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The American Naturalist, Vol. 106, No. 951. (Sep. - Oct., 1972), pp. 581-588.

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r AND *K* SELECTION OR *b* AND *d* SELECTION?

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Hairston, Tinkle, and Wilbur (1970) recently criticized the concepts of *r* and *K* selection as proposed by MacArthur and Wilson (1967). Hairston et al. (1970) noted that selection can not act directly on the instantaneous rate of increase (*r*), but must instead act upon its components, the instantaneous birth rate per head (*b*), and/or the instantaneous death rate per head (*d*). Further, they proposed that the terms “*r* selection” and “*K* selection” be replaced with “*b* selection” and “*d* selection,” respectively. However, these authors seem not to appreciate fully the concepts of *r* and *K* selection (see also Pianka 1970; Gadgil and Solbrig 1972). Here I attempt to reconcile these viewpoints, to reduce confusion, and to clarify concepts of *r* and *K* selection. In addition, I briefly discuss the central theoretical role of *r* and *K* selection in modern population biology.

In simplest terms, *r* selection refers to the density-independent component of natural selection, whereas *K* selection is density dependent (see also Roughgarden 1971; Charlesworth 1971; Clarke 1972). A very simple equation which models population growth is:

$$\frac{dN}{dt} = xN - yN^z, \quad (1)$$

where *x*, *y*, and *z* are constants with *z* being greater than one. In this equation, selection on the constant *x* would be *r* selection whereas that operating on constants *y* and/or *z* would constitute *K* selection. Hairston et al. develop their argument from a modified version of equation (1), the Verhulst-Pearl logistic equation:

$$\frac{dN}{dt} = rN - \frac{rN^2}{K}, \quad (2)$$

where *r* is maximal instantaneous rate of increase per head and *K* is carrying capacity (both constants). Comparing equation (1) with equation (2) shows that *K* selection under the Verhulst-Pearl logistic involves selection on the ratio of *r/K* (= *y*), or the slope of the line relating the constants *r* and *K* (fig. 1). Thus, *K* selection focuses on competitive ability, or the way in which the actual instantaneous rate of increase, $r_a = dN/Ndt = r - (N/K)r$, varies with changing levels of competition (conspecific or otherwise). Given a stable supply of resources, the intensity of competition should be proportional to population density (figs. 1-3). The interaction of r_a and *N* is then of prime concern in considerations of *r* and *K* selection. Increased competi-

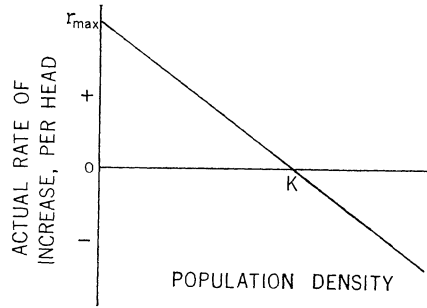


FIG. 1.—Plot showing how actual instantaneous rate of increase per head, r_a , decreases linearly with increasing population density under the Verhulst-Pearl logistic equation. See text.

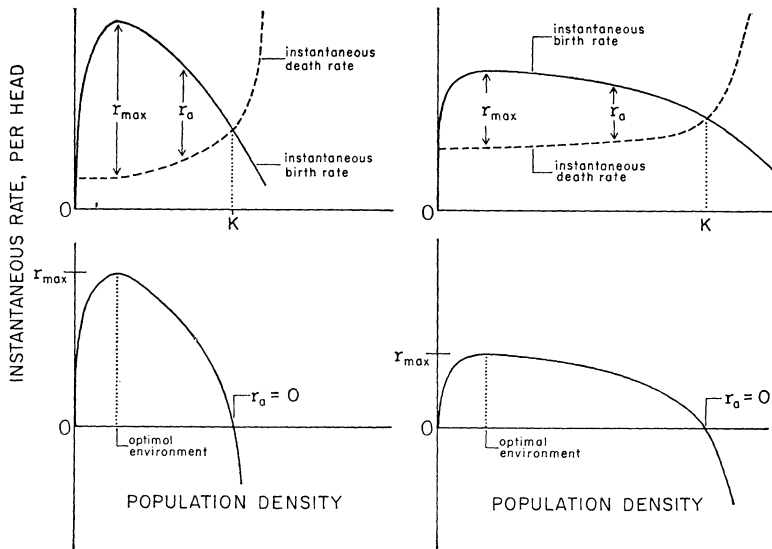


FIG. 2.—Diagrammatic plots of the various instantaneous rates per head versus the intensity of competition (here represented by population density), showing how these might vary in an r strategist (*left*) and in a K strategist (*right*). At densities below the optimal environment, birth rate per head is low because probabilities of mating are reduced. The peak of the birth-rate curve need not correspond with the trough in the death-rate curve. The lower two curves represent the actual instantaneous rate of increase, r_a , obtained by subtracting the instantaneous death rate from the instantaneous birth rate. See text for discussion.

