

DENSITY DEPENDENCE, THE LOGISTIC EQUATION, AND  $\underline{r}$ - AND  $\underline{K}$ -SELECTION:  
A CRITIQUE AND AN ALTERNATIVE APPROACH

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**ABSTRACT:** The logistic equation is a starting point of many ecological theories. Most ecologists agree that this equation is usually not consistent with observations and experimental results but it is argued that the simplicity of this equation is the reason for this inconsistency. In this paper I attempt to prove that the reason for inadequacy of the logistic equation is more fundamental: most systems of equations describing the dynamics of population and its resources cannot be transformed to the single equation for limited growth. Even if this transformation is possible, the  $\underline{K}$  parameter depends on components of  $\underline{r}$ , usually on the ratio of mortality rate to reproduction rate. This fact is commonly overlooked because it is assumed that density affects the abstract term  $\underline{r}$  (population growth rate).

Because of doubts as to density-dependence and the logistic equation, the  $\underline{r}$ - and  $\underline{K}$ -selection concept is criticized, both as a classification system and as a predictive theory. It is shown that when resources are explicitly considered, it is possible to predict traits favored by natural selection on a given resource level directly from the description of the system. This approach seems to be more advantageous than the  $\underline{r}$ - and  $\underline{K}$ -selection concept.

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# I. INTRODUCTION

The logistic equation is a mathematical formulation of the density-dependent factors concept. Though density-dependence may no longer be a burning issue it is difficult to find a contemporary ecology textbook that does not contain the logistic equation. There are also very few papers on theoretical ecology for which this equation would not be a starting point. On the other hand, everybody agrees that the logistic equation does not describe the dynamics of natural populations well enough. Any difference between its predictions and reality is attributed to a too simplified form of the equation. If we assume the inadequacy of the logistic equation, and at the same time we derive from this equation other ecological theories, we cancel the possibility of falsifying either these theories or the density-dependent factor concept on which the equation is based.

The entire body of mathematical descriptions of interspecific competition, as well as the  $\underline{r}$ - and  $\underline{K}$ -selection concept, are based on the logistic equation, hence all these "theories" are not falsifiable. Their quantitative predictions cannot be tested, and their qualitative predictions are so obvious that no mathematical model is required to detect them. When discussing these questions Peters (1976) has pointed out that models of interspecific competition and models of  $\underline{r}$ - and  $\underline{K}$ -selection are not theories but tautologies. Tautologies are, of course, useful for the development of science. Peters (1976) is, however, right when he writes: "Tautologies may be useful logical aids, but they cannot replace real theories. Unless ecologists are careful to distinguish the two, their confusion may produce a body of thought resting on metaphysical rationale rather than empirical, predictive science". As far as I know the part of Peters' views connected with ecological models did not have further repercussions. The reason is simple: the author has not given an alternative method of building the ecological theories.

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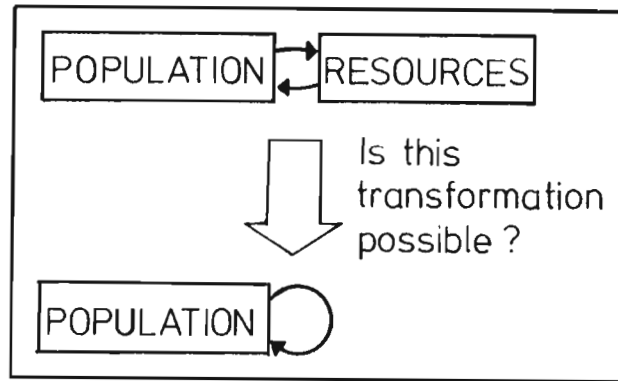


Figure 1. The basic problem of the paper: is resource-dependence equivalent to density-dependence?

