SIZE DISPLACEMENT IN SALAMANDERS: A CRITICISM OF THE CONCEPT OF A DEVELOPMENTAL CONSTANT

In birds and mammals differences in the sizes of feeding structures among sympatric congeners have been interpreted as character displacements which permit coexistence by reducing competition. Hutchinson (1959), in reviewing a number of cases, suggested that a ratio of 1.28 in the linear dimensions of feeding structures of the larger to the smaller species may represent an average lower limit of similarity for coexistence. Such a ratio corresponds to a difference in mass by a factor of about 2. Differences of this magnitude are in accord with a more recent theoretical treatment of competition which predicts separation of species on a resource continuum by \(d/w = 1\), where \(d\) = the distance between means and \(w\) = the standard deviations of the utilization functions (MacArthur 1972; May and MacArthur 1972; May 1973).

Size displacement by a ratio in linear dimensions near 1.28 characterizes not only sympatric congeners but instars of insects and other classes of objects (Horn and May 1977). Maiorana (1978) found that year classes within species of salamanders are sometimes size displaced by a factor of this magnitude, which she designated a developmental constant. She postulated that size displacement either of species or age classes is constant because variability in morphology is relatively constant. Her explanation was that variability in resource use is always greater than that of size of feeding structures, and that a linear displacement of larger to smaller of 1.28 may often correspond to a separation in resource use of \(d/w = 1\).

Wiens and Rotenberry (1981) offered a strong challenge to Maiorana’s interpretation of the ecological (interspecific) constant by demonstrating that size displacements among species vary widely in grassland bird communities. These authors suggested that such communities may not be tightly structured by competition, in which case the rationale for an ecological constant disappears. Ideally, independent confirmation of competition as the organizing factor of a community represents a necessary step for interpreting size displacements, even when the latter conform to the predictions of the displacement hypothesis (Hasterton 1980). A general critique of the ecological constant has recently been provided by Roth (1981), who showed that the concept is deficient on both empirical and theoretical grounds.

Maiorana (1978) equated the ecological constant to an intraspecific developmental constant. Her evidence was drawn from studies of immature insects and salamanders. However, her interpretation of data on the latter is contradictory to the known facts on salamander growth. In any animal, if successive age classes separated by equal age intervals show a constant ratio of body lengths, \(m = 1.28\), then length must be an exponential function of time. Moreover, if body weight varies with the cube of length, according to the power function \(y = ax^b\), where \(y = \)}
and
\[ y = c_1e^{k_1t} \]
\[ x = c_2e^{k_2t}. \]

Following Brody (1945) and Pasternack and Gianutsos (1969) it can be shown that
\[ k_1/k_2 = b \quad \text{and} \quad c_1/c_2b = a \quad \text{of the power function.} \]

Yet growth in amphibians is not ordinarily exponential, but rather sigmoidal, which may be described by one of several functions (Wilbur and Collins 1973). Whichever of these (e.g., logistic, Gompertz, von Bertalanffy) most closely approximates the growth process, there is usually an early inflexion in the growth curve, and a slowing of growth with the approach to either metamorphosis (for larvae) or maturation. Growth of this type yields progressively lower size-displacement ratios as age increases and the growth curve flattens. This is clearly shown in the growth curves of the salamander Desmognathus ochrophaeus (Tilley 1980); the size-displacement ratios are negligible over the greater part of life in this species, such that the average is far less than 1.28. In order to compute an average ratio for a salamander species, the age-specific size attributes need to be far better known that in most of the species which Maiorana (1978) referred to. Moreover, in deriving such averages, there are problems of weighting according to the proportional representation of age classes.

Although Maiorana (1978) contended that size displacement is proportional to variability in size, this may not be a general rule in the salamander species she reported on. To illustrate, in larvae of Pseudotriton ruber from several populations the ratio decreases from 1.74–1.91 to 1.28–1.35 with increasing age; the unweighted averages are between 1.5 and 1.6 (Bruce 1972). In the related species P. montanus, where larval growth is often more rapid, the same trend is evident, but the ratios have higher values, often \( \geq 2.0 \) (Bruce 1974, 1978). Yet variation in body size is quite similar in larvae of the two species of Pseudotriton. As reported in the above papers, age groups having equivalent mean body lengths show correspondingly similar variances. In neither species of Pseudotriton do the data permit estimation of an average size displacement, because adults do not sort by size into identifiable age classes. This is a common difficulty with salamanders.

It is concluded that size displacement ratios in salamanders are not constants but variables, representing by-products of individual growth phenomena. The averages are not necessarily close to the 1.28 value assigned to the "ecological constant." This does not mean that intraspecific competitive interactions do not characterize the developmental period of amphibians, or that such interactions do not affect growth (Wilbur 1980). Rather the argument denies the reality of the constant, and thus its usefulness as a basis for the study of competition.
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LITERATURE CITED


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