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# NATURAL SELECTION AND THE PARAMETERS OF POPULATION GROWTH

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*Abstract:* The intrinsic rate of natural increase,  $r$ , is a constant that measures the ability of a population to grow under a given set of conditions. The Malthusian parameter,  $m$ , is a measure of genotypic rate of increase. Although the mathematical formulations for  $r$  and  $m$  are the same, their biological characteristics are different except in isogenic populations. Selection will always favor genotypes with the highest  $m$  under a given set of conditions, but such selection may result in a reduction of  $r$  for that population. The mechanism by which this process occurs is discussed and simulated, and it is concluded that evolutionary reductions in  $r$  are most likely to have occurred under conditions of density dependence. It is also suggested that the recent terms  $r$  and  $K$  selection have mixed ecological parlance into evolutionary processes in a potentially confusing manner.

Population ecology and population genetics became self-conscious fields of study at approximately the same time (Pearl 1925, Lotka 1956, Fisher 1958, Gause 1934, Haldane 1924). This coincidence should have led to fruitful collaboration, but no such collaboration took place. It is not our purpose to search for causes of the failure, but to discuss some of the anomalous consequences. Among the most obvious of the anomalies is the conflict between theoretical deductions that natural selection tends always to maximize the intrinsic rate of increase or Malthusian parameter (Fisher 1958), and the observations of evolutionary history, in which some descendent species seem clearly to have lower rates of increase than did ancestral ones. This is exemplified in the repeated observations of increasing size over geological time, combined with the observation that larger bodied species have lower rates of increase than smaller ones. Careful at-

tempts to understand fully some of the recent literature (MacArthur 1960, 1962, MacArthur and Wilson 1967, Murphy 1968) in population and evolutionary biology have convinced us of the necessity of bringing the various ideas and usages together, so that proper distinctions can be made and some common misconceptions corrected.

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## ECOLOGICAL USAGE

### Intrinsic Rate of Natural Increase

Population ecologists have a primary interest in the response of the populations which they study to environments in which these populations are found or are placed. If evolutionary processes are considered at all, they are inferred, because the num-

ber of generations usually required for evolutionary change is far greater than the number considered in ecological studies (Fisher 1958:48).

Population ecologists have stressed the value of expressing, in terms comparable for all populations, the populational response to a given set of conditions. In order to make these terms comparable, extensive use has been made of mathematical models, starting with the response of a population unrestricted by density effects as described by the equation for exponential growth,

$$\frac{dN}{dt} = rN. \quad (1)$$

This equation describes an exponentially decreasing as well as an exponentially increasing population in which  $r$  can take any value, the only restriction being that it must be *constant*. Because of its implication in population growth,  $r$  can be called the "natural rate of increase," the "true rate of increase," the "potential rate of multiplication," the "Malthusian parameter of population increase," the "intrinsic rate of natural increase," and probably a number of other similar terms. This constant is the difference between birth rate and death rate. It thus represents in a single number all of the physiological responses of all members of the population to a given set of environmental conditions, since ultimately all physiological responses must be relatable to the ability to reproduce or to the ability to survive. The value of such a term is obvious in comparing the favorableness of different environments for one species, or in comparing the relative favorableness of a given environment for different species. In microbiology and cell biology, the easily equatable terms "division time" or "daily division rate" have

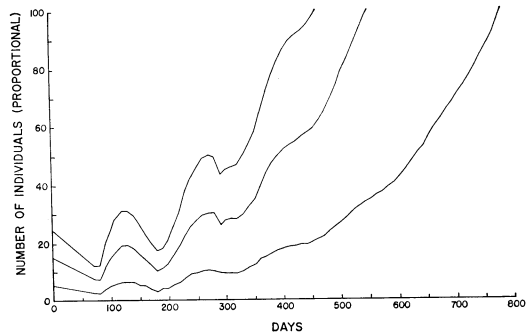


Fig. 1. The growth of three populations of an amphibious snail, *Oncomelania hupensis*. All three curves were calculated from the same age-specific death rates and egg-laying rates, and all were assumed to start with the same single age-class. The scale of the ordinate is arbitrary. (Pesigan et al. 1958:541).

been used for the same purpose for many years.

