

A Mathematical Model with a Modified Logistic Approach for Singly Peaked Population Processes

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When a small number of individuals of a single species are confined in a closed space with a limited amount of indispensable resources, breeding may start initially under suitable conditions, and after peaking, the population should go extinct as the resources are exhausted. Starting with the logistic equation and assuming that the carrying capacity of the environment is a function of the amount of resources, a mathematical model describing such a pattern of population change is obtained. An application of this model to a typical set of population records, that of deer herds by V. B. Scheffer (1951, *Sci. Monthly* 73, 356–362) and E. C. O’Roke and F. N. Hamerstrom (1948, *J. Wildlife Management* 12, 78–86), yields estimates of the initial amount of indispensable food and its availability or nutritional efficiency which were previously unspecified. © 1999 Academic Press

INTRODUCTION

The logistic or the Lotka–Volterra model has long been a mathematical frame work for studying population dynamics tending to a stationary or oscillating equilibrium due to intra- or interspecific interactions (e.g., Pielou, 1974; Begon *et al.*, 1996; Borrelli and Coleman, 1996; Glesson and Wilson, 1986; Reed *et al.*, 1996). Also, there is another pattern of population change which is singly peaked. A typical one is the population change of deer herds observed by Scheffer (1951). It was reported that the deer were freed in closed spaces at some definite

time and the populations first increased nearly exponentially to reach a peak and then decreased or finally went extinct. The change was considered to be fluctuation or overabundance from the sigmoidal pattern and ascribed to changes in the reproduction rate and/or mortality due to unspecified reasons. But, such patterns should be generally observable if living organisms are confined in a closed space with a constant amount of growth resources which are actually not reproducible although initially given. Effects of food availability or resource limitation on population dynamics are one of recent concerns (e.g., Ogushi and Sawada, 1985; Edgar and Aoki, 1993). To our knowledge, however, rather few mathematical models have been studied to analyse such patterns of population change and the carrying capacity for

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population has been traditionally assumed to be a constant characterizing its environment. In this report, we propose a new mathematical model to interpret such a pattern of population change by introducing the new assumption that the carrying capacity is a function of the amount of resources. After its formulation and its application to the deer herd population, we discuss several characteristics of our model as compared with the existing models.

MATHEMATICAL MODELS

We start with the logistic equation for a single species living in some limited space,

$$\frac{1}{N} \frac{dN}{dt} = r \left(1 - \frac{N}{K} \right), \quad (1)$$

where N is the population size of the species, r the potential net reproduction rate, and K the carrying capacity of the population. Now we assume that the carrying capacity depends on the amount of indispensable resources in the space for the organisms and the resources are consumed by the organisms after they begin to live. In such a situation, we may assume that the carrying capacity is a function of the amount (X) of the resource, $K = f(X)$. Thus, we have

$$\frac{1}{N} \frac{dN}{dt} = r \left(1 - \frac{N}{f(X)} \right). \quad (2)$$

We may further assume that the decreasing rate of X is proportional to the population size and the reproduction rate of the resources is negligible compared with the consumption rate, i.e.,

$$\frac{dX}{dt} = -aN, \quad (3)$$

where $a (>0)$ is the consumption rate of the resources per individual per unit time. From Eqs. (2) and (3), we have

$$\ln \frac{N}{N_0} = r(t - t_0) + \frac{r}{a} \int_{X_0}^X \frac{dX}{f(X)}, \quad (4)$$

where N_0 , X_0 , and t_0 are the initial values of N , X , and t , respectively. There may be various choices for $f(X)$ as an integrable function which represents a possible

dependence of carrying capacity on resources. We choose here the simplest, a linear function $f(X) = bX$, with the proportional constant $b (>0)$, which we call the nutritional efficiency. Thus we have

$$N(t) = N_0 \left[\frac{X(t)}{X_0} \right]^{r/ab} \exp(rt), \quad (5)$$

with $t_0 = 0$. Equation (5) predicts that the amount of resources per individual, X/N , in the case of $a = r/b$, decreases exponentially with time from the initial value X_0/N_0 . Solving the simultaneous Eqs. (3) and (5), we obtain the following solutions: For $a = r/b$,

$$N(t) = N_0 \exp \left[rt + \frac{a N_0}{r X_0} \{1 - \exp(rt)\} \right], \quad (6)$$

and for $a \neq r/b$,

$$N(t) = N_0 \left[1 + \left(\frac{a}{r} - \frac{1}{b} \right) \frac{N_0}{X_0} \{1 - \exp(rt)\} \right]^{r/(ab-r)} \times \exp(rt). \quad (7)$$