tive ability (evidenced by higher actual rates of increase at high densities in figs. 2 and 3) is assumed to be necessarily accompanied by *reduced* maximal instantaneous rate of increase per head (r_{\max}) in a demographically optimal environment, although this is not true of r_a at all densities (fig. 3). This assumption is plausible in that limited resources of time, matter, and energy available for reproduction should normally result in an inverse rela-

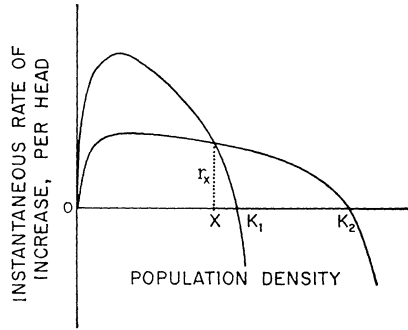


FIG. 3.—Instantaneous rates of increase for the two hypothetical populations in fig. 2 plotted on the same axes. K_1 and K_2 are the carrying capacities of the r and the K strategist, respectively. At density X actual rates of increase of both genotypes (or species) are identical; to the right of X the K strategist is competitively superior, while to the left of X the r strategist is superior. Density-independent rarefaction reduces actual rates of increase by the same amount at all densities; such a removal rate greater than r_x selects for the r strategist (r selection), while a rarefaction rate less than r_x favors the K strategist (K selection).

tionship between number of progeny produced and their individual fitness (including survival ability and competitive ability). (The argument can be developed equally well without holding reproductive effort constant, although it is slightly more cumbersome.) Thus, all else being equal (genetic background, etc.), one would expect a positive relationship between expenditure upon an individual offspring and that progeny's individual fitness.

Vandermeer (1972) and Gill (1972) recently proposed to recognize still another sort of selection for interspecific competitive ability, which they term “ α selection” after the competition coefficients of the Lotka-Volterra competition equations. K selection as discussed here and such “ α selection” are intricately intertwined and interdependent, since by definition the inhibitory effect of one member of species j on the actual rate of increase per individual of species i is α_{ij}/K_i . Since α_{ii} equals unity by definition, the inhibitory effect of one conspecific individual (i) on the actual rate of increase of other members of its population is simply $1/K_i$. In view of the difficulty of assuming constant K 's and because competitive inhibition in nature clearly does not obey the assumptions of these classical equations (Wilbur 1972), it seems appropriate to consider species-specific selection acting upon the entire class of interactions between competing species as “ K selection,” or selection for competitive ability. In competition of the exploitation type, competitors reduce resource availability in much the same manner as other members of one's own population, leaving little logical reason to distinguish intraspecific from interspecific competition.

In order to perpetuate its genes in a saturated environment (i.e., one in which the instantaneous demand/supply ratio is near unity), an organism must produce offspring that are competitively very fit (and, because of the

relationship between expenditure per progeny and fitness, relatively *few* of them). Such K -selected organisms must inevitably have a low r_{\max} simply because of their low fecundity (even an instantaneous death rate of zero cannot produce a high r_{\max} when instantaneous birth rate is low).

Conversely, in a rarefied environment (one with an instantaneous demand/supply ratio considerably less than one), competition is reduced and an organism need not produce progeny with high competitive abilities. Under such circumstances, resources allocated to reproduction can advantageously be divided up among several to many offspring, often with each one having a lowered probability of surviving to reproduce itself. Indeed, in such an environment, there is actually a strong advantage to early reproduction and high fecundity because of the low expectation of future offspring due to high rarefaction; opportunistic populations exploiting such habitats are often expanding (see Pianka 1970). (Variability of r_a in time, in fact, might often be a good indicator of an organism's position along the r - K continuum.) Such r -selected organisms usually have relatively high r_{\max} values due largely to their high fecundities (recall that r_{\max} is the instantaneous rate of increase per head under a theoretical set of demographically perfectly optimal conditions for both reproduction and survivorship).