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There are two arguments for the density-dependence concept. The older one is that since the other factors are unable to stop the exponential population growth or to protect the population against extinction it is necessary that the density-dependent factors should exist (see e.g. Solomon, 1957; Lack, 1966)<sup>1</sup>. The second argument is more convincing and more widespread at the present time. It is assumed that resources are limited and, since there is a feedback between the amount of resources and the population size, the single equation of limited growth

$$(1) \quad \frac{dn}{dt} = f(n)$$

can be formulated. In this paper I discuss the second argument only (Fig.1). All arguments based on necessity of existence as well as undoubted examples of density-dependent factors (e.g. cannibalism, unintentional ruining of other individuals' eggs) are beyond the scope of the paper.

The systems of equations for populations and their resources are a starting point of the considerations presented here. It is assumed that such systems are closer to reality than single equations of limited growth. In the next section an attempt is made to reduce the equation systems to a single equation, when space, mineral nutrients and food are the limiting factors. If such a reduction is possible, special attention is given to test whether the  $K$  parameter, called carrying capacity, has the same meaning as its common interpretation. The mathematics in this section is rather simple, but the entire section can be omitted if desired; the results are briefly summarized in the other sections.

Development of the density-dependence concept is further discussed. When considering population dynamics two critical points are suggested. One of them seems to be especially unjustified but strongly influential on ecological theories: it is assumed that density acts immediately on an abstract population parameter. In the context of doubts concerned the logistic equation three different aspects of the  $r$ - and  $K$ -selection concept are discussed. As an alternative to this concept, natural selection is considered in the systems when the resources are explicitly specified.

My suggestion to describe the dynamics of population-resource systems instead of the dynamics of populations alone is not a new idea, of course. Unfortunately both approaches are usually mixed: nearly always the logistic term is involved in the system description. Thus it is difficult to recognize what patterns are the results of population-resources relationship, and what are the products of logistic thinking. The main aim of this paper is to separate them, at least in very simple systems.

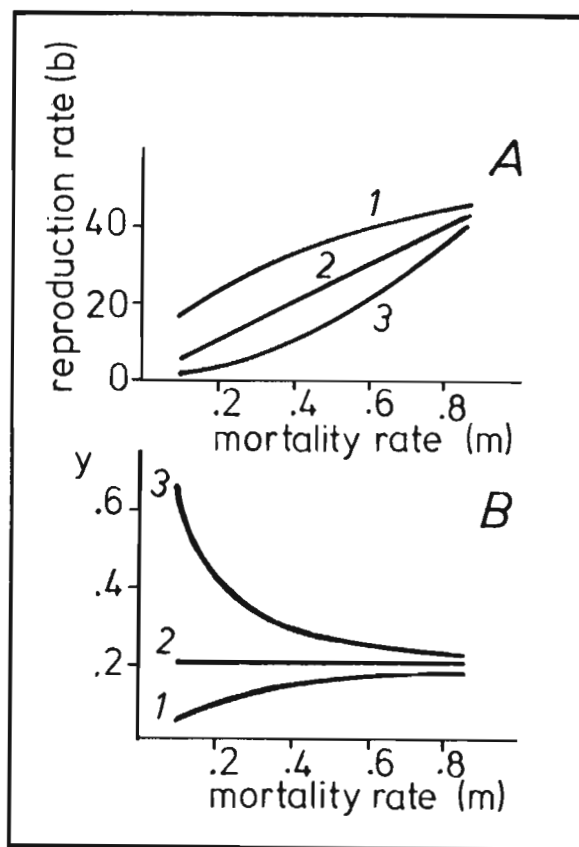


Figure 2. Hypothetical relation of mortality and reproduction rate (A), and the corresponding fraction of free space  $y$  at which population increase is stopped (B).  $b = 5m^{0.5}$  for curves 1,  $b = 5m$  for curves 2, and  $b = 5m^{1.5}$  for curves 3.

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## II. AN ATTEMPT AT REDUCING DIFFERENT KINDS OF SYSTEMS TO A SINGLE EQUATION

Let us assume that the rate of growth of the population depends on the amount of one of the resources (space, light, food, mineral nutrients, etc.). The dynamics of such a system can be described by the system of equations:

$$(2a) \quad \frac{dx}{dt} = h_1(x, n)$$

$$(2b) \quad \frac{dn}{dt} = h_2(x, n)$$

where  $x$  = amount of resource,  $n$  = number of individuals. For transforming the system (2) to the single equation of limited growth (1) the equation  $\frac{dx}{dn} = g(n)$

should be calculated from (2), and its solution  $x = k(n)$  should be found. After putting this solution into (2b) we obtain

$$\frac{dn}{dt} = h_2(k(n), n) = f(n)$$

i.e. an equation of the same form as (1).