Most unicellular organisms have populations with negligible age structures, and rapidly grow to very large numbers of independent units, thereby approximating an autocatalytic reaction, such as inspired the formulation of many of the mathematical models of population growth (Pearl and Reed 1920, Smith 1952, 1963b, Caperon 1967).

The difficulty of measuring  $r$  for a population with a well-defined age structure, such as occurs in most metazoa, is easily visualized from Fig. 1, which traces the history of growing populations, starting from groups composed entirely of one age-class. The successive waves of abundance result from different proportional representation of different age-classes and any attempt at the direct measurement of  $r$  faces the difficulty imposed by these successive waves of abundance.

The problem was solved through the theorem of the stable age distribution as discussed in Lotka (1956) and the demonstration that  $r$  can be calculated for any

population for which the age-specific birth rates and death rates are known. The solution is obtained from

$$\int_0^{\infty} l_x m_x e^{-rx} dx = 1 \quad (2)$$

or approximated from

$$\sum l_x m_x e^{-rx} = 1. \quad (3)$$

In these equations,  $l_x$  is the proportion of females surviving from birth (or egg-laying) to age  $x$ , and  $m_x$  is the number of female young produced per female at age  $x$ . In practice, as in equation (3),  $l_x$  is measured to the midpoint of the age band over which  $m_x$  is observed. This approach is now universally used in studies of populations which have been divided into age-classes.

It is reiterated that for the calculation of  $r$  from either equation above the assumption must be made that the age-specific rates of survival and of reproduction are constant; otherwise  $r$  would vary, and comparisons with other conditions or other populations would be valueless.

#### Density-dependence and Sigmoid Growth

It is universally recognized that Equation (1) can be observed for only one or a few generations. The image of elephants overrunning the earth was evoked by Darwin, and serves well to illustrate the point. For most populations when started with few individuals in an environment in which some limiting resource is supplied at a constant rate, a graph depicting numbers plotted against time follows a sigmoid form. Several mathematical models have been devised to describe such growth, but we only need to be concerned with one of these, since the relevant property is shared by all.

The best-known such model is the

logistic equation, in which all terms are easily interpreted biologically,

$$\frac{dN}{dt} = rN \left( \frac{K - N}{K} \right), \quad (4)$$

where  $K$  is the maximum number of individuals which the environment will support.

It is perhaps at this point that the meaning and proper use of  $r$  have become confused. Whereas in the exponential growth equation (1),  $r$  is equal to the instantaneous change in abundance per individual, or  $(dN)/(N dt)$ , and both are constant, in the logistic this equivalence no longer holds;  $r$  remains a constant, but  $(dN)/(N dt)$  declines in a linear manner with density until it reaches zero when the population reaches  $K$  (see Slobodkin 1961, for discussion). Andrewartha and Birch (1954:53 and Chap. 9) write as if  $r$  varied with size of population. We regard this as an improper use of the concept of  $r$  and restrict  $r$  to their meaning of  $r_m$  (p. 33): ". . . the maximal rate of increase attained at any particular combination of temperature, moisture, quality of food, and so on, when the quantity of food, space, and other animals of the same kind are kept at an optimum and other organisms of different kinds are excluded from the experiment."

Like most models, the logistic breaks down when the supposed relationships between the details of the model and the biology of the population are examined closely. Thus, the logistic describes mathematically how the *effect* of  $r$ , as measured by  $(dN)/(N dt)$ , is modified by increasing the density of individuals in the population, as expressed by  $(K - N)/K$ . However, the change in abundance per individual can only be affected biologically by altering the birth rate or the death rate or both. One is faced, then, with the paradox that

the birth rate ( $b$ ) and the death rate ( $d$ ) are fixed constants, contained in  $r$ , yet the actual biological changes are in the manner in which the expression of these two constants is modified by the density effects  $(K - N)/K$ . We regard this difficulty as the inevitable result of over-dissection of a model (Levins 1968, Chap. 1), which in spite of many admitted faults has provided a useful framework for valuable ecological thought and research. Other derivations of the logistic equation separate the action of birth and death processes (Bartlett 1960). Although Bartlett's treatment is useful for understanding the mechanisms of population growth, it does not have the advantage of a single rate constant in comparing populations. Moreover, in such a model the operations of these functions affect their own magnitude (see below).