In developing their notions of b and d selection, Hairston et al. (1970) insist that r , b , and d are not functions of population density; they object to Andrewartha and Birch's (1954) use of $r_m (= r_{\max})$ and to MacArthur and Wilson's (1967) contention that r varies inversely with population size. Hairston et al. point out, rightly, that r , b , and d are constants in the Verhulst-Pearl logistic equation. These assertions are, however, merely a matter of definition and they somewhat restrict discussion of b and d curves (fig. 2). The biologic reality of these curves is apparent from the fact that fecundity (and therefore, b) is often *inversely* related to population density (Lotka 1925; Odum 1959; Lack 1966); similarly, survivorship (the inverse of d) has often been shown to be influenced by population density (Lotka 1925; Lack 1966).

By distinguishing the two components of r (b and d), Hairston et al. (1970) have actually pointed the way toward a more refined analysis of r and K selection. Treating r , b , and d as constants, however, occludes such an analysis, since under this condition, so-called b selection and d selection are in fact both *density independent* and merely components of r selection. As such, Hairston et al.'s (1970) notions of b and d selection have nothing to do with K selection, per se. By allowing r , b , and d to be variables and functions of population density, one can consider the selective forces molding the *shapes* of the two curves in figure 2, rather than just the maximal difference between them. Obviously, at any given density, the *difference* between the two curves determines an organism's fitness. Selection should thus act to raise the b curve and to lower the d curve, and, in addition, to make both curves as flat as possible (such flatness confers a reduced degree of sensitivity to increased levels of competition).

Much of the theory of population genetics has traditionally assumed

density-independence and/or constant fitness; consider, for example, the "fundamental theorem of natural selection" (Fisher 1930). In contrast, most of both classical and current theory in population ecology assumes that habitats are saturated with individuals and/or that rates of increase (the analogues of fitness) are inversely density dependent; as examples, consider the concepts of character displacement (Brown and Wilson 1956; Hutchinson 1959) and the competitive exclusion principle (Hutchinson 1957; Hardin 1961), or the Lotka-Volterra competition equations and their modern outgrowths, such as those developed by Levins (1968) and Vandermeer (1970, 1972). (A notable exception is the classic paper of Cole [1954], which assumes constant fitness and complete density independence.) Thus one school assumes that nature is a perfect ecological vacuum, while the other assumes that, at equilibrium, it is always fully saturated. Both assumptions are biologically unsound, and the real world doubtlessly lies somewhere in between, being partially saturated. Moreover, the degree of saturation must vary from area to area, from time to time, and from population to population. The artificial dichotomy between considering natural phenomena either as completely density independent or completely density dependent led to the great dispute during the last two decades over how populations are regulated (e.g., Andrewartha and Birch 1954; Lack 1954, 1966; Smith 1961, 1963; Andrewartha 1963; Orians 1962; Horn 1968; McLaren 1971). Modern population biologists are relaxing these assumptions and are trying to build more inclusive and stronger theories which allow for various degrees of saturation (e.g., Gadgil and Bossert 1970; King and Anderson 1971). The concepts of *r* and *K* selection have played, and will doubtless continue to play, a central role in such theoretical developments. These emerging theories will help bridge the gap between, as well as blend, the disciplines of population genetics and population ecology. An important empirical foundation for the new theories of population biology will be to understand how competition varies as a function of the differential between supply and demand. Because competition should be intensified as the ratio of demand over supply increases, one would predict that maximum tolerable (allowable) niche overlap should be greater in relatively less saturated communities and/or portions of communities (I call this the "niche-overlap hypothesis"—see fig. 4). A key to testing such aspects of the emerging theory will lie in the development of appropriate empirical indices of such quantities as the following: (1) level of competition, (2) degree of saturation, and/or (3) the ratio of demand over supply. All these properties are abstract and will be difficult to quantify. It may, however, be possible to approach the problem more indirectly, using the time and energy budgets of organisms as indicators of the degree of competition and saturation.