This transformation is possible if  $\frac{dx}{dt} / \frac{dn}{dt}$  is independent of  $x$ . It is

intuitively clear that this condition is satisfied when (i) changes of number of individuals are the only reason for the changes of amount of resources, and (ii) the resources are re-usable, i.e. they return into the system at the moment of an individual's death. The equation (2a) takes in this case the form:

$$(3) \quad \frac{dx}{dt} = h_1(x, n) = -a \frac{dn}{dt},$$

where  $a$  is the amount of resource kept by one individual.

#### SPACE as the limiting factor

Space is an example of a resource to which equation (3) can be applied. Space can be a limiting factor for plants (in this case space can be considered as an access to light or water), for sedentary crustaceans or molluscs, for territorial animals, for hole-nesting birds, etc. It can be assumed sometimes in these cases that the reproduction and recruitment depend only on the amount of free space. Each living and resident individual produces its progeny at the constant rate  $b$  but the young individuals will survive only when they find an unoccupied space (crustaceans, plants) or if reproduction occurs only when the parents find an unoccupied place (e.g. territorial animals, hole-nesting birds). In both cases a simplified system of equations describing the dynamics of free space  $x$  and plant or animal number  $n$  takes the form:

$$(4a) \quad \frac{dx}{dt} = -a \frac{dn}{dt}$$

$$(4b) \quad \frac{dn}{dt} = (-m + b \frac{x}{x_0}) n$$

The parameter  $a$  denotes the amount of space occupied by each individual,  $m$  is mortality rate,  $b$  is maximum reproduction rate, and  $x_0$  is total amount of space (occupied and free). From the system (4) it can be deduced that  $\frac{dx}{dn} = -a$ , and further  $x = x_0 - an$ . Substituting the equation for  $x$  into (4b) yields:

$$(5) \quad \frac{dn}{dt} = (-m + b(1 - \frac{an}{x_0})) n$$

The equilibrium state  $K$  appears when:

$$(6) \quad K = (1 - \frac{m}{b}) \frac{x_0}{a}$$

Equation (5) can be transformed into the following form:

$$\frac{dn}{dt} = (b - m) (1 - \frac{n}{K}) n = r (1 - \frac{n}{K}) n,$$

i.e. the form of classical logistic equation, where  $r$  is the maximum growth rate. But it is necessary to point out that  $K$  is not equal to the number of individuals which fill up the space. The space can store  $\frac{x_0}{a}$  individuals, while the equilibrium number  $K$  depends also on the ratio  $\frac{m}{b}$  (note 2).

#### MINERAL NUTRIENT as the limiting factor

Let us consider a closed experimental system, without input and output of mineral nutrients, in which algae live. Algae use nutrients to produce their

own bodies and their progeny. Assume further that one of those nutrients is the limiting factor. Such a system can be described, in the simplest case by the system of equations as follows:

$$(7a) \quad \frac{dx}{dt} = -cxn + amn$$

$$(7b) \quad \frac{dn}{dt} = \left(-m + \frac{cx}{a}\right)n,$$

where  $x$  is nutrient concentration,  $c$  is efficiency of nutrient intake (proportion of free nutrient taken up per unit time per individual),  $a$  is amount of nutrient contained in one organism, and  $m$  is mortality rate. Therefore:

$$\frac{dx}{dn} = -a$$

$$x = x_0 - a(n - n_0),$$

where  $x_0$  and  $n_0$  denote the initial amount of nutrient and initial number of algae, respectively.

