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EFFECTS OF POPULATION DENSITY ON GROWTH RATES
OF ANIMAL POPULATIONS*

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Abstract. The growth rate of a population is defined as the change in numbers per unit population at the time of the change per time ($r_t = dN/N_t dt$). The objective of this study was to determine whether the growth rate is or is not a function of the population density.

In most mathematical models of populations whose changes resemble those of actual populations, the growth rate is a decreasing function of population density. The relation between the growth rate and population density of actual animal populations was determined from the records of 111 different populations representing 71 species. Growth rates were calculated for each interval of time; regression methods were then used to calculate a coefficient of growth rate on population density and to test whether or not this coefficient was significantly different from zero.

Of the 71 species represented, 7 were eliminated from further analysis because their census records were not significantly different from a series of random numbers, 42 had negative coefficients significantly different from zero, 21 had coefficients not significantly different from zero (all but one of these estimated coefficients were negative), and one, the world's human population, had a positive coefficient significantly different from zero. There were no differences between taxonomic groups (insects, other invertebrates, fish, birds, mammals). The primary conclusion is that in most animal species a population's growth rate is a decreasing function of density. This

explains the relative stability of animal populations, which rarely continue to increase at rates their fertility would allow and rarely decrease to extinction.

Tentative conclusions are presented regarding the processes regulating population numbers. Populations of herbivorous insects at low and moderate levels are regulated by predators and parasites causing mortality that is an increasing function of density. Favorable conditions may allow an increase in insect numbers so rapid that the population temporarily escapes regulation by its enemies. Nonterritorial species of vertebrates are normally controlled by predation and, when that fails, by competition; in both cases juvenile individuals are most affected. In territorial vertebrates competition for suitable territories determines the size of the breeding population. Populations of vertebrate species (excepting man) are in general regulated by the production of adult individuals being a decreasing function of population density.

INTRODUCTION

Changes in size of animal populations usually follow seasonal and other variations in the environment. An important question is: Are these changes determined solely by the environment, or does the density of the population itself affect these changes? This study aimed at determining the relation between the rate at which a population grows or declines and the population density. Two approaches were used: (1) an examination of mathematical models of populations, and (2) an analysis of the records of many different animal populations. In the second approach, data were obtained from the literature and statistically analyzed to test whether the growth rate of each population was or was not a function of population density.

The change in numbers of a population with respect to time, dN/dt , equals rN , where N is the number in the population and r is the rate of change per unit population: $r = dN/Ndt$. For conciseness r will hereafter be called a population's "growth rate," even though it can measure a decrease as well as an increase in population size. The growth rate equals the conventional birth rate (number born per unit population per time) minus the death rate (number died per unit population per time), and the growth rate will be positive, negative, or zero depending on the relative values of its two components.

If r is a positive constant, the population will grow exponentially; if it is a negative constant, the population will decline exponentially; and if it is zero, the size will not change. Since

populations never do any of these for an indefinitely long period, the value of r must vary from time to time. If its value is determined solely by the environment, r is independent of the population density. Otherwise r is some function of the population density. If r is a decreasing function of density, declining as the density increases as in Fig. 1A, and if the environment is relatively stable for a sufficiently long time, the population will stabilize at the density where r is zero. If r is an increasing function of density, as in Fig. 1B, the population will increase to infinity or decline to extinction, again assuming that the environment does not change.

This research was completed while I was working in the Radiation Ecology Section, Health Physics Division, Oak Ridge National Laboratory; members of this section helped me to clarify many of the ideas expressed in this paper. Most of the statistical calculations were performed by the Mathematics Panel of the Oak Ridge National Laboratory.

RATES IN MATHEMATICAL MODELS

Mathematical models for animal populations present the population size, N , as a function of time, or the derivative of this with respect to time, dN/dt . The growth rate of the population, r , equals this derivative divided by N . The relation between r and N in these equations can be determined by differentiating r with respect to N . If the resulting derivative is negative, r is a decreasing function of N as in Fig. 1A; if it is positive, r is an increasing function as in Fig. 1B; if it is zero, r is independent of N . The only models

examined here are those which have been found to describe the changes in actual populations.

The logistic equation, widely used in population studies, is discussed by Allee et al. (1949, Ch. 21), who give numerous examples of this equation fitted to the growth of actual populations. The derivative, dr/dN , of the logistic equation is negative, showing that the growth rate decreases with increasing N , as in Fig. 1A. Several persons (Gause and Witt, 1935; Smith, 1963b) have modified the logistic for one reason or another, but in these modified forms r remains a decreasing function of N .

Neyman, Park, and Scott (1958) constructed mathematical models for Tribolium populations based on extensive experiments in rearing these beetles; one model is for the numbers of a species living alone and another consists of two equations for two species of Tribolium living together. Nicholson and Bailey (1935) developed equations for the numbers of a host and its parasite; the first part of the oscillating curve predicted by these equations was followed by seven generations of a host-parasite population (DeBach and Smith, 1941). In all of these equations the derivative of the growth rate with respect to numbers is negative. Utida (1957b) presented different equations which predicted the course of his oscillating host-parasite populations. The derivative for the parasite population is negative; that for the host population is positive or negative depending upon conditions other than the density of the host.

In summary, in mathematical models which have been shown to parallel the changes of actual populations, the derivative of r with respect to N is usually negative, i.e., the growth rate is a decreasing function of the density.

RATES IN ANIMAL POPULATIONS

Few persons have appraised the effect of population density on population growth rates. Errington (1945, 1954) plotted per cent gain in bobwhite and muskrat (scientific names are listed in Appendix B) populations as a function of density and obtained curves showing smaller rates of increase with higher densities. Smith (1961, 1963a) found that in populations of thrips the growth rate over a month was negatively correlated with the population density at the start of the month. He also (1963b) showed that cultured daphnia populations possessed growth rates that were non-linear, decreasing functions of density.

For this part of the study, I obtained from the literature the records of many different animal populations, calculated the growth rates from the recorded numbers, and tested the hypothesis that these rates were independent of the population densities.

Sources of data

The data were obtained from censuses of animal populations that met the following requirements: (1) actual counts of a population

inhabiting a definite space so that density was directly proportional to the number, or a reliable index of the density of the population; (2) counts or estimates made periodically so that the growth rates were based on constant intervals (Δt); (3) a sufficiently long series of such counts to enable a meaningful test despite random variations.

