



## Patterns and Populations

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Soviet production and other U.S. production of  $Rh^{102}$ , it might be worth making a plea for greater coordination, preferably on an international basis, of possible future world-wide tracer experiments (23). Again, in view of the results for this experiment, it should be possible to plan in a better way the sampling program for future experiments. Certainly, the greatest value from future experiments will be obtained by increased coordination and participation of the world scientific community (24).

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## Patterns and Populations

Basic problems of population biology transcend artificial disciplinary boundaries.

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An important and rapidly developing area of biological science is the study of aggregations of organisms. This field, which we call population biology, may be defined as including all aspects of groupings of organisms and organisms in groups. Often, however, it is considered to comprise only ecology in a relatively narrow sense, or even population genetics alone. We feel that there is much to be gained from taking a broad view in the study of populations, in which emphasis is on the many simi-

larities in the phenomena studied by the taxonomist, the ecologist, the geneticist, the behaviorist, the economist, and perhaps the mathematician as well. Despite the apparent heterogeneity of this assemblage it seems to us that there are many basic problems common to these diverse disciplines. Often these areas of mutual interest have not been recognized, even though many workers have urged broad interdisciplinary approaches. Perhaps the time has come to dissolve disciplinary boundaries. Such a unification will require a careful study of techniques and procedures, in addition to an analysis of the lan-

guage and the conceptual frameworks involved, with particular attention to the Whorfean hypothesis (1). Conceivably, a new mathematics must be developed in order to handle the problems of population biology. The mathematics of information theory (2) and game theory (3) already are being shown to have possible applications in this field, but so few biologists are versed in these mathematics that their importance and utility are only beginning to be investigated. A general mathematical theory of population biology may be formulated eventually, but a great deal of intellectual brush-clearing must necessarily precede even preliminary groping for overall principles. In the discussion which follows it may seem that we have restricted ourselves largely to destructive criticism, demonstrating the disadvantages of established procedures and modes of thought. But these must be pointed out before it is possible to develop improvements. Although we have not always discussed possible improvements in detail, these often are presented in the works cited. In science it frequently is necessary to criticize existing theoretical structures to clear the way for new ideas.

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## Facts and Concepts

The thinking concerning many problems in population biology has been colored strongly by the terms invented to deal with them. People are inclined to confuse concepts with established facts and then consider it unnecessary to investigate the facts further. Often terminology differs with different disciplines, and thus areas of study are isolated and relationships are obscured. For example, it is difficult to find a neutral term for "more than one organism" which has not already been used in a restrictive sense in one or more disciplines. Whereas earlier we used the word *aggregations* to refer merely to a plurality of organisms, it has several different meanings in ecology. The fact that semantic problems of this sort cause serious difficulty throughout all human endeavor should not deter us from attempting to correct the situation.

Many concepts in population biology have low information content and little or no operational meaning. In this category we would place such concepts as "competition," "niche," "community," "climax," "species," "population fitness," and to some extent "population" itself. Dissatisfaction with the concepts of population biology is widespread. Ecologists recently have attempted to develop an operational definition of "niche"—that is, to specify the set of physical operations which would assign to every niche a unique value, such as the coordinates of an  $n$ -dimensional hypervolume (4). The language of ecology has been analyzed (5) with the aim of eliminating semantic confusion; the idea of natural selection as an ecological concept has been investigated (6). The concept of population fitness, one of the most difficult problems in population genetics, has received a great deal of attention recently (3, 7). Boulding (8) has discussed conceptual problems as they relate to economics, and the behavioral literature is filled with discussions of the value of such ideas as "instinct," "releaser," "displacement activity," and "learning."

Any attempt to avoid this confusion of concepts and facts would seem to entail changing our approach to the entire "population" level of biological organization. Perhaps the best way to start is by asking questions in a manner which is divorced as much as possible from our present conceptual framework. For example, three very broad and basic questions in population bi-

ology which are of particular interest to us are the following: (i) What are the patterns of variation which may be observed in nature? (ii) How can we evaluate the reality of the observed patterns? (iii) What hypotheses can be advanced to account for the observed patterns?

The reality of such concepts as "fish," "bird," "mammal," "conifer," and "grass" is rarely questioned; it seems obvious that they represent major clusters in patterns of variation. That peoples of other cultures order natural phenomena differently bothers most of us very little [for example, Eskimos have no generic term for water but have a detailed and useful terminology describing the various kinds of frozen water; gauchos have some 200 terms for horse colors, but they divide the vegetable world into four species: *pasta*, fodder; *paja*, bedding; *cardo*, woody materials; and *yuyos*, all other plants (9)]. It also seems to bother biologists very little that other scientists—for example, physicists—take a rather disturbingly different view of what is real and what is unreal, what is fact and what is construct. For instance, the Newtonian concept of absolute time is not employed by modern physicists because no phenomenon with the postulated properties of absolute time has been found experimentally. As we shall demonstrate, the concept of genetic (or "biological") species, the idea of the community as a unit, and many other concepts current in subdisciplines of population biology have much in common with the idea of absolute time.