One useful measure is "reproductive effort," which consists simply of the proportion of the total resources (time, matter, and/or energy) available to an organism that is allocated to reproduction at any given time or over a particular time interval (Williams 1966; Tinkle 1969; Harper, Lovell, and Moore 1970; Harper and Ogden 1970; Gadgil and Bossert 1970; Gadgil and

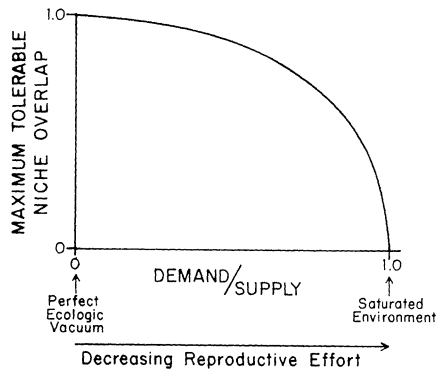


FIG. 4.—Hypothetical relationship between the level of competition and maximum tolerable niche overlap. Maximal niche overlap in a saturated environment may not be zero as figured, but rather might be some positive quantity related to the character displacement ratio of 1.3 (Hutchinson 1959).

Solbrig 1972). If we assume that selection normally maximizes the amount of energy gathered per unit time, an organism's competitive milieu can have either or both of two distinct types of effects upon its time and energy budget: (1) increased competition can reduce the overall amount of energy an organism can gather per unit time, and, hence, its total budget; and/or (2) an altered competitive environment may require some reapportionment of time and energy allocated to various conflicting demands. Thus, when faced with heightened competition, an organism might have to expend relatively more of its limited time and energy on territorial defense and other competitive activities, leaving less for reproduction. From either effect, total reproductive effort should generally decrease with increasing degree of saturation. Similarly, because competitive ability is at a premium under K selection, a successful competitor puts relatively more energy into each of its offspring and *expenditure per progeny* is high. In contrast, r -selected organisms expend less on each individual progeny and produce more of them, and their offspring are less likely to encounter high intensities of competition. Intense density-independent mortality (r selection), by decreasing an individual's expectation of future offspring, should reduce returns from allocation of energy to somatic tissues and activities, thereby favoring increased reproductive effort. Hence, r strategists should produce more offspring than K strategists, both because of their increased reproductive effort and because of reduced expenditure per progeny. Obviously, no organism is completely r selected or completely K selected, but rather all must reach some compromise between the two extremes. The relative positions of organisms along the continuum of r and K selection (Pianka 1970) are of considerable interest.

Female lizards are especially suitable organisms for examination of reproductive effort and expenditure per progeny; they seldom exert parental care and the weight of a clutch or litter is easily measured, as is the weight of

individual oviducal eggs and/or offspring. Estimates of the percentage of total body weight going into egg production, coupled with data on clutch size and estimated number of clutches, should allow assignment of crude relative positions along the r - K continuum to various lizard species (Pianka, in preparation). Niche overlap can be estimated using data on microhabitat usage, stomach contents, and times of activity (Pianka 1969) and new measures of niche breadth and niche overlap (Colwell and Futuyma 1971). By plotting reproductive effort and expenditure per progeny against niche overlap (and ratios of niche overlap over niche breadth), the niche-overlap hypothesis presented in figure 4 could be tested.

Although the terms r and K selection themselves may perhaps be somewhat unfortunate to the extent that they invoke the much overworked Verhulst-Pearl logistic equation, the concepts which accompany them are independent of that equation and are both clear and extremely useful in modern population biology.

SUMMARY

The concepts of r and K selection and b and d selection are discussed and compared. The former pair of concepts will play a central role in the development of new theories in population biology which relax the assumptions that communities (and portions thereof) are either fully saturated or completely unsaturated. It is hypothesized that maximal tolerable niche overlap should vary inversely with the level of competition, and a test is suggested.

ACKNOWLEDGMENTS

Students in my 1971 graduate population ecology class read the Hairston et al. paper and their confusion and comment helped me in formulating ideas presented here; this help is much appreciated. Discussions with J. H. Gillespie and W. E. Neill were of great value. I thank J. C. Avise, J. A. Bissonette, D. H. Feener, C. E. King, L. Moore, P. E. Smouse, D. Yardley, and my wife Helen for helpful comments on the manuscript. Finally N. G. Hairston, D. W. Tinkle, and H. M. Wilbur read the manuscript and made useful criticism which allowed resolution of several misunderstandings. I am also grateful to the National Science Foundation (grant numbers GB-8727 and GB-31006) for financial support.

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