About half of the populations reported in Table I were censused. For the remainder an index of density was available. This index for the fish populations was calculated from the annual commercial catch corrected for variations in fishing intensity. Fur returns were used as indexes of density for some northern mammals; Keith (1962) gave reasons for believing that these were valid indexes of density when the returns came from constant geographic areas where fur prices had not failed. Hunting kill statistics were not considered to be a reliable index of density because of variations in hunting pressure with periods of war, changing economic conditions, and changing recreational habits. Exceptions to this were some bag records made on British game preserves which had been managed intensively for decades; Keith (1962) believed that these were reliable indexes of density. Fur returns from the Hudson Bay Company and game bag records for some British preserves supplied the longest series of records for this study.

I found records of 111 populations, representing 71 species, that met the requirements of this study.

Methods of analysis

A population at time t has a size N_t . Its growth rate proportional to population size at this time is r_t . Expressing this rate in terms of the measured change in numbers, N_t , over a definite period, Δt ,

$$r_t = \frac{\Delta N_t}{N_t \Delta t} = \frac{N_{t+1} - N_t}{N_t \Delta t} \quad (1)$$

Hypothetically, r_t is a function of the environmental conditions and the density of the population at this time.

Let: $a \equiv$ a constant

$E_t \equiv$ the suitability of the environment at time t
(climate, predators, food, etc., but not numbers
of the same species, all combined into one value).

$b_E \equiv$ the coefficient of regression of r_t on E_t .

$N_t \equiv$ the number in the population at time t ; the density
will be directly proportional to N_t if the popula-
tion inhabits a definite area or volume.

$b_N \equiv$ the coefficient of regression of r_t on N_t .

$\epsilon \equiv$ a random variable (the difference between an actual
 r_t measured as $\Delta N_t / N_t \Delta t$ and an ideal r_t , a function
only of E_t and N_t and the parameters a , b_E , and b_N).

$$r_t = a + b_E E_t + b_N N_t + \epsilon \quad (2)$$

E_t is unknown, but the following possibilities exist:

1) E_t is constant. This could be true in short term studies and in cultures of animals where physical conditions are regulated and food is constantly renewed. It is obviously not the case in most natural situations. If E_t is constant, $(a + b_{E_t}E_t)$ is a constant and equation (2) becomes

$$r_t = a' + b_{N_t}N_t + \epsilon \quad (2a)$$

2) E_t fluctuates randomly so that there is no correlation between successive values of E_t . If the successive values of E_t are independent, $b_{E_t}E_t$ can be considered as part of ϵ and equation (2) becomes

$$r_t = a + b_{N_t}N_t + \epsilon \quad (2b)$$

3) For many species periods of abundance alternate with periods of scarcity (e.g., rainy and dry seasons). In such cases we can assume that E_t has one value, E_h , during periods of high numbers and another, E_s , during periods of scarcity. Let $a + b_{E_h}E_h = a_h$ and $a + b_{E_s}E_s = a_s$, then equation (2) becomes two equations:

$$\begin{aligned} r_t &= a_h + b_{N_t}N_t + \epsilon, \text{ when populations are high;} \\ r_t &= a_s + b_{N_t}N_t + \epsilon, \text{ when populations are low.} \end{aligned} \quad (3)$$

This idea could be applied to more than two population levels, but that is not attempted in this paper.

The question of whether r_t is or is not a function of population density was answered by the following argument and procedure. In a population inhabiting a definite space and censused at regular intervals, ΔN_t equals N_{t+1} minus N_t . The density is directly proportional to N_t and Δt can be called 1. The record of population censuses provides a measure of r_t (equation 1) for each N_t except the last; the number of paired values of r_t and N_t is one less than the number of censuses of the population. If the environment fits either possibility (1) or (2) described above, equations (1) and (2a) or (2b) can be combined into the regression equation

$$r_t = \frac{N_{t+1} - N_t}{N_t} = a \text{ (or } a') + b_N N_t + \epsilon \quad (4)$$

If the environment has changed as hypothesized above in possibility (3), the same procedure can be followed except for calculating two regression equations (equation 3) with the same coefficient, b_N .

The null hypothesis to be tested is that $b_N = 0$. If the null hypothesis is accepted, r_t is considered to be independent of N_t . If the null hypothesis is rejected, r_t is a decreasing function of N_t (Fig. 1A) if b_N is negative, or an increasing function (Fig. 1B) if b_N is positive.

Linear regression methods were used to estimate b_N for each species listed in Table I. When two or more censuses were available for one species, a single weighted mean coefficient (weighted by the inverse of the variances of the separate censuses) was calculated for the species. To test the null hypothesis, the distribution of Student's t was used as a test of significance.

In the above discussion, r_t was assumed to be a linear function of population size. Smith (1963b) has shown that in Daphnia magna the population growth rate is a non-linear, decreasing function of density (Fig. 1C). Ricker (1954) hypothesized a series of "reproduction curves" from which r_t can be calculated; the curve which he considered best fits the data from a number of fish and invertebrate populations has the non-linear, decreasing relation between r_t and density shown in Fig. 1D. It can be seen from Figs. 1C and 1D that these curves can be approximated by straight lines which will indicate correctly that r_t is a decreasing function of density. Therefore for the purposes of this study, r_t can be assumed to be a linear function of density.

Before performing the regression analyses, it was necessary to prove that the values of N_t for each population are serially correlated or are non-random, because a series of random numbers analyzed by the method used for the populations will produce a b_N significantly different from zero. The reason for this result is that if N_{t+1} is independent of N_t , for each N_t the expected value of N_{t+1} is its mean value, $\overline{N_{t+1}}$. Then $r_t = (\overline{N_{t+1}} - N_t)/N_t = \overline{N_{t+1}}/N_t - 1$. Since $\overline{N_{t+1}}$ is a constant, this is the equation of a hyperbola, and a regression of r_t on N_t will necessarily result in a value of b_N different from zero. If on the other hand N_{t+1} is correlated with N_t , b_N will be different from zero only if $\Delta N_t/N_t$ changes approximately linearly with changing N_t .

Each series of population counts was tested for non-randomness

by the method of runs. Any in which the probability of randomness was not less than 5% was eliminated.

To enable comparisons of the relative sizes of the coefficients (b_N) among the different species, the coefficients must be adjusted for several factors, because the absolute value of b_N depends upon the length of the time interval between censuses, the number in the population, and some relation between the animals' size and habits and the effect of density.

