose of increasing its realism. The rationale for some of these improvements is discussed in Section 2 of this paper, as an introduction to a mathematical model proposed in Section 3 for a specific case of predator-prey interaction: the moose and wolf populations of Isle Royale, Michigan.

During the past decade this island has been the subject of many studies. An interesting account of the animal life on Isle Royale has been written by L. D. Mech [3]. It contains a detailed description of the life habits of moose and wolves and some basic data concerning the ecological balance of the island. More recently, Jordan, et al. [4] have given some additional information on the biomass balance on the island, and a computer simulation of this balance.

If one examines the available data on Isle Royale and compares it with the Lotka-Volterra model, or variations thereof, he finds that none of these simple models matches the data very well. Among the most important sources of mismatch is the fact that individual moose are not equally vulnerable to predation. Very young and very old or sick moose are vulnerable; but healthy adults are almost invulnerable. This and other characteristics of the Isle Royale populations point to the need for a more elaborate, age-specific, model for the description of these populations. In what follows, we discuss the development of a model that matches some essential features of the Isle Royale ecosystem.

Before discussing this model, we give some remarks on Lotka-Volterra types of models and the effect of various alterations on these models. Then we construct a model describing the interaction of three different categories of moose with each other and with a single population of wolves. In developing the model, our main objectives were to provide it with sufficient versatility to realistically reproduce population trends and simultaneously to keep it simple enough to hold promise of its being validated against available data.

2. The Lotka-Volterra model and various elaborations

In its primitive form, the Lotka-Volterra model [1,2] concerns two species labelled 1 and 2. It is postulated that the population of species 1, N_1, would grow expo-

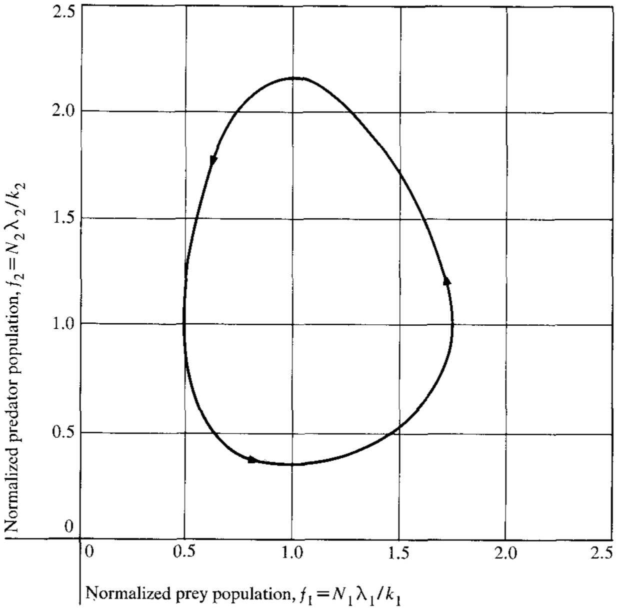


Figure 1 A typical trajectory in state space showing the periodic behavior of the Lotka-Volterra model.

nentially in the absence of its predator species while the population of species 2, N_2, would decline exponentially in the absence of its prey species 1. Thus, without interaction

$$\frac{dN_1}{dt} = k_1 N_1 ,$$
$$\frac{dN_2}{dt} = -k_2 N_2 . \tag{1}$$

The interaction mechanism proposed by Lotka and Volterra is that of binary collisions, so that the death rate of 1 due to interaction with 2 is proportional to $N_1 N_2$, as is the rate of population growth of 2. This mechanism yields the Lotka-Volterra equations

$$\frac{dN_1}{dt} = k_1 N_1 - \lambda_1 N_1 N_2 ,$$
$$\frac{dN_2}{dt} = -k_2 N_2 + \lambda_2 N_1 N_2 . \tag{2}$$

These equations have been investigated and generalized by a number of authors. We note in passing several characteristics of their solution. First, equilibrium populations q_i are obtained by setting $dN_i/dt = 0$. They are given by

$$q_1 = k_2/\lambda_2 ,$$
$$q_2 = k_1/\lambda_1 . \tag{3}$$

If we define $f_i = N_i/q_i$, $(i = 1, 2)$, it can be shown that the normalized state variables, f_1, f_2, satisfy the relationship

$$G(f_1, f_2) = (-f_1 + \ln f_1)/k_1 + (-f_2 + \ln f_2)/k_2 = C_0 , \tag{4}$$

where the constant, C_0, depends on the initial conditions.