If the population could grow to the total depletion of nutrients, it would reach the number equal  $\frac{x_0}{a}$ . In reality the population growth must be stopped earlier. Let us assume the initial population number so small that it is possible to neglect  $n_0$ . We have then:

$$(8) \quad \frac{dn}{dt} = (b - m) \left(1 - \frac{n}{K}\right)n,$$

where:

$$(9) \quad b = \frac{cx_0}{a}, \quad K = \frac{x_0}{a} - \frac{m}{c} = \frac{x_0}{a} \left(1 - \frac{m}{b}\right).$$

Equation (8) has the form of the logistic equation. The parameter  $b$  means rate of reproduction at the initial nutrient concentration. Equilibrium number  $K$  here depends on the ratio  $\frac{m}{b}$ .

When the system under study is not confined, i.e. it has an input and an output of nutrient, or when the dead individuals are decomposed either slowly or outside the system (e.g. at the bottom), then it is impossible to reduce the system of equations describing such an ecological system to the logistic equation or to a similar equation of limited growth.

#### FOOD as the limiting factor

Food is probably a limiting factor for a great number of animals. Based on the fact that the world is green, some authors believe that there is an excess of food in terrestrial ecosystems, at least for the phytophagous animals (Hairston et al., 1960). Emlen (1973) argued this point, drawing attention to the fact that a relative shortage of a resource often occurs (Andrewartha and Birch, 1954). From the equations of the population dynamics of animals limited by food given below, it is also clear that a decrease of animal numbers may start a long time before the resources are fully consumed, which supports Emlen's analysis.

Let  $M$  denote individual maintenance cost, measured in the same units as the amount  $x$  of food in the habitat. Assume that an individual consumes no more than  $L$  units of resource per unit of time. Therefore we obtain:

$$(10a) \quad \frac{dn}{dt} = (-m - f(\alpha x))n \quad \text{for } \alpha x \leq M$$

$$(10b) \quad \frac{dn}{dt} = (-m + k(\alpha x - M))n \quad \text{for } M < \alpha x < L$$

$$(10c) \quad \frac{dn}{dt} = (-m + k(L - M))n \quad \text{for } \alpha x \geq L$$

where  $m$  is the mortality rate for all causes except starvation,  $\alpha$  is a parameter measuring the efficiency in searching for food,  $\alpha x$  is the amount of food consumed in a unit of time by an individual,  $f(\alpha x)$  is mortality due to starvation, and  $k$  is a parameter which allows the conversion of any surplus of the consumed food into progeny, measured as the number of young animals. The population can reach the equilibrium state ( $\frac{dn}{dt} = 0$ ,  $n \neq 0$ ) only when  $M < \alpha x < L$  (10b).

Let us consider now some very simple equations for resources: irretrievable (eq. 11a), appearing at a constant rate (eq. 11b), or appearing at a rate proportional to the amount of existing resources (eq. 11c):

$$(11a) \quad \frac{dx}{dt} = -\alpha x n \quad (11b) \quad \frac{dx}{dt} = C - \alpha x n \quad (11c) \quad \frac{dx}{dt} = cx - \alpha x n$$

None of the equation systems composed of the equations (10) and of any of the equations (11) can be reduced to a single equation of limited growth, in spite of the considerable simplicity of the examples. This is due to the fact that the energy is used irretrievably, i.e. it does not return into the system after the animal is dead<sup>3</sup>.

### III. LOGISTIC DEVIATION OF ECOLOGY

In previous section I have stated that all population-resource systems can be divided into two groups with respect to the possibility of reducing resource-dependence to density-dependence. Reducible systems can be described by the logistic equation but it must be remembered that there is an intrinsic tradeoff between the parameter  $K$  and the components of  $r$  (maximum growth rate). If two populations have the same  $r$  but different  $b$  (birth rate) and  $m$  (mortality rate), and when other assumptions are kept constant, equilibrium numbers will be different. This fact is usually overlooked. To be sure Emlen (1973) has considered the possibility of interdependence of  $r$  and  $K$  but he has found nothing interesting and disturbing in this respect.

The stages of the development of ecological reasoning regarding population dynamics are given in Table 1, to show the logical invalidity of the logistic equation. They have been chosen and formulated subjectively, but they may be useful when looking for critical points of the logistic theory.