Adjusting b_N to the generation time of the species gave values of the same relative size for species censused at different intervals. Generation time is here defined as the age at which a female usually first reproduces. The generation times included in Table I were compiled from a variety of sources.

$$b_N \text{ for generation time} = b_N \text{ for } \Delta t \times (\text{generation time})/\Delta t \quad (5)$$

Each population censused was believed to inhabit a constant area or volume so that the population density was proportional to its numbers. In most cases the actual space inhabited was unknown, but it was probably proportional to the mean size of the population, \bar{N} ; i.e., area = $k\bar{N}$. Let D_t be the population density at time t and b_D be the coefficient of regression of r_t on D_t ; then

$$D_t = N_t/\text{area} = N_t/k\bar{N}$$

$$r_t = a + b_N N_t + \epsilon = a + b_D D_t + \epsilon = a + b_D (N_t/k\bar{N}) + \epsilon$$

$$b_N \bar{N} = b_D/k \quad (6)$$

This coefficient, b_D/k , is independent of the size of the population on which the regression is based and is characteristic of the species. An attempt to evaluate k did not add any meaning to the value of the adjusted regression coefficient, so the coefficients reported in Table I have been adjusted only for generation time and the mean size of the population. This adjustment of b_N , the coefficient of regression in equation (4), is summarized in a combination of equations (5) and (6):

$$b_N \times (\text{generation time})/\Delta t \times \bar{N} = b_D/k \quad (7)$$

Results and discussion of results

The results of the regression analyses are presented in Table I. For each species the table contains information on the populations and on the censuses or other measurements. The regression coefficient, b_D/k , has been adjusted by equation (7) for generation time and the size of the population censused. The probability of the result under the null hypothesis (the regression coefficient equalling zero) is in the last column. The populations eliminated because their records were not significantly different from a series of random numbers are listed at the end of the table.

The results in Table I were obtained by using equation (4), based on the assumption that the environment either was constant or varied in a random manner. Equations (3) and the associated explanation shows how it is possible to allow for two levels of the environment, and this equation was used for two species. The number of thrips

(Davidson and Andrewartha, 1948) increased each year to a high level during the Australian spring and then dropped to a low level during approximately ten months of drouth and low temperatures. The starling population inhabited an area where the death of many trees beginning about the sixteenth year of the series (Kendeigh, 1956) produced many more nesting sites and a period of relative abundance of these birds. For each of these records two regression equations were calculated with the same coefficient of regression but with different constants representing different levels of the environment. The regression coefficients for the thrrips calculated in this way is -0.278 with the probability of this under the null hypothesis being less than 0.001 ; that for the starling is -0.738 with the probability being less than 0.001 . Thus these regression coefficients are very significantly different from zero while those calculated from a single regression are not so (see Table I). This procedure was used only for these two species; for all the others the coefficients as calculated by a single equation were significantly different from zero (at the 0.05 level or better) or there was no direct evidence of environmental changes to justify using equation (3).

Some of the populations for which the coefficient is not significantly different from zero exhibited characteristics helping to explain the lack of significance. The wax scale insect and the four lepidopterous insects showed marked and occasionally very sudden changes in population size; the causes of these changes are not known. The

blowfly had a time lag between population density and the response to density, resulting in oscillating numbers (Nicholson, 1954). The lake trout population became almost extinct with a sudden and accelerating decline in numbers (Eschmeyer, 1957).

The results in Table I are summarized in Table II. Of the 64 species remaining after 7 were eliminated, 42 species had coefficients that were significantly different from zero and were negative; the thrrips and starling, for which the use of equations (3) as described above produced a coefficient significantly different from zero, are counted here. Only one, the human population of the world, which has been increasing at a greater rate with the increase in population density, has a coefficient that is significantly positive. Furthermore, of the 21 species for which the regression coefficient did not differ significantly from zero, only one did not have a negative estimated value (see Table I). Population rates of change are usually, therefore, a decreasing function of population density; as can be seen from Tables I and II, this conclusion applies to animals which are taxonomically very different.

Changes between spring and fall

Spring and fall censuses over a number of years were made for the four species listed in Table III, enabling a test of whether or not the population rate of change is a function of density during a period of increase, from spring to fall, and during a decrease, from fall to spring. The procedure is the same as that described for

equation (4) except that, when considering spring to fall changes, N_t becomes the number in spring and N_{t+1} the number the following fall; there is a parallel procedure in studying fall to spring changes. In adjusting the regression coefficient by equation (7), the generation time for all four species is one year, Δt is six months, and \bar{N} is the average spring population.

The results of the regression analyses are shown in Table III and are the same for all four species. For the spring to fall changes, the coefficient with respect to density is negative and significantly different from zero; for the fall to spring changes, the coefficients are not significantly different from zero. Possible explanations for the seasonal differences are discussed in the following section.

CAUSES OF POPULATION CHANGES

The analyses described in the preceding sections have shown that in most of the species tested the population growth rate is a decreasing function of density. Different ways of saying the same are (1) that as a population increases, its growth rate decreases, or if it is declining the negative rate increases toward zero, so that a curve depicting its rise or fall will flatten as it approaches a certain level; or (2) that as a population becomes more dense the probability of a further increase becomes less and that of a decrease becomes greater, and vice versa. The net result is that population numbers tend to remain stable, rarely increasing to excessive numbers and rarely decreasing to extinction. It is true that many animal populations

in constant environments do fluctuate in size, but fluctuation within limits is a degree of stabilization. Many fluctuations or oscillations of animal populations result from a delay or time lag in the response of growth rate to density (Frank, 1960; Wangersky and Cunningham, 1957).

My purpose now is to discuss the causes of population change, the processes that affect the size of a population, to determine which are responsible for the growth rate being a decreasing function of density.

I am avoiding the use of the term "density-dependent factor" which has been used frequently in connection with this subject but with different meanings by different ecologists; see Macfadyen (1963, p. 152-157) for a review of the literature concerning this term. The phrase "increasing (or decreasing) function of density" is explicit and is used here for any change whose rate increases (or decreases) with increasing population density, and for the processes causing such a change. The term "density-independent" is used in the absence of any relation between rate and density.

The growth rate equals the birth rate minus the death rate. If the growth rate is a decreasing function of density and only the birth rate varies, the birth rate must also be a decreasing function of density. Ecologists often assume that each species has a potential reproductive rate determined by its physiology and life history, and that environmental factors reduce the actual rate to something below the potential. These factors reducing the birth rate at higher densities must then be operating as increasing functions of density. If, on the

other hand, only variations in the death rate are producing the changes in the growth rate, death rates are increasing with greater population density and so must the effectiveness of the processes producing the mortality. In summary, the growth rate is usually a decreasing function of density, but the causes of population change operate as increasing functions of density.

The statistical analyses of population changes do not give any clue as to which processes are producing the changes, except that in four species (Table III) changes that were functions of density occurred only between spring and fall and therefore the processes must be confined to that season. The most frequently suggested processes that may operate as increasing functions of density are competition, predation, and disease.