From this observation, one can deduce that the solutions of the basic equations (2) are periodic. There exists a closed trajectory in the state-plane f_1, f_2 for each value of C_0. We have plotted the solution of Eq. (4) for a typical case in Fig. 1. Volterra generalized the two-species equations to n species, and it can be shown that in the latter case a "constant of motion" like C_0 still exists.

A deficiency of the Lotka-Volterra model, which is important in some applications, is the nonexistence of a saturation level of the population of species 1 in the absence of predator species 2. Generally, a population in a given environment, in a limited space, cannot exceed some saturation level, which we denote by θ. Typical equations for population growth of a single species with saturation are the Verhulst [5] equation

$$\frac{dN}{dt} = kN\left[1 - \frac{N}{\theta}\right] \tag{5a}$$

and the Gompertz [6] equation

$$\frac{dN}{dt} = -kN \ln\left(\frac{N}{\theta}\right), \tag{5b}$$

which are special cases (with $\alpha = 1, 0$) of

$$\frac{dN}{dt} = \frac{kN}{\alpha}\left[1 - \left(\frac{N}{\theta}\right)^{\alpha}\right]. \tag{5c}$$

The extension of the Lotka-Volterra equations that includes a Verhulst term for species 1 is

$$\frac{dN_1}{dt} = k_1 N_1 \left[1 - \frac{N_1}{\theta}\right] - \lambda_1 N_1 N_2 , \tag{6a}$$

$$\frac{dN_2}{dt} = - k_2 N_2 + \lambda_2 N_1 N_2 . \tag{6b}$$

The equilibrium solution of these equations is

$$q_1 = k_2/\lambda_2 ,$$
$$q_2 = \left[1 - \frac{k_2}{\lambda_2 \theta}\right]\frac{k_1}{\lambda_1}. \tag{7}$$

Since there is no "constant of motion" for the set of Eqs. (6), the curve in the state plane f_1, f_2 is not a closed loop as in the solution of Eq. (4). Solutions of (6) are not periodic; but in the stable regime, with $(k_2/\lambda_2\theta) < 1$, the variation of N_2 with N_1 spirals into the equilibrium point (q_1, q_2), as is evident in Fig. 2. The variation of the normalized species populations with time is plotted in Fig. 3, where the time τ is a normalized variable given by $\tau = k_2 t$. In an experimental or observational situation in which the ratio of the initial population of species 1, $N_1(0)$, to the saturation level θ, is very small, a large number of cycles may be necessary before the system comes close to its equilibrium point. The experiment may be discontinued, or the environment may change significantly in a natural situation, before equilibrium is achieved. In that case, the appropriateness of a Verhulst type of nonlinearity in (6) is difficult to ascertain.

A second type of saturation effect might be important in the interaction terms of the system of Eqs. (2) and (6) in the regime of small N_2 and large N_1. The appetite of a given predator is limited, so that the total number of prey eaten per day cannot exceed a number proportional to N_2 and independent of N_1, provided that N_1 is large compared with the number required to satiate the predators. Hence, the N_1-dependent factor on the collision term should be proportional to N_1 when N_1 is small and should tend to a constant when N_1 is large. A simple function with this property, first introduced by Watt [7], is

$(\lambda_1/c)\ [1 - \exp(-cN_1)]$,

where the constant c is proportional to the biomass of a unit of prey and reflects the contribution of such a unit to the satiation of the prey population.

