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NATURAL SELECTION AND ECOLOGICAL THEORY

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A long and intense controversy over the mechanisms of control of animal populations in nature has accompanied the development of ecology as a vigorous science during the past two decades. While admitting that this has stimulated a great deal of research, I shall argue that much of the controversy has involved peripheral issues and that its perpetuation will continue to result in wasted efforts on the part of ecologists and will add to the confusion among interested non-ecological biologists as to what ecologists are really concerned about. Many share the view of Dobzhansky as expressed during one of the discussions at the Cold Spring Harbor Symposium on Population Studies (1957). "To a non-ecologist, the controversy which has made our session so lively is, I confess, somewhat bewildering. I have had a feeling for several years now that this is a controversy chiefly about words, about 'semantics,' to use a fashionable word. Having tried to the best of my ability to understand the issue involved, I still continue to feel that way."

In advancing the view that there is really a basic issue involved, which is much deeper than its peripheral manifestation in the form of the argument over density-dependence and density-independence, I shall base my case largely on two important books on population ecology, those of Lack (1954) and Andrewartha and Birch (1954). Recognizing that no two books can effectively speak for an entire field, I still select this course because of the great impact of these books on current thinking and because their views are clearly stated. As with most arguments, the most critical portion concerns the initial assumptions upon which theories are erected. Hence, attention will be concentrated upon these fundamental assumptions, rather than upon corollaries which follow if the assumptions are granted.

The basic goals of ecology are seldom stated clearly by ecologists, if, indeed, most ecologists even have opinions about them, but Andrewartha and Birch are characteristically explicit on this point. To them it is the job of the ecologist to explain why a certain animal is found in one place and not in another, why it is more numerous in one place than another, and why there are fluctuations in its numbers. To accomplish this, a three-pronged approach is proposed — the physiology and behavior of the animal must be

investigated; the physiography, climate, soil, and vegetation of the area must be studied; and the numbers of individuals in the population in question must be measured as accurately as possible. Other organisms are to be investigated as they appear important in the ecology of the species under special investigation.

This method of study is not only presented as being extremely profitable, but also as being definitely preferable to other methods commonly employed by ecologists. Community studies, which are motivated by the hope that predictable relationships between the relative abundance and interactions of species can be discovered leading to insights into community structure, are rejected as having contributed nothing, and as being unlikely to contribute anything in the future, to general theory. When too much attention is put upon the community, too little attention is paid to the species whose distribution and abundance are to be explained. Moreover, the community studies are said to stress the importance of other plants and animals to the neglect of other components of the environment.

In my view, the rejection of community ecology by Andrewartha and Birch is the corollary of a still more basic position, namely, that evolutionary concepts have no place in ecological theory. The importance of natural selection is not disputed, for the final section of the book is devoted to evolutionary aspects of ecology, and Birch (1955, 1961) has made important contributions to the study of evolution. Rather it is claimed that a general and satisfying theory of ecology can and should be constructed without recourse to evolutionary thinking and concepts. This view is clearly illustrated by the now famous case of the bees in the auger-holes (page 23). It is the job of the ecologist to count auger-holes and so to predict the number of bees to be found and the job of the evolutionist to measure genetic change as a result of competition. Conceptually, the two fields are kept quite distinct.

Their general theory of ecology states that the numbers of animals in natural populations may be limited in three ways: (1) by shortage of material resources, (2) by inaccessibility of resources, and (3) by the short period of time in which the intrinsic rate of natural increase (r) is positive. The fact that the third of these factors belongs to a category quite distinct from the first two need not be pursued now. For the present it is sufficient to note that, unfortunately, the current controversy is centered around the relative importance of these factors and not upon the assumptions which have led to them.

Lack does not attempt to state a formal theory of ecology but his approach to ecological problems is clearly outlined in the introduction to the the book. Since the book is oriented toward population control, Lack does not consider community studies, but there is an implicit acceptance of their fundamental importance. On points other than those pertaining to communities, he is clear. The distinguishing feature of his approach to ecology is an emphasis upon the need to recognize the distinction between proximate and ultimate factors. Believing that ultimate factors provide the key to the understanding of current population adaptations, Lack has oriented

his own research toward the elucidation of evolutionary mechanisms in ecology. Andrewartha and Birch are, of necessity, concerned only with proximate factors and it is at this point that the most fundamental dichotomy exists.