Competition results when the supply of some resource is inadequate for the population, or if interference or struggle for a common resource results in harm to individuals. Competition is obviously an increasing function of density. Examples of scarcity of a resource, usually food, limiting a population, lowering fertility, or increasing mortality are many (Andrewartha and Birch, 1954, p. 368-376; Andrewartha and Browning, 1961; Armstrong, 1964; Gibb, 1960; Klomp, 1964; Lack, 1954, Ch. 7 and 11; Slobodkin, 1954). Among vertebrates, competition for food frequently results in higher mortality of juvenile individuals rather than of adults; examples of this are known for fish (Beverton, 1962; Ivlev, 1961), for owls (Southern, 1959), for voles (Hoffman, 1958), and for deer (Leopold, Sowls, and Spencer, 1947).

Individuals of some species defend a territory against encroachment by other individuals, and in these territorial species the amount of suitable habitat may be a limiting resource. Examples of vertebrates where the size of the breeding population appears to be limited by the number of suitable territories are golden eagles (Brown and Watson, 1964), red grouse (Jenkins, 1963), titmice (Kluyver and Tinbergen, 1953), chaffinches (Glas, 1960), song sparrows (Tompa, 1962), several bird species nesting in the spruce-fir forest (Hensley and Cope, 1951; Stewart and Aldrich, 1951), and muskrats (Errington, 1946). Dragonflies (Odonata) offer one example of this phenomenon in insects (Moore, 1964).

The amount of suitable habitat for a territorial species may limit the population in another way. Errington (1946, 1956) has shown that in muskrats mortality from predation is much higher among individuals that fail to establish themselves in a suitable territory than among territory holders. Mortality is also higher in red grouse that do not obtain territories in suitable habitats (Jenkins, 1963; Jenkins, Watson, and Miller, 1963).

The information included in Table III is consistent with the hypothesis that the populations of these four species are regulated by competition, either by territoriality determining the size of the breeding population or by competition for food and perhaps other resources determining the survival of the juveniles through the summer and early fall. The growth rate for these four species was a decreasing function of density only during the period from spring to fall; it was density-independent for the rest of the year when no reproduction was

occurring and when young animals were becoming mature. Of the species listed in Table III, the bobwhite and muskrat are territorial, the first only during the nesting season, and the pheasant and grouse are territorial only in the sense that the polygamous males defend a display area during the breeding season.

Interference between individuals affects population growth, as is illustrated by the following examples. Allee et al. (1949, p. 349-352) summarize the detrimental effects of interference on the reproductive rates of a few species of insects. The food intake of individual fishes in a crowded situation decreased because of interference from others, fright, or actual fighting (Ivlev, 1961, Ch. 5). Titmice fought over food most often in midwinter when they spent the greatest proportion of their time searching for food (Gibb, 1954). As a result of stress from increased social contacts, the birth rate of rodents and hares decreased, and the mortality of infant rodents increased because of failure of lactation, with increasing population density (Christian, 1959 and 1963).

Predation is a cause of mortality that may be an increasing function of density under some conditions and density-independent or even a decreasing function under others. Holling (1961), in a review of the effects of predation on insect numbers, concluded that the number of prey killed per predator generally increases with prey density, until prey density becomes so great that either the predators are satiated or the prey obtains protection from the large group; predation may therefore be an increasing function of density at low prey

densities and a decreasing function at high densities. Holling's conclusions are supported by studies of predation on insects by birds made by Gibb (1962), Tinbergen (1960), and Tinbergen and Klomp (1960).

The role of predation among vertebrates appears to be more complex. Errington (1946, 1956) was convinced that in territorial species those individuals that failed to establish good territories were removed by predation, which therefore removed only the surplus, but in nonterritorial species whose behavior allows crowding, predation may determine the size of the population. Deer are nonterritorial species and deer populations were at least originally controlled by predators as all overpopulations of deer in the United States followed, and none preceded, the disappearance of large predators or the initiation of predator control (Leopold, Sowls, and Spencer, 1947).

The effects of predation on populations of small mammals were studied by Craighead and Craighead (1956) on an area in Michigan for two fall and winter seasons. Their published results do not contain an estimate of the mortality rate due to predation, but from some of their data I have estimated this rate for four species of small mammals preyed upon by nine species of hawks and owls; mammalian predators appeared to be insignificant. Appendix A describes the method of estimating the rate. Table IV summarizes the results. Large mouse populations were present in the 1941-42 fall and winter, smaller numbers in the 1947-48 season. The rate of mortality due to predation on the two species of mice was about the same for each year, or density-independent. The rabbit and fox squirrel populations were, on the other

hand, lowest in 1941-42 but suffered the higher mortality rate from predation this year; for these two species predation was a decreasing function of density. The obvious reason for this is that the large numbers of mice present in 1941-42 attracted to the area many more hawks and owls than normal, and this increased the probability of an attack upon an individual rabbit or squirrel.

The results presented in Table III indicate that for these four species predation is a density-independent cause of mortality. In the period from fall to spring population changes result solely from mortality, and predation is responsible for most of this. During this period the rates of population decline were independent of population density.

Young or juvenile individuals are more likely to be killed by predators than are adults. Beverton (1962) concluded that populations of plaice are regulated by varying mortality from starvation and predation of the larval fish. Murie (1944) reported that predation on caribou and Dall sheep was concentrated on young animals.

Cannibalism is a special case of predation, resembling competition in that the process is intraspecific. It appears to be an increasing function of density in flour beetles, Tribolium (Allee et al., 1949, p. 370-371; Neyman, Park, and Scott, 1958), and it is at least an important cause of mortality in planarian worms (Armstrong, 1964). Ricker (1954) discusses the hypothetical effects of cannibalism on population size.

Mortality due to parasites or disease is an increasing function of density for insects and does regulate population size according to Macfadyen (1936, p. 263). For birds and mammals, however, Lack (1954) believes that disease is with few exceptions not a cause of mortality increasing with density. The evidence for both of these conclusions was obtained from a few cases, and the conclusions may not have general validity. Disease often follows starvation, and then starvation should be considered the primary cause of mortality.

There are two other possible mechanisms for regulating population size, although few observations and measurements pertain to either. The secretion of substances into the environment which inhibit the activities of other organisms would have results similar to those of competition; this subject is briefly reviewed by Rose (1960). Wynne-Edwards (1962) describes a number of behavior patterns which he suggests can reduce reproductive rates in dense populations.

The processes regulating natural populations of herbivorous insects and some vertebrates are beginning to be understood. Herbivorous insects are normally regulated by their predators and parasites. When favorable conditions for reproduction and survival exist, the numbers of insects may increase so rapidly as to "escape" their predators and parasites and an outbreak occurs. The peak population is subdued by the favorable period ending or by parasites and disease overtaking the dense population. The hypothesis that fluctuating insect populations are regulated only when at their lower levels is supported by the data in Table V. The five species of insects listed

here had populations which fluctuated greatly. The statistical analyses based on their entire series of population counts indicated that their population changes were independent of density (Table I). When each population record was divided into periods of scarcity and abundance, however, and a test was made only for the periods of scarcity, the regression coefficient of growth rate on density was negative and significantly different from zero (at the 0.05 level or better) for three of the five species. This is evidence that the low or "normal" levels of these populations were being controlled by processes operating as increasing functions of density.

