

A Predator–Prey Viewpoint of a Single Species Population

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The growth of a single species mammalian population in an environment with unlimited food, water, and nesting materials is modeled. The model provides for crowding effects by considering the population divided into a “young” group and an “old” group, with menopausal age the dividing criterion. The old group is viewed as a predator on the young prey and the classical predator-prey coupled differential equation system is used as the basic mathematical description. It is modified by introducing an Allee effect in the predator death rate to account for an observed decrease in predator death rate as predator density rises.

The five year history of an experimental colony of mice is used to evaluate five parameters of the model. The evaluated model exhibits excellent correspondence with its experimental data, in particular the instability which led to rapid growth and subsequent collapse of the experimental population. Each mathematical expression in the differential equation system is discussed in terms of its biological and/or social significance. The potential of considering non-linear interactions between age groups of a single species as a predator–prey effect is also discussed.

1. Introduction

In most studies of the growth of single species populations a mechanism for density dependence is incorporated to account variously for crowding effects, limited essential resource, carrying capacity of the environment, etc. A wide variety of deterministic and stochastic models have been based on such mechanisms. These models have been formulated using differential equations (Lotka, 1956), differential-delay (May *et al.*, 1974), difference equations (May, 1972), and integral equations (Pielou, 1969).

The early models were of two types:

- (1) Those which are amenable to analysis but ignored structural differences, such as age of organisms, between members of a population which are important in determining the dynamics of real populations; and
- (2) Age-structured models of the Leslie type (Leslie, 1945; Pielou, 1969), which incorporated age-specificity but were difficult to apply to populations in

which non-linear demographic parameters varied strongly with time or population density. Leslie (1948) extended his basic model to include a rather restrictive form of density-dependence (Beddington, 1974) and Cooke & Leon (1976) have developed more general treatments of density effects for age-structured populations. Oster & Takahashi (1974) and Beddington & Free (1976) have explored the effects of age structure on models of trophic interaction. However, many populations, particularly of higher vertebrates, may be regulated by interactions between age classes of conspecifics. Calhoun (1973) has described the growth of such a laboratory population of house mice. The model discussed in this paper combines a differential equation model incorporating density-dependence with a first approximation of age structure.

2. The Mouse Population

The population chosen to test the model was the mouse colony of Calhoun (1973). Initially four pairs of approximately 30 day old Balb C strain house mice were introduced into a square enclosure 2.57 m on a side and 1.37 m high. Nest boxes, food hoppers and water bottles were fastened to the walls of the enclosure expanding the usable space beyond that of the floor. The compartmentalization of the pen into nesting areas, feeding areas etc., was designed to create an optimal environment (in a fixed space) for the animal's prosperity, corresponding to man's best understanding of its social behavior. Details of the environment have been described by Calhoun (1973). The population was allowed to grow with minimal disturbance for 1590 days. During this time, the mice were supplied with *ad lib* food, water, and nest material and there were no observed diseases or predators (Calhoun, 1973). Each mouse was weighed and examined every 21 days for the first 400 days of the study and about every 40 days thereafter. Mortality of young mice associated with handling (Calhoun & Slade, in prep.) was probably the only departure from maximum reproduction and survival in this population. Because of the structure of the environment and surplus of resources, the only influences on population growth were socially related (Calhoun, 1973).

The population grew rapidly at first but began to exhibit pathological symptoms as crowding increased. Among the observed symptoms were smothering of the young, inadequate weaning, and the diversion of male energies from the sexual to agonistic behavior concerned with territoriality. A severe decrease in copulation frequency was evident as the density of animals increased. Eventually mating stopped entirely, the birth rate vanished, and natural mortality began to reduce the population (dead animals were removed daily). When the population returned to a level that had been prosperous in

the initial phase of the experiment, the birth rate did not recover because most of the females were beyond the reproductive age.

Calhoun (1973) has given a general description of the changes in mouse numbers through time. The population grew from 8 to over 2200 mice and then began to decrease at an accelerating rate. Our data differ from those of Calhoun only in our separating the mouse population into two groups—those 560 days of age or younger and those greater than 560 days old. We estimated numbers in the two groups at 23 day intervals through the entire study. Dates of birth and death were estimated to the day by Calhoun and his coworkers so population estimates are reasonably accurate even when falling between census dates.

