ON r- AND K-SELECTION

Dobzhansky (1950) proposed that natural selection in the tropics operates in a fundamentally different way than it does in temperate zones. He argued that much of the mortality in the temperate zones is *relatively* independent of the genotype (and phenotype) of the organism concerned, and has little to do with the size of the population. Traditional examples of mass winter kills of fish and sparrows are extremes of this sort. Dobzhansky reasoned that in the relatively constant tropics, most mortality is more directed, generally favoring those individuals with better competitive abilities. Thus, in the temperate zones selection often favors high fecundity and rapid development, wheras in the tropics lower fecundity and slower development could act to increase competitive ability. By putting more energy into each offspring and producing fewer total offspring, overall individual fitness is increased. The small clutch sizes characteristic of many tropical birds are consistent with Dobzhansky's hypothesis. Dobzhansky's ideas were framed in terms too specific to reach the general ecological audience and have gone more or less unnoticed until fairly recently.

MacArthur and Wilson (1967) coined the terms "K-selection" and "r-selection" for these two kinds of selection, which are clearly not restricted to the tropics and the temperate zones (K refers to carrying capacity and r to the maximal intrinsic rate of natural increase [r_{max}]). To the extent that these terms invoke the much overused logistic equation, they are perhaps unfortunate. However, it is clear that there are two opposing kinds of selection, which usually have to be compromised. Certainly, no organism is completely "r-selected" or completely "K-selected," but all must reach some compromise between the two extremes. Fisher (1930) stated the problem as follows: "It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction." Fisher's early statement is one of the clearest on the idea of the budgeting of time, matter, and energy into these components (see also, Williams 1966; Gadgil and Bossert 1970). Presumably, natural selection will usually act to maximize the amounts of matter and energy gathered per unit time; the problem is to understand how this matter and energy are partitioned among somatic and reproductive tissues and activities.

We can visualize an r-K continuum, and a particular organism's position along it. The r-endpoint represents the quantitative extreme—a perfect ecologic vacuum, with no density effects and no competition. Under this situation, the optimal strategy is to put all possible matter and energy into reproduction, with the smallest practicable amount into each individual offspring, and to produce as many total progeny as possible. Hence r-selection leads to high productivity. The K-endpoint represents the qualitative

TABLE 1
SOME OF THE CORRELATES OF r-AND K-SELECTION

	r-Selection	K-Selection
Climate	Variable and/or unpredictable: uncertain	Fairly constant and/or predictable: more certain
Mortality	Often catastrophic, nondirected, density-independent	More directed, density-dependent
Survivorship	Often Type III (Deevey 1947)	Usually Type I and II (Deevey 1947)
Population size	Variable in time, nonequilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra- and interspecific competition	Variable, often lax	Usually keen
Relative abundance	Often does not fit MacArthur's broken stick model (King 1964)	Frequently fits the MacArthur model (King 1964)
Selection favors	1. Rapid development 2. High r_{max} 3. Early reproduction 4. Small body size 5. Semelparity: single reproduction	1. Slower development, greater competitive ability 2. Lower resource thresholds 3. Delayed reproduction 4. Larger body size 5. Iteroparity: repeated reproductions
Length of life	Short, usually less than 1 year	Longer, usually more than 1 year
Leads to	Productivity	Efficiency

extreme—density effects are maximal and the environment is saturated with organisms. Competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring. Replacement is the keynote here. K-selection leads to increasing efficiency of utilization of environmental resources. Table 1 summarizes some of the correlates of the r- and K-selected extremes. However, even in a perfect ecologic vacuum, as soon as the first organism replicates itself, there is the possibility of some competition, and natural selection should favor compromising a little more toward the K-endpoint. Hence, as an ecologic vacuum is filled, selection will shift a population from the r- toward the K-endpoint (MacArthur and Wilson 1967).

One whole class of terrestrial organisms (vertebrates) seems to be relatively K-selected, while another large group (most insects, and perhaps terrestrial invertebrates in general) apparently is relatively r-selected. There are, of course, a few exceptions among both the insects (e.g., 17-year cicada) and the vertebrates (some amphibians). Nevertheless, many of the correlates of the two kinds of selection listed in table 1 are characteristic of these two natural groups of terrestrial organisms. Presumably perennial and annual plants differ in a similar way. Aquatic organisms do not appear to obey this generalization; fish, in particular, span the range of the r-K continuum.
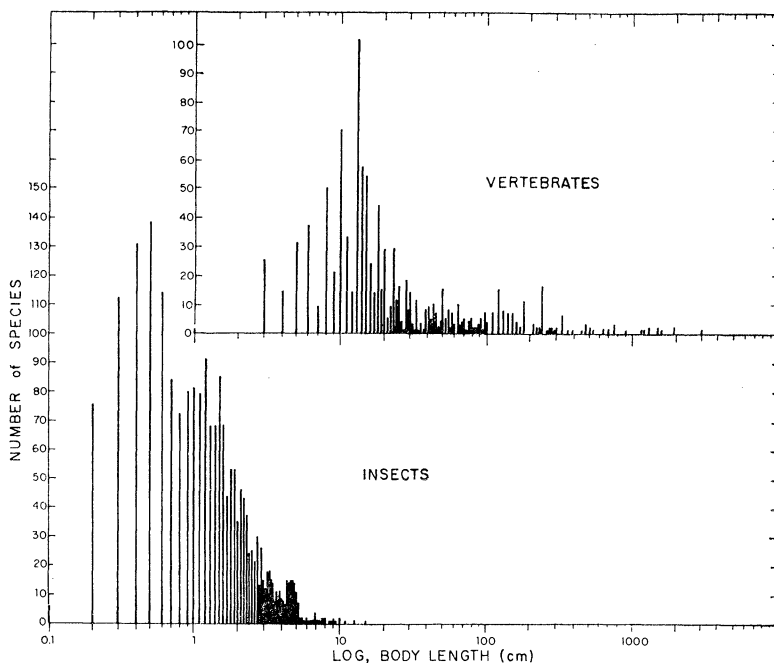
FIG. 1.—Frequency distributions of body lengths for many species of terrestrial insects and vertebrates from eastern North America (data taken from numerous field guides and taxonomic accounts).