In vertebrates, the processes controlling population size are different between non-territorial and territorial species. Non-territorial species, including probably most fish, deer, hares, and most rodents, are normally regulated by predation. When this fails, as when predators of deer are removed by man, competition for food becomes important. In deer and probably in fish, this results in starvation of younger individuals. In hares and some rodents the reproductive rate drops and the mortality of juveniles increases. The numbers of territorial species are determined by competition for suitable territories. Those that fail to obtain territories, usually immature individuals, are not able to reproduce and are the first to be eliminated by predation or starvation. Because the processes regulating vertebrate populations either lower the birth rate or increase the mortality of young individuals, the general result of increased population density in vertebrates is a lowering of the production of young adults.

Hairston, Smith, and Slobodkin (1960) inferred from some obvious facts that populations of herbivores are generally controlled by predators and those of predators by competition. This generalization is supported only in part by my conclusions presented above. Although herbivorous insects and some herbivorous mammals are normally controlled by predators or parasites, competition is important for territorial herbivores like muskrat and red grouse and also in some rodents whose reproductive rate falls with increased crowding. Competition does appear to be the regulating process in predaceous birds and mammals, largely through the mechanism of territoriality; by far the majority of species known to be territorial are carnivorous birds and mammals.

The processes regulating natural populations of animals other than herbivorous insects, birds, and mammals are still mostly unknown. The statistical analyses summarized in Tables I and II indicate that these processes, like those discussed in this section, must somehow regulate by varying the population's growth rate so that it is a decreasing function of density.

APPENDIX A

Data published in the book by Craighead and Craighead (1956) were used to calculate the mortality rates due to avian predators shown in Table IV. Because this calculation involved drawing data from scattered parts of the book, and because the conclusion drawn from Table IV does not agree with their conclusion (p. 309) that the predation observed tended to regulate the prey populations, the procedure I used is here outlined. Table and page numbers cited below refer to Craighead and Craighead (1956).

Let:

W_r \equiv grams of food consumed by each species of raptor during fall and winter (from Table 90).

w_s \equiv average individual weight for each prey species (from Table 100).

n_{sr} \equiv number of individuals of each prey species (s) consumed during fall and winter by each species of raptor (r).

N_r \equiv total number of all prey individuals consumed by each species of raptor, $= \sum_s n_{sr}$

f_{sr} \equiv frequency of each prey species in food of each species of raptor, $= n_{sr}/N_r$ (estimated in samples reported in Tables 25-28).

$$W_r = \sum_s n_{sr} w_s = \sum_s N_r f_{sr} w_s = N_r \sum_s f_{sr} w_s$$

N_r can then be calculated since the other factors have been estimated.

$$\text{Total number of each prey species consumed} = \sum_r N_r f_{sr}$$

The rate of mortality due to predation is this number divided by the size of the prey population (p. 356-357).

APPENDIX B

Scientific names for species named in text and tables.

PELECYPODA. Clam Tivela stultorum.

ARACHNIDA. Herbivorous mite Eotetranychus sexmaculatus. Predatory mite Typhlodromus occidentalis.

CRUSTACEA. Daphnia Daphnia magna (unless otherwise stated).

INSECTA. Thrips Thrips imaginis. Florida wax scale Ceroplastes floridensis. Chaff scale Parlatoria pergandei. Bordered white moth Bupalus piniarius. Pine spinner moth Dendrolimus pini. Pine hawk moth Hyloicus pinastri. Pine beauty moth Panolis griseovariegata. Rice weevil Calandra oryzae. Bean weevil Callosobruchus chinensis. Broad-horned flour beetle Gnathocerus cornutus. Red flour beetle Tribolium castaneum. Confused flour beetle Tribolium confusum. Granary beetle Trogoderma versicolor. Parasitic wasp Heterospilus prosopidus. Sheep blowfly Lucilia cuprina. Housefly Musca domestica. Sewage fly Spaniotoma minima.

OSTEICHTHYES. Atlantic salmon Salmo salar. Lake trout Salvelinus namaycush. Goldeye Hiodon alosoides. Northern pike Esox lucius. Yellow perch Perca flavescens. Walleye Stizostedion vitreum. Freshwater drum Aplodinotus grunniens. Plaice Pleuronectes platessa.

AVES. Fulmar Fulmarus glacialis. Gannet Morus bassanus. Heron Ardea cinerea. Stork Ciconia ciconia. Golden eagle Aquila chrysaetos.

Appendix B, continued

Ruffed grouse Bonasa umbellus. Red grouse Lagopus scoticus.
 Sharp-tailed grouse Pedioecetes phasianellus. Prairie chicken
Tympanuchus cupido. Bobwhite quail Colinus virginianus. Partridge
Perdix perdix. Ring-necked Pheasant Phasianus colchicus. Pied
 flycatcher Muscicapa hypoleuca. Coal tit Parus ater. Blue tit
Parus caeruleus. Crested tit Parus cristatus. Great tit Parus
major. House wren Troglodytes aedon. Wood thrush Hylocichla
mustelina. Starling Sturnus vulgaris. Red-eyed vireo Vireo
olivaceus. Ovenbird Seiurus aurocapillus. Hooded warbler
Wilsonia citrina. Chaffinch Fringilla coelebs. Song Sparrow
Melospiza melodia. Indigo Bunting Passerina cyanea.

MAMMALIA. Wolverine Gulo luscus. Fisher Martes pennanti. Mink Mustela
vison. Weasel Mustela vulgaris. Arctic fox Alopex lagopus.
 Coyote Canis latrans. Wolf Canis lupus. Gray fox Urocyon
cinereoargenteus. Colored fox Vulpes fulva. Lynx Lynx canadensis.
 Fur seal Callorhinus ursinus. Fox squirrel Sciurus niger.
 Levant vole Microtus guentheri. Meadow vole Microtus pennsylvanicus.
 Muskrat Ondatra zibethicus. White-footed mouse Peromyscus leucopus.
 Snowshoe hare Lepus americanus. European hare Lepus europaeus.
 European rabbit Oryctolagus cuniculus. Cottontail rabbit
Sylvilagus floridanus. Caribou Rangifer arcticus. Reindeer
Rangifer tarandus. Pronghorn Antilocapra americana. Dall sheep
Ovis dalli.

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Fig. 1. Graphs of r , population growth rate ($r = dN/Ndt$) as a function of population density.

