Intrinsic Rate of Natural Increase: The Relationship with Body Size

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Summary. The relationship between previously published values of “the intrinsic rate of natural increase” \( (r_m) \) and body weight is studied. When organisms covering a wide range of body weights are compared, a correlation is found which can be described by the equation \( r_m = aW^n \) where \( r_m \) is the intrinsic rate of natural increase per day and \( W \) is the average body weight in grams; \( a \) is a constant which takes three different values for unicellular organisms and heterotherm and homoiotherm animals respectively. The constant \( n \) has a value of about \(-0.275\) for all three groups. This result is compared to the previously found relationship between the metabolic rate per unit weight and body size. It is shown that \( r_m \) can be interpreted as the productivity of an exponentially growing population and thus must correlate with metabolic rate. The values of the constants \( a \) and \( n \), however, show that for each of the three groups, unicellular organisms, heterotherms and homoiotherms the ratio of energy used for maintenance to that used for production increases with increasing body size and that the evolution from protozoa to metazoa and the evolution from heterotherm to homoiotherm animals in both cases resulted in not only an increased metabolic rate, as shown previously, but also in a decreased population growth efficiency. It is shown that the increase in reproductive potential of homoiotherms relative to that of heterotherms is due to a shorter prereproductive period in the former group.

Previous estimates of \( r_m \) for different species and comparisons between these values in relation to their ecology are discussed in context with the found “\( r_m \)-body weight” relationship. Attempts to show that such comparisons will be more meaningful when body size is included in the considerations are made. It is suggested that the found relationship may represent the maximum values \( r_m \) can take rather than average values for all species, since it is likely that the species used for laboratory population-studies are biased in favor of species with high reproductive potentials.

Introduction

It has long been recognized that in a constant environment all populations tend asymptotically to grow at an exponential rate described by the equation \( \frac{dN}{dt} = r_mN \), where \( N \) is population size. The constant \( r_m \), which measures the growth rate in absence of density dependent limitation of a population which has attained a stable age distribution (Birch, 1948), is usually designated the “Malthusian parameter”, “intrinsic rate of natural increase” or “innate capacity for increase”. Some authors
(e.g. Cole, 1954) have implied that natural selection will always, and in one sense exclusively, favor an increase of $r_m$, a problem which is not, however, trivial. More recently this problem has been discussed in terms of "r-" and "K-selection" (MacArthur, 1962). According to this idea, selection will always favor an increase in $r_m$ of populations which are dominantly controlled by density independent factors, i.e. populations living in unstable and unpredictable environments or occurring early in ecological successions. For populations of stable and predictable environments and predominantly limited by density dependent factors, however, selection will tend to increase the number of individuals which can be sustained at equilibrium conditions, i.e. at the "carrying capacity" ($K$) of the environment. In such populations selection will favor that a larger part of the available resources are spent on competitive ability, defense mechanisms and a more efficient utilization of limiting resources at the expense of features which increase the reproductive potential in absence of density dependent limitation, i.e., $r_m$. All real populations will, of course, be found somewhere in between these two extremes. These ideas, which are related to the concept of "colonizing" or "opportunistic" versus "equilibrium" species, have recently attracted much interest and a large number of theoretical and experimental studies have been carried out (e.g. Clarke, 1972; Cody, 1966; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Hairston et al., 1970; Heron, 1972 b; Lewontin, 1965; Mertz, 1971; Pianka, 1970; Roughgarden, 1971).

The study of these concepts implies for a large part comparisons of "reproductive potential" or "reproductive effort" between different species or between genotypes within one species. However, it has previously been recognized that when organisms with different body sizes are compared there is a tendency for $r_m$ to decrease with increasing body size (Fenchel, 1968; Pianka, 1970; Smith, 1954) and comparisons between $r_m$ of different organisms are therefore not easily interpreted independently of body sizes of the species in question.

The purpose of the present paper is to report a study on the relationship between $r_m$ and body size using the available data from the literature. The found relationship should make comparisons between reproductive potentials of different species more meaningful.

The value of $r_m$ for any population is, of course, dependent on a large number of environmental factors (food, temperature, humidity, etc.) and any stated value of $r_m$ must therefore be followed by a specification of such factors. However, at least one set of environmental factors will for any species correspond to a maximum value of $r_m$. Such maximum values of $r_m$ can often be closely approximated in experimental populations. In many previous works (e.g. Evans and Smith, 1952; Heron, 1972 b; Smith, 1954) this maximum value is in reality implied when comparisons of $r_m$