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THE POPULATION CONSEQUENCES OF LIFE HISTORY PHENOMENA

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PREFACE

FEW branches of biology have attracted more analytical mathematical treatment than has the study of populations. Despite this, one may read in the most complete treatise of ecology yet published (Allee, et al., 1949, p. 271) that "theoretical population ecology has not advanced to a great degree in terms of its impact on ecological thinking." This unfortunate gap between the biologists and the mathematicians has elicited comments which need not be repeated in detail here (Allee, 1934; Gause, 1934; Allee et al., 1949, p. 386). The neglect of the analytical methods by biologists may be attributed in part to the tendency of writers in this field to concentrate on the analysis of human populations and in part to skepticism about the mathematical methods of analysis. Early analyses of population growth (Verhulst, 1838, 1845; Pearl and Reed, 1920) employed human populations as examples, although it is clear from other publications (e.g., Pearl and Miner, 1935; Pearl, 1937) that comparative and general population studies were the principal interest of some of these students. Similarly, the pioneer works of Lotka (1907b, 1910, 1925) were very general in conception but made their greatest impact in the field of demography (Dublin and Lotka, 1925; Dublin, Lotka, and Spiegelman, 1949). The skepticism expressed by biologists toward theoretical studies has ranged from antagonism (Salt, 1936) to ap-

proval given with the warning that "... for the sake of brevity and to avoid cumbersome expressions, variables are omitted and assumptions made in the mathematical analyses which are not justified by the biological data" (Allee, 1934). It may be unfortunate that warnings about mathematical oversimplification are especially pertinent in connection with the study of interactions between species (Ross, 1911; Lotka, 1920, 1925; Volterra, 1927, 1931; Nicholson and Bailey, 1935; Thompson, 1939), which is just that portion of the subject which has remained most closely associated with general ecology. Hence we have a situation in which the analytical theories which are recognized by ecologists deal with complex phenomena and are susceptible to cogent criticisms (e.g., Smith, 1952) while the simpler analysis of the ways in which differences between the life histories of species may result in different characteristics of their populations has remained relatively unexplored. It is the purpose of the present paper to consider some parts of this neglected branch of ecology which has been called "biodemography" by Hutchinson (1948).

It is possible, but often impracticable, to compute exactly the characteristics of the hypothetical future population obtained by assuming an unvarying pattern of the pertinent life history features which govern natality and mortality. It is often more practicable to employ approximate methods of computation of the type which have

aroused skepticism among biologists. It will be shown that the two approaches can be reconciled and that for many cases of ecological interest they lead to identical conclusions. Some of these conclusions reached by the writer have appeared surprising when first encountered, and they seem to give a new perspective to life history studies. They also suggest that pertinent bits of information are frequently ignored in life history studies simply because their importance is not generally recognized.

The total life history pattern of a species has meaning in terms of its ability to survive, and ecologists should attempt to interpret these meanings. The following sections are intended primarily to indicate some of the possibilities in this direction. The writer wishes to express his gratitude to Professor Howard B. Adelmann for a critical reading of the manuscript of this paper, for suggesting numerous ways of clarifying the text and improving terminology, and for translating from the Latin parts of the text from Fibonacci (1202). Thanks are also due to Professors Robert J. Walker and Mark Kac who have been consulted about technical mathematical questions raised by the writer while considering various phases of this subject.

INTRODUCTION

If it is to survive, every species must possess reproductive capacities sufficient to replace the existing species population by the time this population has disappeared. It is obvious that the ability of the ancestors of existing species to replace themselves has been sufficient to overcome all environmental exigencies which have been encountered and, therefore, that the physiological, morphological, and behavioral adaptations that enable offspring to be produced and to survive in sufficient numbers to insure the persistence of a species are of fundamental ecological interest.

On the other hand, it is conceivable that reproductive capacity might become so great as to be detrimental to a species. The many deleterious effects of overcrowding are well known. It also seems obvious that a species which diverts too large a proportion of its available energies into unnecessary, and therefore wasteful, reproduction would be at a disadvantage in competition with other species.

In this paper it will be regarded as axiomatic that the reproductive potentials of existing species are related to their requirements for survival; that any life history features affecting reproductive potential are subject to natural selection; and that such features observed in existing species should be considered adaptations, just as purely morphological or behavioral patterns are commonly so considered.

Some of the more striking life history phenomena have long been recognized as adaptations to special requirements. The great fecundity rather generally found in parasites and in many marine organisms is commonly regarded as an adaptation insuring the maintenance of a population under conditions where the probability is low that any particular individual will establish itself and reproduce successfully. Again, parthenogenesis obviously favors the rapid growth of a population because every member of a population reproducing in this fashion can be a reproductive female. In turning seasonally to parthenogenesis, organisms like cladocerans and aphids are responding in a highly adaptive way during a limited period of time when the environmental resources are sufficient to support a large population. Parthenogenesis, hermaphroditism, and purely asexual reproduction may clearly offer some advantages under conditions that restrict the probability of contacts between the sexes. Protandry, as exhibited, for example, by some marine molluscs, and various related phenomena where population density affects the sex ratio (Allee et al., 1949, p. 409) may be considered as compromise devices providing the advantages of biparental inheritance while maintaining an unbalanced sex ratio which makes most of the environmental resources available to reproductive females.

Reproductive potentialities may be related to the success of a species in still other ways. It was an essential part of Darwin's thesis that the production of excess offspring provided a field of heritable variations upon which environmental conditions could operate to select the most favorable combinations. A high degree of fecundity may also aid the dispersal of species. An extreme example of this is afforded by the ground pine, *Lycopodium* (Humphreys, 1929), whose light windborne spores may be scattered literally over the whole face of the earth and so make it likely that all favorable habitats will come to be occupied. Another adaptational interpretation of the overproduction of offspring postulates that the excessive production of young fish which are frequently cannibalistic is a form of maternal provisioning,

the majority of the young serving merely as food for the few that ultimately mature.

Many additional examples of life history phenomena that have been regarded as adaptive could be cited. Here, however, we wish rather to call attention to the striking fact that in modern ecological literature there have been relatively few attempts to evaluate quantitatively the importance of specific features of life histories. The apparent mathematical complexity of the general problem is undoubtedly partly responsible for this. When the biologist attempts to compute from observed life history data the numbers of organisms of a particular type that can be produced in a given interval of time he may find it necessary to make assumptions which biologists in general would hesitate to accept. And even with these simplifying assumptions the computations may become so tedious as to make the labor involved seem unjustifiable in view of the seemingly academic interest of the result. In particular, such computations involve biological parameters which are not necessarily fixed characteristics of the species and which are not ordinarily expressible in convenient mathematical form. It is necessary to know the way in which the chance of dying (or of surviving) and the reproductive activities vary during the life span of an individual. These quantities are nicely summed up by the familiar life-table function, survivorship (l_x), which is defined as the probability of surviving from birth to some age x, and by the age-specific birth rate (b_x), which is defined as the mean number of offspring produced during the interval of age from age x to age $x + 1$. The biologist immediately recognizes that these quantities vary with environmental conditions and that he cannot expect to obtain a realistic result if he must assume, for example, that the probability of surviving a day, a week, or a month, is the same for individuals born in the autumn as for those born in the spring. He also recognizes that the population consists of discrete units and that offspring are produced in batches (here called litters whether in plants or animals) rather than continuously; hence he necessarily regards with suspicion any formulation of the problem in terms of differential equations where these considerations are apparently ignored.

Actually a tremendous variability is observed in life history phenomena which could affect the growth of populations. Some organisms are semelparous, that is to say, they reproduce only once in a lifetime and in these semelparous forms reproduction may occur at the age of only 20 minutes in certain bacteria (Molisch, 1938), of a few hours in many protozoa, or of a few weeks or months in many insects. Many semelparous plants and animals are annuals; in other semelparous organisms reproduction may occur only after a number of years of maturation, for example, two or more years in dobson flies and Pacific salmon, and many years in "century plants" (*Agave*) and the periodic cicada or "17-year locust" (*Magicicada septendecim*). The number of potential offspring produced by semelparous individuals varies from two in the case of binary fission to the literally trillions (2×10^{13}) of spores produced by a large puffball (*Calvatia gigantea*).

In iteroparous forms, that is to say, those which reproduce more than once in a lifetime, the period of maturation preceding the first production of prospective offspring may vary from as little as a few days in small crustaceans to over a century in the giant sequoia (U. S. Forest Service, 1948), and practically any intermediate value may be encountered. After the first reproduction has occurred in iteroparous organisms it may be repeated at various intervals—for example, daily (as in some tapeworms), semiannually, annually, biennially, or irregularly (as in man). As in semelparous organisms, the litter size of iteroparous forms may also vary greatly; here it may vary from one (as is usual, for example, in man, whales, bovines, and horses) to many thousands (as in various fishes, tapeworms, or trees). The litter size may be constant in a species, vary about some average, or change systematically with the age of the parent, in which case it may increase to some maximum (as in tapeworms) or climb to a maximum and then decline as in some cladocerans (Banta et al., 1939; Frank, 1952). Furthermore, individuals may live on after their reproduction has ceased completely, and this post-reproductive period may amount to more than one-half of the normal life span (Allee et al., 1949, p. 285).

There is similar variability in the potential longevity of individual organisms. Man, various turtles, and trees may survive more than a century, while, on the other hand, the life span of many other species is concluded in hours or days. Innumerable intermediate values of course occur.

Additional sources of variation (such as biased sex ratios and the occurrence of asexual reproduction in developmental stages so as to result in the

production of many offspring from one egg or spore) force the conclusion that the number of theoretical combinations of observed life history phenomena must greatly exceed the number of known species of organisms. And if all these phenomena have potential adaptive importance the interpretation of the possible merits of the particular combination of features exhibited by a species presents a problem of apparent great complexity.

The usual mathematical approach to the problem of potential population growth is straightforward. It is assumed that the growth of a population at any instant of time is proportional to the size of the population at that instant. If r is the factor of proportionality and P_x represents the population size at any x time this leads to the differential equation

$$\frac{dP}{dx} = rP \qquad (1)$$

which upon integration gives:

$$P_x = A\,e^{rx} \qquad (1')$$

where A is a constant. This is an equation of continuous compound interest at the rate r or of a geometric progression where the ratio between the sizes of the populations in two consecutive time intervals, say years, is e^r.

While formulas (1) and (1') represent only the usual starting point for mathematical discussions of population growth, they already exhibit points about which there has been, and still is, a great deal of controversy. Explicit statements to the effect that human populations potentially increase by geometric progression can be traced back at least to Capt. John Graunt (1662), who estimated that a human population tends to double itself every 64 years (which would correspond to $r = .0108$ in formula 1). This belief in geometric progression as the form of potential population increase was endorsed by numerous students prior to the great controversy initiated by Malthus in 1798 (see review by Stangeland, 1904). Among these early writers we may here note only Linnaeus (1743), who considered the problem of geometric increase in the progeny of an annual plant, and Benjamin Franklin (1751), who estimated that the population of "America" could double at least every 20 years (corresponding to $r = .035$), and who clearly regarded the geometric nature of potential population increase as a general organic phenomenon.

The great controversy over growth in human populations which was initiated by the publication in 1798 of Malthus' *Essay on Population* engendered numerous arguments regarding geometric progression as the potential form of population growth. This controversy is still alive and in much its original form, with the "Neo-Malthusian" position maintaining that potential population growth is indeed in the form of a geometric progression, whereas the capacity of the environment to absorb population is necessarily limited, and with their opponents denying both the geometric progression and the finite capacity of the environment. Essentially the modern arguments against the Malthusian thesis, although not presented in modern concise form, are to be found in the treatise by Sadler (1830) which, whatever its shortcomings from the modern point of view, contains in places (especially in the appendix to Book IV) a very remarkable pre-Darwinian statement of such ecological phenomena as food chains, species interactions, and the balance of numbers between predators and prey.

The entire problem of potential population growth and its relationship to the resources of the environment is clearly one of the fundamental problems of ecology, but one which has never been adequately summarized in a way to reconcile the mathematical approaches, such as those of Lotka (1925), Volterra (1927), Kuczynski (1932, 1935), Kostitzin (1939), and Rhodes (1940), and the purely biological approaches which have concentrated on life history features such as longevity, fecundity, fertility, and sex ratios. In the present paper we will consider the mathematical form of potential population growth and certain subsidiary phenomena and the way in which these are related to particular life history phenomena. It is hoped that this will bring to attention some of the possible adaptive values of observed life history phenomena and will lead ecologists to a greater consideration of population problems which are essentially ecological. Life history features do in fact control potential population growth, as Sadler recognized, but the quantitative relationships have still been so insufficiently elucidated that even today ecologists generally do not attempt to answer queries such as the following, written by Sadler in 1830 (Vol. 2, p. 318):

"For instance, how would those who have the folly to suppose that population in this country advances too fast by one per cent., so operate, had they even

their wish, as to diminish the number of marriages by one in one hundred, or otherwise contract the fecundity of the existing number by about one twenty-fifth part of a birth each, or calculate, upon their own erroneous suppositions, the term of that postponement of marriage on which they insist so much, so as to produce this exact effect? The very idea is, in each instance, absurd to the last degree."

FUNDAMENTAL CONSIDERATIONS

Sadler (1830) makes clear in numerous places his belief that "... the geometrical ratio of human increase is, nevertheless, in itself, an impossibility ..." (Vol. 2, p. 68). However, when one examines his argument it is apparent that he is not actually opposing the principle that with fixed life history features populations would grow at compound interest, but rather is proposing the thesis that life history features change with population density, e.g., his fundamental thesis: "The prolificness of human beings, otherwise similarly circumstanced, varies inversely as their numbers" (Vol. 2, p. 252). Some of Sadler's computations assuming fixed ages at marriage and fecundity rates, in fact, lead to geometric progressions.

The modern conception of population growth regards the *potential* rate of increase as a more or less fixed species characteristic (cf. Chapman, 1935) governed by life history features; but it considers that this potential rate is ordinarily only partially realized, the "partial potential" characteristic of a particular situation being dependent on environmental conditions. Ecologists commonly associate this concept of "biotic potential" with the name of Chapman (1928, 1935), but actually the concept of populations as systems balanced between a potential ability to grow and an "environmental resistance" dates back at least to the Belgian statistician Quetelet (1835), who considered (p. 277) that potential population growth is a geometric progression, while the resistance to population growth (by analogy with a body falling through a viscous medium) varies as the square of the rate of growth. Only three years later Quetelet's student and colleague Verhulst (1838) set forth the thoroughly modern concept that potential population growth is a geometric progression corresponding to our formula (1'), and that the environmental resistance varies inversely with the unexploited opportunities for growth. By this conception, if K represents the capacity of the environment or the ultimate size which the population can attain, the resistance to population growth increases as $K - P$, the amount of space

remaining to be occupied, decreases. As the simplest case Verhulst considered that the resistance is related in a linear manner to the remaining opportunities for growth and thus derived the familiar logistic function as a representation of population growth (for discussion see Allee et al., 1949).

The modern mathematical formulation of population growth, as given, for example, by Rhodes (1940), proceeds by expressing the environmental resistance as some function of population size, $f(P)$, and writing a differential equation of the type

$$\frac{dP}{dx} = rPf(P). \qquad (2)$$

By employing different functions for $f(P)$, any number of population growth laws may be derived and the mathematical connection between P and x determined, providing equation (2) can be integrated. Rhodes gives several examples of the procedure.

Formula (1'), the equation of the geometric progression representing population growth in an unlimited environment, represents the special case of formula (2) where the factor $f(P)$ is replaced by a constant, most conveniently by the constant value unity. By the foregoing interpretation it is clear that the constant r must be regarded as a quantity of fundamental ecological significance. It is to be interpreted as the rate of true compound interest at which a population would grow if nothing impeded its growth and if the age-specific birth and death rates were to remain constant.