- A. r is a decreasing linear function of density.
- B. r is an increasing linear function of density.
- C. r is a decreasing nonlinear function of density, found in growing daphnia populations (Smith, 1963b).
- D. r is a decreasing nonlinear function of density, from the reproduction curves of Ricker (1954).

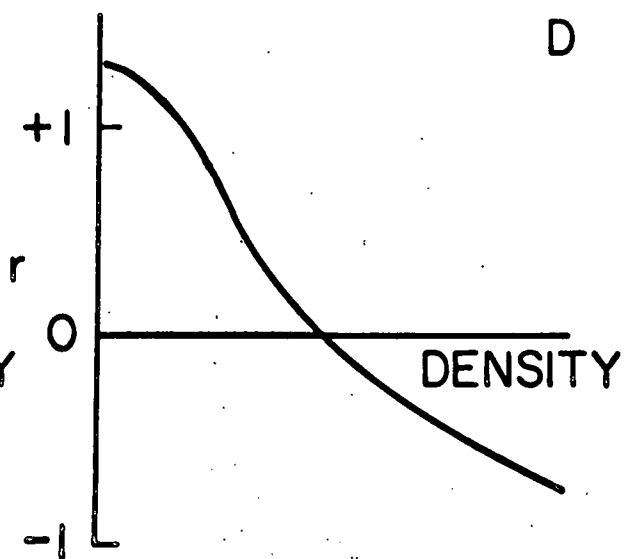
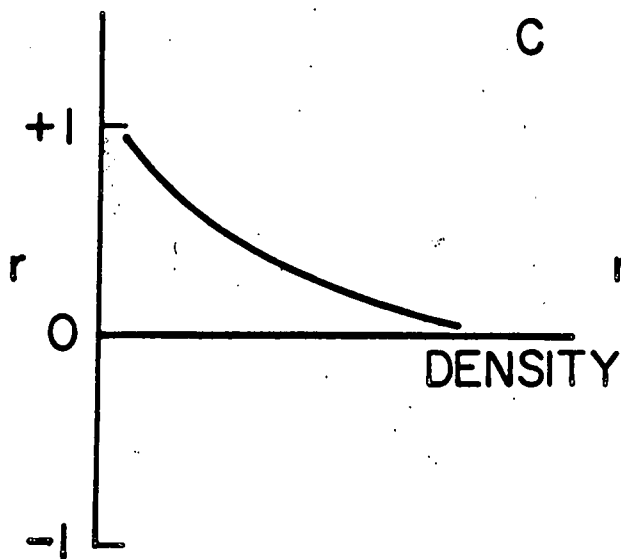
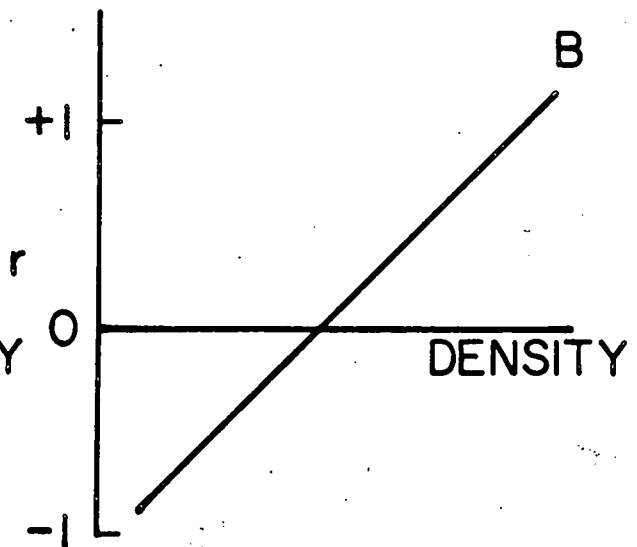
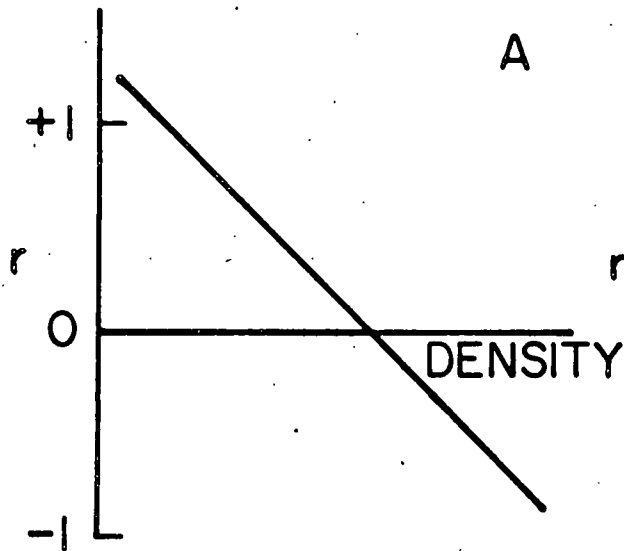


TABLE I. Populations subjected to regression analysis, the regression coefficient (coefficient of r_t on population density), and results of tests of significance on the regression coefficient.

Column A: Nature of population and source of data. Scientific names are in Appendix B.

B: Number of populations combined.

C: Average size of population(s).

D: Interval between counts or measurements
generation time (see text)

E: Number of intervals (average number if two or more populations have been combined).

F: Calculated value of $\frac{b_D}{k}$, (b_D is the regression coefficient of r_t on population density, see text for meaning of k).

G: Level of significance; the probability is less than this figure that the null hypothesis ($H_0: b_D = 0$) is true.

* - see also further analysis in text.

A	B	C	D	E	F	G
Herbivore mite in culture. (Huffaker, 1958)	4	2586	$\frac{5 \text{ day}}{10 \text{ day}}$	30	- 1.69	0.001
Predatory mite in culture. (Huffaker, 1958)	1	17	$\frac{5 \text{ day}}{20 \text{ day}}$	30	- 3.00	0.02
<u>Daphnia magna</u> in cultures. (Pratt, 1943)	1	41	$\frac{4 \text{ day}}{4 \text{ day}}$	53	- 1.27	0.02
<u>Daphnia obtusa</u> in cultures. (Slobodkin, 1954)	2	284	$\frac{10 \text{ day}}{4 \text{ day}}$	29	- 1.54	0.001
Thrips in roses in garden. (Davidson and Andre- wartha, 1948)	1	352	$\frac{\text{month}}{20 \text{ day}}$	80	- 0.14	0.20*