Lack also strongly supports the belief that controlling mortality factors must be density-dependent. He thus rejects climate *per se* as a controlling mechanism and discusses climate only with respect to changes in range and not with respect to population regulation. In contrast, Andrewartha and Birch ascribe major importance to control of populations by climate and regard distribution and abundance as two aspects of the same problem.

Given these striking differences in viewpoint, it remains to analyze their significance. Since Lack has studied primarily birds and Andrewartha and Birch, insects, it is fruitful to consider whether the differences in viewpoints might be attributable to their choice of organisms since it is to be expected that different organisms will have differing autecologies. It is important to note, however, that Andrewartha does not believe this to be the case, for in his recent book (1961) he is at great pains to cite vertebrate examples, conspicuous by their absence in the earlier book, to substantiate views derived from studies of insects.

Despite this, however, several major possibilities immediately suggest themselves. First, insects are heterothermic and therefore more at the direct mercy of climatic variations than homeothermic birds which can stand wide variations in climate provided resources are available, especially in desert or near-desert environments. Second, a large proportion of insects which have been intensively studied are herbivores, whereas most birds are insectivores or carnivores. Since the apparent inability of herbivores to make effective use of the primary productivity in most terrestrial ecosystems is a puzzling problem, it could be argued that control mechanisms in herbivores are basically different (Hairston, Smith and Slobodkin, 1960). From this it might follow that orderly predictions about insect populations are more difficult to make and, hence, such populations are more appropriately treated by different methods (MacArthur, 1961). Moreover, most birds exhibit well-defined territorial behavior which may act strongly as a density-regulating factor (Orians, 1961), thus modifying the impact of the population upon its resources to a much greater degree than in insects with less highly developed intrapopulational control mechanisms. However, this argument ignores the complexity of the problem of utilization of primary productivity in terrestrial ecosystems. The assumption of different control mechanisms for herbivores and carnivores is based upon inadequate evidence and fails to consider the problem of food quality, often of prime importance to herbivores (Cowan et al., 1950; Taber, 1956, Harlan, 1956; Orians and Pitelka, 1960). Moreover, though the action of natural selection may be more difficult to trace in insect populations than birds, this provides no convincing basis for rejecting an evolutionary approach.

Further, we may consider differences in the nature of the communities studied by field ecologists. As economic entomologists, primarily concerned with insect pests of croplands and their predators, Andrewartha and

Birch work in the highly artificial and recently derived communities of pure-stand crops. One result is that most insects are studied not in the native vegetation to which they have been evolutionarily adapted but in recently colonized habitats many of which are geographically remote from the natural range of the species. In most cases nothing is known of the ecology of the species in diversified natural communities so that the adaptive significance of many life history features is obscure. It is at present impossible to assess the impact of these circumstances in relation to empirical results on population fluctuations in cropland pests, but there is clearly sufficient ground for caution in generalizing from these results to natural communities. Moreover, the growth of economic entomology has been stimulated by particular practical demands, namely the prediction of outbreaks of pests and their control, either through predators or through the discovery of a particularly vulnerable stage of the life history. Since correlation may permit prediction, these goals can often be achieved by obtaining climatic correlations with population fluctuations, despite the fact that the correlation need not imply causation.

However important the differences in the autecologies and environments of organisms studied by ecologists of different schools of thought may be, I believe that the fundamental dichotomy in modern ecology, as illustrated by the books under consideration, can only be understood as a manifestation of the fundamental division of biology into two major categories — functional biology and evolutionary biology (Mayr, 1961). The differences in method and basic concepts of these major fields is sharply focused in this controversy though its roots have apparently not been grasped either by the participants or interested observers. As functional ecologists, Andrewartha and Birch are concerned with the operation and interaction of populations and one of their major concerns is with experimental control of environmental variables. This approach leads to the rejection of results directed toward the elucidation of the action of natural selection upon populations, such as the distribution of chaffinches (*Fringilla coelebs* and *F. coerulea*) in the Canary Islands (Lack and Southern, 1949) and character displacement (Vaurie, 1951; Brown and Wilson, 1956). To the evolutionary ecologist, this rejection is quite inconsistent with their easy acceptance of climatic correlations that appear far less critical and may easily be misinterpreted through improper application of statistics (Smith, 1961).