With this satiation term, Eq. (6a) becomes

$$\frac{dN_1}{dt} = k_1 N_1 \left[1 - \frac{N_1}{\theta}\right] - \frac{\lambda_1 N_2}{c}\,[1 - \exp(-cN_1)]\,. \quad (8a)$$

When the same saturation effect is introduced into (6b) it yields an expression of the form

$$\frac{dN_2}{dt} = -k_2 N_2 + \frac{\lambda_2 N_2}{c}\,[1 - \exp(-cN_1)]\,. \quad (8b)$$

As $c \to 0$, the system (8) reduces to (6).

All the above elaborations on the Lotka-Volterra model appear to be essential for the Isle Royale ecosystem. Prey saturation is needed if we do not want to consider explicitly the limitation on growth imposed by the limited supply of plants consumed by the moose. Also, the number of wolves ranges between 20 and 30, while the population of moose is generally upwards of 500. Hence, the satiation of the predators, as in the Watt-type model, is essential in the ecosystem.

Other possible elaborations to the Lotka-Volterra model are the introduction of a time-lag between the consumption of prey and the birth of a predator, and age-specificity in either the predator or the prey populations or both. The time-lag between a prey kill and a predator birth, while important, is not considered as a major correction to the model, which anyway neglects seasonal variations in the behavior of the populations. However, the age-specificity is particularly important, because of the different vulnerability of the various age groups of moose to predation. Wolves exercise not only population control on the moose, but also some form of eugenics. They kill many of the young calves, thus limiting the number of moose (and saving them from cycles of famine); they also kill the old and sick moose, and leave a robust adult population on the island.

With these observations in mind, let us now propose a basic mathematical model for the Isle Royale ecosystem.

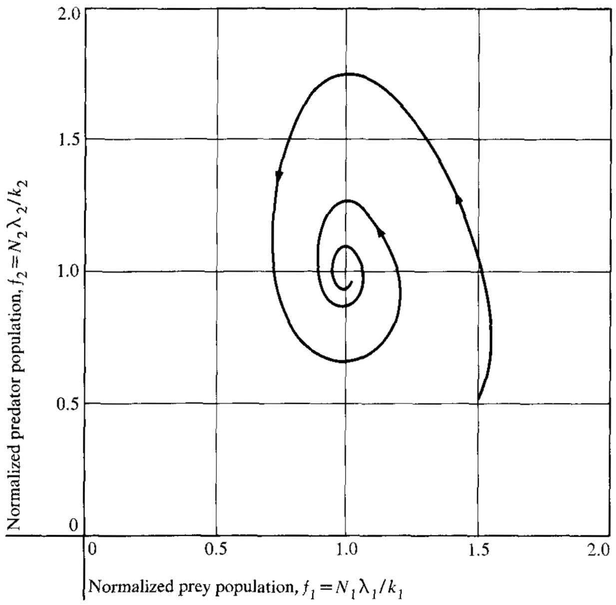
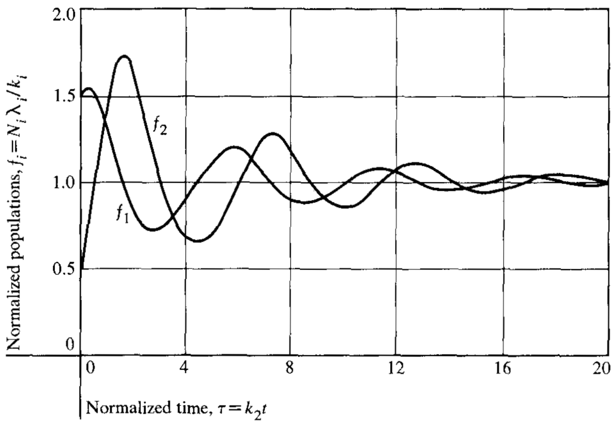


Figure 2 Effect of a Verhulst-type saturation correction on the Lotka-Volterra model. The two populations spiral toward equilibrium.