Quite recently a number of ecologists have recognized the importance of a knowledge of the value of r for non-human populations and have computed its value for various species by employing empirical values of age-specific birth rates and survivorship (Leslie and Ranson, 1940; Birch, 1948; Leslie and Park, 1949; Mendes, 1949; Evans and Smith, 1952). While Chapman's term "biotic potential" would seem to have ecological merit as the name for this parameter r it has been variously called by Lotka the "true," the "incipient," the "inherent," and the "intrinsic" rate of increase, and by Fisher (1930) the "Malthusian parameter" of population increase. Probably for the sake of stabilizing nomenclature it is advisable to follow the majority of recent writers and refer to r as "the intrinsic rate of natural increase."

In the works of Dublin and Lotka (1925),

Kuczynski (1932), and Rhodes (1940) on human populations and in the papers mentioned above dealing with other species, the value of *r* has typically been determined by some application of three fundamental equations developed by Lotka (1907a, b; Sharpe and Lotka, 1911). He showed that if the age-specific fecundity (b_x) and survivorship (l_x) remained constant, the population would in time assume a fixed or "stable" age distribution such that in any interval of age from x to $x + dx$ there would be a fixed proportion (c_x) of the population. Once this stable age distribution is established the population would grow exponentially according to our formula (1′) and with a birth rate per head, β. Then the following equations relate these quantities:

$$\int_0^\infty e^{-rx} l_x b_x \, dx = 1 \qquad (3)$$

$$\int_0^\infty e^{-rx} l_x \, dx = 1/\beta \qquad (4)$$

and

$$\beta e^{-rx} l_x = c_x. \qquad (5)$$

While the use of formulas (3), (4), and (5) to compute the value of *r* often presents practical difficulties owing to the difficulty of approximating the functions l_x and b_x by a mathematical function, and also because the equations usually must be solved by iterative methods, it may fairly be stated that Lotka's pioneer work establishing these relationships provided the methods for interpreting the relationships between life history features and their population consequences.

However, the exceedingly important ecological questions of what potential advantages might be realized if a species were to alter its life history features have remained largely unexplored. Doubtless, as already noted, this is largely to be explained by a certain suspicion felt by biologists toward analyses such as those of Lotka, which seem to involve assumptions very remote from the realities of life histories as observed in the field and laboratories. A particularly pertinent statement of this point of view is that of Thompson (1931), who recognized the great practical need for methods of computing the rate of increase of natural populations of insects adhering to particular life history patterns but who insisted that the reproductive process must be dealt with as a discontinuous phenomenon rather than as a compound interest phenomenon such as that of formula (1′). His methods of computation were designed to give the exact number of individuals living in any particular time period and, while he recognized that the population growth can be expressed in an exponential form such as (1′), he rejected its use on these grounds:

"In the first place, the constant (*r*) cannot be determined until the growth of the population under certain definite conditions has been studied during a considerable period; in the second place, no intelligible significance can be attached to the constant after its value has been determined; in the third place, the growth of the population is considered in this formula to be at every moment proportional to the size of the population, which is not true except with large numbers and over long periods and cannot be safely taken as a basis for the examination of experimental data."

In the following sections of the present paper an effort will be made to reconcile these two divergent points of view and to show under what conditions Thompson's "discontinuous" approach and the continuous methods lead to identical results. Practical methods of computation can be founded on either scheme, and there are circumstances where one or the other offers distinct advantages. It is hoped that a theoretical approach to population phenomena proceeding from exact computational methods will clarify the meaning of some of the approximations made in deriving equations such as (3), (4), and (5) by continuous methods, and will stimulate students of ecology to a greater interest in the population consequences of life history phenomena.

Before proceeding to a discussion of potential population growth, one point which has sometimes caused confusion should be mentioned. This concerns the sex ratio and the relative proportions of different age classes in the growing population. Once stated, it is obvious that if a population is always growing, as are the populations in the models used for determining potential population growth, then each age and sex class must ultimately come to grow at exactly the same rate as every other class. If this were not the case the disproportion between any two classes would come to exceed all bounds; the fastest growing class would continue indefinitely to make up a larger and larger proportion of the total population. It is thus intuitively recognizable that with fixed life history features there must ultimately be a fixed sex ratio and a stable age distribution. In discussing potential population growth it is often convenient to confine our attention to females or

even to a restricted age class, such as the annual births, while recognizing that the ultimate growth rate for such a restricted population segment must be identical to the rate for the entire population.

SIMPLEST CASES OF POPULATION GROWTH

Non-overlapping generations

The simplest possible cases of population growth from the mathematical point of view are those in which reproduction takes place once in a lifetime and the parent organisms disappear by the time the new generation comes on the scene, so that there is no overlapping of generations. This situation occurs in the many plants and animals which are annuals, in those bacteria, unicellular algae, and protozoa where reproduction takes place by fission of one individual to form two or more daughter individuals, and in certain other forms. Thus in the century plants (*Agave*) the plant dies upon producing seeds at an age of four years or more, the Pacific salmon (*Oncorhynchus*) dies after spawning, which occurs at an age of two to eight years (two years in the pink salmon *O. gorbuscha*), and cicadas breed at the end of a long developmental period which lasts from two years (*Tibicen*) to 17 years in *Magicicada*. For many other insects with prolonged developmental stages such as neuropterans and mayflies potential population growth may be considered on the assumption that generations do not overlap.

In these cases, perhaps most typically illustrated in the case of annuals, the population living in any year or other time interval is simply the number of births which occurred at the beginning of that interval. Starting with one individual which is replaced by b offspring each of which repeats the life history pattern of the parent, the population will grow in successive time intervals according to the series: 1, b, b^2, b^3, b^4, $\cdots$ b^x. Hence the number of "births," say B_x, at the beginning of any time interval, T_x, is simply b^x which is identical with the population, P_x, in that interval of time. If the population starts from an initial number P_0 we have:

$$P_x = P_0 b^x \qquad (6)$$

which is obviously identical with the exponential formula (1'), $P_x = Ae^{rx}$, where the constant A is precisely P_0, the initial population size, and $r = \ln b$; the intrinsic rate of increase is equal to the natural logarithm of the litter size.

If litter size varies among the reproductive individuals, with each litter size being characteristic of a fixed proportion of each generation, it is precisely correct to use the average litter size, say $\bar{b}$, in the computations, so that we have $r = \ln \bar{b}$. Furthermore, if not all of the offspring are viable, but only some proportion, say l_1, survive to reproduce, we shall have exactly $r = \ln \bar{b}^{l_1}$. Thus, mortality and variations in litter size do not complicate the interpretation of population growth in cases where the generations do not overlap. On the other hand, even in species which reproduce only once, if the generation length is not the same for all individuals, this will lead to overlapping generations, and the simple considerations which led to formula (6) will no longer apply. In other words, we can use an average figure for the litter size b but not for the generation length x. It will be shown in the next section, however, that the more general formula (1') is still applicable.

In these simplest cases the assumption of a geometric progression as the potential form of population growth is obviously correct, and numerous authors have computed the fantastic numbers of offspring which could potentially result from such reproduction. For example, according to Thompson (1942), Linnaeus (1740?) pointed out that if only two seeds of an annual plant grew to maturity per year, a single individual could give rise to a million offspring in 20 years. (In all editions available to the present writer this interesting essay of Linnaeus' is dated 1743, and the number of offspring at the end of twenty years is stated by the curious and erroneous figure 91,296.) That is, $P_{20} = 2^{20} = e^{20 \ln 2} = 1,048,576$. Additional examples are given by Chapman (1935, p. 148).

Formulas (1') or (6) may, of course, also be used in an inverse manner to obtain the rate of multiplication when the rate of population growth is known. For the example given by Molisch (1938, p. 25), referring to diatoms reproducing by binary fission where the average population was observed to increase by a factor of 1.2 per day, we have $1.2 = e^{x \ln 2}$, where x is the number of generations per day. Solving for $1/x$, the length of a generation, we obtain $1/x = \dfrac{\ln 2}{\ln 1.2} = \dfrac{.69315}{.18232} = 3.8$ days.

Overlapping generations

Interest in computing the number of offspring which would be produced by a species adhering to a constant reproductive schedule dates back at

least to Leonardo Pisano (= Fibonacci) who, in the year 1202, attempted to reintroduce into Europe the study of algebra, which had been neglected since the fall of Rome. One of the problems in his *Liber Abbaci* (pp. 283–84 of the 1857 edition) concerns a man who placed a pair of rabbits in an enclosure in order to discover how many pairs of rabbits would be produced in a year. Assuming that each pair of rabbits produces another pair in the first month and then reproduces once more, giving rise to a second pair of offspring in the second month, and assuming no mortality, Fibonacci showed that the number of pairs in each month would correspond to the series

$$1, 2, 3, 5, 8, 13, 21, 34, 55, \text{etc.},$$

where each number is the sum of the two preceding numbers. These "Fibonacci numbers" have a rather celebrated history in mathematics, biology, and art (Archibold, 1918; Thompson, 1942; Pierce, 1951) but our present concern with them is merely as a very early attempt to compute potential population growth.

Fibonacci derived his series simply by following through in words all of the population changes occurring from month to month. One with sufficient patience could, of course, apply the same procedure to more complicated cases and could introduce additional variables such as deductions for mortality. In fact, Sadler (1830, Book III) did make such computations for human populations. He was interested in discovering at what ages persons would have to marry and how often they would have to reproduce to give some of the rates of population doubling which had been postulated by Malthus (1798). To accomplish this, Sadler apparently employed the amazingly tedious procedure of constructing numerous tables corresponding to different assumptions until he found one which approximated the desired rate of doubling.

Although we must admire Sadler's diligence, anyone who undertakes such computations will find that it is not difficult to devise various ways of systematizing the procedure which will greatly reduce the labor of computation. By far the best of these methods known to the present writer is that of Thompson (1931), which was originally suggested to him by H. E. Soper.

In the Soper-Thompson approach a "generation law" (*G*) is written embodying the fixed life history features which it is desired to consider. The symbol

T^x stands for the xth interval of time, and a generation law such as $G = 2T^1 + 2T^2$ would be read as "two offspring produced in the first time interval and two offspring produced in the second time interval." This particular generation law might, for example, be roughly applicable to some bird such as a cliff swallow, where a female produces about four eggs per year. Concentrating our attention on the female part of the population, we might wish to compute the rate of population growth which would result if each female had two female offspring upon attaining the age of one year and had two more female offspring at the age of two years. The fundamental feature of the Thompson method is the fact that the expression:

$$\frac{1}{1 - G} \tag{7}$$

is a generating function which gives the series of births occurring in successive time intervals. In the algebraic division the indices of the terms T^1, T^2, etc., are treated as ordinary exponents and the number of births occurring in any time interval T^x is simply the coefficient of T^x in the expansion of expression (7). Thus, for our example where $G = 2T^1 + 2T^2$ we obtain:

$$\frac{1}{1 - 2T^1 - 2T^2} = 1 + 2T^1 + 6T^2 +$$

$$16T^3 + 44T^4 + 120T^5 + 328T^6 + \cdots,$$

showing that one original female birth gives rise to 328 female offspring in the sixth year. The series could be continued indefinitely to obtain the number of births any number of years hence. However, in practice it is not necessary to continue the division. In the above series the coefficient of each term is simply twice the sum of the coefficients of the two preceding terms; hence the generation law gives us the rule for extending the series. $G = 2T^1 + 2T^2$ instructs us to obtain each new term of the series by taking twice the preceding term plus twice the second term back. In the case of the Fibonacci numbers we would have $G = T^1 + T^2$, telling us at once that each new term is the sum of the two preceding it.

From the birth series we can easily obtain the series enumerating the total population. If each individual lives for λ years, the total population in T^x will be the sum of λ consecutive terms in the expansion of the generating function. Multiplying formula (7) by the length of life expressed in the form $1 + T^1 + T^2 + T^3 + \cdots + T^{\lambda-1}$ will give

the population series. In our above example if we assume that each individual lives for three years, although, as before, it only reproduces in the first two, we obtain for the population

$$\frac{1 + T^1 + T^2}{1 - 2T^1 - 2T^2} = 1 + 3T^1 + 9T^2 +$$

$$24T^3 + 66T^4 + 180T^5 + 492T^6 + \cdots,$$

a series which still obeys the rule $G = 2T^1 + 2T^2$.

Thompson's method for obtaining the exact number of births and members of the population in successive time intervals is very general. As in the case of non-overlapping generations, the coefficients in the generation law may refer to average values for the age-specific fecundity. Also the length of the time intervals upon which the computations are based can be made arbitrarily short, so that it is easy to take into account variations in the age at which reproduction occurs. For the above example, time could have been measured in six-month periods rather than years so that the generation law would become $G = 2T^2 + 2T^4$, with the same results already obtained.

Furthermore, the factor of mortality can easily be included in the computations. For example, suppose that we wish to determine the rate of population growth for a species where the females have two female offspring when they reach the age of one, two more when they reach the age of two, and two more when they reach the age of three. Neglecting mortality, this would give us the generation law $G = 2T^1 + 2T^2 + 2T^3$. If we were further interested in the case where not all of the offspring survive for three years, the coefficients in the generation law need only be multiplied by the corresponding survivorship values. For example, if one-half of the individuals die between the ages of one and two, and one half of the remainder die before reaching the age of three we would have $l_1 = 1$, $l_2 = \frac{1}{2}$, $l_3 = \frac{1}{4}$, and the above generation law would be revised to $G = 2T^1 + T^2 + \frac{1}{2}T^3$. The future births per original individual would then be

$$\frac{1}{1 - G} = 1 + 2T^1 + 5T^2 + 25/2T^3 + 31T^4 +$$

$$151/2T^5 + \cdots.$$

Very generally, if the first reproduction for a species occurs at some age α and the last reproduction occurs at some age ω, and letting b_x and l_x represent respectively the age-specific fecundity

and survivorship, we may write the generation law as:

$$G = l_\alpha b_\alpha T^\alpha + l_{\alpha+1} b_{\alpha+1} T^{\alpha+1} + \cdots$$

$$+ l_\omega b_\omega T^\omega = \sum_{x=\alpha}^{\omega} l_x b_x T^x. \tag{8}$$

Therefore, in the Thompson method we have a compact system of computation for obtaining the exact number of births and the exact population size at any future time, assuming that the significant life history features (α, ω, l_x, and b_x) do not change.

Not all of the possible applications of Thompson's method have been indicated above. For example, formula (7) may be used in an inverse manner so that it is theoretically possible to work back from a tabulation of births or population counts made in successive time intervals and discover the underlying generation law. Formulas (7) and (8), together with the procedure of multiplying the birth series by the length of life expressed as a sum of T^x values, provide the nucleus of the system and offer the possibility of analyzing the potential population consequences of essentially any life-history phenomena. The system has the merit of treating the biological units and events as discontinuous variates, which, in fact, they almost always are. The members of populations are typically discrete units, and an event such as reproduction typically occurs at a point in time with no spreading out or overlapping between successive litters. While survivorship, l_x, as a population quantity, is most realistically regarded as continuously changing in time, the product $l_x b_x$ which enters our computations by way of formula (8) is typically discontinuous because of the discontinuous nature of b_x.