3. Model

Our approach is to view the population as divided into “young” and “old” groups, with the estimated average age of female menopause (560 days) as the partitioning criterion (Calhoun, 1973) and to model population growth by coupled differential equations as suggested in Ch. 12 of Keyfitz (1968). The older group, in its role as competitor for the limited space with attendant negative influence on the production and maturing of young, is considered a predator. The younger group, whose well-being and prosperity is limited by the density of the predator, is viewed as prey. However, instead of using the system of linear differential equations of Keyfitz (1968) we used Lotka’s (1956) classic coupled non-linear differential equations (Lotka, 1956). With this model both populations show periodic variations with amplitudes dependent on the displacement of the initial populations from a neutrally stable equilibrium (Pielou, 1969).

The classical model expresses predator mortality in the absence of prey as a linear function of predator density y ,

$$\frac{dy}{dt} = -ky. \quad (1)$$

Data taken from the latter phases of the experimental population, after the “young” group had vanished, exhibited a convexity in the logarithm which suggested the alternate mortality formulation

$$\frac{dy}{dt} = -ky^{1-\varepsilon}, \quad \varepsilon \text{ small, positive.} \quad (2)$$

The solution $(y_0^\varepsilon - \varepsilon kt)^{1/\varepsilon}$ to (2) approaches the exponential solution to (1), $y = y_0 e^{-kt}$ as ε approaches 0 and, for fixed $\varepsilon > 0$ intersects the exponential at a time T_0 when the model populations have decreased to less than unity (see

Appendix). Therefore, in the time range of interest for population studies, populations modeled by (2) decrease more slowly than their exponential counterparts.

Model Parameters

To adduce the relationship between the experimental data and the model proposed we break down population history into three non-overlapping phases:

(A) PHASE I

Only the younger group is present; the population $x(t)$ grows exponentially with rate k_1 , i.e. $x(t) = x(0) e^{k_1 t}$. The rate k_1 was derived from a regression of the appropriate data and has value 0.0075 day^{-1} .

(B) PHASE II

Both groups coexist. The interaction is realized as the young pass the critical age. The passing of individuals from the younger group to the older, the repressive effect of the older on the population of young and the shrinking of the reproductive age span from increased crowding, is represented as a predator-prey interaction. In view of the observation concerning mortality, the differential-equation formulation is

$$\frac{dx}{dt} = k_1 x - k_2 xy, \quad \frac{dy}{dt} = k_3 xy - k_4 y^{1+\epsilon} \quad (3)$$

Justification of the quadratic interactive term is taken up in the discussion.

(C) PHASE III

Only the older group survives. The extinction of the group is governed by

$$y(t) = (y_0^\epsilon - \epsilon k_4 t)^{1/\epsilon} \quad (4)$$

and the parameter choices $k_4 = 0.0127 \text{ (mice)}^{0.8} \text{ day}^{-1}$, $\epsilon = 0.08$ optimally conform to the experimental data. The interaction parameters k_2 and k_3 were evaluated from data collected in Phase II of the population history.

The variable metric extension of the steepest descent algorithm (Davidon, 1959) was employed to minimize the difference between model simulations and population data with respect to parameters k_2 and k_3 . Optimal values obtained were $k_2 = 0.63 \times 10^{-3} \text{ (mice)}^{-1} \text{ day}^{-1}$, $k_3 = 0.295 \times 10^{-4} \text{ (mice)}^{-1} \text{ day}^{-1}$. Experimental data together with model solutions for the