While the existence of this dichotomy can (and doubtless will) be challenged, there are a number of reasons to believe it is real. For instance, figure 1 shows the distribution of body lengths for a wide variety of terrestrial insects and vertebrates from eastern North America. Body length is far from the most desirable measurement to demonstrate the polarity, but the strong inverse correlation of r_{max} with generation time and body size (below) suggests that, when frequency distributions for the former two parameters become available, a similar bimodality will emerge.

Some interesting and important generalizations have been made concerning the relationships between body size and r_{max} and generation time. Bonner (1965) plotted the logarithm of body length against the logarithm of generation time for a wide variety of organisms and demonstrated a strong, nearly linear, positive correlation. Smith (1954) demonstrated a similar, but inverse, correlation on a log-log plot of r_{max} versus generation time. Smith pointed out that r_{max} measures the rate at which an organism can fill an ecologic vacuum (at zero density); it is therefore one of the better indices of an organism's position on the r-K continuum. He also noted that r_{max} was inversely related to body size (i.e., that larger organisms are usually more K-selected than smaller ones). Now, r_{max} is inversely related to generation time, T, by the following formula: $r_{max} = \log_e R_0/T$, where R_0 is the net reproductive rate. From this equation it can be seen that variations in R_0 alter r_{max} only slightly compared to changes in T.
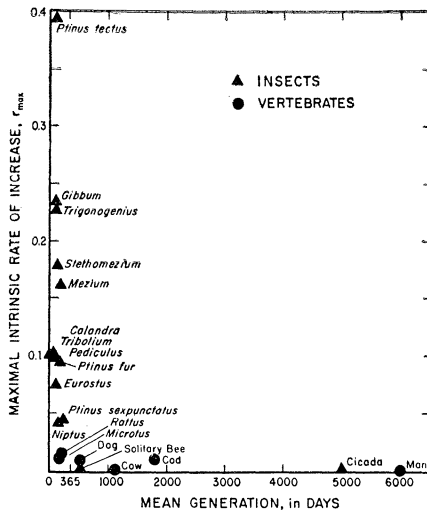
FIG. 2.—Arithmetic plot of r_{max} against generation time, using data of Howe (1953) and Smith (1954).

Hence a hyperbola is expected. When Smith's data and that of Howe (1953) are plotted on arithmetic axes (fig. 2), the data do fit a strong hyperbola, the arms of which appear to represent the two ''natural'' groups of organisms referred to earlier. Cole (1954) presents a similar plot showing the reduction in r_{max} associated with delayed reproduction (or increased generation time).

Over a long period of time, the average r of any stable population must equal zero. Smith (1954) pointed out that organisms like *Escherichia coli* with very high r_{max} values are much further from realizing their full ''biotic potential'' than organisms with low r_{max} values, such as man. He suggested that r_{max} represents a rate of increase necessary for the population to persist in the face of its inevitable ''environmental resistance.'' Furthermore, he argued that the resistance of the environment must exactly balance the biotic potential for an actual r equal to zero. Hence r_{max} also measures environmental resistance. Increased body size no doubt reduces environmental resistance in many ways; an obvious one is that a larger organism has fewer potential predators. Larger organisms are also better buffered from changes in their physical environment. But the dividends of reduced environmental resistance attained by increased body size are offset by loss of biotic potential. Nonetheless, the fossil record does show frequent evolutionary trends toward larger size (Newell 1949).

There are three major cycles in nature—daily, lunar, and annual. Most organisms live longer than a day. Lunar cycles are probably of relatively little importance to the majority of terrestrial organisms. Thus it is unlikely that either daily or lunar rhythms underlie the apparent bimodality of these organisms. However, the annual cycle is another case. To survive, any resident organism with a generation time greater than a year must be

adapted to cope with the full range of physical and biotic conditions which prevail at a given locality. An organism which lives less than a year encounters only a portion of the total annual range of conditions. The latter usually survive the harshest periods by forming resting eggs or pupae. Their population sizes vary with the particular local climatic conditions and the length of time during which r is positive (for descriptions and discussions of such organisms, see Andewartha and Birch 1954). Because longer-lived larger organisms are better buffered from environmental vicissitudes, their population sizes do not vary as much as those of smaller, shorter-lived organisms. Furthermore, presumably their competitive relationships are also more predictable and constant.

The attainment of a generation time exceeding a year may well be a threshold event in the evolutionary history of a population. When perenniality is reached, there are substantially fewer environmental "surprises" and a rather drastic shift from r- to K-selection. I conclude that there may well be a natural bimodality in environmental resistance.

There are, of course, other possible reasons for the apparent bimodality of relatively r- and relatively K-selected organisms in nature. It could be simply historic accident that body sizes and generation times of insects and vertebrates are largely non-overlapping. It is also quite possible that an either/or strategy is usually superior to some compromise. This might be a simple consequence of the hyperbolic inverse relationship between $r_{\max}$ and T.

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