It is quite obvious that equations of continuous variation such as (1′) are often much more convenient for purposes of computation than the series of values obtained by expanding (7). This is especially true in dealing with the life histories of species which have long reproductive lives. In writing a generation law for man by (8) we should have to take α at least as small as 15 years and ω at least as great as 40 years, since for the population as a whole reproduction occurs well outside of these extremes and it would certainly be unrealistic to regard b_x as negligibly small anywhere between these limits. Thus there would be at least 25 terms in our generation law, and the computations would be extremely tedious. By selecting special cases
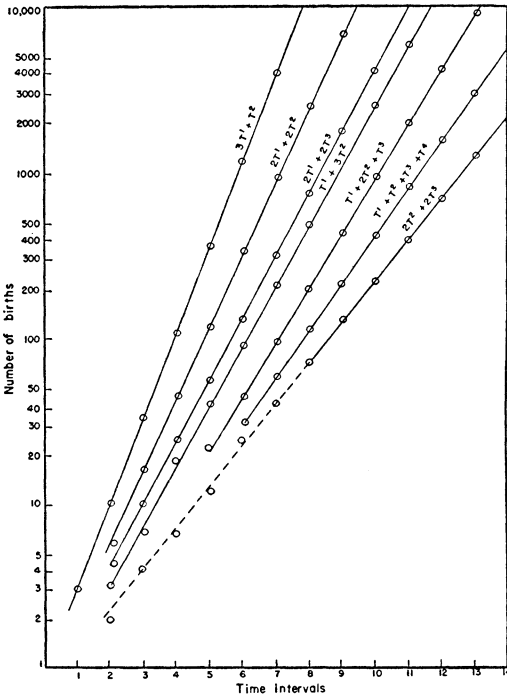
FIG. 1. EXACT VALUES OF POPULATION GROWTH IN TERMS OF BIRTHS PER UNIT TIME UNDER SEVERAL GENERATION LAWS, WHEN EACH FEMALE HAS A TOTAL OF FOUR FEMALE OFFSPRING

In each case it is assumed that a single female exists at time zero and produces her four progeny on or before her fourth birthday. The plotted points represent exact values as determined by Thompson's method. To the extent that the points for any generation law fall on a straight line in this logarithmic plot, they can be represented by the exponential growth formula (1′), and the slope of each line is a measure of the intrinsic rate of natural increase (r).

for study it is sometimes possible greatly to simplify the procedures. For example, if one is interested in the case where there is no mortality during the reproductive span of life and where the litter size is a constant, say b, the expression for the generation law (8) can be simplified to:

$$G = bT^{\alpha} + bT^{\alpha+1} + \cdots bT^{\omega} = \frac{bT^{\alpha} - bT^{\omega+1}}{1 - T}.$$

Since one can also write the length of life as

$$1 + T^1 + T^2 + \cdots + T^{\lambda-1} = \frac{1 - T^{\lambda}}{1 - T},$$

the generating function for the total population simplifies to

$$\frac{1 - T^{\lambda}}{1 - T - bT^{\alpha} + bT^{\omega+1}}.$$

This last formula is much more convenient for computations than one containing 25 terms or so in the denominator, but it applies only to a very special case and is much less convenient than formula (1′). Consequently, great interest attaches to these questions: can (1′) be used as a substitute for (7)? (i.e., does Thompson's method lead to a geometric progression?) and, if it is so used, can the constants, particularly r, be interpreted in terms of life-history features?

THE GENERALIZATION OF THOMPSON'S METHOD

Fig. 1 shows the exact values, as determined by Thompson's method, of the birth series arising from several generation laws (life-history patterns) which have in common the feature that in each case every female produces a total of four female offspring in her lifetime and completes her reproductive life by the age of four "years." The number of births is plotted on a logarithmic scale, hence if it can be represented by formula (1′), $P = Ae^{rx}$ or, logarithmically, $\ln P = \ln A + rx$, the points should fall on a straight line with slope proportional to r. It is apparent from Fig. 1 that after the first few time intervals the points in each case are well represented by a straight line. Therefore, except in the very early stages, formula (1′) does give a good representation of potential population growth. The question remains, however, as to whether we can meet Thompson's objection to (1′) and attach any intelligible significance to the constants of the formula. From Fig. 1 it is obvious that the lines do not, if projected back to time 0, indicate exactly the single individual with which we started. Thus, in these cases the constant A cannot be precisely P_0 as was the case with non-overlapping generations.

Before proceeding to interpret the constants of formula (1′) for the case of overlapping generations it will be well to notice one feature of Fig. 1 which is of biological interest. In the literature of natural history one frequently encounters references to the number of offspring which a female can produce per lifetime, with the implication that this is a significant life-history feature. The same implication is common in the literature dealing with various aspects of human biology, where great emphasis is placed on the analysis of total family size. From Fig. 1 it will be seen that this datum may be less significant from the standpoint of contributions to future population than is the age schedule upon which these offspring are

produced. Each life history shown in Fig. 1 represents a total production of four offspring within four years of birth, but the resulting rates of potential population growth are very different for the different schedules. It is clear that the cases of most rapid population growth are associated with a greater concentration of reproduction into the early life of the mother. This is intuitively reasonable because we are here dealing with a compound interest phenomenon and should expect greater yield in cases where "interest" begins to accumulate early. However, the writer feels that this phenomenon is too frequently overlooked in biological studies, possibly because of the difficulty of interpreting the phenomenon quantitatively.

In seeking to reconcile the continuous and discontinuous approaches to potential population growth, let us first note that Thompson's discontinuous method corresponds to an equation of finite differences. We have seen above that the generation law gives us a rule for indefinitely extending the series representing the population size or the number of births in successive time intervals by adding together some of the preceding terms multiplied by appropriate constants. If we let $f_{(x)}$ represent the coefficient of T^x in the expansion of the generating function (7) and, for brevity, write in (8) $V_x = l_x b_x$, then our population series obeys the rule:

$$f_{(x)} = V_\alpha f_{(x-\alpha)} + V_{\alpha+1} f_{(x-\alpha-1)} + \cdots + V_\omega f_{(x-\omega)}, \quad (9)$$

which may be written in the alternative form,

$$f_{(x+\omega)} - V_\alpha f_{(x+\omega-\alpha)} - V_{\alpha+1} f_{(x+\omega-\alpha-1)} - \cdots - V_\omega f_{(x)}, = 0. \quad (10)$$

Thus for our "cliff swallow" example, where we had $G = 2T^1 + 2T^2$ we have

$$f_{(x)} = 2f_{(x-1)} + 2f_{(-2)} \text{ or,}$$
$$f_{(x+2)} - 2f_{(x+1)} - 2f_{(x)} = 0.$$

Formula (10) represents the simplest and best understood type of difference equation, a homogeneous linear difference equation with constant coefficients. It is outside the scope of the present paper to discuss the theory of such equations, which has been given, for example, by Jordan (1950). By the nature of our problem as summarized in formula (9), all of our V_x values are either equal to zero or are positive real numbers and all of the signs of the coefficients in (9) are positive: features which considerably simplify

generalizations. By virtue of these facts it can be shown that there is always a "characteristic" algebraic equation corresponding to (10). This is obtained by writing ρ^x for $f_{(x)}$ and dividing through by the ρ value of smallest index. This gives

$$\rho^\omega - V_\alpha \rho^{\omega-\alpha} - V_{\alpha+1} \rho^{\omega-\alpha-1} \cdots - V_\omega = 0 \quad (11)$$

an algebraic equation which has the roots ρ_1, ρ_2, etc.

The general solution of the corresponding difference equation (10) is

$$f_{(x)} = C_1 \rho_1^x + C_2 \rho_2^x + \cdots + C_n \rho_n^x \quad (12)$$

where the C's are constants to be determined by the initial conditions of the problem. Formula (12) is precisely equivalent to Thompson's method and is a general expression for the number of births or the population size in any future time interval.

As an example we may consider the case where $G = 2T^1 + 2T^2$. The difference equation, as already noted, is $f_{(x+2)} - 2f_{(x+1)} - 2f_{(x)} = 0$ and the characteristic algebraic equation is $\rho^2 - 2\rho - 2 = 0$ which is a quadratic equation with the roots $\rho_1 = 1 + \sqrt{3}$, and $\rho_2 = 1 - \sqrt{3}$. Hence the general solution is $f_{(x)} = C_1(1 + \sqrt{3})^x + C_2(1 - \sqrt{3})^x$. To determine the constants C_1 and C_2 we look at the beginning a of the seriesnd note that we have $f_{(0)} = 1$ and $f_{(1)} = 2$. Substituting these values in the general solution we obtain $C_1 = \dfrac{\sqrt{3} + 1}{2\sqrt{3}}$ and $C_2 = \dfrac{\sqrt{3} - 1}{2\sqrt{3}}$. Therefore, the general expression for the number of births in time interval T^x is

$$f_{(x)} = \frac{\sqrt{3} + 1}{2\sqrt{3}}(1 + \sqrt{3})^x + \frac{\sqrt{3} - 1}{2\sqrt{3}}(1 - \sqrt{3})^x$$

which can be simplified to $f_{(x)} = \dfrac{\rho_1^{x+1} - \rho_2^{x+1}}{\sqrt{3}} = \rho_1^x + \rho_1^{x-1}\rho_2 + \cdots + \rho_2^x$.

In order to have the difference equation (12) correspond to the equation of exponential growth (1′), the ratio between populations in successive time intervals must assume a constant value giving

$$\frac{f_{(x+1)}}{f_{(x)}} = e^r. \quad (13)$$

By the nature of our problem, as already noted, the potential population growth is always positive, so

that any limit approached by the ratio $\dfrac{f_{(x+1)}}{f_{(x)}}$ must be a positive real number.

It is beyond the scope of the present paper to discuss the conditions, for difference equations in general, under which this ratio does approach as a limit the largest real root of the characteristic algebraic equation. (See, for example, Milne-Thompson, 1933, chap. 17). Dunkel (1925) refers to the homogeneous equation with real constant coefficients corresponding to our formulas (10) and (11). The algebraic equation (11) has a single positive root which cannot be exceeded in absolute value by any other root, real or complex. Using (12) to express the ratio between successive terms, we have

$$\frac{f_{(x+1)}}{f_{(x)}} = \frac{C_1\rho_1^{x+1} + C_2\rho_2^{x+1} + \cdots + C_n\rho_n^{x+1}}{C_1\rho_1^{x} + C_2\rho_2^{x} + \cdots + C_n\rho_n^{x}}. \quad (14)$$

If we let ρ_1 represent the root of (11) of greatest absolute value and divide both numerator and denominator of (14) by $C_1\rho_1^{x}$ we obtain

$$\frac{f_{(x+1)}}{f_{(x)}} = \rho_1 \left[\frac{1 + \frac{C_2}{C_1}\left(\frac{\rho_2}{\rho_1}\right)^{x+1} + \frac{C_3}{C_1}\left(\frac{\rho_3}{\rho_1}\right)^{x+1} + \cdots + \frac{C_n}{C_1}\left(\frac{\rho_n}{\rho_1}\right)^{x+1}}{1 + \frac{C_2}{C_1}\left(\frac{\rho_2}{\rho_1}\right)^{x} + \frac{C_3}{C_1}\left(\frac{\rho_3}{\rho_1}\right)^{x} + \cdots + \frac{C_n}{C_1}\left(\frac{\rho_n}{\rho_1}\right)^{x}} \right]. \quad (15)$$

The expressions in parentheses are all less than unity, on the assumption that ρ_1 is the largest root, and the entire expression in brackets approaches unity as x increases. Consequently we have, for x large

$$\frac{f_{(x+1)}}{f_{(x)}} \sim \rho_1 \sim e^r. \quad (16)$$

This then explains the shape of the potential birth and population series as illustrated in Fig. 1. In the very early stages population growth is irregular, because the expressions in (12) and (15) involving the negative and complex roots of (11) are still large enough to exert an appreciable influence. As x increases, the influence of these other roots becomes negligible and the population grows exponentially, conforming to (16). In considering potential population growth we are concerned with the ultimate influence of life-history features, and the equation of geometric progression or compound interest does actually represent the form of potential population growth. We are interested only

in the single positive root of (11) for the purpose of determining the constant r, and this can readily be computed with any desired degree of precision by elementary algebraic methods.

Having established the relationship of formula (13) or (16), it is easy to reconcile Thompson's discontinuous approach to population growth with Lotka's continuous approach, as exemplified by formulas (3), (4), and (5).

Employing formula (9) we may write the ratio between populations in successive time intervals as

$$\frac{(f_{x+1})}{f_{(x)}} = V_\alpha \frac{f_{(x-\alpha+1)}}{f_{(x)}} + V_{\alpha+1}\frac{f_{(x-\alpha)}}{f_{(x)}} + \cdots + V_\omega \frac{f_{(x-\omega+1)}}{f_{(x)}}.$$

Substituting the relationship given by (13), this becomes

$$e^r = V_\alpha e^{-r(\alpha-1)} + V_{\alpha+1}e^{-r\alpha} + \cdots + V_\omega e^{-r(\omega-1)}, \text{ or}$$

$$1 = V_\alpha e^{-r\alpha} + V_{\alpha+1}e^{-r(\alpha+1)} + \cdots + V_\omega e^{-r\omega}.$$

Replacing V_x by its equivalent, $l_x b_x$, this is

$$1 = \sum_{x=\alpha}^{\omega} e^{-rx} l_x b_x. \quad (17)$$

Formula (17) is the precise equivalent in terms of finite time intervals of Lotka's equation (3) for infinitesimal time intervals. In Lotka's equation, as in (17), the limits of integration in practice are α and ω since b_x is zero outside of these limits. Formula (17) was in fact employed by Birch (1948) as an approximation to (3) in his method of determining r for an insect population. The only approximation involved in our derivation of (17) is the excellent one expressed by formula (13); otherwise the formula corresponds to Thompson's exact computational methods. It is hoped that recognition of this fact will make some of the approaches of population mathematics appear more realistic from the biological point of view.

Formulas (4) and (5), originally due to Lotka, are also immediately derivable from the relationship (13). In any time interval, T_x, we may say that the population members aged 0 to 1 are

simply the births in that interval, say B_x. The population members aged 1 to 2 are the survivors of the births in the previous interval, that is $l_1 B_{x-1}$, or employing (13), $l_1 B_x e^{-r}$. Quite generally, the population members aged between z and $z + 1$ are the survivors from the birth z intervals previous, or $l_z B_x e^{-rz}$. If λ is the extreme length of life for any population members $(l_{\lambda+1} = 0)$ we have for the total population

$$P_x = B_x(1 + l_1 e^{-r} + l_2 e^{-2r} + \cdots$$
$$+ l_\lambda e^{-r\lambda} = B_x \sum_{x=0}^{\lambda} e^{-rx} l_x.$$

The birth rate per individual, β, is B_x/P_x, therefore,

$$1/\beta = \sum_{0}^{\lambda} e^{-rx} l_x \tag{18}$$

which is the equivalent in finite time intervals of Lotka's equation (4). Also the proportion, c_z, of the population in the age range z to $z + 1$ is $\dfrac{l_z B_x e^{-rz}}{P_x}$ which is simply,

$$c_z = \beta e^{-rz} l_z. \tag{5}$$

COMPUTATIONAL METHODS

In the following sections we will examine some of the population effects which are the consequences of particular life history patterns. Probably the most significant comparisons are those involving the effects of life-history features on the intrinsic rate of natural increase, r. Of course, any change in r is accompanied by other effects, such as those on the age-structure and on the population birth-rate. However, the intrinsic rate of increase is a parameter of fundamental ecological importance. If a species is exposed to conditions which would favor the ability to outbreed competitors or where exceptional hazards limit the probability that an individual will become established, we might expect to find life-history adjustments tending to increase the value of r. Conversely, if a species has evolved life-history features of a type tending to hold down the intrinsic rate of increase, a fertile field of inquiry may be opened regarding the selective factors to which such a species is subject.

It is probably fairly obvious to anyone that in general a species might increase its biotic potential by increasing the number of offspring produced at a time (litter size), by reducing mortality at least until the end of active reproductive life, by reproducing oftener, by beginning reproduction at an earlier age, or by minimizing any wastage of environmental resources on sterile members of the population. Any biologist will at once recognize, however, that a great deal of evolution (an extreme case is the evolution of sterility in the social insects) has proceeded in precisely the wrong direction to increase biotic potential by some of these devices. Presumably, this can only mean that the optimum biotic potential is not always, or even commonly, the maximum that could conceivably be achieved by selecting for this ability alone. Comparative life-history studies appear to the writer to be fully as meaningful in evolutionary terms as are studies of comparative morphology or comparative physiology.