Figure 3 Variation of the populations with time for a Lotka-Volterra model with a Verhulst-type saturation correction.



3. The model

The basic assumptions of the model are the following:

a) The moose and wolf populations are assumed isolated from the rest of the ecosystem. That is, we assume that there is always enough food for the moose, except as indicated in (e) below, and any other animal species provides a negligible percentage of the wolves' diet.
b) There are three main age groups of the moose, the very young, N_1, the "adults", N_2, and the very old or sick, N_3. The first and third groups are vulnerable to predation, but the adult group is not.
c) The wolves are lumped together into one population, N_4.
d) Calves are born to both the "adult" group 2 of moose, and group 3 of old and sick moose, but with different birth rates.
e) The birth rate of moose is limited according to a Verhulst-type correction, to account for the saturation effect due to limited space and browse.

Accordingly, we propose the following model for the description of the moose and wolf populations:

$$\frac{dN_1}{dt} = (-k_{11}N_1 + k_{12}N_2 + k_{13}N_3)\ V - c_{14}\frac{D_1N_1N_4}{D_1N_1 + D_3N_3} \times [1 - \exp(-D_1N_1 - D_3N_3)]\,,$$

$$\frac{dN_2}{dt} = k_{21}N_1 - k_{22}N_2\,,$$

$$\frac{dN_3}{dt} = k_{32}N_2 - k_{33}N_3 - C_{34}\frac{D_3N_3N_4}{D_1N_1 + D_3N_3} \times [1 - \exp(-D_1N_1 - D_3N_3)]\,,$$

$$\frac{dN_4}{dt} = k_{44}N_4\{-1 + c[1 - \exp(-D_1N_1 - D_3N_3)]\}\,, \quad (9a)$$

where V is the Verhulst saturation factor given by

$$V = \left(1 - \frac{N_1}{\theta_1} - \frac{N_2}{\theta_2} - \frac{N_3}{\theta_3}\right). \quad (9b)$$

N_1, N_2, N_3 are the population sizes of the three moose groups, θ_1, θ_2, θ_3 their saturation levels, and N_4 is the number of wolves. The various coefficients of Eqs. (9a) describe the rates of birth, death, kill, and "graduation" from one class of moose to another. Some of these coefficients describe more than one process. For example, k_{11} describes the graduation from the calf to the adult class of moose plus infant mortality. This is why k_{11} is, in general, different from k_{21}, which represents the ratio of calves who reach adulthood. The biological interpretations of most of the constants in Eqs. (9a) are shown in Table 1. We note that we have used the Watt modification [7] to the kill terms in the first and third equation. In addition, Eqs. (9) express the idea that the probability of a kill of a member from the class N_i is proportional to the relative abundance of the "biomass" D_iN_i, compared to the total prey biomass, $(D_1N_1 + D_3N_3)$.

Table 1 Biological interpretation of the constants used in Eqs. (9a).

k_{11} =	Graduation rate from the calf to the adult class of moose plus infant mortality.
k_{12} =	Fertility rate of adult moose
k_{13} =	Fertility rate of old or sick moose
k_{21} =	Graduation rate from the calf to the adult class of moose
k_{22} =	Graduation rate from the adult to the old or sick class of moose, plus adult mortality
k_{32} =	Graduation rate from the adult to the old or sick class of moose
k_{33} =	Natural mortality rate of old or sick moose
k_{44} =	Rate of depletion of the wolf population in the absence of moose
D_1 =	Contribution (proportional to the weight) of a single calf to the satiation effect (abundance of prey) on the wolf population
D_3 =	Contribution (proportional to the weight) of an old or sick moose to the satiation effect on the wolf population
c, c_{14}, c_{34} =	Constants to be determined so that all populations remain stable at their equilibrium values.