Now let us consider Table 1 step by step. The theory of unlimited growth is the oldest and clearest of all ecological concepts. When unlimited growth is considered, it is possible to find the stable age distribution, to calculate the intrinsic rate of increase, and even to define the fitness rather precisely. Therefore numerous papers, especially ones concerning population genetics but also papers on life-history tactics, assume unlimited growth. Unfortunately it is obvious that no population can grow to infinity (Table 1, step 3), and therefore it is necessary to take the limiting factors into account. Population growth may be stopped by the depletion of different resources (e.g. space, mineral nutrients, food) or by predator pressure (Table 1, step 4). I will consider only the first case further.

There are differences between limiting factors in time and space; on the other hand ecologists look for general theories. As a result it is usually assumed that the dynamics of limiting resources may be neglected, but it is sufficient to assume that the increase of population size causes a decrease of the resources (Table 1, step 7). This assumption is based on the negative feedback between population size and the resource level, which seems to be quite obvious (Table 1, step 5). On the other hand the negative feedback does not imply that the population increase affects the decrease of resources without any time lag. E.g., when predators depend on their prey, both populations can grow or decrease simultaneously in parts of a cycle. I have considered in the previous section the necessary conditions to justify a transition from step 5 to step 7, i.e. validity of equivalence between density dependence and resource dependence. The condition is very simple: the resource must be used up in a reversible way. Space is the best example, probably quite common in nature.

It should be noted that May (1976) reduced the predator-prey system to a single equation whereas Zwanzig (1973) reduced certain competition systems to a single equation of limited growth. Nevertheless it should be pointed out that these equations contain the integrals of density over time - more exactly, integrals of functions of density. Then the dynamics of a population can be predicted if its history is known. So the regulation is "history-of-density-dependent" but not density-dependent. Thus a historical aspect appears here. Ockham's razor is an argument for rejecting the approach used by May and Zwanzig. Another argument is the significant complication of the limited growth equations.

Let us assume that the system under consideration can be reduced to a single equation of limited growth, i.e. that density-dependence is really equivalent to resource-dependence. The next step of reasoning (Table 1, step 9) seems always to be logically unjustified. Density can never influence the abstract parameter  $r$  (population growth rate) directly. Density can decrease birth rate or increase mortality rate, or can do both but independently. Therefore we never obtain the form of the logistic equation in which actual growth rate (per capita) is simply proportional to maximum growth rate multiplied by  $(1 - \frac{n}{K})$  and  $K$  is independent of the components of  $r$ . Neglecting this fact may not seem very important but really leads to numerous implications, probably false but nevertheless very influential on the present ecology. A subjective and incomplete list of them is given in Table 1, steps 10-14. The population equilibrium number,  $K$ , seems to be independent of life-history traits (Stearns, 1977). Many authors consider carrying capacity to be a population parameter. This phenomenon is called by Stearns (1977) "an artifact of logistic thinking". A further implication of this artifact is the treatment of populations (and beyond them, ecosystems) as units similar to a single individual, with the concepts of homeostasis, evolution toward efficiency maximization of the system, etc. Fortunately, such concepts, very close to metaphysics, are not popular among theoreticians, but they have been expressed by numerous empirically-oriented ecologists (e.g. Margalef, 1968, Odum, 1971).

Considering  $K$  as a population parameter leads also to the conclusion that natural selection can act on  $K$ . This is a basis for the  $r$ - and  $K$ -selection concept. The conclusion may be treated as an abbreviated paraphrase of the statement that natural selection acts on traits which affect  $K$ . The most common example of such a trait is the efficiency of food gain. Increase of this efficiency can bring about a decrease of resources and eventually diminish the population equilibrium size  $K$  (Levins, 1975), but unfortunately the above paraphrase conceals such a possibility. In fact  $K$ -selection may decrease  $K$ , which seems to be strange and even illogical.