Although a great many empirical data on life histories have been accumulated, attempts to interpret these data comparatively have lagged far behind the corresponding efforts in morphology and physiology. The methods exhibited in the preceding parts of the present paper are adaptable for the quantitative interpretation of life history features and, while the number of conceivable life-history patterns is infinite, we propose to examine some of the cases which appear to possess particular ecological interest.

The life-history features with which we are concerned are the age at which reproduction begins (α), the litter size and frequency of reproduction (both summarized by a knowledge of the function b_x, which can also be computed so as to take account of the sex ratio), the maximum age at which reproduction occurs (ω), survivorship (l_x), and maximum longevity (λ). Corresponding to any given set of values for these quantities there is a definite value for the intrinsic rate of natural increase (r) and a definite stable age distribution of the population (c_x). In general, these population features will be altered by any alteration of the life-history features and we wish to examine some of these possible changes quantitatively.

The most efficient way of making the desired computations will vary from problem to problem. Thompson's method (formulas (7) and (8)), could be used to obtain exact population values arising from any life history, but the computations would in many cases be exceedingly laborious and would actually uield no more information about the ultimate course of population growth than would be obtained by solving (11) for the positive root.

In either case it will usually be most efficient to measure time in terms of the shortest interval between the pertinent life-history events with which we are concerned.

Except in very special cases, it is necessary to use iterative methods for obtaining the value of r corresponding to particular life-history patterns. In most cases the solutions are quite rapidly obtained by employing a calculating machine and detailed tables of natural logarithms (e.g., Lowan, 1941) or of the exponential function (e.g., Newman, 1883). In the majority of the cases considered by the writer, the most efficient procedure has been to rewrite formula (17) in the form:

$$e^{r\alpha} = V_\alpha + V_{\alpha+1}e^{-r} + V_{\alpha+2}e^{-2r} + \cdots \\ + V_\omega e^{-r(\omega-\alpha)} \qquad (19)$$

and then to obtain the sum of the series on the right-hand side of (19) for different patterns of variation in the function $l_x b_x = V_x$. This method corresponds exactly to the discontinuous approach, granting only that potential population growth is a geometric progression, and it leads to relatively simple equations in a number of the cases of greatest ecological interest.

A more general approach from the standpoint of formal mathematics can be obtained by rewriting (3) in the form of a Stieltjes integral (Widder, 1940). We may define a maternity function $M(x)$ representing the average number of offspring which an individual will have produced by the time it has attained any age x, and such that its derivative with respect to time is $\left(V_x \dfrac{d}{dx}M(x) = V_x\right)$. We then have

$$\int_0^\infty e^{-rx} dM(x) = 1 \qquad (20)$$

which can represent cases where $V_{(x)}$ is either continuous or discontinuous because the integral vanishes for values where V_x is discontinuous. When V_x can be expressed as a function of time (x), formula (20) is identical with (3) and the use of the Laplace transformation, a procedure of considerable importance in engineering and physical mathematics, makes it possible to avoid the numerical integration and express V_x as a function of r. If V_x is considered as a series of single impulses regularly spaced from α to ω, equation (20) assumes the form (17). Laplace transformations for a number of functions are tabulated by Churchill (1944) and Widder (1947) and, no doubt, there

are cases where this procedure would lead to simpler iterative solutions than those obtained from equation (19). For the cases considered in the present paper, however, the solution of equation (19) generally leads to somewhat simpler results.

In dealing with any particular life-history pattern the computational method of choice may depend upon the types of features to be investigated. The pure numbers α, ω, and λ typically offer no particular computational problems, as they are assigned different values, but this is not always the case with the functions b_x and l_x.

In the cases considered by the writer the intervals between successive periods of reproduction have been considered to be equal. There is no particular difficulty in altering this assumption so as to consider cases where the frequency of reproduction varies with age, but regular spacing seems to be so much more usual in nature as well as representing a limiting case that it seems to merit first consideration. Litter size often does vary with the age of the parent organism, and this fact may introduce complexities into the behavior of the function V_x. In this case also, it appears that the ecologically most interesting cases are those in which the average litter size is a constant. Furthermore, as will become apparent in later sections, the first few litters produced by an organism so dominate its contribution to future population growth that later changes in litter size would have only very minor population consequences. In dealing with empirical data on human populations attempts have been made to express analytically the changes in b_x with age [cf. "Tait's law" that fertility declines in a linear manner (Yule, 1906; Lotka, 1927)] but for the present we shall consider that b_x assumes only the values zero and some constant, b.

The shape of the survivorship (l_x) curve is more difficult to deal with in a realistic manner. Pearl and Miner (1935) originated the classification of survivorship curves which is most employed for ecological purposes (cf. Deevey, 1947; Allee et al., 1949). The "physiological" survivorship curve is the limiting type in which each individual lives to some limit characteristic of the species and the age at death (λ) is regarded as a constant. In this case $l_x = 1$ when $x \leqslant \lambda$ and $l_x = 0$ when $x > \lambda$. This is the simplest case for computations, and actual cases are known which approach this type. Furthermore, there are other types of survivorship curves of ecological interest which may be treated

in the same manner. In what Deevey (1947) calls Type III there is an extremely heavy early mortality with the few survivors tending to live out a "normal life span." For the computation of r we are only concerned (cf. formula 19) with survivorship during the reproductive span of life, and it appears likely that "Type III" curves can be treated as constant throughout this age range without serious error. Another interesting type of survivorship curve which appears to be consistent with empirical data at least on some wild populations (cf. Jackson, 1939; Deevey, 1947; Ricker, 1948) is that in which a constant proportion of the population dies in each interval of age. This, of course, implies that life expectancy is independent of age, an assumption which cannot in general be considered realistic but which might apply to catastrophic causes of mortality. When this type of l_x curve applies, the V_x values will be in geometric progression and the right side of formula (19) can be summed as easily as in the case where V_x is constant. This case is, therefore, easily dealt with.

The type of survivorship curve usually observed in actual cases is a reverse sigmoid curve, interpreted by Deevey as intermediate between the "physiological" type and the geometric progression. This can be interpreted in various ways as a "wearing-out" curve. Gompertz (1825) attempted to find an analytical form on the assumption that the ability of individuals to "resist destruction" decreases as a geometric progression with age. Elston (1923) has reviewed formulas proposed to represent human mortality; none of these has proved generally applicable, despite great complexity in some cases. Another approach is to assume that some sort of a "vital momentum" (Pearl, 1946) or ability to survive is distributed among the members of the population in the form of a bell-shaped or "normal" frequency distribution. This point of view is a familiar and controversial one in the recent literature on bio-assay problems (Finney, 1947, 1949; Berkson, 1944, 1951) and, at least to the extent that a bell-shaped curve can represent the empirical distribution of ages at death, a probit function or a logit function (Berkson, 1944) can be used to represent l_x.

In the present paper we are concerned primarily with the limiting cases or the *potential* meaning of life-history phenomena. Consequently the writer has chosen to deal with survivorship curves of the physiological type and thus to investigate the ultimate effects of life-history phenomena for a species which is able to reduce mortality during the reproductive part of the life span to a negligible value. Our general conclusions will not be seriously altered even by rather startling drastic alterations of this assumption, and, in any case, our results will indicate the maximum gain which a species might realize by altering its life-history features.

Perhaps the most fundamental type of life-history pattern to be investigated in terms of population consequences is that in which the individuals are assumed to produce their first offspring at the age of α "years" with the mean litter size being a constant, b. A second litter is produced at age $\alpha + 1$ and an additional litter in each subsequent interval of age out to, and including, age ω. The total number of litters produced per individual is then $n = \omega - \alpha + 1$.

We then have, from (19),

$$e^{r\alpha} = b(1 + e^{-r} + e^{-2r} + \cdots + e^{-r(\omega-\alpha)}).$$

The expression in parentheses is a geometric progression the sum of which is $\dfrac{1 - e^{-rn}}{1 - e^{-r}}$. Consequently, the general implicit equation for r under these conditions may be written

$$1 = e^{-r} + be^{-r\alpha} - be^{-r(n+\alpha)} \qquad (21)$$

which may be solved by trial and error by employing a table of the descending exponential function.

Alternative formulas corresponding to (21) may be obtained by the use of the Laplace transformation. In the case where reproduction is considered to occur as a series of regularly spaced impulses, this approach leads to formula (21). Another approach is to consider that $V_x = 0$ when $x < \alpha$, $V_x = b$ when $\alpha \leqq x \leqq \omega$, and $V_x = 0$ when $x > \omega$. The Laplace transformation of a step-function is then employed, leading to the formula

$$\frac{be^{-r\alpha}}{r} - \frac{be^{-r(\omega+1)}}{r} = 1. \qquad (22)$$

Formula (22) and formula (21) would be identical under the condition that $r + e^{-r} = 1$, which is approximately true when r is small. If one desires more nearly to reconcile the continuous and discontinuous approaches in this case, he may note that in formula (21) he is finding the area under a "staircase-shaped" curve with the first vertical step located at $x = \alpha$, whereas in formula (22) he

is finding the area under a straight line paralleling the slope of the staircase. It is apparent that the two areas will be more nearly identical if the straight line is started about one-half unit of time earlier. If we substitute in (22) $\alpha - \frac{1}{2}$ for α and $\omega - \frac{1}{2}$ for ω we obtain a formula which gives results for practical purposes identical with those obtained from (21). The formulas are about equally laborious to solve, and the writer has employed (21) for the following computations because of its more obvious relationship to the exact computational methods.

POSSIBLE VALUES OF REPEATED REPRODUCTION
(ITEROPARITY)

One of the most significant of the possible classifications of life histories rests on the distinction between species which reproduce only once in a lifetime and those in which the individuals reproduce repeatedly. This being the case, it is very surprising that there seem to be no general terms to describe these two conditions. The writer proposes to employ the term semelparity to describe the condition of multiplying only once in a lifetime, whether such multiplication involves fission, sporulation, or the production of eggs, seeds, or live young. Thus nearly all annual plants and animals, as well as many protozoa, bacteria, insects, and some perennial forms such as century plants and the Pacific salmon, are semelparous species. The contrasting condition will be referred to as iteroparity. Iteroparous species include some, such as small rodents, where only two or three litters of young are produced in a lifetime, and also various trees and tapeworms where a single individual may produce thousands of litters. The distinction between annual and perennial plants is doubtless the most familiar dichotomy separating semelparous and iteroparous species, but general consideration of the possible importance of these two distinct reproductive habits illustrates some points of ecological and evolutionary interest. For purposes of illustration we shall first consider cases where the time interval between reproductive efforts is fixed at one year.

Many plants and animals are annuals. This is true, for example, of many of the higher fungi and seed plants, of insects, and even of a few vertebrates. One feels intuitively that natural selection should favor the perennial reproductive habit because an individual producing seeds or young annually over a period of several years obviously

has the potential ability to produce many more offspring then is the case when reproduction occurs but once. It is, therefore, a matter of some interest to examine the effect of iteroparity on the intrinsic rate of natural increase in order to see if we can find an explanation for the fact that repeated reproduction is not more general.

Let us consider first the case of an annual plant (or animal) maturing in a single summer and dying in the fall at the time of reproduction. We have seen earlier (formula 16, seq.) that if b is the number of offspring produced by such an annual the intrinsic rate of increase would be the natural logarithm of b. We wish to determine by how much this would be increased if the individual were to survive for some additional years, producing b offspring each year. Obviously, an annual species with a litter size of one (or an average of one female per litter in sexual species) would merely be replacing current population and no growth would be possible (ln 1 = 0); therefore, when the litter size is one the species must necessarily be iteroparous.

The most extreme case of iteroparity, and the one exhibiting the absolute maximum gain which could be achieved by this means, would be the biologically unattainable case of a species with each individual producing b offspring each year for all eternity and with no mortality. In this case we have $\alpha = 1$ "year" and, since ω is indefinitely large, the final term $be^{-r(\omega+1)}$ in equation (21) becomes zero. Thus we have

$$r = \ln(b + 1) \qquad (23)$$

which is to be contrasted with $r = \ln(b)$ for the case of an annual. *For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size.* Of course, this gain might be appreciable for a species unable to increase its average litter size. The extreme gain from iteroparity for a species with a litter size of two would be (ln 3/ln 2) or an increase of about 58 per cent, for a species with a litter size of four the increase would be about 16 per cent, but for one producing 30 offspring in a single reproductive period the extreme gain would amount to less than one per cent. It seems probable that a change in life history which would add one to the litter size would be more likely to occur than a change permitting repeated reproduction, which in many

cases would necessitate adjustments to survive several seasons of dormancy. It appears that for the usual annual plants and insects with their relatively high fecundity any selective pressure for perennial reproduction as a means of increasing biotic potential must be negligible.

The above conclusion, which appears surprising when first encountered, arouses curiosity as to why iteroparity exists at all. Perhaps some species are physiologically unable to increase their fecundity. This must, however, be unusual and we are led to investigate whether the situation would be different for a species with a prolonged period of development preceding reproduction. One thinks immediately of the giant Sequoias which require a century to mature and begin reproduction but which, once started, produce large numbers of seeds biennially for centuries.

In order to investigate this question we may again compare the intrinsic rate of increase for a single reproduction with that corresponding to an infinite number of reproductions. This procedure will, of course, tend to overestimate the possible gain from iteroparity although it will set an upper limit, and the first few reproductive periods so dominate the situation that even for very modest litter sizes there is a negligible difference between the results of a very limited number of reproductive periods and an infinite number.

For α not necessarily equal to one, formula (21) gives

$$b = e^{r\alpha} - e^{r(\alpha-1)}, \qquad (24)$$

an implicit equation for r which must be solved by iterative means.

Fig. 2 was constructed from formula (24) to show the relationship between the age at which reproduction begins (α) and the litter size (b) in terms of the possible gain in intrinsic rate of increase which could be achieved by iteroparity. The ordinates represent the proportionate increase in the value of r which could be achieved by changing from a single reproductive effort at age α to an infinite number at ages α, $\alpha + 1$, $\alpha + 2$, etc. The curves all slope upward, indicating that species with long pre-reproductive periods could gain more
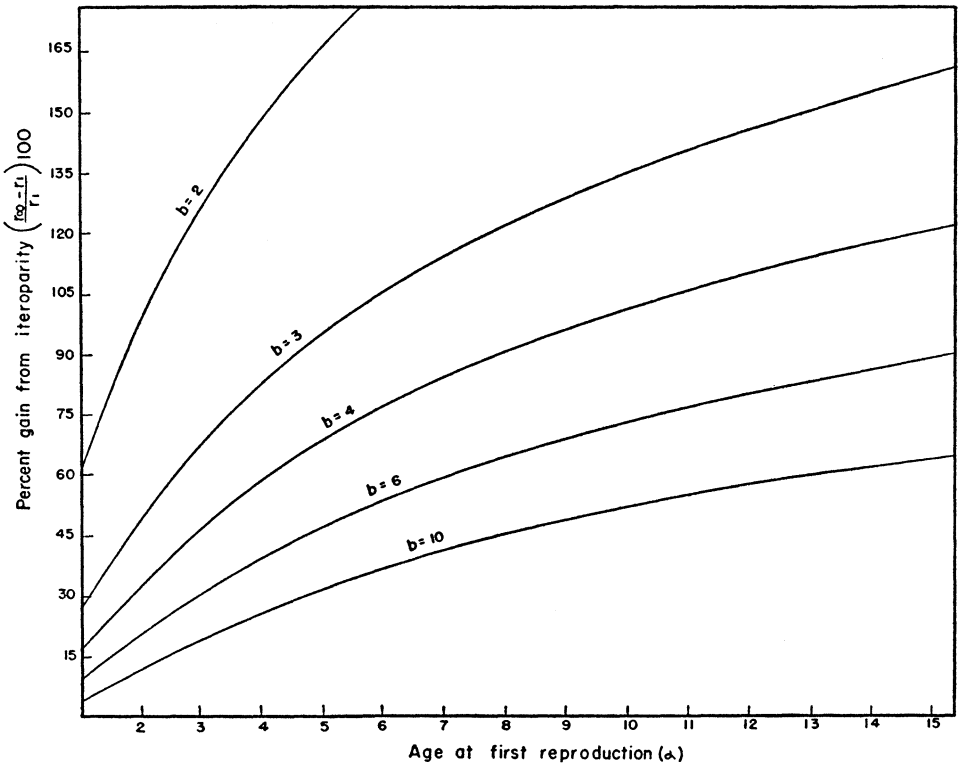

FIG. 2. THE EFFECTS OF LITTER SIZE (b) AND AGE AT MATURITY (α) ON THE GAINS ATTAINABLE BY REPEATED REPRODUCTION

The litter size, b, is the number of female offspring per litter in the case of sexual species.

from iteroparity than forms which mature more rapidly. The tendency of the curves to flatten out with large values of α, however, indicates that the advantages of repeated reproduction increase somewhat less rapidly as the pre-reproductive period is prolonged.