## The New Taxonomy

Traditions and force of habit have influenced present-day workers in taxonomy more than they have influenced workers in most other disciplines. For nearly 200 years taxonomists have followed Linnaeus in arranging organisms in "natural groups." Darwin supplied a rationale for the existence of such groups, and in the minds of many workers the existence of groups and their probable cause have become inseparable. This has led to the so-called phylogenetic approach to taxonomy, in which, in the absence of satisfactory fossil records, taxonomic systems often are used as the basis for constructing phylogenetic trees. Unfortunately, these trees sometimes are then employed to alter the original taxonomic system. This circular procedure produces sys-

tems with some predictive value and information content, although the process of creating these systems through repeated revision is time-consuming and relatively inefficient.

About 5 years ago in the United States and England, taxonomists began to investigate multivariate methods of assaying similarities among organisms (10). The newer methods have methodological and philosophical advantages over older methods of multivariate analysis (11), and there is the additional advantage that data may be handled by modern automatic data-processing equipment. Several different techniques have been developed which give similar and repeatable results. The systems of logical relationship obtained in this manner have relatively high information content. They supply a base for phylogenetic speculation, but the speculation is not involved in establishing the base.

This general approach thus seems to provide a means of answering the first question posed above, and it presents a possible basis for answering the second question as well. The genetic relationships among a group of organisms (that is, the pattern of similarities or differences among genotypes) might be considered a parameter which one could estimate by taking samples of the genetic information for each individual and then calculating the matrix of similarity (or distance) coefficients among the samples. The practical way to sample the vast store of information in a genotype is to sample the phenotype and accept the error introduced by the interaction of the genetic information and its milieu. The magnitude of this error (which is implicit in virtually all systematic studies and most genetic work) cannot be estimated accurately at the present time. We need much more knowledge of phenomena of the kind that may be lumped conveniently under the heading "developmental homeostasis" (12). Indeed, if this sampling procedure is legitimate, then patterns of (logical) relationship which are essentially congruent should be produced by working with any large sample of characters.

This hypothesis of congruence is being tested at several institutions and on diverse groups of organisms. For example, Ehrlich is now engaged in a detailed investigation of the comparative external and internal morphology of a representative series of butterflies. When his study is completed it will be possible to compute a matrix of coeffi-

cients for some 75 characters (13) from the external anatomy and another based on a roughly equivalent number of characters from the internal anatomy. To test the assumption that there is a reasonable degree of congruence in the patterns for adults and for larvae, the next step in these investigations will be to see whether the same pattern is obtained when characters of the larvae are considered. Recent work by Rohlf (14) indicates that such congruence is not complete in the patterns of relationship of mosquito larvae and adults, and other studies, by Michener and Sokal (15), of patterns for males and females and for head and body characters of bees also show incomplete congruence. Studies such as these should give information on the "reality" of currently accepted patterns of relationship and also may help shed light on basic problems of development. Present thinking leads to the assumption that systems of relationships based on adult characters will be essentially the same as those based on immature stages or alternate generations. This is an aspect of development which is poorly understood; in addition, it is not certain whether the genetic code functions cyclically or in different ways in cells at different levels of ploidy.

There seems to be no theoretical reason why there *must* be complete congruence among estimates of relationships based on characters from different developmental stages or on characters from different organ systems of the same stage. Thus, for highest information content and predictive value, specialized taxonomies designed for optimal usefulness under restricted conditions could be created. The day may be at hand when, instead of saying "mammal taxonomy" or "butterfly taxonomy," we will discuss "adult mammal taxonomy" or "pupal butterfly neurotaxonomy." In a taxonomy based on ecological requirements, whales will be more closely related to sharks than to bears. Such a relationship is no more or less "true" or "natural" than the classical one; it is merely based on different attributes. Special systems would, of course, be created on demand—not in expectation of need, as today's taxonomies are. What sort of taxonomy is desirable depends upon what one wishes to use it for. Ecologists have used special taxonomies (such as that of Raunkiaer) for many years. In dealing with a multiplicity of special taxonomies, it is obvious that the cre-

ation of structures of formal names should be avoided.