Table 1. Author's personal view on the development of ecological reasoning concerning density regulation and interpretation of the parameter  $K$ .

| No of step | Step description                                                                                                                                                               | Step evaluation          | Mathematical formulation                                                                      | Symbols                                                             |
|------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|-----------------------------------------------------------------------------------------------|---------------------------------------------------------------------|
| 1          | When resources are unlimited, per-capita population growth rate is proportional to the difference between birth rate and mortality rate.                                       | justified                | $\frac{1}{n} \frac{dn}{dt} = b - m$                                                           | b=birth rate<br>m=mortality rate<br>n=number of organisms<br>t=time |
| 2          | The abstract concept of growth rate is involved in such a situation.                                                                                                           | justified                | $\frac{1}{n} \frac{dn}{dt} = r$                                                               | r=population growth rate<br>r = b - m                               |
| 3          | The population cannot grow in an unlimited way for a long time.                                                                                                                | justified                | $\lim_{t \rightarrow \infty} n(t) \neq \infty$                                                |                                                                     |
| 4          | Growth of the population must be stopped by resource depletion.                                                                                                                | justified                |                                                                                               |                                                                     |
| 5          | There is negative feedback between population number and amount of resources.                                                                                                  | justified                |                                                                                               |                                                                     |
| 6          | Population increase and resource decrease must occur simultaneously                                                                                                            | justified or unjustified | $\frac{dn}{dt} > 0 \Rightarrow \frac{dx}{dt} < 0$                                             | x=amount of resource                                                |
| 7          | The effect of the decrease of the amount of resource can be expressed as an effect of crowding (population size)                                                               | justified or unjustified | $\frac{dn}{dt} = h(x, n)$<br>is equivalent to<br>$\frac{dn}{dt} = f(n)$<br>because $x = k(n)$ | f, h, k=functions which can potentially be found                    |
| 8          | It is possible to formulate an equation of limited population growth. I will consider further explicitly the most common form of such an equation, i.e. the logistic equation. | justified or unjustified | $\frac{dn}{dt} = f(n)$                                                                        |                                                                     |

Table 1. continued

| No of step | Step description                                                                                                                                                                 | Step evaluation | Mathematical formulation                                     | Symbols                 |
|------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------|--------------------------------------------------------------|-------------------------|
| 9          | It is assumed that the abstract population parameter $\underline{r}$ is affected by density.                                                                                     | unjustified     | $\frac{1}{n} \frac{dn}{dt} = r \left(1 - \frac{n}{K}\right)$ | $K$ =equilibrium number |
| 10         | The population equilibrium number, $\underline{K}$ , seems to be independent of birth and death rates.                                                                           | unjustified     |                                                              |                         |
| 11         | $\underline{K}$ is called carrying capacity. $\underline{K}$ is assumed to depend on resource amount and efficiency of individuals only.                                         | unjustified     |                                                              |                         |
| 12         | Carrying capacity is treated by numerous but not all ecologists as a cause of population dynamics, although $\underline{K}$ is simply a result of population-resources dynamics. | unjustified     |                                                              |                         |
| 13         | $\underline{K}$ is treated as population parameter.                                                                                                                              | unjustified     |                                                              |                         |
| 14         | It is assumed that natural selection can act on $\underline{K}$ .                                                                                                                | unjustified     |                                                              |                         |

IV. THE  $\underline{r}$  AND  $\underline{K}$ -SELECTION CONCEPT

The concept of  $\underline{r}$  and  $\underline{K}$ -selection formulated by MacArthur and Wilson (1967) can be briefly summarized as follows. Let us assume that organisms with a higher intrinsic rate of natural increase  $\underline{r}$  have a lower carrying capacity  $\underline{K}$ . If the density of the population is low, then natural selection favors individuals (or populations, if a multi-species system is considered) with a high  $\underline{r}$ ; when the density increases the individuals or populations with a high  $\underline{K}$  are favored. Therefore it is possible to say that natural selection favors individuals with the highest value of the expression  $\frac{1}{n} \frac{dn}{dt}$ , this is, in fact, equivalent to the

definition of natural selection. Thus, the  $\underline{r}$  and  $\underline{K}$ -selection concept in such a form is a tautology and not a scientific theory. Peters (1976) drew attention to this fact, but several authors have dealt with this tautological form of the concept (e.g. Anderson, 1971; Anderson and King, 1970; King and Anderson, 1971; Charlesworth, 1971; Roughgarden, 1971).