The relationship of iteroparity to litter size is clearly illustrated by Fig. 2. When the litter size is small, as shown by the curve for $b = 2$ (which would correspond to a litter of four individuals when the sex ratio is 1:1), iteroparity can yield important gains in biotic potential, and the possible gains are greater the longer maturity is delayed. The possible advantages diminish quite rapidly as litter size is increased, although it is clear that iteroparity as contrasted with a single reproductive effort would always add something to biotic potential.

Fig. 2 suggests that for semelparous species with large litters there would be very slight selective pressure in favor of adopting the iteroparous habit, and that for iteroparous species with large litters there would be little selection against loss of the iteroparous habit, especially in forms which mature rapidly. On the other hand, in a species which is established as iteroparous there would be slight selection for increasing fecundity or if litter size is relatively large, even against loss of fecundity. This perhaps explains the notoriously low level of viability among the seeds of many trees.

From these considerations it is obvious that when a species could benefit by an increase in the intrinsic rate of natural increase, this advantage might be achieved either by increasing fecundity in a single reproductive period or by adopting the iteroparous habit. A selective advantage would accrue to a mutation altering the life history in either of these directions, and it is an interesting field for speculation as to which type of mutation might be most likely to occur. In this connection it may be interesting to determine the amount of increase in litter size which, for a semelparous species, would be equivalent to retaining the initial litter size but becoming iteroparous.

From (6) we have seen that the intrinsic rate of increase for a semelparous species is defined by $e^{r\alpha} = b$. We wish to find an equivalence factor (E) which will indicate by how much b must be increased to make the value of r for a semelparous species equal to that in formula (21) referring to an iteroparous species. By neglecting the last term in (21) so as to consider the most extreme case of

iteroparity and substituting $Eb = e^{r\alpha}$, we obtain

$$E = \frac{1}{1 - e^{-r}} = \frac{e^{r\alpha}}{b} \qquad (25)$$

where the value of r must be obtained by solving equation (21). When E is plotted against α for various values of b, as shown in Fig. 3, the resulting curves are essentially straight lines.

Fig. 3 illustrates some interesting points bearing on the life histories of organisms, such as tapeworms and many trees, which are iteroparous in addition to producing large litters. From the arrangement of Fig. 2 one might suspect that the iteroparous habit would provide very little advantage to a species that could produce a thousand or so offspring in a single litter, but Fig. 3 indicates that the selective value of iteroparity may be greatly increased when the pre-reproductive part of the life span is prolonged.

A mature tapeworm may produce daily a number of eggs on the order of 100,000 and may continue this for years (Allee et al., 1949, p. 272; Hyman, 1951). With so large a litter size one wonders if iteroparity in this case may not represent something other than an adaptation for increasing biotic potential. Perhaps the probability that a tapeworm egg (or a *Sequoia* seed) will become established may be increased by distributing the eggs more widely in time and space, and this could conceivably be the reason for the iteroparous habit. No definite answer to this problem is possible at present, but Fig. 3 indicates that a knowledge of the length of the life cycle from egg to egg is an essential datum for considering the question. In at least some tapeworms a larva may grow into a mature worm and reproduce at an age of 30 days (Wardle and McLeod, 1952). If this represented the length of the entire life cycle, then Fig. 3 indicates, assuming $b = 100,000$, that a threefold increase in litter size would be the equivalent of indefinite iteroparity. However, with the larval stage in a separate host, the average life cycle must be much longer. If the total cycle requires as much as 100 days, Fig. 3 shows that it would require almost an eight-fold increase in litter size (a single reproductive effort producing 790,167 offspring) to yield the same biotic potential as iteroparity with a litter size of 100,000. Obviously, it is possible, when the life cycle is sufficiently prolonged, to reach a point where any attainable increase in litter size would be less advantageous for potential population growth than a change to the iteroparous
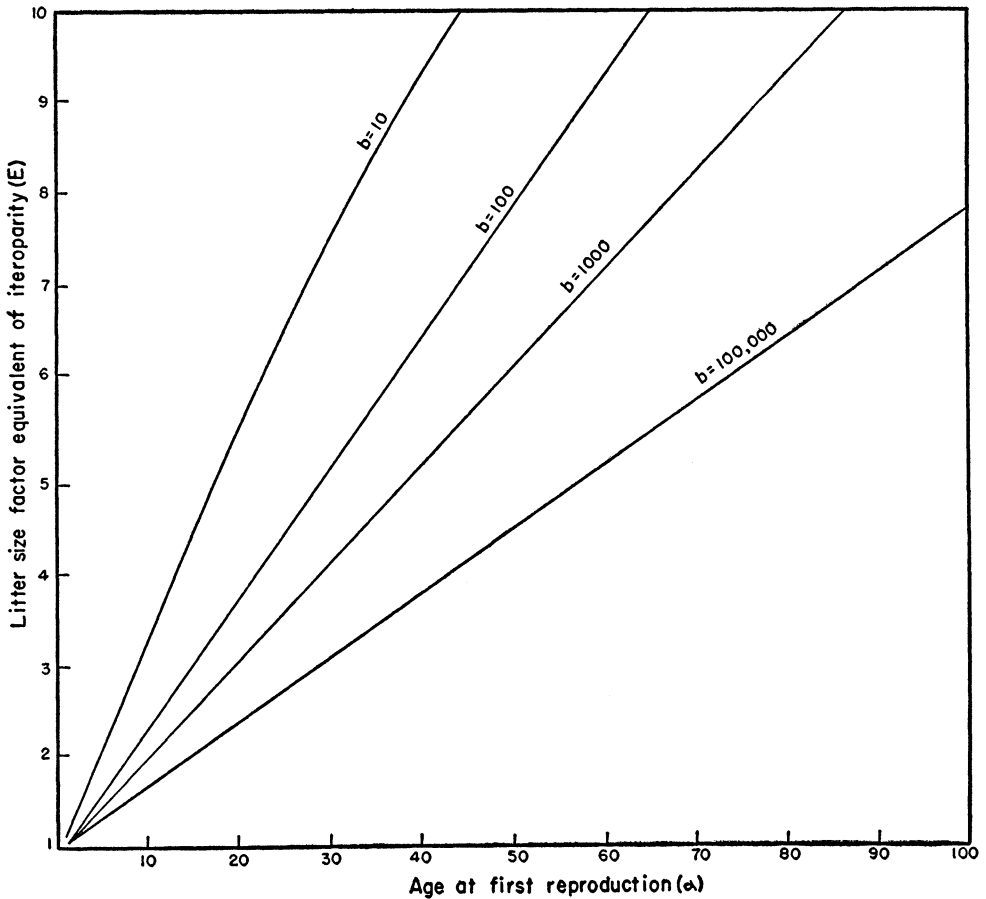
FIG. 3. THE CHANGES IN LITTER SIZE WHICH WOULD BE REQUIRED TO ACHIEVE IN A SINGLE REPRODUCTION
THE SAME INTRINSIC RATE OF INCREASE THAT WOULD RESULT FROM INDEFINITE ITEROPARITY

b represents the litter size for an iteroparous species and the ordinate scale (E) represents the factor by which b would have to be multiplied to attain the same intrinsic rate of increase when each female produces only one litter in her lifetime.

habit. Hence a selective pressure can operate in favor of iteroparity even when the litter size is large. It is clear from Fig. 3, noting the greater slope of the lines representing smaller litter sizes, that in these cases the point will be reached more quickly at which the potential gains from itero-parity outweigh those attainable by increasing the litter size.

Man has a life cycle which is rather unusual in that it combines a long pre-reproductive period with a very small litter size; the very conditions under which iteroparity should be most advantageous. Everyone is, of course, aware that multiple births occur in man but with such a low frequency in the population that they are of negligible importance in population phenomena. It is also rather generally accepted that there is a hereditary basis for the production of multiple births. The question

arises as to why increased litter size should not become more common simply as a result of increased contributions to subsequent population resulting from the increase in biotic potential associated with large litters. It should be of interest, therefore, to determine how large a litter would have to be produced in a single reproductive effort to provide an intrinsic rate of increase equal to that resulting from three or more single births.

In the case of man we may rather confidently accept the value $b = \frac{1}{2}$ to signify that the average number of female offspring produced per human birth, and which will ultimately mature, is one-half. Accepting this value means that a mother must on the average produce two "litters" merely to replace herself (to give $r = 0$), so we shall examine the intrinsic rate of increase only for cases where n, the total number of births, is greater

than two. To examine the maximum gain attainable by iteroparity we assume that successive births are spaced one year apart and obtain the value of r from formula (21), employing different values of n and α. It is easily seen that the necessary litter size, say b', to give the same value of r by means of a single reproductive effort at age α, would be precisely $e^{r\alpha}$.

The value of r from formula (21) corresponding to three annual births beginning at age 12 is .0312. At the other extreme, if the first of the three births occurs at age 30 we obtain $r = .0131$. The corresponding values of $e^{r\alpha} = b'$ are successively 1.41 and 1.48. Under these conditions *it would require essentially a three-fold increase in litter size to achieve in one reproductive effort the same biotic potential as that obtained from three successive births.* The same conclusion is obtained when we consider larger numbers of births. In the case of man very little could be gained by increasing the litter size by any reasonable amount and it is probable that the biological risk involved in producing multiple

births is more than sufficient to outweigh the very slight gain in biotic potential which could be obtained by this means. This would not be the case if the pre-reproductive period was drastically shortened, so we see that even in the case of man there is an interaction of life-history phenomena such that the importance of any conceivable change can only be evaluated through consideration of the total life-history pattern.

THE EFFECT OF TOTAL PROGENY NUMBER

In the preceding section we compared the two possible means by which an increase in total progeny number might lead to an increase in biotic potential. Our general conclusion was that the relative importance of changes in litter size and changes in the number of litters produced depends upon the rate of maturation. For species which mature early a modest change in litter size might be the equivalent of drastic changes in litter number but the possible value of iteroparity increases as the pre-reproductive part of the life span
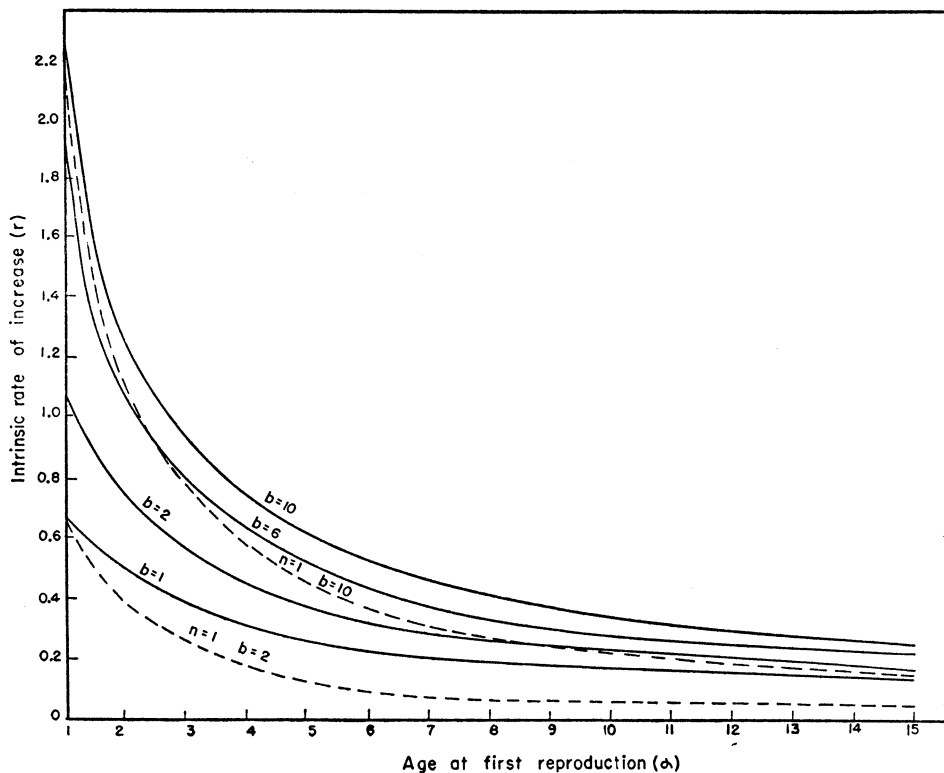

FIG. 4. THE EFFECT OF DELAYED MATURITY ON THE INTRINSIC RATE OF NATURAL INCREASE

The two broken lines represent semelparous species. The solid lines represent indefinitely iteroparous species where each female, after producing her first litter of size b, produces another similar litter in every succeeding time interval.

is lengthened. The importance of discovering the age at which reproduction begins has commonly been overlooked by students of natural history, hence it appears worthwhile to explore the matter further by examining the actual values of the intrinsic rate of natural increase corresponding to specified patterns of reproduction.

Fig. 4 was constructed from formula (21) to show, for several litter sizes, how the intrinsic rate of increase, r, is affected by lengthening the pre-reproductive period, α. Both semelparous ($n = 1$) and indefinitely iteroparous ($n = \infty$) species are illustrated. The striking feature of Fig. 4 is the way in which the lines representing different litter sizes converge as α increases. This occurs whether there is a single reproduction per lifetime or an infinite number, hence it is a general phenomenon. This supplements our earlier conclusions by suggesting that in species where reproductive maturity is delayed there should be relatively slight selection pressure for increased litter size. Here we are referring, of course, to the effective litter size or number of offspring which are capable of maturing. In cases where early mortality is very high, as is known to be the case with many fishes, it might require a tremendous increase in fecundity to produce a very small increase in effective litter size, and such increases might not be very important from the population standpoint. For example, a semelparous species reproducing at age 20 and with an effective litter size of 10 would have, $r = 0.120$. A ten-fold increase in litter size, to $b = 100$, would give $r = 0.231$ or an increase in biotic potential of 92 per cent. Another ten-fold increase to $b = 1000$ would give $r = 0.345$, or a gain of 50 per cent. The diminishing returns attainable by increasing litter size are obvious. For an iteroparous species reproducing first at age 20 and thereafter in each subsequent time interval, the increase in effective litter size from 10 to 100 would give only a 50 per cent increase in biotic potential and a further ten-fold increase in litter size would increase r by only another 35 per cent. In late-maturing species the litter size must be great enough to make it highly probable that *some* of the progeny will mature, but any further increases in fecundity will yield rapidly diminishing returns.

It is also clear from Fig. 4 that for any fixed litter size the biotic potential could be increased by shortening the period of maturation. Any specified amount of decrease in the pre-reproductive period will, however, be most effective for species where this part of the life span is already short.

Fig. 5 illustrates the way in which the two factors of length of the pre-reproductive part of the life span (α) and the number of offspring produced interact to determine the intrinsic rate of natural increase. These values were also computed from formula (21), in this case considering the litter size, b, as a constant with the value one-half. The figure then applies to species which, like man, produce one offspring at a time and where one-half of these offspring are females. Under these conditions it obviously requires two births just to replace the parents, but the population consequences of producing more than two offspring per lifetime vary tremendously with the age at which reproduction begins.

