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Evolutionary History and Population Biology

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While accepting evolutionary theory, should ecologists be more sceptical about hypotheses derived solely from untestable assumptions about the past ? The authors put forward the view that many ecologists underestimate the efficacy of natural selection and fail to distinguish between phylogenetic and ecological questions.

SOME biologists claim that an understanding of the evolutionary history of organisms is a prerequisite to any comprehension of ecology. We believe that this notion is having the effect of sheltering large areas of population biology from the benefits of rigorous thought. It is clear that the phylogenetic origins of an organism, structure, or process may be of great interest, and that the elucidation of such origins is a legitimate subject for investigation and speculation. We contend, however, that such investigation or speculation is not required for many studies of ecology and taxonomy. Indeed, since the level of speculation (rather than investigation) is inevitably high in phylogenetics of any kind, a preoccupation with the largely unknown past can be shown to be a positive hindrance to progress.

The data for the contemporary investigation of ecology and taxonomy are the distribution, numbers and variation of existing organisms in their present environments. When this ecology and taxonomy is understood we may, in some cases, be in a position to make reasonable guesses about phylogenetic origins. On the other hand, to reverse the process and attempt to investigate ecology and taxonomy through a series of inferences about the past is to base these sciences on non-falsifiable hypotheses. The protocol for this reversal is difficult to imagine and, of course, it is never achieved in actual practice. All that is accomplished by those who feel that evolutionary history is the only pertinent aspect of population biology is a confusion of data and untestable hypotheses. This confusion is often compounded when a simple rewording of the problem is accepted as a solution to the problem. For example, the mutually exclusive ranges of X and Y are "explained" by "competition". How do you know there was competition ? Answer, because each "obviously" excluded the other from its range ! A *sine qua non* for rectifying this way of thinking is the more rigorous

proposal and testing of falsifiable hypotheses. We make some suggestions along these lines and discuss the problem of phylogenetic thinking in ecology. The confusion created by phylogenetic thinking on taxonomy has been discussed in detail elsewhere[1,2].

Two recent articles by Orians[3] and Lack[4] can be used to exemplify the thinking of historical ecologists. Orians pleads for an evolutionary approach to the study of ecology. He claims that in the view of Andrewartha and Birch[5] "evolutionary concepts have no place in ecological theory", and he believes that this attitude of Andrewartha and Birch can be traced to their investigations of insect pests "in the highly artificial and recently derived communities of pure stand crops". He points out that in most cases nothing is known of the ecology of the species in their original natural communities so that the adaptive significance of many life history features is obscure. Lack also remarks that he overlooked for many years the importance of investigating what he calls "evolutionary ecology", in the natural habitat of the species, "as many of its ecological adaptations may not be well suited to habitats modified by man. Moreover man has so greatly modified so many habitats that adaptations may be hard to recognize as such . . . the English countryside is itself a huge artefact, so that ecological research carried out there may give misleading results". The implication of these statements is that organisms that now live in an environment different from the one they occupied decades or centuries ago will have biological characteristics that were adaptive in the old but not necessarily in the more recent environment.

We believe that the views of Orians and Lack are deficient on two counts: (1) that they may underestimate the efficacy of natural selection, and (2) that they fail to distinguish between two different questions, one a phylogenetic question and the other an ecological question.

Underestimation of Efficacy of Natural Selection

Orians and Lack expect to find non-adaptive characters in present day populations because these populations have not yet evolved in response to present day conditions. Nevertheless the species they write about are sufficiently well adjusted to the environments changed by man to be plentiful and widespread. On the other hand, our investigations of the ecology of invertebrates and vertebrates, both those that are pests and those that are not, have impressed us with the genetic plasticity of natural populations and with the rapidity with which natural populations are moulded by changing environment.