If this concept was a theory it would be possible to predict the favored traits under given conditions. Pianka (1970, 1974) enumerates a set of the correlates of  $\underline{r}$ - and  $\underline{K}$ -selection. But it must be remembered that those "correlates" do not result from the mathematical model (here: the logistic equation) but from additional considerations, which are not quite clear, especially in the case of  $\underline{K}$ -selection.

Let us consider  $\underline{r}$ -selection; the theory of unlimited growth is well developed and rather clearly formulated mathematically. It is well known that  $\underline{r}$  is more sensitive to generation time than to fecundity. Since it is impossible to imagine large species with short generation time, early reproduction, rapid development, etc., it is merely obvious that  $\underline{r}$ -strategists must be small. Thus instead of enumerating all correlates of  $\underline{r}$ -selection a statement may be made:  $\underline{r}$ -strategists must be small. As a matter of fact Southwood et al. (1974) and Southwood (1976) practically reduced the  $\underline{r}$ -strategist's traits to small size of organisms.

The problem with  $\underline{K}$ -strategists is more difficult. As Stearns (1977) pointed out, it is impossible to find a tradeoff between the parameter  $\underline{K}$  and different life-history traits. Most of Pianka's correlates of  $\underline{K}$ -selection are just opposite to the correlates of  $\underline{r}$ -selection. The unjustified reasoning was applied that if  $\underline{r}$ -strategists must be small,  $\underline{K}$ -strategists must be large (and further that they must have slower development, delayed reproduction, etc.). The small size of  $\underline{r}$ -strategists was deduced as a physiological necessity but the larger size of  $\underline{K}$ -strategists by analogy only.  $\underline{K}$ -strategists can be large but do not need to be large. Therefore it is not surprising that many of the hypothesized correlates do not always appear.

Two other correlates of  $\underline{K}$ -selection, i.e. greater competitive ability and efficiency, are unfortunately not clearly defined and it is therefore difficult to examine them further.

The concepts of  $\underline{r}$ - and  $\underline{K}$ -selection are commonly accepted, especially among empirically oriented ecologists. The concepts have become rather diverse. Stearns (1977) mentions three ways of using these concepts: as a system of classification, as explanations, and as predictions. The letters  $\underline{r}$  and  $\underline{K}$  may be used as labels for combinations of traits. But, as stated above, almost all correlates are size-dependent. It is really better to say " $\underline{r}$ - and  $\underline{K}$ -strategists" instead of "small or large animals"?

The concept of  $\underline{r}$ - and  $\underline{K}$ -selection gives an "explanation" of almost all ecological facts: e.g., clutch size trends in tropical birds and difference between clutch sizes of blue tits and condors (Southwood, 1976). Those "explanations" completely ignore obvious physiological limits which are responsible for a large part of the observable clustering of some life-history traits. This concept is even considered able to give a compromise between Lack's and Wynne-Edwards' views because, as

Southwood et al. (1974) write, "the evidence that most strongly supports Wynne-Edwards (1962) is derived from species that have been strongly K-selected, while Lack's interpretation is most applicable to those species that are, for birds, toward the r-end of the selection spectrum". In fact all "explanations" given by this theory are too general to be useful. They give an illusion of explanation and thus are very dangerous: they inhibit looking for the real explanations.

Inadequacy of the concept as a predictable theory is discussed above. Additional doubts are given by the facts that not all population-resource systems can be reduced to the logistic equation, and that even when such a transformation is possible r- and K-parameters are interdependent.

#### V. AN ALTERNATIVE TO THE r- and K-SELECTION CONCEPT

The concept of r- and K-selection cannot predict which traits are really favored by natural selection. I suggest that the main reason is in not considering limiting resources explicitly. To test this suggestion I will try to predict the results of natural selection when space, mineral nutrients, and food are the limiting factors.