The $N(t)$ curve given by Eq. (6) or Eq. (7) has a single peak for a limited range or combinations of parameters a , b , r , X_0 , and N_0 . The range giving the single peak is determined from the extreme condition of $N(t)$. The solution (6) for $a = r/b$ has a peak if $rX_0/aN_0 > 1$. We note that $rX_0/aN_0 = bX_0/N_0$ in this case. The maximum of N is given by

$$N_m = \frac{rX_0}{a} \exp \left(\frac{aN_0}{rX_0} - 1 \right), \quad (8)$$

at time $t_m = (1/r) \ln(rX_0/aN_0)$. For $a \neq r/b$, the peak exists again when $bX_0/N_0 > 1$. The maximum is

$$N_m = N_0 \left[\frac{1}{ab} \left\{ r + (ab - r) \frac{N_0}{bX_0} \right\} \right]^{r/(ab-r)} \times \left(\frac{rX_0}{aN_0} + 1 - \frac{r}{ab} \right) \quad (9)$$

with $t_m = (1/r) \ln(rX_0/aN_0 + 1 - r/ab)$. We show the range where a single peak exists on the $(N_0/X_0, b)$ plane in Fig. 1. It should be noted that our model is soluble exactly. We also note that it is scale invariant under the change of $(a, 1/b, X_0)$ into $(\lambda a, \lambda/b, \lambda X_0)$ with an arbitrary constant λ , and the units of X define the units of a and b .

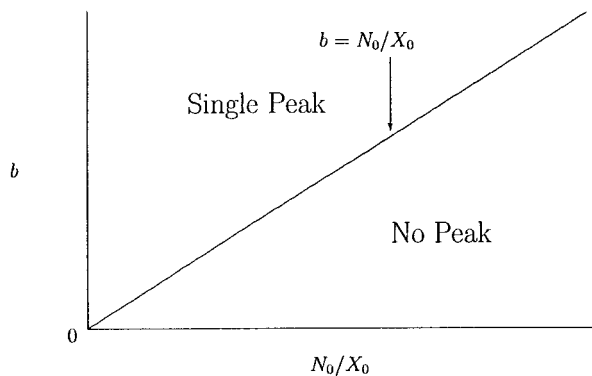


FIG. 1. The range in which the condition giving a peak in $N(t)$ curves is fulfilled: $b > N_0/X_0$. Notation is defined in the text.

APPLICATION TO THE DEER POPULATIONS

What can be analysed by the present model? To show this, we apply the model to the population changes of reindeer on St. Paul Island (SPI) from 1911 to 1950 and on St. George Island (SGI) from 1911 to 1949 (Scheffer, 1951). The population data are well known to be from an ideal observation in an outdoor laboratory where the animals lived under small hunting pressure and were free of predator attack for 40 years; a definite number of animal were placed in the closed spaces at a definite time, after which the population showed singly peaked changes. The accuracy of the numbers was estimated to be about 10%. We also apply the model to the population change of white-tailed deer at the George Reserve of the University of Michigan (GRM) which showed a similar trend from 1928 to 1947 (O'Roke and Hamerstrom, 1948).

For the application, we need to fix one of three parameters, a , b , and X_0 , and we need to assume the presence of an indispensable resource for the animals. We may assume that it was lichen at least for the SPI herd. This is because lichen was considered to be the key forage for reindeer, especially in winter (Scheffer, 1951). The grass disappeared on SPI 40 years after the introduction of reindeer, which was regarded as the cause of the extinction of the reindeer. We may apply Eq. (3) here without adding any reproduction term for plant breeding since it was reported that recovery of the lichen range may take 15 or 20 years. A caribou is reported to eat 4.5 kg of lichen a day (Bandfield, 1996). We infer that real values of the consumption rate of the three deer herds are near to this value since they belong to the same family (a