It is necessary to reiterate that the logistic was derived for use in an ecological context. Even in such a context, there are many valid criticisms that can be made (Smith 1952, 1963*b*, Slobodkin 1953, Andrewartha and Birch 1954, Bartlett 1960), but it is not proper to remove the frame of reference to an evolutionary one, and to try to force the terms into those required by the operation of natural selection. In particular, we object to models in which  $r$  is permitted to vary inversely with population size. Such an arrangement has been claimed, for example, by MacArthur and Wilson (1967:68). A model in which this happens allows  $r$  to change as a result of its own action, and the equation may as well be written equating  $(dN)/(N dt)$  with itself, since the model permits all outcomes. It is unfortunate that they chose to name their parameters the same as those of the logistic equation when their model does not behave in a logistic manner.

## EVOLUTIONARY USAGE

### The Malthusian Parameter

The linking of  $r$  with selection was proposed in a non-obvious way by Fisher (1958) and we would like to discuss explicitly the way in which selection and  $r$  are related.

Fisher used what he called the Malthusian parameter of population increase to measure the relative rates of increase or decrease of a population with a stable age distribution. His formulation (1958:26)

$$\int_0^{\infty} e^{-mx} l_x b_x dx, \quad (5)$$

equated to unity, is identical to the integral form of the Lotka equation given earlier. In this context  $r$  and the Malthusian parameter,  $m$ , are the same. Despite this identity it is clear that when Fisher (1958) used  $m$  to speak in an evolutionary context he is speaking not of the  $m$  for a population, but the  $m$  of each conceivable genotype in that population. For example, he states (p. 47) ". . . the actuarial information necessary for the calculation of the genetic changes actually in progress in a population of organisms, will always be lacking: if only because the number of different genotypes for each of which the Malthusian parameter is required will often, perhaps always, exceed the number of organisms in the population, . . ." Also (p. 50): "The Malthusian parameter will in general be different for each different genotype, and will measure the fitness to survive of each." Finally (p. 51), "Any net advantage gained by an organism will be conserved in the form of an increase in population, rather than in an increase in the average Malthusian parameter, which is kept by this adjustment always near zero." For the purposes of the subsequent discussion we will use Fisher's  $m$

when we are speaking of genotype rates of increase and  $r$  when we speak of population rates of increase. Unlike  $r$ ,  $m$  cannot be calculated, for the reasons stated in the first quotation above. Therefore  $m$  is in effect an imaginary rate.

In emphasizing the distinction between  $r$  and  $m$ , we first consider natural selection under three ecological conditions: (1) in a population growing exponentially for a long period in a favorable environment; (2) in a population saturating its environment under conditions of complete density dependence; (3) in a fluctuating population affected principally by density-independent factors.

In the exponentially growing population there is no negative feedback on growth rate imposed by dwindling resources or by other effects of increasing density, so that  $r$  is fully expressed. Under such conditions those genotypes with phenotypic expressions of early maturity, high fecundity and multiple reproduction each season must increase at a rapid rate and become more and more abundant in that population. It must be realized at this point that Fisher's formulation of  $m$  is identical to the ecological  $r$  (Equations 2 and 3) so that he is talking about increasing numbers of a genotype just as an ecologist would speak of increasing numbers of individuals. However, for those used to thinking of selection in terms of increased *frequency* of particular genotypes or genes the following example is appropriate. Consider a population comprised initially of two genotypes in equal numbers which are not allowed to interbreed; the population is increasing exponentially. That genotype with the highest  $m$  will increase at a faster rate than the other one and, at an infinite population size, will approach a frequency of 1.0. Because  $r$  depends upon the genetic con-

stitution of the whole population, its value will increase in evolutionary time because the genotype with higher  $m$  comes to predominate. Under these conditions, which we consider rare or very transient in nature, selection will inevitably result in a higher  $r$ .

In the second situation of complete density dependence a new selective pressure has been imposed upon the population. In this case the genotype with the highest  $m$  will also increase in frequency but this genotype may be different from the one favored in an unlimited environment (Lewontin 1965). Furthermore, the increase in one genotype must be at the expense of another whose numbers and frequency must decrease because the size of the population is relatively stationary. Under these density dependent conditions a selective advantage may accrue to individuals which reduce their mortality by producing smaller broods, devoting parental care to them and perhaps maturing at a larger size, but older. The genotypes conferring such phenotypes will certainly not be the same as those in the first example, but in this case they will have the highest  $m$ 's. The life history characteristics affected, however, are virtually certain to result in a lower  $r$  for this population. Inasmuch as trends toward larger size and more complex age structure are characteristic of many groups of organisms, we conclude that such trends were associated with density-dependent regulation of the populations involved. We recognize, of course, that opposite trends also occur and may take place in a density-dependent system and result in higher  $r$ , but increases in  $r$  in evolution are not inevitable.