Let us consider again a system with space as the limiting factor. Let us make the simplified assumption that the amount of space occupied by an individual does not change when free space is reduced. Under this assumption it is clear from equation (6) that the individuals with smaller  $\frac{m}{b}$  ratio (mortality to birth rate) gain a selective advantage when the space becomes more and more filled up. Reproduction rate and mortality are usually connected in such a way that they both increase or decrease simultaneously (MacArthur and Connell, 1966; Pianka, 1974). When the dependence of birth rate on mortality is concave, natural selection acts to decrease mortality; when the relationship is convex, increase of reproductive rate is favored in dense populations, despite a simultaneous increase of mortality (Figure 2). The relationship is probably concave among plants: almost all ground plants in the climax forest, where space and access to light are extremely limited, are longlived. They develop such organs as bulbs, rhizomes, and onions or lignified browse (e.g. bilberry) instead of putting more effort into sexual reproduction (see e.g. Collier et al., 1973).

The above results are clear. When there is a lack of unused resource, the best strategy is to keep possession by a decrease of mortality. An increase of death risk must be compensated for by an enormous increase of fertility (convex curve).

When mineral nutrients are the limiting factors and they became scarce, an advantage is also obtained by the genotypes minimizing the ratio  $\frac{m}{b}$  (see equation 9). This ratio can be minimized by an increase of the efficiency of nutrient-capturing c, a decrease of the mortality m, or a decrease of body size (the parameter a is proportional to body size). The parameters which are favored by natural selection could be predicted if the properties of individuals were known. E.g., small individuals are exposed to greater mortality but they capture nutrients more efficiently. It is necessary, of course, to describe relationships like this by functions.

Considering food as the limiting factor, it was assumed above that the cost of maintenance of an animal is constant. In reality it can be expected that an animal which looks for food more actively spends more energy. Let us have:  $M = p(\alpha)$  and let us put this into Equation (10). Individuals should adopt a behavior which maximizes the expression:

$$(12) \quad \begin{array}{ll} \alpha x - p(\alpha) & \text{for (10a) and 10b, when } \alpha x \leq L \\ L - p(\alpha) & \text{for (10c), when } \alpha x > L \end{array}$$

Natural selection will act similarly. The expression (12) is equivalent to "expansive energy", suggested by Van Valen (1976) as a fitness measure. On the other hand the increase of activity can also increase mortality, e.g. by increasing the risk of discovery by predators. In many cases m is certainly a function of a too. It is

important that the function  $p(\alpha)$  and the parameter  $L$  can be measured from individual bioenergetics. The dependence of mortality rate on activity can be also calculated from observations or experiments.

I hope that all the above examples support the offered suggestion: a system of equations for the population and its resources is a good starting point when traits favored by natural selection at a given resource level are considered. Some results are very similar to those given by the  $r$ - and  $K$ -selection concept. The main difference is that here they are deduced from simple mathematical formulas describing a system, but not from additional considerations. They are predictions from the theory, not correlates of the theory. When resources are explicitly considered, theoretical ecology can easily collaborate with physiology, bioenergetics, and other individual-oriented branches of biology.

#### NOTES:

1/ This reasoning was criticized by Andrewartha and Birch (1954) and Andrewartha (1961). The discussion between these authors and Lack (1966) was in my opinion a misunderstanding. The methodological strictures of Andrewartha and Birch have been argued away by Lack, quoting the empirical data. In spite of that the density-dependent factors concept has been commonly accepted.

2/ It is assumed here that  $b$  depends only on the amount of unoccupied area. If reproduction rate decreases and mortality increases with a decrease of proportion of free space, then the parameters  $b$  and  $m$  both appear in the definition of  $K$ .

3/ Strictly speaking it is possible to find an equation for resources which together with (10b) satisfies the condition that  $\frac{dx}{dt} / \frac{dn}{dt}$  is independent of  $x$ . This equation takes form:  $\frac{dx}{dt} = a(-m + k \alpha x - kM)n$ . Let us assume that  $x$  is measured in energy units;  $a$  is the conversion coefficient of individuals to energy (the opposite of  $k$ ).

Therefore,  $\frac{dx}{dt} = \alpha x n - amn - Mn$ . What can cause the resources to adopt such a strange behavior?

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