It seems to us rather unlikely that, as Lack[4] suggests, clutch size in certain birds is so non-protean as to be unable to shift rapidly in response to a changing environment. In any case, the example which Lack gives to support the importance of the past appears to be a much better example of the need for a thorough understanding of the present. In a broad-leaved wood near Oxford the commonest clutch-size in a population of the great tit (*Parus major*) is nine eggs. In most years those nests with nine eggs have also been, on the average, those with the most surviving young per brood. In conifers the average clutch size "is similar to the oak woods, presumably because extensive conifer plantations are recent in England and the great tits breeding there are not genetically isolated from those in broad-leaved woods". Because of a shortage of food in the pine woods, however, many of the nestlings starve and the rest are badly underweight, suggesting to Lack that a smaller brood size would be advantageous.

If we accept Lack's hypothesis that a smaller clutch size would be advantageous in the pine woods, how can the persistence of the "wrong" clutch size be explained ? It seems to us that a critical piece of evidence necessary for answering that question is knowledge of the genetics of clutch size in great tits. Some information could doubtless be gained by comparing the clutch sizes of offspring with those of the parents, if these data can be extracted from the observations. The literature on clutch size gives us the impression that either there is considerable genetic variance in clutch size, or that clutch size is quite responsive to environmental change. Lack, Gibb and Owen state on page 314 of ref. 6 that "There is much circumstantial evidence that the clutch size of great and blue tits is adapted to local and temporary conditions". They go on to quote results showing that clutch size varies among years in relation to the abundance of caterpillars. Perrins[7] states that mean clutch size has varied between 7·8 and 12·5 in different years, and lists four sorts of variation in clutch size: clutches are smaller late in the season, smaller at higher densities, smaller in habitats with fewer large trees, and smaller when laid by birds which are breeding for the first time. Furthermore, Lack[8] comments on variation in clutch size of the great tit and blue tit thus: "This section shows, once again, how variable and adaptable clutch size is . . . clutch size is much more adaptable to the particular conditions than I formerly supposed . . ."

In the face of even this limited information it seems to us unlikely that the great tits in the pines are hanging on to their "old adaptations". A much more likely explanation may be that hinted at by Lack, namely, that rather than being adjusted to the conditions of another time, they are adjusted to the conditions of another place. That is, they are peripheral populations which cannot adjust to local conditions because of the rate of flow of genes from broad-leaved woods. It is clear that considerably more thorough investigations of the present day population biology of these birds, with the emphasis on the genetics of clutch size, magnitude of selection pressure on clutch size, and rates of gene flow, will be necessary before we fall back on an untestable historical hypothesis. If gene flow from the broad-leaved woods is responsible, then the situation is entirely explicable without any guesswork about the "ancestral habitat of the British great tit", or other untestable hypotheses about the evolutionary past.

In fairness to Lack, however, we must state that in our own work we have not been impressed merely with the speed with which selection can shape a population; we have also been impressed with the speed with which environments can change. One may well be able to detect populations "out of step" with their current environments, but we insist that all testable hypotheses be thoroughly falsified before resorting to "adaptation to the past".

Distinction between Phylogenetic and Ecological Questions

The statements we have quoted from Orians and Lack confuse two questions. When an ecologist investigates a species he may ask: given the existing characteristics of the species, as for example its temperature tolerances, birth rates, death rates, capacity for dispersal and so on, what determines the distribution and numbers of the species in the world ? In order to answer that question we do not need to know how the species evolved its particular characteristics. The phylogenetic question is interesting in itself but it is not relevant to the investigation of the question of distribution and abundance. How the species acquired its present adaptive characteristics is a second and independent question. To deny the relevance of the investigation of phylogeny in seeking an answer to the ecological question of abundance is not to deny, as Orians and Lack imply, that the adaptive characteristics of the species evolved. In correspondence Orians makes it clear that he agrees that the two questions (or "proximate and ultimate factors") should be kept distinct, and that his statement[3] of the point of view of Andrewartha and Birch[5] regarding the celebrated case of the Canary Islands' chaffinches is misleading.