As an evolutionary ecologist, Lack is primarily concerned with the causes behind observable ecological adaptations and has made his major contribution in the subject of the evolution of reproductive rates. This approach leads to the rejection of climate as a significant regulating factor for populations, a rejection which the functional ecologist finds incomprehensible.

It is pointless to debate the validity of these contrasting approaches to ecology as both have clearly justified their usefulness in all fields of biology. However, it is of great importance to consider the claim of Andrewartha and Birch that general ecological theory can and should be built solely upon the functional approach. Just as many physiologists treat the animal body as a highly interesting and complex mechanism which has not been and

is not going anywhere, Andrewartha and Birch treat ecology as the study of complex relationships between animal populations and their environments which are to be best understood as neither having evolved nor continuing to evolve.

It is becoming increasingly apparent that a complete answer to any question should deal with physiological, adaptational and evolutionary aspects of the problem (Pittendrigh, 1958). The evolutionary process of becoming yields the most profound understanding of biological systems at all levels of organization (Simpson, Pittendrigh and Tiffany, 1957). The non-evolutionary answer to the question of why an animal is abundant in some parts of its range and rare in others is of necessity incomplete. The functional ecologist can and does make an important contribution to the understanding of the dynamics of populations, but for the formulation of theory it is essential that the approaches be combined. The functional approach by itself cannot provide a basis for theory and, in fact, the "theory" of Andrewartha and Birch really states that no general theory of ecology is possible and that each case must be considered individually, which is really a statement of research technique rather than theory.

The application of selectionist thinking to natural populations has already led to deeper insights about the proximate relationships of populations. In fact, it is difficult to think about populations without considering the selective advantage of various life history features. Lack's work on avian reproductive rates is an excellent example of ecological insight derived from selectionist thinking. Another is R. A. Fisher's theory on the evolution of sex ratios, originally proposed in 1930 and recently amplified by Kolman (1960) and Bodmer and Edwards (1960). To this we may add Medawar's (1957) stimulating discussion of the evolution of death rates, a fundamental ecological and physiological problem; all competition studies; the ecology of vertebrate social organization (Pitelka, 1959; Orians, 1960, 1961); and the nature of animal niches (Hutchinson, 1959; MacArthur, 1961). Recent studies of species abundance and diversity (Kohn, 1959; MacArthur, 1957, 1960; MacArthur and MacArthur, 1961) are also producing promising results, but it still is too early to evaluate them adequately. Also, animal ecologists are adopting more widely the community approach which has been intensively and extensively used by plant ecologists for decades (Elton, 1949).

On the other hand, Lack and others of similar viewpoint probably overstate the case for density-dependence when they assume that regulation and evolution cannot occur unless there is so-called biological control and competition. The role of climate as a controlling mechanism is often doubted on this ground alone, but Birch (1960) has made a valid claim for the operation of natural selection through climate. Moreover, environments do fluctuate and may do so regularly enough to prevent competition from proceeding to its conclusion (Hutchinson, 1953).

Finally, it may be asked whether or not there is any such thing as a general theory of ecology, satisfying or unsatisfying. Is there a theory of behavior or comparative anatomy or embryology or physiology? Whereas there

are descriptive generalizations in all of these fields, the only general theory which now seems possible is that of natural selection. Ecology, too, has its descriptive generalizations, such as the principle of competitive exclusion, but as in other fields, evolution would seem to be the only real theory of ecology today. Even if one strongly believes in the action of natural selection it is exceedingly difficult, as Darwin pointed out, to keep it always firmly in mind. Neglect of natural selection in ecological thinking is, therefore, understandable though regretable. However, its deliberate exclusion in these years following the Darwin centennial would seem to be exceedingly unwise.

CONCLUSIONS

The roots of the current controversy which so deeply divides ecology lie much deeper than their peripheral manifestations in the argument over density-dependence and density-independence. Rather, they stem from the division of the field into two major categories — functional ecology and evolutionary ecology. Both of these approaches are valid and useful and it is a mistake to erect general ecological theory exclusively on either.

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