Equations (9) are now reduced to a canonical form, with the minimum number of parameters. Let q_i represent the equilibrium values for N_i, corresponding to the solution of Eqs. (9) when we set $dN_i/dt = 0$ for all i, and

$$f_i = N_i/q_i,\ (i = 1,\cdots,4)\,. \quad (10)$$

Then, Eqs. (9) may be reduced to the form

$$\frac{df_1}{d\tau} = K_1\left[\left(1 - \frac{f_1 + f_2 + f_3}{F}\right)(-f_1 + \lambda_{12}f_2 + \lambda_{13}f_3) - \left(1 - \frac{3}{F}\right)(\lambda_{12} + \lambda_{13} - 1)\,f_1f_4G\right],$$

$$\frac{df_2}{d\tau} = K_2(f_1 - f_2)\,,$$

$$\frac{df_3}{d\tau} = K_3\,[\lambda_{32}f_2 - f_3 - (\lambda_{32} - 1)f_3f_4G]\,,$$

$$\frac{df_4}{d\tau} = f_4\left[-1 + \frac{1 - \exp(-d_1f_1 - d_3f_3)}{1 - \exp(-d_1 - d_3)}\right], \quad (11)$$

where

$$G = \frac{d_1 + d_3}{d_1f_1 + d_3f_3}\left[\frac{1 - \exp(-d_1f_1 - d_3f_3)}{1 - \exp(-d_1 - d_3)}\right] \quad (12)$$

and the Verhulst saturation factor was chosen so that the saturation levels of the three classes are proportional to the equilibrium levels. The latter choice was made because it is plausible, and in order to limit the number of independent parameters. The new parameters are related to the ones of Eqs. (9) according to the relationships

$$K_i = \frac{k_{ii}}{k_{44}},\ (i = 1, 2, 3)\ ,$$

$$\lambda_{12} = \frac{k_{12}k_{21}}{k_{11}k_{22}},\ \lambda_{13} = \frac{k_{13}q_3}{k_{11}q_1},$$

$$\lambda_{32} = \frac{k_{32}q_2}{k_{33}q_3},$$

$$d_i = q_i D_i,\ (i = 1, 3)\ ,$$

$$\tau = tk_{44}\ . \tag{13}$$

The biological interpretation of the constants K_i can be seen by referring to Table 1. They are the ratios of the three rates,

k_{11} = Graduation plus mortality rate of calves,
k_{22} = Graduation plus mortality rate of adult moose, and
k_{33} = Natural death rate of old or sick moose,

to the depletion rate of the wolf population in the absence of prey, k_{44}. The constants λ_{ij} are best interpreted by referring to the equilibrium state of the system, in which $N_i = q_i$. Thus we find that, in this steady-state situation.

$$\lambda_{12} = \frac{\text{Number of calves born to adult moose}}{\text{Number of calves graduating to adult class}}$$

$$\lambda_{13} = \frac{\text{Number of calves born to old or sick moose}}{\text{Number of calves graduating to adult class}}$$

$$\lambda_{32} = \frac{\text{Number of adults graduating to old or sick class}}{\text{Number of old or sick moose dying naturally}}\ .$$

It is seen that the λ_{ij} are constrained by physical considerations. For example, we cannot have more calves graduating to the adult class than those that are born, therefore, $\lambda_{12} + \lambda_{13} \geqslant 1$. Also, we must have at least as many adult moose graduating to the old or sick class as the number of moose from the latter class that die; therefore, $\lambda_{32} \geqslant 1$.

Equations (11) have the equilibrium solution

$$\left.\begin{aligned} f_i &= 1 \\ \frac{df_i}{d\tau} &= 0 \end{aligned}\right\}\ (i = 1, \cdots, 4)\ . \tag{14}$$

The population variation near equilibrium may be investigated by a study of the stability about equilibrium.