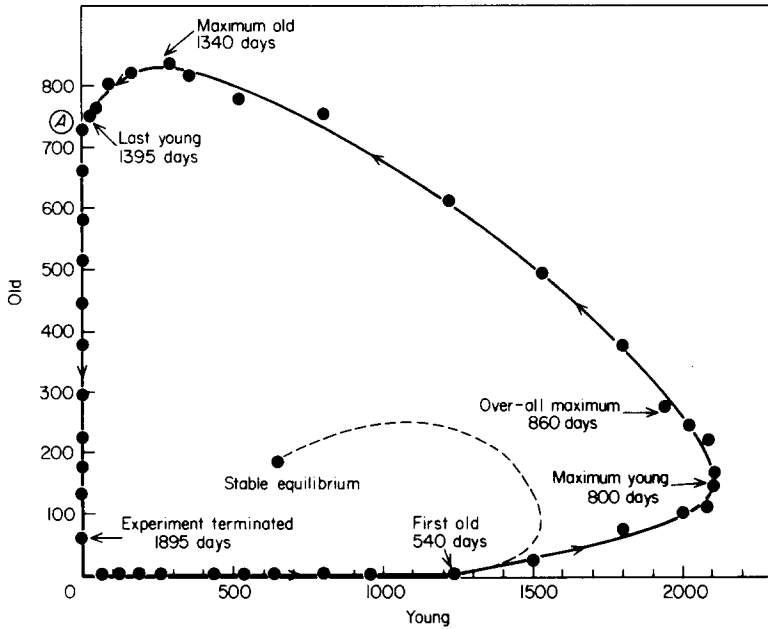


FIG. 1. Comparison of experimental data with model simulations. Abscissa: Population of younger age group. Ordinate: Population of older age group. ●: Experimental data (46 day intervals). —: Model simulations for optimal parameter values: $\epsilon = 0.08$, $k_1 = 0.0075 \text{ day}^{-1}$, $k_2 = 0.63 \times 10^{-3} (\# \text{ old age group})^{-1} \text{ day}^{-1}$, $k_3 = 0.295 \times 10^{-4} (\# \text{ young age group})^{-1} \text{ day}^{-1}$, $k_4 = 0.0127 (\# \text{ old age group})^{0.08} \text{ day}^{-1}$. - - -: Typical behavior of rejected model with linear predator gain.

above parameter values are shown in Fig. 1. The gap in the upper left-hand corner represents model transition from Phase II to Phase III. Figure 2 shows the time dependence of the optimized model solution $x(t)$, $y(t)$.

It is of interest to observe that an effect of positive ϵ is to destabilize the population trajectory in its progression around the stationary point

$$x^* = \frac{k_4}{k_3} \left(\frac{k_1}{k_2} \right)^{-\epsilon}, \quad y^* = \frac{k_1}{k_2} \quad (\text{Lotka, 1956}). \quad (5)$$

When $\epsilon = 0$ the trajectory is neutrally stable with population amplitudes depending on initial populations, and the eigenvalues of the stability matrix are purely imaginary. Positive ϵ provides the eigenvalues with a positive real part and the trajectory spirals away from the stationary point.

Excellent accounts of graphical stability analysis of various predator-prey interactions and the evolution of the predator isocline appear in the literature (Rosenzweig & MacArthur, 1963; Rosenzweig, 1973).

null cline analysis shows that the figure must have been produced using $k_2=0.62e-4$

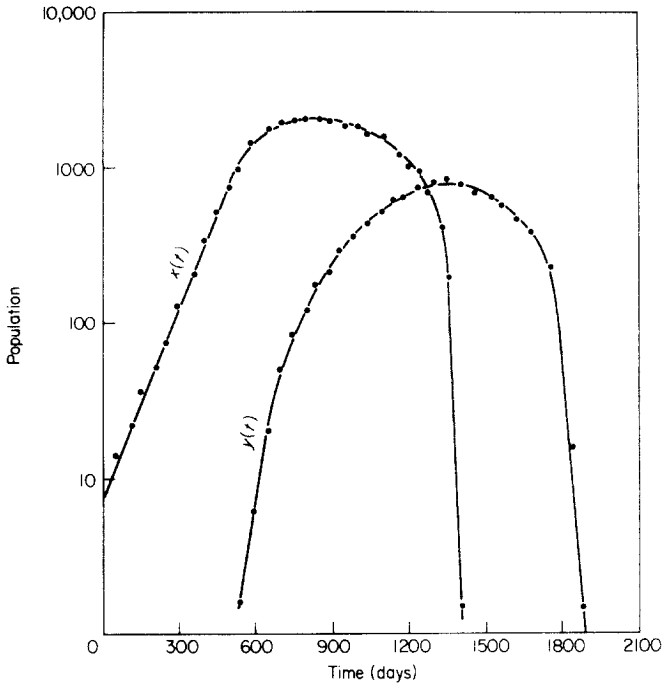


FIG. 2. Time dependence of model solutions. Abscissa: Population (log scale). Ordinate: Time (days, arithmetic scale). •: Experimental data. $x(t)$ young population, $y(t)$ old population.

5. Discussion

The choice of 560 days of age as a dividing point between young and old roughly separates the productive and unproductive females. This age is about midway through what Calhoun (1971) termed the adult stage of life, being preceded by preweaning, juvenile, subadult, and establishing adult and followed by declining and senescent stages. The parameters ϵ , k_1 , k_2 , k_3 , k_4 were found to be relatively insensitive to changes in the boundary defining young and old. In Phase II the quadratic interaction terms allow of three biological interpretations.

- (a) Transition of individuals from younger to older group.
- (b) Direct repression of reproductive rate by deteriorating maternal behavior.
- (c) Early sexual withdrawal of young mice.