The female of the extinct passenger pigeon presumably produced her first brood consisting of a single egg at the age of one year. From the steep slope of the line representing $\alpha = 1$ in Fig. 5 it is clear that, beyond the minimum of two eggs per average female, several additional eggs produced in successive years would each add very appreciably to the value of r. Accordingly, a relatively slight reduction of the life expectancy for such a species might greatly reduce the biotic potential. The flattening out of the curves in Fig. 5 again illustrates the fact that each litter contributes less to potential population growth than the one preceding it. However, in a case such as that of the passenger pigeon even the seventh and eighth annual "litters" would add appreciable increments to the value of r.

Fig. 5 also shows that as the age at maturity increases the possible gains in biotic potential attainable by producing many offspring rapidly diminish. When $\alpha = 3$, as in the economically important fur-seal, each pup contributes much less to biotic potential than was the case for the eggs of the passenger pigeon. Nevertheless, it is apparent from the figure that if the life expectancy for females should be reduced to seven or eight years (corresponding to the fifth or sixth pup), or less, the species would be in a vulnerable position. The curve is steep in this portion of the graph and relatively slight changes in average longevity could produce disproportionately large population effects.

The lowest curves in Fig. 5 represent ages at maturity falling within the possible range for man. The curves come close together as α increases, so that in this range a change of a year or two in the age at which reproduction begins is less significant than in the case of a species that matures **more**
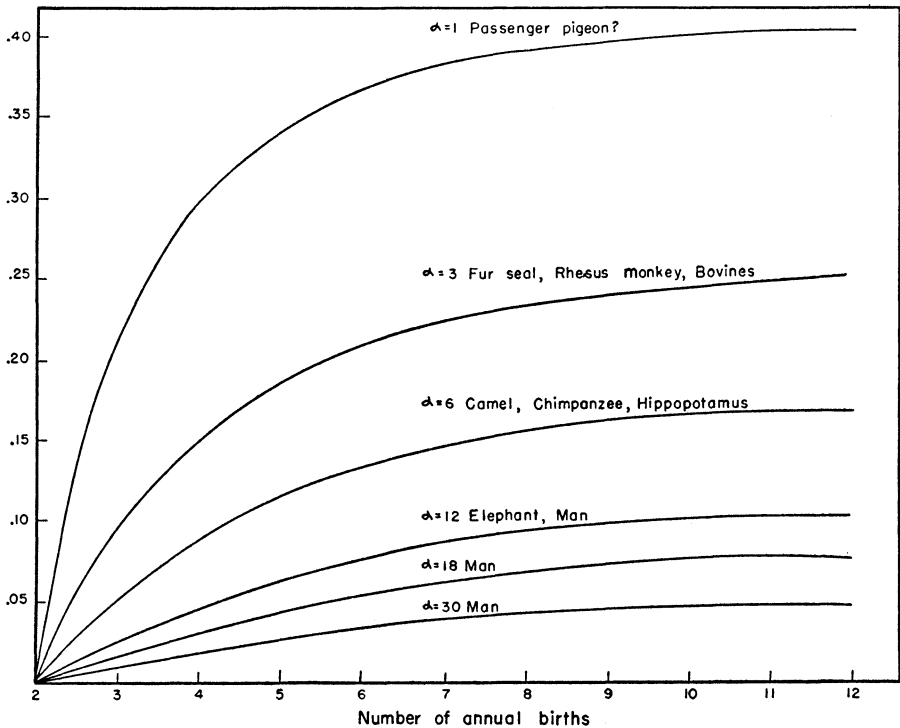
FIG. 5. THE EFFECTS OF PROGENY NUMBER ON THE INTRINSIC RATE OF NATURAL INCREASE WHEN THE LITTER SIZE IS ONE ($b = \frac{1}{2}$)

The ordinate scale shows the intrinsic rate of increase for species which produce an average of one-half female offspring per litter. For any given total progeny number, the intrinsic rate (r) is seen to be greatly affected by the age (α) at which the first offspring is produced.

rapidly. Furthermore, the curves flatten out rapidly so that families which are very large by ordinary standards actually contribute little more to potential population growth or to future population than do families of quite moderate size. As an explicit illustration consider the intrinsic rate of increase which would result if, on the average, human females produced their first offspring at the age of 20 and had a total of five children spaced at one-year intervals. In this case we would have $r = 0.042$. If, on the other hand, we assume that, instead of producing only five children, the females could live forever producing a child each year we would obtain $r = 0.0887$. Under these conditions we conclude that in terms of biotic potential five children are almost one-half (actually 47 per cent) the equivalent of an infinite number. With larger values of α the effect of very large families would be even further reduced. From these considerations the writer feels that human biologists, as well as other natural historians, often overemphasize the importance of total number of progeny while underestimating the significance of the age at which reproduction begins. It is impossible to conclude that one segment of the population is contributing more to future population than is some other segment without examining the total life-history pattern. Age at marriage could, in studying human populations, be a more significant datum than total family size.

The foregoing discussion suggests that a species such as man which is characterized by a long period of maturation and a small litter size can exhibit considerable variability in the details of its life history without greatly affecting the intrinsic rate of natural increase. The population consequences to be anticipated if the average age at which reproduction begins were to be altered by a few years or if the average number of progeny per female were slightly altered are much less striking than is the case for many other species. This implies that the intrinsic rate of increase should be relatively constant over the range of possible variations in the life-history features for man.

Such a conclusion would seem to be of both practical and theoretical interest and to merit closer examination.

The intrinsic rate of increase for man would be the rate of compound interest at which a human population, unrestrained by environmental resistance, would grow. We have already noted that Franklin (1751) estimated that a human population could double in 20 years and that this would correspond to r = .035. Malthus (1798) estimated that an unrestrained human population such as that of the United States at that time could double in 25 years. Malthus' estimate corresponds to r = .0277 which is remarkably close to the value of r = .0287 obtained by Lotka (1927) using much more refined methods for estimating the rate of increase prevailing in 1790 in the United States. Pearl and Reed (1920) fitted a logistic curve to the population figures for the United States, and their equation gives the value r = .03134. Additional examples of estimates based on empirical data

could be given, but these are sufficient to suggest that the value of the intrinsic rate of increase for man is not far from 0.03.

Fig. 6 was constructed from formula (21) in order to examine the question whether or not the life-history features of man would actually lead us to anticipate the approximate value, r = 0.03. Fig. 6 suggests rather definitely that the value r = 0.02 is too low, since it falls well below the obvious reproductive capabilities of humans. If females, on the average, had their first child at the age of 12 years (which is possible, cf. Pearl, 1930, p. 223) it would require an average of 2.6 surviving annual births per female to correspond to the rate r = .02. This curve is quite flat, so that if the first birth was delayed until the age of 20 years, which seems to be roughly the beginning of the semi-decade of maximum human fertility (Pearl, 1939), three annual births would still be adequate to give r = .02. Even if the first birth is delayed until the age of 28 years, this intrinsic rate of increase calls
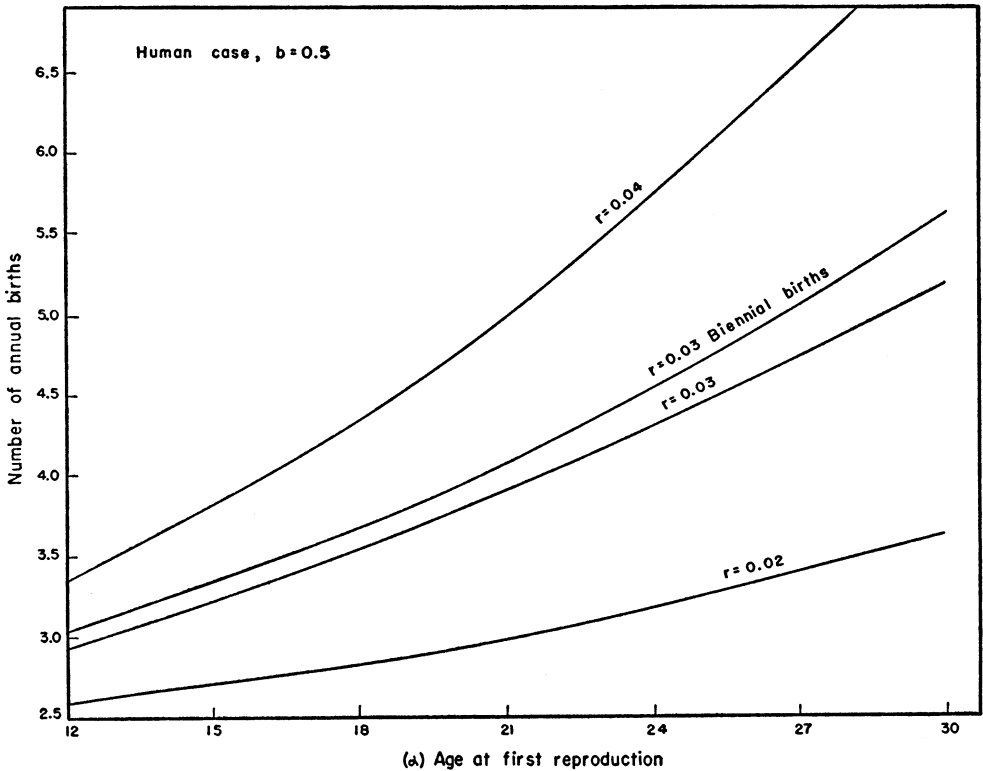

FIG. 6. AVERAGE REPRODUCTIVE PERFORMANCES REQUIRED TO GIVE SPECIFIED VALUES OF r, THE INTRINSIC RATE OF NATURAL INCREASE, IN HUMAN POPULATIONS

Assuming the average number of female offspring per human birth to be one-half (b = 0.5), this graph shows the extent to which total progeny number would have to be altered to maintain a specified intrinsic rate of increase while shifting the age at which reproduction begins. The figure also makes it possible to estimate the intrinsic rate of increase for a population when the average reproductive performance per female is known.

for an average progeny number of only 3.5. Clearly, man can easily exceed this average level of performance. On the other hand, the value $r = .04$ seems to require reproductive performance which would be astonishingly high as an average condition. If the first birth occurred when the mother was aged 13 years, an average of 3.5 children per female would suffice to give $r = .04$. However, the curve turns upward and if the first birth was delayed until the age of 20 it would require an average of 4.8 children to obtain this value. A delay of one more year, to the age of 21 for the first child, would increase the necessary mean progeny number to 5.0, while six children would be necessary if the first birth came when the mother was 25 years old. This intrinsic rate of increase then seems to call for exceptional rather than average reproductive performance, and the writer believes that Fig. 6 would lead us to expect that the intrinsic rate of increase for man lies between the limits .02 and .04 and might be estimated at about .03. Of course, the figure makes no allowance for mortality or for spacing the births at intervals of more than one year, so in actual cases the reproductive performance would have to be somewhat greater than indicated. The interval between births, however, is less critical than might be anticipated. The reproductive performances necessary to give $r = .03$ are shown both for one-year spacing and for two-year spacing between births and, to the writer, at least, either of these curves appears to represent a more reasonable picture of average human reproduction than do the cases representing the higher and lower intrinsic rates of increase.

THE POPULATION BIRTH-RATE AS A CONSEQUENCE OF LIFE-HISTORY PHENOMENA

We have noted earlier formulas (4) and (5) which were originally derived by Lotka (1907a, b; Sharpe and Lotka, 1911) and which show that when life-history features remain constant from generation to generation the population will ultimately settle down to a "fixed" or "stable" age distribution and will exhibit a fixed birth rate. We have also noted that this conclusion could be expected intuitively and can be obtained (formula 18) from discontinuous computational methods, once it is established that the potential form of population growth is a geometric progression. These potential consequences appear to provide the best justification for studying the life histories of various species, yet when such studies are conducted it is common practice not to attempt any interpretation in terms of population phenomena.

It is evident from formulas (3), (4), and (5) that the birth rate and the stable age distribution are tied together with the intrinsic rate of increase and that any extensive discussion of the way in which changes in life-history features would affect these population features might repeat many of the points already covered. Consequently, we shall here note very briefly the relationships between life-history features and the resultant phenomena of birth rates and age structure.

If we consider a "closed" population, which changes in size only through the processes of birth and death, it is apparent that the intrinsic rate of increase, r, in formula (1), $\dfrac{dP}{dx} = rP$, must represent the difference between the instantaneous birth rate and the instantaneous death rate. In practice, however, we are more interested in a finite rate of population change. If we employ formula (1') to express the rate of population growth and consider that the changes result entirely from the birth rate (BR) and the death rate (DR), we obtain:

$$BR - DR = \frac{P_{x+1} - P_x}{P_x} = e^r - 1. \quad (26)$$

A birth rate, β, appropriate to this approach has already been defined by formula (18). However, because we are dealing with finite time intervals the B_x births regarded as occurring at the beginning of some time interval, T_x, should properly be credited to the P_{x-1} individuals living in the previous time interval. The birth rate would, therefore, be:

$$BR = e^r\beta. \quad (27)$$

On the other hand, the death rate should properly be the ratio of the D_x deaths in interval T_x to the total population exposed to the risk of death; that is D_x/P_x. Hence the simple relationship of formulas (5) and (26) can be misleading, especially when there is a rapid population turnover. For example, the birth rate β in Lotka's formula (5) is by definition identical with c_0, the fraction of the population aged between zero and one. Consequently β can never exceed unity no matter how many offspring are on the average produced per individual during a time interval.

In practical population problems the crude birth rate is often observed and employed as a criterion of the state of the population. This

practice can be misleading, especially in comparing species which differ widely in their life-history features. It would be redundant to undertake a detailed analysis of the way in which life-history phenomena affect the crude birth rate because, as is evident from formulas (5), (26), and (27), any change which affects the value of r also affects the population birth-rate. However, the birth rate is subject to additional influences and these may be briefly examined.

The methods used in computing the value of r (formulas 17, 21, and 22) have involved survivorship only out to the age ω at which reproduction ceases. In species having a post-reproductive part of the life span, the crude birth rate corresponding to a given value of r will be reduced simply because post-reproductive individuals accumulate and are counted as part of the population on which computations are based. It is clear, therefore, that

any increase in longevity (λ) which is not accompanied by an increase in ω will tend to lower the observed birth rate; conversely, the birth rate must affect the age structure of the population.