Finally, we have considered populations affected by density-independent mortality factors and have found that such situations

can also lead to lower  $r$ . Murphy (1968) has considered one such possibility in the case of populations in which survival of pre-reproductives is highly variable. According to his simulations such a situation leads to selection of genotypes favoring long life expectancy and iteroparity. Such long life expectancies may then result in evolutionary reductions in clutch size or increase in age at first breeding, thereby resulting in lower  $r$ . The explanation of iteroparity and long life-expectancy is that following a year with very low recruitment, the population will be composed mostly of older animals. During that year most of the reproduction would be by these older animals. To the extent that their longevity had a genetic basis, then genes resulting in improved adult survivorship would increase in frequency.

If juvenile mortality were truly density independent, then high mortality of pre-reproductives could well follow a poor breeding year and cause extinction of the population. Furthermore, Murphy (1968) in reality introduced strong density-dependence into his simulations by setting an upper limit on the population and by adjusting recruitment to the limit. If this restriction were removed, then genotypes resulting in high  $r$  might still come to predominate in Murphy's populations even though one or more high mortality years for pre-reproductives might reduce the numbers of these genotypes.

To test the significance of Murphy's model under a more nearly density-independent system his algorithm was modified (a listing of the FORTRAN program is available from the authors) so that the survivorship of zygotes to maturity was a normally distributed, random variable uncorrelated with the size of the population. Individuals homozygous for the semel-

parous gene ( $A$ ) had a clutch size of ten at age one and then died. Individuals homozygous for the iteroparous gene ( $a$ ) had a clutch size of five at both age one and at age two. The heterozygotes ( $Aa$ ) had an intermediate survivorship and fecundity: the clutch size at ages one and two was eight; one quarter of the adults lived to age two. By these rules individuals of all genotypes produced ten zygotes. With no mortality of immatures, the values of  $r$  for monomorphic populations would have been  $AA$  (2.302),  $Aa$  (2.099),  $aa$  (1.767). At each time period all gametes were combined according to binomial probabilities. Random mortality affected only the survivorship of the zygotes to age one. There was no feedback of population size upon the rate of increase of the population; correlation coefficients between  $(dN)/(N dt)$  and  $N$  were nonsignificant (see Green 1968). In our simulations the normal distribution of survivorships had a mean of 0.10, which equalized the birth rate, and a standard deviation of 0.04 which was found to be small enough to prevent rapid extinction or expansion but large enough to demonstrate the effect of variation on the genetic structure of the population.

The persistence of populations affected only by density-independent factors requires very restrictive conditions. The birth rate must equal the death rate on the average, and the variance of the difference between the two rates must be small (Smith 1961, 1963a) or the population will either expand during a succession of favorable years until a resource limitation imposes density effects, or the population becomes extinct during a succession of unfavorable years (Andrewartha and Birch 1954). The arbitrary restriction of the magnitude of the variance in average

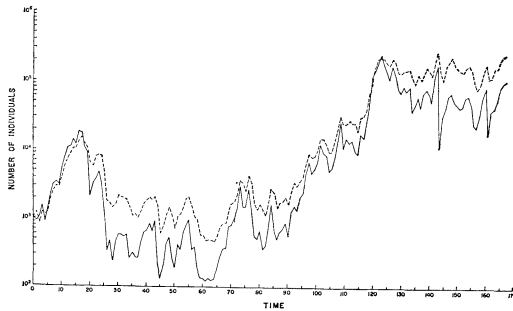


Fig. 2. Population change of iteroparous (broken line) and semelparous (solid line) homozygotes. For full explanation see text.

survivorship might be claimed by some to represent an unidentified source of density dependence. We maintain, however, that the restriction can be thought of as analogous to having the population occupy an environment in which variations affecting survivorship are not severe in magnitude and are random with respect to the density of the population.