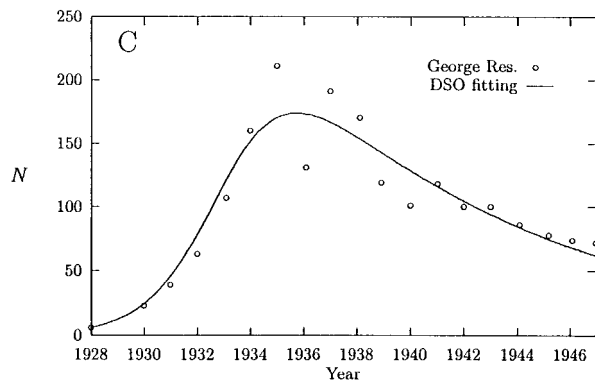
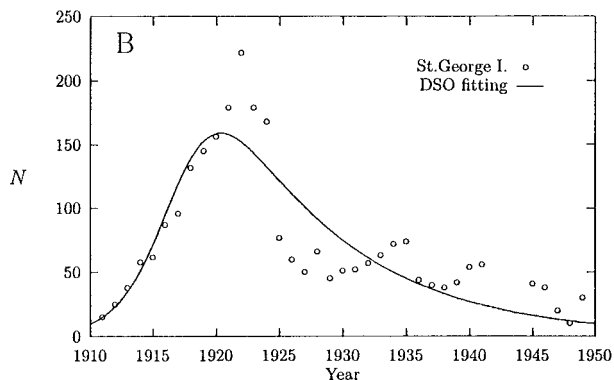
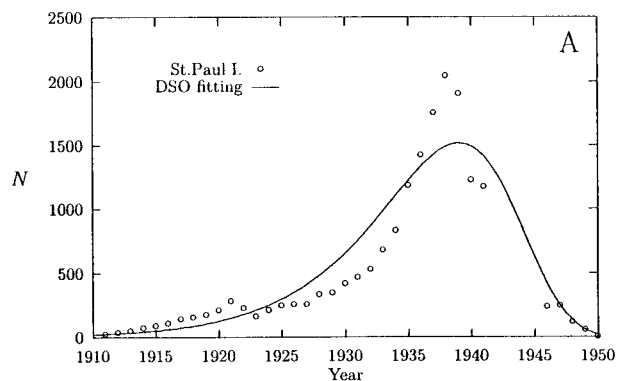


FIG. 2. Population curves obtained with Eqs. (6) and (7) in the text to fit the population records of the three deer herds. The nutritional efficiency (b), the initial stock of indispensable food (X_0), and the potential reproduction rate (r) which are defined in the text are optimized. (A) Reindeer on St. Paul Island (Scheffer, 1951); (B) reindeer on St. George Island (Scheffer, 1951); and (C) white-tailed deer in the George Reserve, Michigan (O'Roke and Hamerstrom, 1948).

TABLE I

Population Data of Three Deer Herds

Herd	Habitat area (acres)	N_0	N_m	$r(y^{-1})$	b (individual/ton)	X_0 (tons)	K_0
St. Paul Island reindeer	26,500	25	2046	0.182	0.111	37,000	4090
St. George Island reindeer	22,400	15	222	0.469	0.0512	4,460	229
George Reserve w.t. deer	1,200	6	211	0.740	0.0561	4,150	233

Note. The habitat area and the initial and maximum population sizes (N_0 and N_m) are from Scheffer (1951) and O'Roke and Hamerstrom (1948). The nutritional efficiency (b), the initial stock of indispensable food (X_0), and the reproduction rate (r) which are defined in text are obtained in this work after direct search optimization of the theoretical curve (Eqs. (6) and (7) in the text) to fit the population records in the references and shown with significant figures of three digits. The consumption rate of indispensable food (a) is fixed to be 1.64 tons per year per individual for the three herds. $K_0 (= bX_0)$ is the initial carrying capacity given in the text.

Japanese deer is reported to eat 11 kg of grass a day). As the choice of this value is not essential when considering the actual population, we use $a = 1.64$ tons a year per individual for the three herds.

The population change (N) of the SPI reindeer from Scheffer's table is shown in Fig. 2A with empty circles. To fit the curve of Eq. (7), we use direct search of optimization (DSO) for three parameters, r , b , and X_0 , and we obtain $r = 0.182$ per year, $b = 0.111$ individual per ton, and $X_0 = 37,000$ tons. We notice here some deviation of the curve from the data points which might be caused by changes in hunting effects or weather. We cannot clarify the reason at present, however. After a similar application of DSO to the population on SGI and that in GRM, the optimized curves are compared with the observed data in Figs. 2B and 2C. All parameters thus obtained are summarized in Table I together with the areas of three habitats and the respective initial and maximum population sizes.