4. Stability investigation

Let us assume a small perturbation about equilibrium, namely

$$f_i = 1 + \epsilon_i,\quad \epsilon_i \ll 1,\ (i = 1, \cdots, 4)\ . \tag{15}$$

Entering Eqs. (15) into Eqs. (11), expanding in power series of ϵ_i and retaining only first-order terms, we obtain a linearized set of equations

$$\frac{d\epsilon_i}{d\tau} = \sum_{j=1}^{4} M_{ij}\, \epsilon_j\ , \tag{16}$$

where

$$M_{11} = K_1 \left\{ -\left(1 - \frac{3}{F}\right) + (1 - \lambda_{12} - \lambda_{13}) \right.$$
$$\left. \times \left[\frac{1}{F} + \left(1 - \frac{3}{F}\right)\left(\frac{Ed_1}{1 - E} + \frac{d_3}{d_1 + d_3}\right)\right]\right\},$$

$$M_{12} = K_1 \left[\left(1 - \frac{3}{F}\right)\lambda_{12} + \frac{1}{F}\,(1 - \lambda_{12} - \lambda_{13})\right],$$

$$M_{13} = K_1 \left\{\left(1 - \frac{3}{F}\right)\lambda_{13} + (1 - \lambda_{12} - \lambda_{13})\right.$$
$$\left. \times \left[\frac{1}{F} + \left(1 - \frac{3}{F}\right) d_3\left(\frac{E}{1 - E} - \frac{1}{d_1 + d_3}\right)\right]\right\},$$

$$M_{14} = K_1 \left(1 - \frac{3}{F}\right)(1 - \lambda_{12} - \lambda_{13})\ ,$$

$$M_{21} = -M_{22} = K_2\ ,$$

$$M_{31} = K_3(1 - \lambda_{32})\left(-\frac{d_1}{d_1 + d_3} + \frac{Ed_1}{1 - E}\right),$$

$$M_{32} = K_3\lambda_{32}\ ,$$

$$M_{33} = K_3\left[-1 + (1 - \lambda_{32})\left(\frac{d_1}{d_1 + d_3} + \frac{Ed_3}{1 - E}\right)\right],$$

$$M_{34} = K_3(1 - \lambda_{32})\ ,$$

$$M_{41} = \frac{Ed_1}{1 - E},$$

$$M_{43} = \frac{Ed_3}{1 - E},$$

$$M_{23} = M_{24} = M_{42} = M_{44} = 0\ ,$$

$$E = \exp\,[-d_1 - d_3]\ . \tag{17}$$

The stability of the equilibrium solution, Eqs. (14), against small perturbations is determined by the nature of the eigenvalues of the matrix M_{ij}. The equilibrium solution is stable if, and only if, all eigenvalues have a negative real part. A complete investigation of stability would require a search of regions of stability in the domain of the nine independent parameters, F, K_1, K_2, K_3, λ_{12}, λ_{13}, λ_{32}, d_1, and d_3.

We have determined numerically that stability is particularly sensitive to a variation of the parameters λ_{12}, λ_{13} and λ_{32}. Therefore, we have determined the bound of stability in the plane λ_{12} versus λ_{32} for some representative values of the other five parameters. The results are shown in Fig. 4, where the stable region lies above the