Table I, continued - 2

A	B	C	D	E	F	G
Florida wax scale on citrus leaves (Bodenheimer, 1958)	1	322	$\frac{\text{month}}{4 \text{ month}}$	95	- 2.67	0.50
Chaff scale on citrus leaves (Bodenheimer, 1958)	1	282	$\frac{\text{month}}{4 \text{ month}}$	87	- 1.71	0.001
Bordered white moth pupae hibernating in forest floor. (Varley, 1949)	1	1214	$\frac{\text{year}}{\text{year}}$	59	- 0.24	0.30
Pine spinner moth larvae hibernating in forest floor. (Varley, 1949)	1	672	$\frac{\text{year}}{\text{year}}$	59	- 0.11	0.50
Pine hawk moth pupae hiber- nating in forest floor. (Varley, 1949)	1	38	$\frac{\text{year}}{\text{year}}$	49	- 0.23	0.40
Pine beauty moth larvae hibernating in forest floor. (Varley, 1949)	1	43	$\frac{\text{year}}{\text{year}}$	59	- 0.58	0.30
Rice weevil in culture. (Birch, 1953)	2	533	$\frac{4 \text{ week}}{6 \text{ week}}$	23	- 1.55	0.001
Bean weevil in culture. (Utida, 1957a)	1	382	gener- ation	111	- 1.12	0.001
Red flour beetle in culture. (Park and Frank, 1950)	1	157	$\frac{30 \text{ day}}{45 \text{ day}}$	68	- 1.06	0.01
Confused flour beetle in culture. (Park et al., 1941; Park and Frank, 1950)	2	1361	$\frac{30 \text{ day}}{45 \text{ day}}$	43	- 4.50	0.001
Parasitic wasp in culture. (Utida, 1957a)	1	358	gener- ation	111	- 0.61	0.001
Sheep blowfly in culture. (Nicholson, 1954)	1	2544	$\frac{2 \text{ day}}{15 \text{ day}}$	132	- 3.61	0.10
Housefly in culture. (Pimentel et al., 1963)	1	4	$\frac{7 \text{ day}}{4 \text{ week}}$	82	- 1.92	0.20

Table I, continued - 3

A	B	C	D	E	F	G
Sewage fly in sewage beds. (Lloyd, 1943)	1	1703	$\frac{\text{month}}{43 \text{ day}}$	79	- 0.67	0.01
Atlantic salmon weight of catch (Allee et al., 1949)	1	(56,300 pounds)	$\frac{\text{year}}{3 \text{ year}}$	63	- 0.95	0.01
Lake trout abundance index based on fisheries catch. (Eschmeyer, 1957)	1	(2218000 pounds)	$\frac{\text{year}}{5 \text{ year}}$	25	+ 1.74	0.10
Goldeye abundance index based on fisheries catch. (Smith and Krefting, 1954)	1	(66,659 pounds)	$\frac{\text{year}}{2 \text{ year}}$	23	- 2.37	0.30
Northern pike abundance index based on fisheries catch. (Smith & Krefting, 1954)	1	(39,100 pounds)	$\frac{\text{year}}{5 \text{ year}}$	23	- 2.07	0.05
Yellow perch abundance index based on fisheries catch. (Smith & Krefting, 1954)	1	(212,365 pounds)	$\frac{\text{year}}{3 \text{ year}}$	23	- 3.16	0.05
Walleye abundance index based on fisheries catch. (Pycha, 1961)	1	(258,034 pounds)	$\frac{\text{year}}{5 \text{ year}}$	28	- 2.17	0.01
Freshwater drum abundance index based on fisheries catch. (Smith & Krefting, 1954)	1	(17,108 pounds)	$\frac{\text{year}}{3 \text{ year}}$	23	- 0.51	0.30
Fulmar breeding birds in Britain. (Fisher, 1962)	1	23,000	$\frac{5 \text{ year}}{7 \text{ year}}$	14	- 0.36	0.20
Gannet estimated world popu- lation. (Fisher and Vevers, 1944)	1	102,600	$\frac{5 \text{ year}}{5 \text{ year}}$	24	- 0.06	0.20
Heron nesting birds. (Lack, 1953)	3	423	$\frac{\text{year}}{2 \text{ year}}$	19	- 0.59	0.01
Stork nesting birds. (Lack, 1954)	1	342	$\frac{\text{year}}{4 \text{ year}}$	24	- 0.10	0.80
Ruffed grouse census in habitat. (Hickey, 1955; Marshall, 1954)	2	278	$\frac{\text{year}}{\text{year}}$	30	- 2.46	0.05

Table I, continued - 4

A	B	C	D	E	F	G
Red Grouse game bag records (Mackenzie, 1952; Middleton, 1934)	6	1387	$\frac{\text{year}}{\text{year}}$	66	- 1.20	0.001
Sharp-tailed grouse census in habitat (Hickey, 1955)	1	28	$\frac{\text{year}}{\text{year}}$	34	- 0.33	0.05
Prairie chicken counts of displaying males. (Shelford & Yeatter, 1955)	1	66	$\frac{\text{year}}{\text{year}}$	17	- 0.35	0.10
Partridge game bag records; breeding birds. (Middleton, 1934; Severtzoff, 1934)	4	1010	$\frac{\text{year}}{\text{year}}$	86	- 0.92	0.001
Pheasant introduced popu- lation (Lack, 1954)	1	405	$\frac{\text{year}}{\text{year}}$	5	- 0.89	0.10
Pied flycatcher breeding population (Lack, 1954)	1	66	$\frac{\text{year}}{\text{year}}$	9	- 0.86	0.05
Coal tit breeding population (Kluyver, 1951)	1	20	$\frac{\text{year}}{\text{year}}$	31	- 1.32	0.01
Blue tit breeding population (Kluyver, 1951)	1	27	$\frac{\text{year}}{\text{year}}$	31	- 1.90	0.001
Crested tit breeding population (Kluyver, 1951)	1	10	$\frac{\text{year}}{\text{year}}$	31	- 0.81	0.02
House wren breeding bird census (Kendeigh, 1944; Kendeigh et al., 1948-63)	2	41	$\frac{\text{year}}{\text{year}}$	24	- 0.62	0.001
Wood thrush breeding bird census (Williams, 1947-50)	1	29	$\frac{\text{year}}{\text{year}}$	18	- 0.56	0.10