Now we explain some characteristics of the population processes, referring to the figures and to Table I. The most significant result in Table I is that the initial stock X_0 on SPI is more than eight times larger than that on SGI although the land areas are almost the same. In the present model, the deviation of X_0 is proportional to that of a due to the scale invariance of the parameters mentioned above. However, this difference in the X_0 's is much more than can be caused by a probable difference in the a 's. Rather, this may correspond to an approximately 10 times larger N_m observed on SPI than on SGI and suggests that SPI was much more fertile than SGI. Scheffer remarked on some environmental differences between the two islands. Here we propose that the initial values of the carrying capacity are given by $K_0 = bX_0$ (data also included in Table I). K_0 is free from the effect of ambiguity of a . The significant difference between the

K_0 's of SPI and SGI in Table I also supports the above view. We find next that the net reproduction rate r of the SPI herd is much smaller than that of SGI which further is smaller than that of GRM. Values of r are free from the effects of a . A biological reason may exist for the differences in r , although we cannot explain it now. The b value of the SPI herd is about twice that of the SGI herd (and the GRM herd). However, this difference might be caused by any difference in possible a values.

Further, we find significant differences between population processes on SPI and on SGI (and in GRM): The population on SPI increased rather slowly and went extinct steeply after the maximum while that on SGI increased fast and decayed slowly. For the SPI herd, the ratio of the obtained r to the b value is very near to the a value, meaning that the curve fitting for SPI reindeer is attained with Eq. (6) or as the case $a = r/b$, as far as the a value is acceptable. In contrast with this, some similarities are found in the population processes of SGI

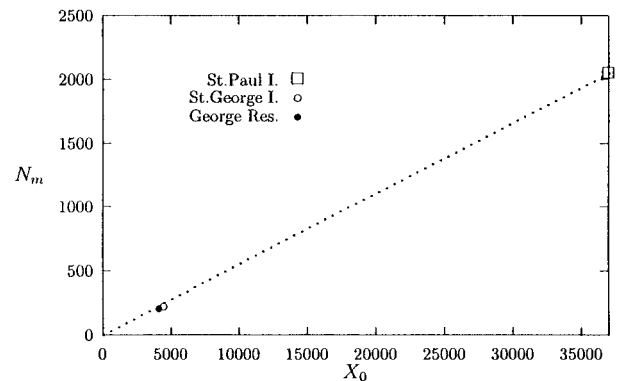


FIG. 3. The maximum size of deer populations observed (N_m) vs the initial amount of indispensable food (X_0) estimated in the text.

TABLE II

The Estimations of N_m/X_0 of Three Deer Herds

Herd	$N_m(\text{DATA})/X_0$	$N_m(\text{LNR})/X_0$	$N_m(\text{DSO})/X_0$
St. Paul Island reindeer	0.0553	0.0407	0.0409
St. George Island reindeer	0.0498	0.0352	0.0356
George Reserve w.t. deer	0.0508	0.0417	0.0419

Note. $N_m(\text{DATA})$, $N_m(\text{LNR})$, and $N_m(\text{DSO})$ are defined in the text. They are divided by X_0 , which takes the value corresponding to each herd in Table I.

reindeer and GRM white-tailed deer: r/b is much less than the assumed a for both herds, meaning that the fitting is realized with Eq. (7) or as the case $a < r/b$. In spite of the large difference in the areas of the two habitats, the two magnitudes of b are nearly equal to each other and the two X_0 's are too. Between the two habitats, the ecological characteristics for the deer should have been similar.