If the maximum longevity for a species is λ, a continued birth rate of $1/\lambda$ would just suffice to leave a replacement behind at the time each individual dies. Hence $1/\lambda$ represents an absolute minimum for a steady birth rate which is capable of maintaining the population. For example, if it were possible to keep every human female alive for 100 years a birth rate as low as 0.01 or 10 births per thousand population per annum (assuming ½ of the offspring to be females), could theoretically suffice for population maintenance. However, for human females the value of ω is not much beyond 40 years; in general, if a female has not produced a replacement by the age of 40 she is not going to do so. The latter consideration might lead one to
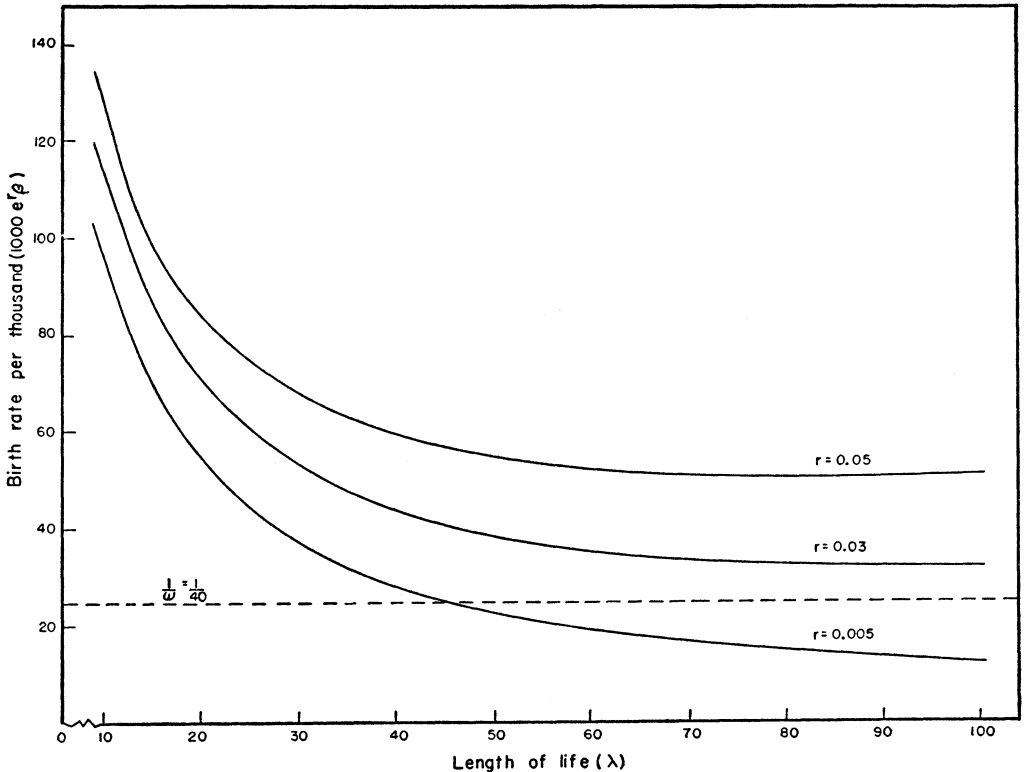

FIG. 7. POPULATION BIRTH RATES CORRESPONDING TO DIFFERENT LIFE HISTORY PATTERNS
The figure shows that the intrinsic rate of natural increase (r), the birth rate, and mean longevity (λ) are all interdependent. The broken line represents the minimum birth rate which would maintain a population if females did not survive beyond the age of 40 "years," which is here used as an estimate of the normal age (ω) at which reproduction is concluded. As longevity is increased, slow population growth becomes possible even when birth rates fall below $1/\omega$. Such low birth rates, however, have sometimes caused unwarranted concern about excessive population increase when abnormal conditions have temporarily reduced the death rate so that there is a large excess of births over deaths.

designate as a minimum maintenance birth rate the value $1/\omega$, or 0.025 in the case of man. But it is clear from the foregoing sections that offspring produced prior to the time that a female reaches the age of 40 will already have begun to "accumulate interest" before the mother can reach the age of 100. The compound interest nature of potential population growth complicates the relationship between birth rate and life-history phenomena and makes it conceivable that populations of species where $\lambda > \omega$ could even continue to grow while exhibiting birth rates lower than $1/\omega$.

No end of interesting combinations of birth rates, death rates, and life-history phenomena might merit consideration, but a single simple example will be selected here to illustrate the general relationship between changing longevity and population birth-rates. If we assume, as before, a physiological type of survivorship such that each individual that is born lives to attain its λth birthday but dies before reaching the age of $\lambda + 1$, we can sum the right-hand side of formula (19) as a geometric progression and combine this with formula (27) to obtain the following expression for the population birth rate (BR):

$$BR = e^r \beta = \frac{e^r - 1}{1 - e^{-r\lambda}}. \qquad (28)$$

Formula (28) shows, as would be expected, that as longevity (λ) is increased, with the other life-history features remaining unchanged, the birth rate will fall and approach as a limit the value $e^r - 1$, which is in accord with (26) when the death rate is set equal to zero.

Fig. 7 was constructed from formula (28) to illustrate the interrelations between BR, r, and λ within a range of values of life history features roughly applicable to man. The condition for a stationary population would, of course, correspond to $r = 0$, while all positive values of r correspond to growing populations. r must become negative when the birth rate falls below $1/\lambda$, and it will be noted that the birth rates below about 20 per thousand which are sometimes observed in human populations (see tabulation in Allee et al., 1949, p. 288) must, unless they represent abnormal temporary phenomena, correspond to populations with very low potential growth rates. The curve for $r = .005$, in fact, does not differ greatly from $1/\lambda$. The curves in Fig. 7 flatten out rapidly for large values of λ, so that drastic and generally unattainable increases in longevity would be re-

quired to make such low birth rates compatible with appreciable population growth.

Looking at these relationships from a different point of view, Fig. 7 shows that a reduction in longevity, such as might result from reducing the life expectancy of game animals, can be expected to result in an increased birth rate even if the intrinsic rate of increase is unchanged. It does not seem worthwhile at present to attempt a quantitative estimate of these relationships because the assumption of a physiological type of survivorship curve is probably not even approximately true for game animals. When more realistic estimates of survivorship are available, however, the type of relationship illustrated in Fig. 7 may assume practical importance.

THE STABLE AGE DISTRIBUTION

The age structure of a population often is a matter of considerable practical concern. In economically valuable species such as timber, game animals, and commercial fishes certain age classes are more valuable than others, and it would be desirable to increase the proportion of the most valuable age classes in a population. Similarly, certain age classes of noxious organisms may be more destructive than others and the relative numbers of these destructive individuals will be governed by life-history phenomena which may conceivably be subject to alteration by control measures. In human populations, also, it is sometimes a matter of concern that the proportion of the population falling within the age limits most suitable for physical labor and military service seems to be below optimum. An article in the New York *Times* for September 24, 1950, headed "population shift in France traced—Study finds too many aged and very young in relation to total of workers" illustrates the potential importance of a knowledge of the age structure of populations.

The mathematical basis for relating the age structure of a population to life-history features was established in Lotka's first paper on population analysis (1907); and in the same year Sundbärg (1907) reached the conclusion that a human population reveals its condition (tendency to grow or decline) through its age structure. These important conclusions have not been sufficiently noted by ecologists. When the mortality factors affecting a population are altered either through natural environmental changes or through human exploitation or attempts at control there will in

general result a change in the age structure of the population, and this may be observable even before changes in population size or in birth rates provide evidence of the consequences of the changed mortality factors. The subject of age structure is a large and difficult one because the various combinations of life-history features, birth rates, death rates, and age structure are analogous to a multidimensional figure where a change imposed in any one feature induces changes in all of the others. The subject has been considered most in connection with human populations, and some empirical generalizations have been obtained which may profitably be examined by means of the computational methods we have been employing. For the purpose of illustrating the general character of the relationships involved, one species will serve as well as another.

For illustrative purposes we may proceed as in the preceding sections and consider the stable age distribution for cases where survivorship is of the physiological type. Letting c_x represent the fraction of the population aged between x and $x + 1$, we may employ formulas (5) and (28) directly to obtain, for $x < \lambda$:

$$c_x = \frac{e^{-rx}(1 - e^r)}{1 - e^{-r\lambda}}. \tag{29}$$

From formula (29) it is apparent that if the extreme longevity for a population is altered without changing the intrinsic rate of increase, the effect on the age structure will be of a very simple type. An increase in longevity from λ_1 to λ_2 will simply reduce the proportion of the population in each age category below λ_1 by the constant proportion $\dfrac{1 - e^{-r\lambda_1}}{1 - e^{-r\lambda_2}}$. Consequently, the effect will be most noticeable on the youngest age classes, because these are the largest classes.

Changes in the value of r affect the stable age distribution in a more complex way than do changes in λ, although the general result of increasing the value of r will be to increase the proportion of young in the population, with a corresponding decrease in the proportion of older individuals. Fig. 8 illustrates this effect for three values of r,
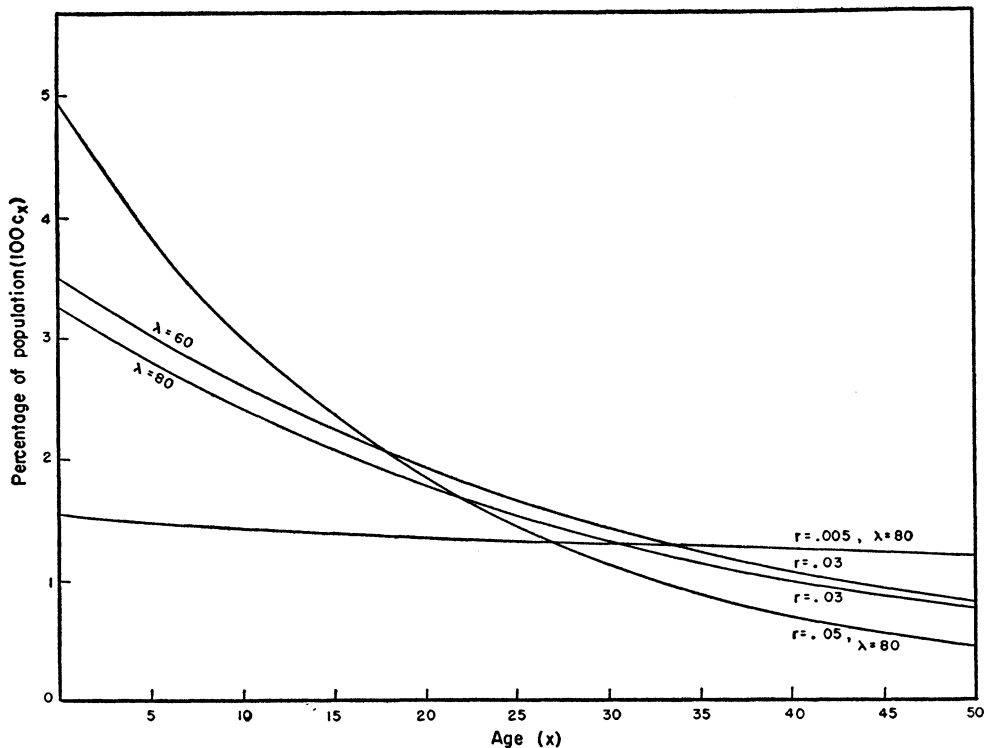

FIG. 8. THE STABLE AGE DISTRIBUTION, OR PROPORTION OF THE POPULATION FALLING WITHIN EACH INTERVAL OF AGE, IS SHOWN HERE AS A FUNCTION OF THE INTRINSIC RATE OF INCREASE (r) AND THE LENGTH OF LIFE (λ)
  These relationships have important ecological correlaries. See text for a discussion relating these to the "optimum yield" problem.

assuming that λ in formula (29) remains constant at 80 "years."

The way in which population age-structure is affected by changes in the value of r and λ, as illustrated by formula (29) and Fig. 8, permits some qualitative conclusions which are of interest in connection with the "optimum yield problem" (for discussion, see Allee et al., 1949, p. 377). If man (or some other species) begins exploitation of a previously unexploited population, the age structure will be affected in a definite manner. An obvious result of increased predation will be to decrease the average longevity, corresponding to a decrease in λ. We have seen earlier (Fig. 7) that this will ordinarily have the effect of increasing the population birth rate, and Fig. 8 and formula (29) show that another effect will be to increase the proportion of young in the population, the very youngest age classes being most affected. However, the increased mortality may also affect the value of r. If the population is initially in equilibrium with the capacity of its environment, its total life history pattern will be adjusted to the effective value, $r = 0$. If exploitation is not too intense, it has the effect of making additional environmental resources available to the surviving members of the population and thus of stimulating population increase; the population "compensates" (see Errington, 1946) for the increased mortality by increasing the value of r. Fig. 8 shows that this will have the effect of increasing the proportion of young in the population, thus supplementing the effect of exploitation on λ. On the other hand, the increase in r will have the effect of reducing the proportion of aged individuals in opposition to the effect of reduced λ which is to increase all of the age classes which still persist. It seems clear that the most obvious population consequence of such exploitation will be to increase the proportion of young members of the population. If predation or exploitation becomes still more intense, as in the case of "overfishing" (Russell, 1942), it will reduce the effective value of r, and, of course, still further reduce average longevity. The decrease in r will tend to decrease the proportion of young individuals, but the decrease in λ will tend to increase this proportion. However, both changes will tend to raise the proportion of older individuals in the population, and this combined effect can then be expected to be the most obvious corollary of overfishing. These conclusions, of course, greatly oversimplify a complex phenomenon. In order to make quantitative estimates of these effects it would be necessary to have detailed information about the life-history features, especially survivorship under the conditions of increased predation. Nevertheless, these qualitative conclusions show the type of effect to be expected when populations are subjected to increased predation, and they suggest that observations of the changes in the age structure of populations may provide valuable evidence of over-exploitation, or, from the opposite point of view, of the effectiveness of control measures. Bodenheimer (1938) comments on the fact that ecologists have neglected this important subject.

From Fig. 8 it will be noticed that changes in life-history features produce their greatest effects on the extreme age classes, whereas the curves representing different patterns are close together in the "middle" age range. The same phenomenon is evident, for example, in a graph (Fig. 27) reproduced by Dublin, Lotka, and Spiegelman (1949) from Lotka (1931) to show the age structure of human populations corresponding to stationary, increasing, and decreasing populations. This suggests that the proportion of a population falling in the middle portion of the life span may be relatively independent of factors which produce drastic shifts in the ratio of very old to very young. This was first postulated by Sundbärg (1907), who concluded that it was "normal" for about 50 per cent of a human population to fall in the age range between 15 years and 50 years. Sundbärg distinguishes three primary population types based on the age distribution of the remaining 50 per cent of the population. In the "progressive" type of population there is a strong tendency for increase and the ratio of young (aged under 15) to old (aged over 50) is, by Sundbärg's criteria, about 40 to 10. In the "regressive" type, exhibiting a tendency toward population decrease, the corresponding ratio of young to old is about 20 to 30, while a "stationary" type with the ratio about 33 to 17 shows no particular tendency either to grow or to decrease. When first encountered Sundbärg's conclusion appears surprising, but in actual human populations differing as radically, for example, as those of Sweden and India, the proportion of the population aged between 15 and 50 is remarkably close to 50 per cent (see tabulation in Pearl, 1946, p. 78). It appears to the writer that this conclusion should be of great interest to students of human populations. The age class between 15 and 50 years includes the bulk of the workers and persons of

military age, and Sundbärg's conclusion implies that the size of this class relative to the remainder of the population must be determined by life-history features which cannot readily be deliberately controlled.

For other species also, the life span may be meaningfully divided into three primary age classes, pre-reproductive (aged 0 to α), reproductive (aged α to ω), and post-reproductive (aged ω to λ), which differ considerably in their biological significance. If we continue with our assumption of physiological survivorship we can obtain the relative sizes of these three age classes directly from formula (29), and Sundbärg's generalization offers an interesting empirical pattern with which to compare our results. For the relative sizes of the three fundamental age classes formula (29) gives:

$$
\left. \begin{array}{ll}
\text{Pre-reproductive} & = \dfrac{1 - e^{-r\alpha}}{1 - e^{-r\lambda}} \\[3ex]
\text{Reproductive} & = \dfrac{e^{-r\alpha} - e^{-r\omega}}{1 - e^{-r\lambda}} \\[3ex]
\text{Post-reproductive} & = \dfrac{e^{-r\omega} - e^{-r\lambda}}{1 - e^{-r\lambda}}
\end{array} \right\} \quad (30)
$$

By putting $\alpha = 15$ and $\omega = 50$, we may examine the relationship between r and λ for Sundbärg's primary population types.

The generalization that about 50 per cent of a human population normally falls in the age range from 15 to 50 is in accord with formulas (30). When $r = .03$ the value of λ to give a stable age distribution with just 50 per cent in the middle age range would be 59 years, but an increase in longevity to 85 years would only reduce this class to 45 per cent of the population. The same general conclusion applies when r is small. The values $r = .005$ and $\lambda = 63$ years correspond to 55 per cent aged 15 to 50 years, and λ would have to be increased to 81 years to reduce this to 45 per cent. It appears that over the usual range of values of human longevity and potential population growth Sundbärg's generalization is very good. This is shown graphically in Fig. 9. It is noteworthy that when the length of life is about 70 years, Sundbärg's generalization holds over a wide range of values of r. In other words, this ratio of "middle-aged" to total population is quite insensitive to changes in other life history features.