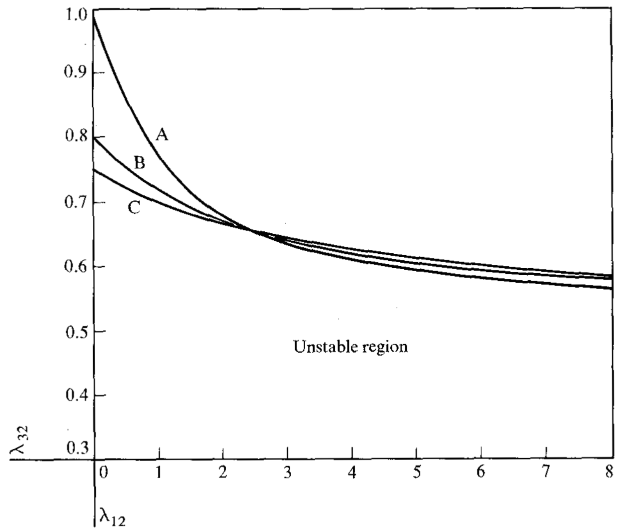
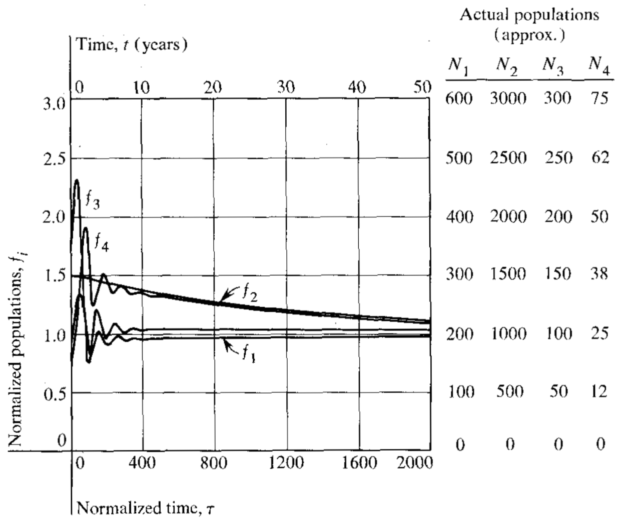


Figure 4 Boundary between stable and unstable regions in the plane λ_{32} versus λ_{12}, for small perturbations about equilibrium. The curves A, B, and C correspond to the values of the parameter $\lambda_{13} = 1$, 2, and 3, respectively. The other parameter values are $K_1 = 0.0125$, $K_2 = 0.00075$, $K_3 = 0.006$, $d_1 = 2.0$, $d_3 = 2.4$ and $F = 8.0$.

Figure 5 Variation of the four normalized populations versus normalized time derived from the model of Eqs. (11). One year corresponds approximately to $\tau = 40$.



appropriate one of the curves labeled A, B, and C. These curves were determined numerically as the loci of the zero of the largest real part of an eigenvalue. It may be seen that the bound of stability corresponding to the curves A, B, and C changes relatively little as λ_{13} changes between the values of 1 and 3. In all three cases shown, the physically acceptable domain, $\lambda_{32} \geqslant 1$, lies within the stable region.

5. Numerical computations and discussion

The existence or lack of stability against small perturbations gives, in general, only partial information concerning large fluctuations about equilibrium. For example, a system of equations that is stable against small perturbations may be unstable against large ones. On the other hand, a system that is unstable against small perturbations about equilibrium may have a limit cycle, as for example, does the Watt modification [7] of the Lotka-Volterra equations.

We have carried out numerical computations of several test cases, using Eqs. (11). The computations appear to indicate that the bounds of stability shown in Fig. 4 are bounds of transition from amplified to attenuated behavior of the perturbations about equilibrium, even when the initial perturbations are large. However, for sufficiently large perturbations, a choice of parameters in the stable region may yield physically unacceptable negative values for some of the population functions and certain periods of time. The differential equations must then be solved under some additional non-negativity constraints.

In modeling Isle Royale, the parameters of the computations were chosen on the basis of information available about life – and death – on Isle Royale. Specifically, we used the following realistic values for the thirteen parameters of Eqs. (9) which are needed in order to determine the constants entering in Eqs. (11).

$k_{11} = k_{12} = k_{13} = k_{21} = 0.5/\text{yr}$

$k_{22} = k_{32} = 0.25/\text{yr}$

$k_{33} = 0.031/\text{yr}$

$k_{44} = 40/\text{yr}$

$q_1 = 160$ moose

$q_2 = 320$ moose

$q_3 = 160$ moose

$D_1 = 0.0125/\text{moose}$

$D_3 = 0.015/\text{moose}$

The class of "adult" moose is assumed to consist roughly of the wear classes I through IV, in the standard classification given, for example, by Mech [3].