As the population enters Phase II, about 500 days after colonization, the

social pressure exerted by the old on the young is expressed as a linear depression of the birth rate of the young

$$\frac{dx}{dt} = x(k_1 - k_2 y), \quad x(t) = \# \text{ of young.}$$

The old age group, in turn, gains in proportion to the number of young present. If a simple linear mechanism is postulated for the interaction

$$\frac{dy}{dt} = k_3 x - k_4 y, \quad y(t) = \# \text{ of old,}$$

the model predicts an approach to a stable nonzero equilibrium, shown typically as the dotted curve in Fig. 1. Such behavior is at variance with the observations of the population and no attempt was made to evaluate the interactive constants k_2 and k_3 . The model was rejected in favor of quadratic predator gain:

$$\frac{dy}{dt} = k_3 xy - k_4 y.$$

In addition, observation of the population in its senescent Phase III, after all the young have disappeared, has resulted in a further attribute of the model for the old group; the nonlinear death rate.

A heuristic explanation of the choice for the quadratic predator gain derives from consideration of the time progression of the age structures of the two groups.

At about 500 days into the experiment, when the first old appear, the age distribution of the young group is exponential. As the density of the old group increases, the birth rate of the young group is depressed and the density of young shows an age distribution whose mode propagates toward higher age. Eventually this maximum age reaches the boundary age between old and young and the number of young "eaten" decreases, causing the pressure depressing the birth rate of the young to decrease. The number of very young in the young group consequently increases again and a second age wave begins to propagate through the young group. The total density of the young again increases in response to the age wave. Periodic fluctuations are indicated. This is typical of classical predator-prey behavior when the death rate of the predator is linear. These considerations led us to the quadratic choice for the predator consumption interaction.

In the early and middle stages of Phase II, when the density of the older cohort was relatively low, considerable social unrest was observed. Among the components contributing to the unrest were a preoccupation with territorial competition and an instability in the normal polygynous social system.

Although the killing of aging males by challengers was responsible for most of the high per capita death rate at this stage of social development, a corresponding high death rate was noticed in the females. The female deaths were due both to direct attack and to exclusion from nests, feeding areas, etc. (mostly by other females).

As the density of the older group increased, traditional social behavior began to deteriorate and an increasing proportion of the group became asocial. These asocial mice spent much of their time eating, sleeping, and grooming themselves, but eschewing normal sexual and territorial activities. They were termed "beautiful ones" by the scientists engaged in the experiment (Calhoun, 1973), and their chances of survival were greater than that of normal mice. We believe that the change in social structure brought about by density pressure accounts for the observed convexity in the logarithm of the older population and, equivalently, a decreased per capita death rate in the latter stages of Phase II and in Phase III.

The observed increase in per capita death rate in the latter stages of Phase III is again the result of an increasing average age within an age group. In Phase III there is no input to the older group from the younger and, as the average age increases toward the natural animal life span, there is a consequent increase in the per capita death rate. The age structure of the model is of course primitive, but does provide an illustration of the application of a traditional model of trophic interaction to a single population. Conceptualization of population dynamics as the result of the interaction of two or more age classes is a potentially valuable modeling tool, and many natural mammalian populations may be regulated by constraints of older individuals upon reproduction or survivorship of younger age classes (Sadler, 1965; Healey, 1976; Slade & Balph, 1974; Dunford, 1977). In as much as aging is a natural process in all populations the dynamics of many populations may follow the general scheme of old "preying" on young. The details of the coupled differential equations will probably vary with the situation. For example the use of a multiplication interaction term for the effect of young on old and the exponent $(1 - \epsilon)$ both were the result of changes in the age structure within an age group and so may well be unique to Calhoun's data. The inclusion of $(1 - \epsilon)$, without restriction on the value of ϵ , may be a desirable modification of the classical predation model because it allows for interaction among the predators, and ϵ is a parameter to be estimated from the data. However, the general form of the impact of young on old is a more complicated function of the young and its choice must be based on the experimenter's conception of the problem, and the specific dynamics of the population. However, we anticipate that extension of the modeling philosophy in which age structures are incorporated with nonlinear

population effects, such as predation and population-dependent death rates, will become a powerful predictive tool in population dynamics.

APPENDIX

We claim that the positive solution $t = T_0$ of

$$y_0 e^{-kt} = (y_0^e - \varepsilon kt)^{1/\varepsilon} \quad (\text{A1})$$

or

$$y_0^e = \frac{\varepsilon kt}{1 - e^{-\varepsilon kt}}. \quad (\text{A2})$$

At the unique positive time T_0 obtained by solution of the above transcendental relation both model populations have been decreased to

$$\left\{ \frac{\varepsilon k T_0 e^{-\varepsilon k T_0}}{1 - e^{-\varepsilon k T_0}} \right\}^{1/\varepsilon}. \quad (\text{A3})$$

The claim follows by observing that the function

$$\frac{x e^{-x}}{1 - e^{-x}} \quad (\text{A4})$$

has positive limit unity at the origin and decreases monotonically through positive values to zero as x increases through positive values.

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