In the 15 trials that were started with equal numbers of each homozygote the iteroparous genotype had a numerical advantage over the semelparous genotype except following a succession of periods of high survivorships. Fig. 2 presents the results of one experiment. The heterozygous genotype had abundances higher than either homozygote throughout most of the run. We emphasize the restrictive conditions which had to be imposed for the population to persist long enough under density-independence to obtain these results. Specifically, these conditions were the long-term equivalence of birth and death rates, the complete absence of variation in birth rates and the restricted variances in death rates.

Our results contradict Murphy's (1968) conclusion that iteroparity can be a response to variation in prereproductive survivorship. In our experiments itero-

parity was advantageous during periods of population decline; its advantage was more a function of the mean rather than of the variance in survivorship. The arbitrarily imposed variance in survivorship was the factor which maintained the polymorphism. In Murphy's genetic simulations, years were randomly assigned survivorships of 1.0 or 0.1. (His results were repeated after assuming that the frequency of good and bad years was equal so that the mean survivorship was 0.55.) This binomial pattern of survivorship was retained in all of his simulations. We ascribe his results (that is, evolution of iteroparity) to the imposition of density dependent reproduction on the model and would conclude from our results that the widespread evolution of iteroparity is evidence for a long history of density dependent population regulation or less likely a long period of population decline. The maintenance of a genetic polymorphism was the unexpected result of the experiments. The relative advantage of the homeostatic property of iteroparity during periods of population decline and the potential for rapid growth of semelparity during population increase was presumably responsible for the life history polymorphism. Although the maintenance of a life history polymorphism is an interesting result, we know of no such life history polymorphisms in nature. An empirical study of the association of iteroparity and variation of survivorship of pre-reproductives is needed, however.

MacArthur and Wilson (1967) have also discussed the evolution of population parameters relative to mechanisms of population regulation. In their introduction to the concepts of "*r*" and "*K*" selection they immediately cast their argument in terms of the selection of genes. In this sense they are referring to *m*, not *r* as they state

(p. 146). Hence "populations" are sub-populations of those individuals which bear only the allele in question.

In the discussion of "K selection," MacArthur and Wilson (p. 148) define "K" as "the 'carrying capacity' of the environment for these homozygous alleles." In some sense they use the classical logistic equation of population growth and the Lotka-Volterra competition equations merely as analogies to explain their model of natural selection. To continue their argument: under a regime of "r selection" with no crowding, density effects are weak and  $(K - N)/K$  is near unity. Selection will favor those alleles which multiply most rapidly in the absence of density effects (see above). Under a "K selection" regime of crowded conditions in which density effects are strong,  $(K - N)/K$  approaches zero. Under these conditions evolution (p. 149) . . . "favors efficiency of conversion of food into offspring—" implying a reduction in family size. Specifically they predict that "r selection" will be important in the early stages of colonization and during periods of increase in fluctuating populations, but see above. "K selection" will be important in populations of established species on islands or populations which maintain uniform sizes.

Before proceeding with the application of these concepts to evolutionary ecology, we should be perfectly clear about the mechanisms and consequences of them. "r selection" is operationally defined as selection in expanding populations; therefore reduction of generation time and increased fecundity are likely. To continue MacArthur and Wilson's analogy, "r" is being maximized. Selection does not operate directly on  $r$  but on some aspect of its component parts, either  $b$ , the birth rate, or  $d$ , the death rate. An increase in  $r$  will

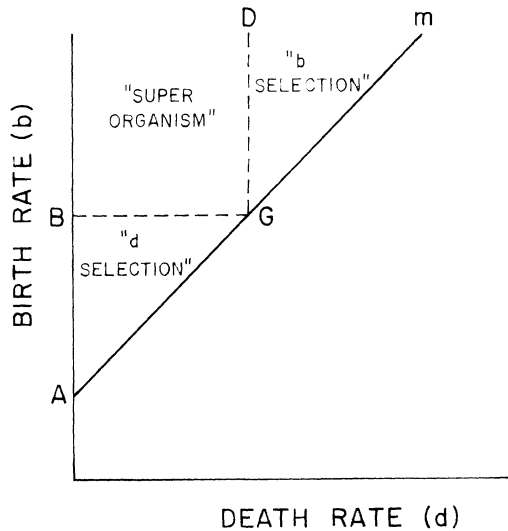


Fig. 3. Evolution of birth rates and death rates and the maximization of the Malthusian parameter of genotypic increase.

result from either an increase in  $b$  or a decrease in  $d$ . MacArthur and Wilson suggest that the probable mechanism is an increase in  $b$ , by the emphasis on production of offspring which, not incidentally, may be achieved by increasing the efficiency of resource utilization. "K selection" is defined as selection in crowded populations. Under this regime it must be the ability of a gene to increase in frequency in a stable, crowded population which is being optimized by selection. Under these conditions of density-dependent population regulation the reduction of  $d$  would be the object of optimization.