The example to which Orians referred concerns the distribution of the chaffinches *Fringella coelebs* and *F. coerulea* in the Canary Islands[9]. The facts as stated by Lack and Southern are that *F. coelebs* is the only species of the genus in Europe. There, it is abundant in both broad-leaved and coniferous woodland. On Tenerife there are two species; *F. coelebs* occurs in broad-leafed forests while *F. coerulea* is restricted to conifers. This is also true of Gran Canaria. On the islands Palma and Hierro, however, *F. coerulea* is absent. Here the "local forms" of *F. coelebs* are common in the conifers. Orians wrote "As functional ecologists, Andrewartha and Birch are concerned with the operation and interaction of populations and one of their major concerns is with the experimental control of environmental variables. This approach leads to the rejection of results directed toward the elucidation of the action of natural selection on populations such as the distribution of chaffinches (*Fringilla coelebs* and *F. coerulea*) in the Canary Islands (Lack and Southern, 1949)[9] . . ." We and others have interpreted this sentence as a criticism of Andrewartha and Birch for rejecting the untestable hypothesis that the observed distribution was caused by competition in the past. We have discussed the matter with Orians, who tells us that he did not mean to imply this. He has pointed out to us that elsewhere Orians and Collier[10] have been critical of basing explanations on the untestable hypothesis of competition in the past. We and Orians now agree that the relevant questions are the following: (1) What keeps *F. coelebs* out of the conifers on Tenerife and Gran Canaria ? In other words, what are the factors responsible today for the observed distribution and abundance of this organism on these islands ? (2) What are the phenetic and genetic relationships of the Tenerife, Gran Canaria, Palma and Hierro populations labelled *F. coelebs* ? Included under phenetic relationships would be a detailed investigation of ecological and behavioural similarities and differences. At

least colour, bill size and food choice differ among these populations. It is a common error for ecologists to consider all populations placed by fiat into the same "biological species" to be somehow the same. (3) Questions 1 and 2 should obviously be investigated first. It is then, of course, quite legitimate to ask what historical events are responsible for the divergence in habits of *F. coelebs* occupying islands where *F. coerulea* is present and those where *F. coerulea* is absent. Any reasonable guess at an answer to this evolutionary question will depend in a large part on the answers to questions 1 and 2, but the reverse is clearly not true. In addition, no hypothesis on the development of this situation, no matter how ingeniously contrived, will add anything to our understanding of today's ecology. It is legitimate to make inferences about past events on the basis of knowledge of the present, but such inferences can make no direct contribution to our knowledge of distribution and abundance today.

We think that in answering this sort of question Lack[11] is too ready to invoke the hypothesis that divergences have been the result of "competition" in the past when the two populations have overlapped. This statement is in itself meaningless (see Birch[12] and Ehrlich and Holm[13]) unless the exact form of this "competition" is specified, including the ways in which it produced selection pressures resulting in the restriction of one or both species. The phenomena which now go under the name of "competition" will never be understood without detailed investigations of the pertinent interactions in nature today. Investigation of the operation of selection will be paramount in such investigations. In fact, we would claim that detailed investigations of the present situation, including field experiments, is the chief approach which will lead to the understanding we seek; the simple statement that competition occurred in the past elucidates nothing. More field investigations such as that of Orians and Collier[10] are badly needed in all groups of animals.

To reiterate, when two similar species have different distributions on a single island it is important to investigate behaviour and other characteristics that are responsible for the observed differences in distribution. It is no answer to say that they are differently distributed because they have evolved different characteristics as a result of having had overlapping distributions in the past. This is an interesting historical hypothesis, but it does not help in elucidating how these different characteristics result in a different distribution today. Moreover, we have yet to be shown how to investigate the ecology of the Triassic or Pliocene. Lacking such techniques it becomes hard to design a test of the overlap hypothesis.