The constants of Eqs. (11) are then the following:

$K_1 = 0.0125$	$\lambda_{12} = 2.0$
$K_2 = 0.00075$	$\lambda_{13} = 1.0$
$K_3 = 0.006$	$\lambda_{32} = 16.0$
$d_1 = 2.0$	$F = 8.0$
$d_3 = 2.4$	

The saturation constant F was selected so that the moose population cannot exceed a combined total of about 1700.

The numerical computations were made using a fourth-order Runge-Kutta integration procedure. Typical results are given in Figs. 5 and 6. Figure 5 shows the variation of the four functions f_i versus the normalized time τ, (and the natural time in years), and Fig. 6 shows the corresponding plot in the state space $f^* = \frac{1}{3}(f_1 + f_2 + f_3)$ versus f_4. (The value of f^* gives a weighted average of the population sizes of the three moose classes, and tends to 1 at equilibrium.) The initial conditions were chosen to approximate the conditions when wolves came to Isle Royale [3] in 1946; namely, a fairly large population of moose and small population of wolves. The numerical results show some initial damped oscillations, and then an almost monotonic trend toward equilibrium, which is reached within about 20 years. The almost monotonic trend toward equilibrium appears to be a fairly good representation of the events of the last two decades. Whether or not the initial fluctuations are realistic is rather difficult to ascertain from available data. There are some indications that they are not, because of one feature of the wolf population that is not contained in the model. The wolves appear to exercise some control over their number, through social rather than logistical pressures. Formation of packs, pack life, territorial dominance, and other social determinants appear to impose a ceiling on the wolf population. There is evidence that a surplus of wolves may emigrate from the island during the winter, over the frozen lake. The growth of the moose population, on the other hand, is limited by the availability of food, and this limitation is not properly accounted for by the Verhulst-type saturation factor. A three-species model, taking into account plants, moose, and wolves, would more adequately describe the periods when the number of moose becomes large and/or the number of wolves becomes small, when the moose population is in danger of starvation. It may be pointed out that over the last two decades or so there has been no evidence of moose starvation. However, some signs of vegetation shortage have been seen in the last few years [8].

In summary, the present model gives a better description of the trend toward equilibrium, observed since the arrival of the wolves on Isle Royale, than that given by simpler, two-population models. With proper calibration, it could be used to describe quite well the effect of increasing the wolf population on the ecological balance of the island. It probably needs some improvements, and possibly an explicit consideration of plant life, before it can be used to describe the effect of limiting the wolf population, and consequently increasing the moose population.

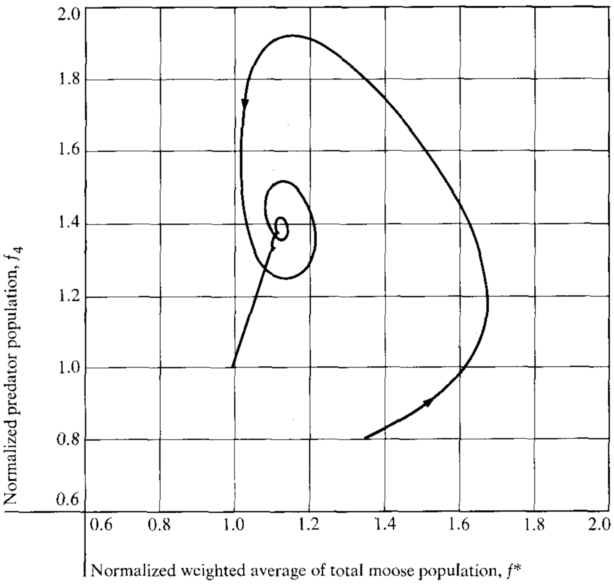


Figure 6 Variation of the average of the three normalized moose populations, $f^* = \frac{1}{3}(f_1 + f_2 + f_3)$ versus normalized wolf population, f_4.

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