These two strategies are represented graphically in Fig. 3. Consider a genotype  $G$  which would confer on a monomorphic population a birth rate  $b$ , a death rate  $d$ , and a Malthusian parameter  $m$  (which equals  $r$  because the population is isogenic). Any change in the genotype which affects  $b$  or  $d$  would move the point  $G$  in the  $b-d$  plane. The locus of points on the line  $A-m$  are combinations of  $b$  and  $d$  which

have equal values of  $m$ . Selection will not move the point  $G$  below this line because this would entail a loss of fitness. Assuming that there is a functional relationship between  $b$  and  $d$  such that optimization of one necessitates a cost to the other, evolution is not possible into the upper left portion of the graph bounded by the lines  $GD$  and  $GB$ . Evolution into the area bounded by  $mGD$  involves an increase in  $b$  with a cost of increased  $d$ . In general, steadily increasing populations will evolve into this region. This kind of selection, called " $r$  selection" by MacArthur and Wilson, may appropriately be called " $b$  selection." Alternatively, evolution could move the genotype into the region  $AGB$  in which  $d$  is reduced at a cost of decreasing  $b$ . This type of response should occur in crowded populations which are regulated by resource limitations. This response, called " $K$  selection" by MacArthur and Wilson, may have more appropriately been called " $d$  selection."

Now, suppose a population is regulated by predators rather than by resource limitation. If the predator-prey system is fluctuating, selection would favor first an increased birth rate and then a decreased death rate as the population alternately increased and declined. This pattern would be modified if the predation pressure per prey individual remained constant. If the prey density were nearly constant two evolutionary strategies would be possible. In Fig. 3 the prey population would evolve into the area  $mGD$  if the response to predation were to shorten the generation time. However, the nature of predation may favor increased survivorship at the expense of  $r$  (evolution into region  $AGB$ ) by an increase in body size, the manufacture of a poison, the development of body armor, or parental care.

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## DETERMINING PARAMETERS FOR POPULATIONS BY USING STRUCTURAL MODELS<sup>1</sup>

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**Abstract:** A method for calculating parameters necessary to maintain stable populations is described and the management implications of the method are discussed. This method depends upon knowledge of the population mortality rate schedule, the age at which the species reaches maturity, and recruitment rates or age ratios in the population. Four approaches are presented which yield information about the status of the population: (1) necessary production for a stable population, (2) allowable mortality for a stable population, (3) annual rate of change in population size, and (4) age ratios in the population which yield a stable condition. General formulas for these relationships, and formulas for several special cases, are presented. Tables are also presented showing production required to maintain a stable population with the simpler (more common) mortality and fecundity schedules.

As hunting pressure increases and game resources become more intensively managed, knowledge of the dynamics of wild animal populations becomes more important. It is important for the wildlife manager to know if the current population is remaining stable and, if so, how it is maintaining this stability. These questions can be examined through the analysis of data regarding population structure: (1) the mortality rate schedule, (2) the age at which the species begins to breed, and

(3) the recruitment rate schedule and/or the sex and age ratios of the population. Even when good census data are available, such analyses are valuable in understanding the mechanisms of population maintenance (or decline); when census data are absent, the evaluation of population *trend* from structure data is especially valuable.

This paper presents models showing the relationships that yield stable populations with the various combinations of mortality and recruitment schedules, and methods for estimating annual rates of increase or decrease in the population level. This subject has been mentioned by many authors, including Lotka (1939), Paynter (1947), Birch (1948), Hickey (1952), and Eberhardt (1969). Paynter evaluated the status

<sup>1</sup> Technical Paper No. 2613, Oregon Agricultural Experiment Station, Corvallis. Financial support was provided by the Department of Interior, Bureau of Sport Fisheries and Wildlife Grant No. 14-16-008-922.

<sup>2</sup> Present address: Migratory Bird Populations Station, Laurel, Maryland 20810.

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