Now we discuss relations among observed and calculated population parameters. Inspection of Table I suggests no definite relation of r to N_m , X_0 , and the respective densities. r is presumably inversely related to N_0 . The observed N_m may have a linear relation to X_0 , which is clearly found in Fig. 3. We have shown a non-linear relation between N_m and X_0 in Eqs. (8) and (9). First, for the case $ab/r = 1$, Eq. (8) is approximated as $N_m \approx rX_0/ea$ since $aN_0/rX_0 \ll 1$ within the present range of parameters (e is the base of natural logarithms). Second, for the case of $ab/r \ll 1$ (the SGI and GRM cases), we rewrite Eq. (9) as $N_m = N_0(r/ab)^{r/(ab-r)} [1 - (1 - ab/r) N_0/bX_0]^{r/(ab-r)} (rX_0/aN_0 + 1 - r/ab)$. If $ab/r + bX_0/N_0 \gg 1$, we have $N_m \approx (r/a)(r/ab)^{r/(ab-r)} X_0$. This condition is fulfilled in the present ranges of the parameters. We then have a linearly increasing trend of N_m with X_0 for both cases. Concerned with the coefficients of the linear increase, we show the quantitative estimates of the ratio N_m/X_0 in Table II; $N_m(\text{DATA})$ is the maximum N , which was actually observed on SPI, SGI, or GRM. N_m (LNR) is estimated by using $N_m \approx rX_0/ea$ for the SPI case or $N_m \approx (r/a)(r/ab)^{r/(ab-r)} X_0$ for the SGI and GRM cases. Equation (8) or (9) gives us the full theoretical value of N_m , which is denoted by $N_m(\text{DSO})$. We may consider that these values of the coefficients are almost constant over the three herds, causing the linear relation between N_m and X_0 .

The minimum required a year-long grazing area of lichen for a reindeer was estimated to be 33 acres on SPI (Scheffer, 1951). This means that the carrying capacity per unit area was 0.030 and the carrying capacity of SPI

was 800 individuals (Dasmann, 1964). The peak densities (N_m/area , estimable in Table I) exceed 0.03 in two habitats, SPI and GRM, which were considered to be fluctuations over the carrying capacity. In our model, we postulate that the carrying capacity is not a constant but a changeable parameter which depends on environmental conditions, e.g., the quantity of indispensable forage for the animal. Referring to K_0 , the initial value of the carrying capacity defined above, we find that $N_m \leq K_0$ in Table I, a reasonable limiting relation of the maximum population to the maximum carrying capacity.

Finally, we compare the present model with the original Lotka–Volterra system (LVS) for predator–prey interaction. In fact, at a glance, the deer may be regarded as the predator and the lichen as the prey. The system is given by

$$\frac{dP}{dt} = -cP + \alpha PS \quad (10)$$

for the predator population size (P) and

$$\frac{dS}{dt} = kP - \beta PS \quad (11)$$

for the prey population (S) with the coefficients c , k , α , and β having their usual meanings (Borrelli and Coleman, 1996). When $k = 0$, this system becomes that of the ordinary differential equations of Kermack–Mckendrick type (KMS) and can reproduce a singly peaked process if the initial value of S is larger than c/α . However, the LVS or KMS includes as its essence an encounter term which is proportional to PS . This means that an encounter between two interacting species should take place with a constant probability uniformly throughout space and time (applicability of the mass-action law). Hence the system should be applicable to the case of thin populations of prey and predator. Our model has no such encounter term (see Eq. (3)) to impose such a limitation

on the population density. The estimated values of X_0 or X per unit area may be interpreted to be for a thin or dense population (or stock) of lichen (or forage) according to its magnitude. For the predator or deer, the present model assumes only intraspecific competition, as does the original logistic. Hence the estimated values of N_m and r may be for a dense population. Of course, effects of overcrowding can be discussed within LVS by introducing the S^2 and P^2 terms to it. However, adding new terms with new parameters may make the analysis more vague unless the parameters are determined by other methods. We should also note that the unimodal curves can be reproduced by a modified logistic equation with a term of integrated toxins for population (Small, 1987). However, the model has no explicit relationship with the resources for the population.

CONCLUSIONS

We have presented a simple mathematical model with which one can analyse singly-peaked population processes. Although simple, the model provides a good account of deer population dynamics by assuming a resource-dependent carrying capacity and by introducing two ecological parameters, the consumption rate of indispensable resources (a) and the nutritional efficiency (b), in addition to such traditional ones as the reproduction rate (r) and the initial stock of the indispensable resources X_0 . Here a and b can be in principle determined by observation. The model is soluble exactly as the original logistic is, providing mathematical benefits. It may be applicable to consumption of fertilizer by the plant (perfectly zero breeding of prey) and to the case of non-zero breeding of the prey by adding a breeding term for it in Eq. (3). Further we add that a population can go extinct steeply, or even suddenly, from its peak in the model. Breeding and extinction of many organisms should depend or should have depended on their access

to a finite amount of indispensable resources; the present model may be applied to such processes.

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