TABLE I, continued - 5

A	B	C	D	E	F	G
Starling breeding bird census. (Kendeigh, 1944; Kendeigh et al., 1948-63)	1	51	$\frac{\text{year}}{\text{year}}$	23	- 0.11	0.30*
Red-eyed vireo breeding bird census. (Kendeigh, 1944; Kendeith et al., 1948-63; Williams, 1947-50)	2	38	$\frac{\text{year}}{\text{year}}$	20	- 0.36	0.05
Indigo bunting breeding bird census. (Kendeigh, 1944; Kendeigh et al., 1948-63)	1	44	$\frac{\text{year}}{\text{year}}$	23	- 0.51	0.02
Wolverine fur yields. (Buckley, 1954)	1	311	$\frac{\text{year}}{2 \text{ year}}$	41	- 0.31	0.20
Fisher fur yields. (Keith, 1962)	2	860	$\frac{\text{year}}{2 \text{ year}}$	38	- 1.12	0.001
Mink fur yields. (Keith, 1962)	1	10,570	$\frac{\text{year}}{\text{year}}$	43	- 0.05	0.70
Weasel game bag returns. (Middleton, 1934)	2	198	$\frac{\text{year}}{\text{year}}$	49	- 0.52	0.001
Arctic fox fur yields. (Buckley, 1954)	1	4772	$\frac{\text{year}}{\text{year}}$	41	- 1.15	0.01
Coyote fur yields. (Keith, 1962)	2	18,600	$\frac{\text{year}}{2 \text{ year}}$	34	- 1.18	0.001
Wolf fur yields. (Buckley, 1954)	1	325	$\frac{\text{year}}{2 \text{ year}}$	41	- 0.52	0.05
Gray fox bounty records. (Richmond, 1952)	1	8724	$\frac{\text{year}}{\text{year}}$	34	- 0.15	0.20
Colored fox fur yields. (Keith, 1962)	1	7927	$\frac{\text{year}}{\text{year}}$	36	- 0.17	0.20
Lynx fur yields. (Buckley, 1954; Elton & Nicholson, 1942b; Keith, 1962)	5	1932	$\frac{\text{year}}{\text{year}}$	55	- 0.23	0.001

TABLE I, continued - 6

A	B	C	D	E	F	G
Fur seal census on breeding grounds. (Scheffer, 1955)	1	547,300	$\frac{\text{year}}{3 \text{ year}}$	19	- 0.69	0.01
Levant vole census in habitat. (Bodenheimer, 1958)	1	8	$\frac{\text{month}}{1.5 \text{ mo}}$	82	- 0.06	0.30
Muskrat census in habitat, fur yields. (Buckley, 1954; Elton & Nicholson, 1942a; Errington, 1954 and 1957; Keith, 1962)	6	207,379	$\frac{\text{year}}{\text{year}}$	48	- 0.41	0.001
Snowshoe hare fur yields. (Lack, 1954; MacLulich, 1957)	2	112,682	$\frac{\text{year}}{\text{year}}$	37	- 1.90	0.05
European hare game bag records. (Middleton, 1934)	2	209	$\frac{\text{year}}{\text{year}}$	80	- 0.52	0.001
European rabbit game bag records. (Middleton, 1934)	2	5,071	$\frac{\text{year}}{8 \text{ month}}$	66	- 0.20	0.001
Reindeer introduced population. (Scheffer, 1951)	2	302	$\frac{\text{year}}{2 \text{ year}}$	30	- 0.20	0.01
Pronghorn census in habitat. (Shelford, 1954)	1	545	$\frac{\text{year}}{2 \text{ year}}$	18	- 1.14	0.02
Human population of the world. (various sources)	1	844×10^6	$\frac{50 \text{ year}}{17 \text{ year}}$	6	+ 0.11	0.05

NOTE: The following censuses were eliminated from the analysis because the series of counts were not significantly different from a series of random numbers: Clams in ocean beach (Coe, 1957). Broad-horned flour beetle in culture (Park et al., 1941). Granary beetle in

TABLE I, continued - 7

culture (Park et al., 1941). Lake trout fisheries catch (Fry, 1949). Walleye fisheries catch (Smith and Krefting, 1954). Bobwhite quail census in habitat (Errington, 1957). Ruffed grouse census in New Jersey habitat (Hickey, 1955). Great tit breeding population (Kluyver, 1951). Ovenbird breeding bird census (Williams, 1947-50). Hooded warbler breeding bird census (Williams, 1947-50). Arctic fox fur yields (Elton, 1942). Mink fur yields (Buckley, 1954).

TABLE II. Summary of results in Table I.

Column A: Total number of species.

B: Number of species eliminated because their population record was not significantly different from a random series.

C: Coefficient, b_D/k , not significantly different from zero, probability of the null hypothesis exceeding .05.

D: Coefficient positive and significantly different from zero.

E: Coefficient negative and significantly different from zero.

	A	B	C	D	E
Invertebrates other than insects	5	1	-	-	4
Insects	17	2	7	-	8
Fish	7	-	3	-	4
Birds	23	4	6	-	13
Mammals	<u>19</u>	-	<u>5</u>	<u>1*</u>	<u>13</u>
Totals	71	7	21	1	42

*The human population of the world.

TABLE III. Results Based on Spring and Fall Censuses of Wild Populations.

Column A: Species and source of data.

B: Number of populations combined.

C: Average size of spring population(s).

D: Number of intervals (average number for the six muskrat populations).

E: Calculated value of b_D/k .

F: Level of significance; the probability is less than this figure that the null hypothesis ($H_0: b = 0$) is true.

A	B	C	Spring to Fall			Fall to Spring		
			D	E	F	D	E	F
Bobwhite Quail, Colinus (Errington, 1957)	1	145	17	- 0.47	0.01	18	- 0.01	.40
Ring-necked Pheasant, Phasianus (Lack, 1954)	1	405	6	- 0.50	0.05	5	+ 0.01	.40
Ruffed Grouse, Bonasa (Bump et al., 1947)	1	177	13	- 0.44	0.05	12	- 0.07	.20
Muskrat, Ondatra (Errington, 1954, 1957)	6	283	16	- 0.46	0.02	15	- 0.01	.90

TABLE IV. Rates of mortality due to predation by nine species of hawks and owls during fall and winter, estimated from the data of Craighead and Craighead (1956).

	Prey Species			
	Meadow Vole	White-foot Mouse	Cottontail Rabbit	Fox Squirrel
<u>1941-42</u>				
Population	303,000	33,000	300	300
Lost by predation	55,600	8,066	162	10
Predation rate	0.184	0.244	0.540	0.033
<u>1947-48</u>				
Population	75,000	27,000	1,200	1,000
Lost by predation	13,500	6,200	234	11
Predation rate	0.180	0.230	0.195	0.011

TABLE V. Insect species from natural habitats analyzed during their periods of scarcity. See Table I for more information.

Column A: Species.

B: Average size of population (during period of scarcity).

C: Number of intervals.

D: Calculated value of b_D/k .

E: Level of significance.

A	B	C	D	E
Florida wax scale	54.7	60	- 0.12	0.05
Bordered white moth	47.3	27	- 2.12	0.01
Pine spinner moth	15.9	42	- 0.42	0.10
Pine hawk moth	8.7	26	- 1.32	0.20
Pine beauty moth	4.9	30	- 0.89	0.01