Lack[4] says that he has been primarily interested in problems for which the explanation has to be sought in the evolutionary history of the species. In pursuing this he says "one must be clear at the start as to which features of a species or population are evolutionary adaptations and which are merely consequences of population dynamics". He then gives as an example of a feature of a species that is an "evolutionary adaptation" as opposed to a "consequence of population dynamics" the "differences in habitat between closely related species of birds". Lack claims that these habitat differences are "due to the fact that two species with similar ecology cannot persist in the same area, and that each is differentially adapted to its habitat". This is Lack's statement of the so-called Gause rule (or competitive exclusion principle). The second part of Lack's statement can be translated as "different species are different". The first part is a loosely drawn argument because, among other things, "similar ecology" and "persist" are not defined.

Lack wants to know how closely related species evolved different requirements. We agree with Lack that this is an interesting problem. We disagree that he has provided any convincing evidence that the Gause hypothesis is a

likely explanation. Furthermore, this hypothesis cannot be tested in this context because it refers to events in the evolution of the species, events about which nothing is known. Despite this, Lack considers the hypothesis to be capable of application and to exclude any possible alternative hypothesis. Andrewartha and Birch[5] criticized Lack's analysis of this problem along the same lines as we have done. Lack[4] replied: "the criticism of this view by Andrewartha and Birch (1954) seems basically due to disagreement with my view that this is a problem of evolutionary ecology and therefore to be interpreted in terms of survival". We agree with the criticism by Andrewartha and Birch[5]. We do not deny at all that the closely related species of birds have come by the properties they possess as a result of an evolutionary history, though we are less convinced than Lack as to what that history is. What we deny is that we need to know the evolutionary history before we can understand the ecology of two related species that happen to occupy the same island today. If ecological studies were to depend on a knowledge of the evolutionary history of the species, as Lack seems to want, then most ecological studies would be halted, for this information is denied us for most species. Indeed, we know nothing whatever of the antecedents of most species for thousands of years. Perhaps these dismal facts account for some of the strangely unsatisfying "explanations" of the evolutionary ecologists.

In any study of distribution and abundance, the ecologist soon becomes aware of critical features of the life cycle (such as the presence of diapause, high birth rate associated with high death rate and low birth rate associated with high survival rate), and community associations (for example, parasites and hosts, herbivores with food plants) which invite analysis and speculation on phylogenetic origins. Cole[14] made an interesting analysis of the relative adaptive advantages of different sorts of life histories, and Lewontin[15] has interpreted life history types in terms of selection. Lack[16] has studied clutch size in birds, and has been able to interpret it in terms of selection for the brood size favouring maximum survival of young. Hamilton and Orians[17] constructed a logical model for the evolution of brood parasitism in altricial birds. Ehrlich and Raven[18] investigated the co-evolution of butterflies and their larval food plant, and were able to infer a pattern in which the butterflies act as a potent selective agent on the plants, and vice versa. These seem worthy subjects for study, despite the inevitable difficulty of providing much more than speculative analyses. It is important to remember that such studies are useful to the ecologist only in so far as they analyse present day situations. For instance, the patterns of plant utilization by butterflies shown by Ehrlich and Raven can be useful to the ecologist in many ways, such as in making predictions about food plants of species the biology of which is unknown and in accounting for certain features of butterfly distribution and abundance. On the other hand, the phylogenetic speculation in this study—about the relative times of divergence of butterfly and plant groups, the past significance of secondary plant substances, and so on—are of no help whatever in explaining present day ecology. They are a series of unfalsifiable hypotheses. These hypotheses do not help us to understand the distribution and abundance of plants and butterflies today, because they are not subject to testing.

While workers in this field often emphasize the importance of the evolutionary past, their work seems peculiarly lacking in selectionist thinking about the present. Where are the studies on selection in competing natural populations, showing how competition alters the genetic characteristics of the two populations ? Where are the works showing that when two populations come together in nature, selection against hybrids can produce character displacement ? Are we to assume that this sort of thing went on only in the past, that evolution as pictured by the evolutionary ecologists has ceased ?