Figure 9 illustrates Sundbärg's population criteria for values of $r > 0$. It is clear that the
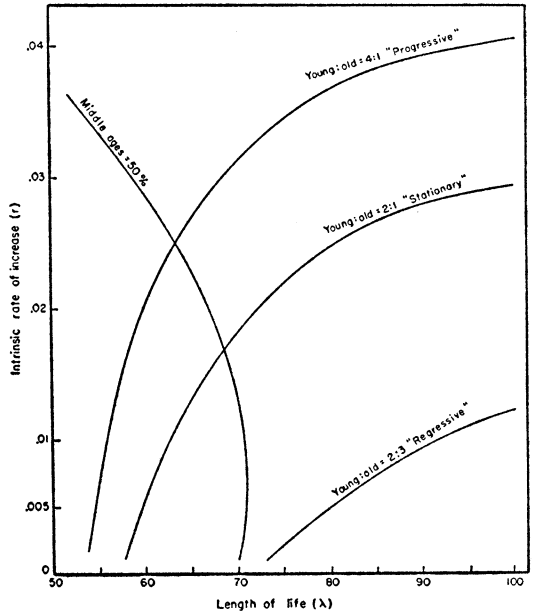

FIG. 9. SUNDBÄRG'S POPULATION CRITERIA IN RELATION TO LIFE-HISTORY FEATURES

The "middle age" range here consists of individuals aged 15 years to 50 years.

"regressive" type of population structure is not consistent with populations possessing a strong tendency to increase and, in fact, for usual longevity figures, will ordinarily correspond to decreasing populations ($r < 0$). On the other hand, the "progressive" type of structure does correspond to large values of r even when λ is not particularly large. The "stationary" type of population structure is less well defined. Any population for which the life-history features correspond to $r > 0$ will tend to grow, and the ratio of two "old" to one "young" can correspond to a large value of r when λ is large. The value of r is, of course, independent of the length of the post-reproductive part of the life span, whereas the age structure is not. For any given value of r, which is determined by the life-history features of individuals aged below ω, the effect of an increase in longevity will be to decrease the proportion of young and, to a lesser extent, the proportion of reproductive members of the population.

At first glance, the type of interactions shown in Fig. 9 might suggest that if the age structure of a population were artificially shifted in the "regressive" direction, for example, through migration or improvements in public health, there would result a reduction in the value of r. This, however, is not

the case, since r is completely determined by life-history events occurring before age ω. Sharpe and Lotka (1911) showed that a characteristic of the "stable" age distribution is the fact that it will become reestablished after temporary displacements. However, practical problems arise in analyzing actual populations because phenomena such as birth rates and death rates may give a very misleading picture of population trends when the age structure is displaced from the stable type and has not yet had time to reestablish a stable age distribution. From Fig. 7 we have noted that in human populations birth rates on the order of 20 per thousand per annum would in general be little more than sufficient to maintain a population. But if the age distribution is displaced from the stable type in the direction of increased frequency of young individuals, the death rate may be temporarily reduced, so that there is a great excess of births over deaths and the population can grow temporarily even if the age-specific birth rates are too low to maintain the population permanently at a constant size. Under these conditions the population is "aging," and in human populations this phenomenon has a number of interesting and important corollaries (see Dublin, Lotka, and Spiegelman, 1949). Fisher (1930) has considered the problem in a more general sense, noting that the apparent value of r given by formula (3) will be incorrect when the age structure is displaced. Fisher suggests the possibility of measuring population size not in terms of the number of individuals present but in terms of "reproductive value," where the "value" of an individual represents his remaining potentialities for contributing to the ancestry of future generations. Some such approach has great potential value for ecological studies of natural populations, but its possibilities in this direction seem not yet to have been explored.

EMPIRICAL APPLICATIONS

In the preceding sections we have been concerned with the influence of specific life-history patterns on the characteristics of populations. In order to examine these effects we have made simplifying assumptions by regarding some of the life-history features as fixed in a certain way while we examined the results of varying other features. While this procedure oversimplifies the biological situation as it exists in actual populations, the writer regards it as a sound way of investigating the meaning of life-history features. The same general attitude may be traced back to Robert Wallace (1753) in his book which profoundly influenced Malthus. Wallace pointed out that "mankind do not actually propagate according to the rules in our tables, or any other constant rule ..." but he emphasized that tables of potential population growth are still valuable because they permit us to evaluate the influences restraining population growth.

Wallace, then, was a pioneer in appreciating the potential value of comparisons between empirical and theoretical population phenomena. In modern actuarial practice, population data are subjected to involved mathematical treatments which are sometimes considered to represent biological laws and at other times to be merely empirical equations, but which, in any case, are known to yield results of practical value. In the words of Elston (1923, p. 68):

> "... it seems to me that even though there be governing causes of mortality that may result in a true law of mortality, any group of lives studied is so heterogeneous, due to differences in occupation, climate, sanitary conditions, race, physical characteristics, etc., that any formula must in practice be considered to be merely a generalization of what is actually happening."

The number of different combinations of life-history features of the type we have been discussing is essentially infinite, and it is out of the question to make detailed examinations of any great proportion of these from the theoretical standpoint. However, we have seen that certain population features, such as the prevailing age distribution and the intrinsic rate of increase, summarize a great deal of information about the potentialities of the population and its relationship to its particular and immediate environment. As mentioned earlier, the recent ecological literature demonstrates that ecologists are becoming interested in determining such features as the intrinsic rate of increase for non-human populations. These computations may have practical value in dealing with valuable or noxious species, and they possess great theoretical interest for ecologists. For example, the logistic equation has been widely employed to represent population growth in a variety of organisms (Allee et al., 1949; Pearl, 1927); and it has also been attacked (Yule, 1925; and succeeding discussion, Gray, 1929; Hogben, 1931; Smith, 1952), on the grounds that it is too versatile and can be made to fit empirical data that might arise from entirely different "laws" of population

growth. This criticism is, of course, directed at the fact that the curve-fitter has three arbitrary constants at his disposal in seeking to obtain a good fit. One of these constants is r, the intrinsic rate of increase. The grounds for accepting or rejecting the logistic equation as a law of population growth (or for seeking some other law) would be greatly strengthened if the value of r was computed directly from observed life-history features and independently of the data on population size.

The computational methods employed in the preceding sections suggest several possible ways of computing the value of r from empirical life-history data. The usual procedure for such computations has been a tedious one based on formula (3) (see Lotka's appendix to Dublin and Lotka, 1925), although Birch (1948) employed formula (17) as an approximation to (3) for his computations. The methods discussed in the preceding sections sug-

gest that a logical procedure for obtaining an empirical value of r would be to observe age-specific birth rates and survivorship under the environmental conditions of interest, and from these to write a "generation law" so that formula (11) can be employed. The single positive root of (11) is e^r and this can be estimated to any desired degree of accuracy without great difficulty even for species where the reproductive life is prolonged. When one is actually solving equation (11) it is strikingly brought to one's attention that the final terms representing reproduction in later life are relatively unimportant in influencing the value of r. This once again reinforces our conclusion that reproduction in early life is of overwhelming importance from the population standpoint, and should be much more carefully observed in field and laboratory studies than has usually been the case.
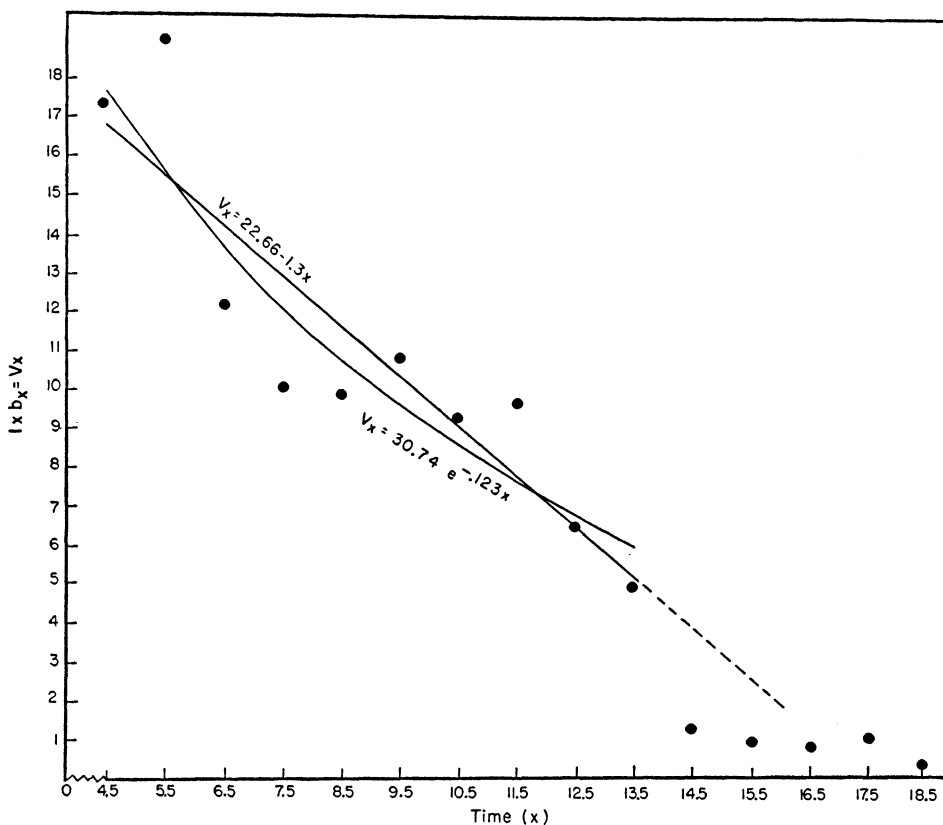

FIG. 10. A STRAIGHT LINE AND AN EXPONENTIAL FUNCTION FITTED TO THE DATA OF BIRCH (1948)

These data are suitable only for illustrating computational methods. Birch observed the age-specific fecundity rates (b_x) for the rice weevil *Calandra oryzae* living under constant conditions of temperature and moisture. He did not observe survivorship (l_x) but carried over the shape of the survivorship curve from the flour beetle *Tribolium confusum*. The black dots represent the product $l_x b_x$.

An alternative approach for obtaining empirical values of r consists of fitting the V_x ($= l_x b_x$) values with mathematical curves of types which make it possible either to obtain the sum of the series on the right-hand side of equation (19) or to employ Laplace transformations to solve equations (3) or (20) by simple iterative methods. Different formulas could be fitted to different sections of the V_x curve, and, when good fits can be obtained with combinations of straight lines, step-functions, exponential functions, and other simple formulas, this procedure will often lead to easy ways of solving for r. As a very simple example of this procedure we may consider the data of Birch (1948), for which he employed formula (17) and, by computations which are given in detail in his paper, obtained the value $r = 0.762$.

The V_x data employed by Birch are shown graphically in Fig. 10 by means of the black dots. The two curves, a straight line and a simple exponential function, were fitted by the method of least squares to the values up to $x = 13.5$. Neither of the functions gives an extremely good fit to the observed data, but, on the other hand, one may question whether the irregularities in the empirical data are not partly artifacts which should be smoothed out when one is attempting to estimate the value of r for a species. In any case, it appears worthwhile to compare Birch's value of $r = .762$ with that obtained by use of the empirically fitted curves.

Using first the exponential curve, if we set $V_x = Ke^{ax}$, formula (19) may be written in the form:

$$Ke^{\alpha(a-r)} = \frac{1 - e^{a-r}}{1 - e^{n(a-r)}}. \qquad (31)$$

When reproduction occurs several times, so that n is fairly large, the denominator in equation (31) becomes for practical purposes unity and may be ignored. In this case we have $\alpha = 4.5$, $K = 30.74$, $a = -.123$, and $n = 9$, so we will ignore the denominator. The equation is easily solved by iterative means, using a table of the exponential function, and the value obtained is $r = .758$, which differs from Birch's value by about one-half of one per cent.

The right-hand side of equation (19) can also be summed for the linear case where $V_x = a + bx$, but in this case the Laplace transformation employed with formula (3) yields a slightly simpler equation:

$$\frac{ar + b}{r^2} = e^{r\alpha}. \qquad (32)$$

Putting $a = 22.66$, $\alpha = 4.5$, and $b = -1.3$ in equation (32), and solving by iterative means we obtain $r = .742$, which differs from Birch's value by nearly three per cent, although this seems to be good agreement in view of the crude approximations employed.

In many practical applications dealing with natural and experimental populations some approximation to the value of r such as those presented above may be all that can be justified by the accuracy of the data. The estimate of r could undoubtedly be improved by fitting different portions of the V_x curve with different functions. Another refinement suggested by observations presented earlier in this paper would be to fit the empirical curves by a method which would give greater weight to the earlier points which have more influence on the value of r than do the later points. Any detailed discussion of these empirical applications would be out of place in the context of the present paper. The writer, however, anticipates that ecologists will in the future devote more attention to the interrelations of life-history features and population phenomena, and it is to be hoped that some of the approaches which have been indicated will accelerate trends in this direction.

SUMMARY

Living species exhibit a great diversity of patterns of such life-history features as total fecundity, maximum longevity, and statistical age schedules of reproduction and death. Corresponding to every possible such pattern of life-history phenomena there is a definitely determined set of population consequences which would ultimately result from adherence to the specified life history. The birth rate, the death rate, and the age composition of the population, as well as its ability to grow, are consequences of the life-history features of the individual organisms. These population phenomena may be related in numerous ways to the ability of the species to survive in a changed physical environment or in competition with other species. Hence it is to be expected that natural selection will be influential in shaping life-history patterns to correspond to efficient populations.

Viewed in this way, comparative studies of life histories appear to be fully as meaningful as studies of comparative morphology, comparative

psychology, or comparative physiology. The former type of study has, however, been neglected from the evolutionary point of view, apparently because the adaptive values of life-history differences are almost entirely quantitative. The recent ecological literature does show a trend toward the increasing application of demographic analysis to non-human populations, but the opposite approach of deducing demographic consequences from life-history features has been relatively neglected. The present paper is presented with the hope that this situation can be changed. In other fields of comparative biology it is usual to examine individual characteristics and to regard these as possible adaptations, and the writer believes that life-history characteristics may also be profitably examined in this way.

It is possible by more or less laborious methods to compute the exact size and composition of the population which at any future time would be produced by any given initial population when the life-history pattern of the individual organisms is regarded as fixed. Thus it is possible to make an exact evaluation of the results of changing any life-history feature, and the value of this type of analysis may be apparent to those biologists who distrust the usual demographic procedures.

Starting with exact computational methods, it has been shown that early population growth may exhibit irregularities or cyclic components which are identifiable with negative or complex roots of an algebraic equation, but that these components vanish in time so that potential population growth

is ultimately a geometric progression. Having established this fact, it is shown that the exact computational methods and the more convenient approximate methods lead to identical conclusions when considered over the long time scale which is of interest in adaptational and evolutionary considerations.

Some life-history patterns of ecological interest are examined and compared by means of relatively simple formulas derived from a consideration of the form of potential population growth. The results have bearing on the possible adaptive value of genetically induced changes of life-history features. It is suggested that this type of approach may add to the value of life-history studies and that an awareness of the possible meanings of empirical life-history data may aid in planning such studies by insuring that all pertinent information will be recorded. One of the most striking points revealed by this study is the fact that the age at which reproduction begins is one of the most significant characteristics of a species, although it is a datum which is all too frequently not recorded in the literature of natural history.

The number of conceivable life-history patterns is essentially infinite, if we judge by the possible combinations of the individual features that have been observed. Every existing pattern may be presumed to have survival value under certain environmental conditions, and the writer concludes that the study of these adaptive values represents one of the most neglected aspects of biology.

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