Our theory of evolution has become, as Popper[19] described, one which cannot be refuted by any possible observations. Every conceivable observation can be fitted into it. It is thus "outside of empirical science" but not necessarily false. No one can think of ways in which to test it. Ideas, either without basis or based on a few laboratory experiments carried out in extremely simplified systems, have attained currency far beyond their validity. They have become part of an evolutionary dogma accepted by most of us as part of our training. The cure seems to us not to be a discarding of the modern synthesis of evolutionary theory, but more scepticism about many of its tenets. In population biology, more work is needed in elucidating the general properties of populations, both those made up of one species of organism, and those made up of two or more species, without reference to dogmas or guesses about how they may have evolved. First we need answers to questions such as (1) How frequently do populations become extinct in nature? (2) Do most populations have self-regulating properties? (3) How frequently do populations utilize the same limited resources in nature? (4) What kinds of selection pressure does such utilization impose on each population? (5) Is great reduction of gene flow necessary for differentiation of populations in nature? (6) How are community complexity and stability best defined and measured? (7) What is the relationship between com-

plexity and stability? Then we can see how the answers fit into the modern synthesis.

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Axonic and Synaptic Lesions in Neuropsychiatric Disorders

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Peculiar vesicular structures in the axons and synaptic terminals of neocortex of a 30 month old boy with psychomotor retardation of unknown origin are similar to the changes observed in other human diseases characterized by disorders of memory and learning. Such changes in the architecture of axons and synapses may cause certain disorders the aetiology of which is at present obscure.

THE part played by the synapse in establishing functional contacts between nerve cells or nerve cells and muscle has been well substantiated[1]. The initiation of the post-synaptic potential by neurotransmitters (neurohumours) is also established beyond any reasonable doubt in the case of several types of synapse[2]. Uncertainties about the structure of the synapse have been clarified by examining this important segment of the neuron under the electron microscope[3-5]. Mitochondria and vesicles containing acetylcholine or other neurotransmitters have been seen in the presynaptic axon terminals (boutons terminaux)[6-8]. It is believed that the synthesis of neurotransmitters takes place at the terminal from substrates and enzymes transported from the perikaryon by axoplasmic flow[9,10]. Energy and probably certain substrates and co-enzymes are provided at the presynaptic ending by mitochondria. The site of actual contact between axon and axon, axon and dendrite or axon and soma is characterized by slight thickening of the apposed membranes; the interstitial space between the pre- and post-synaptic terminals (intersynaptic cleft) is filled with linear or spherical osmiophilic material which probably serves as a cohesive matrix between the pre- and post-synaptic membranes[11,12]. The fine structure of the post-synaptic element has also been the subject of a number of investigations[13-15].

Information is not available about neocortical synapses in neuropsychiatric disease because it is difficult to obtain

fresh specimens and because this vital segment of neocortical neurons is inaccessible to histological methods[16]. It is generally assumed that the synapse plays a secondary part, and degenerates in a non-specific manner after any type of lesion of the perikaryon. Recent evidence suggests that this assumption may not be correct[17,18]. Abnormalities of synaptic fine structure consisting of enlargement of the presynaptic terminal, reduction of the number of synaptic vesicles, and accumulation of fibrillar or vesicular material were observed in biopsy specimens of frontal cortex from patients with psychomotor retardation and Alzheimer's presenile dementia[17,18]. In one case[17], the synaptic lesions were the only recognized changes by light or electron microscopy. These changes are significant in view of the importance of the synapse in establishing functional contacts between neurons[1] and the current belief that the synaptic transmission is an integral part of learning and memory processes[19,20].

This article describes axonic and synaptic changes observed in the frontal cortex of a 30 month old boy with severe psychomotor retardation; the significance of synaptic "lesions" in neuropsychiatric disease will be discussed.

The patient, a Negro male, 30 months old, was admitted to the Hospital of the University of Pennsylvania for evaluation of psychomotor retardation. He was the product of an essentially normal, full-term pregnancy.