It is probable that some type of mean relationship will be utilized as a basis for a general taxonomy giving estimates of overall similarity. This presumably would provide estimates of evolutionary divergence, but the actual parameter being estimated is difficult to specify. If it were possible to compare directly the nucleotide sequences forming the entire genetic code of two organisms, would this be a "true" measure of evolutionary divergence? We think not—the code cannot be considered without its translation. Whatever kind of sampling is used as a basis for new general taxonomic systems, it appears likely that our current systems, based mainly on the external features of adult forms, will seem warped in comparison.

### The Species Problem

One of the most widely accepted ideas of population biology is that higher animals tend to occur in rather well defined clusters called species. Various theoretical definitions of species have been attempted, and most of those accepted by modern evolutionists make some statement about reproductive isolation between, but not within, the clusters. In older definitions, assumptions concerning the occurrence or non-occurrence of interbreeding are implicit. Special definitions such as those of paleontology reflect special problems. The details of such definitions doubtless are familiar. Botanists, on the other hand, have not always found such seemingly well-delimited clusters. It is commonly admitted that species in certain groups of plants simply are not as "good" as those in other groups. In some families the usual terminology may be difficult to apply at the species level (16); in others, "species" may be well marked but higher categories may be difficult to define (17).

Contrary to widely held opinion, the situation in zoology may not be very different from that in botany. In well-investigated groups such as the nearctic butterflies, the distinctness of clusters has been vastly overrated (18). It appears that the idea of preponderance of good species in animals is a generality without foundation—an artifact of the procedures of taxonomy. These procedures require that distinct clusters be found and assigned to some level in a

hierarchy—subspecies, species, subgenus, genus, and so on. Thus, we have the fruitless arguments over whether or not a species or subspecies is "good." Interpolating additional categories (for example, superspecies) has not solved the logical problem; it has merely obscured it. The basic trouble seems to be confusion concerning the evolutionary importance of barriers to gene flow and the actual or potential utility of these barriers as a criterion in establishing a taxonomic system.

Perhaps the most unfortunate aspect of the so-called biological-species definition is the need to estimate the interbreeding potential of allopatric entities. Laboratory tests are not considered definitive. For instance, *Peromyscus leucopus* and *P. gossypianus* will hybridize in the laboratory, but where they occur together naturally in the Dismal Swamp of Virginia they remain distinct. On the other hand, laboratory hybrids between northern and southern populations of *Rana pipiens* do not develop properly, although if intermediate populations became extinct and the terminal ones approached one another naturally, selection *might* alter them so that they would interbreed freely on meeting.

There seems to be an element of crystal-gazing in the idea of potential interbreeding. First, the events at a hypothetical meeting must be predicted. Then, if the formation of hybrids is postulated, the fitness or viability of the hybrid population must be estimated. It need hardly be said that fitness and viability are parameters difficult to estimate in a closed laboratory population of *Drosophila*, let alone a hypothetical hybrid population. As Mayr (19) points out, unpredictability characterizes both large- and small-scale evolutionary events. These difficulties might be partially circumvented by redefining the biological species so that laboratory tests become definitive. However, the problem of cutting a continuum of different degrees of inter-fertility would remain, and the amount of work required to delimit even a single species would be prohibitive. It seems clear that the biological-species definition never has been operational and never will be (20).

A serious problem facing population biologists is the necessity for developing mathematical methods of usefully describing the relationships observed. The ultimate test of a mathematical model is how well it describes a situation in nature; unfortunately, our current

models are of rather uneven performance. Attempts to improve them have taken somewhat diverse paths in different fields; for instance, population ecologists have been exploring applications of information theory with rather interesting results. However, the mathematically inclined population biologists often accept badly formulated concepts of taxonomists as facts. For example, they study "species in competition" when, at most, only individuals can compete. This unfortunate tendency of some nontaxonomists to treat species as entities reaches its naive extreme in papers on topics such as "the embryology of the monkey" or "the physiology of the frog." The partially indeterminate results of Park's sophisticated work (21) on two kinds of competing *Tribolium* beetles clearly show the dangers of treating "species" as units. After a number of generations at high temperature, the surviving individuals were of one kind; at low temperatures, the survivors were of the other; at intermediate temperatures, the results varied from experiment to experiment. It is likely that, as Park suspected, the genetic variance among the beetles (all of the same kind) used to start the various experiments is one of the factors causing the indeterminacy at intermediate temperatures (22). *Tribolium confusum* is not an entity, it is a taxonomic concept.

The term *species* should be retained only in its original, less restrictive sense of "kind." There seems to be no reason why quantitative methods should not be used to study phenetic relationships (those based on similarity rather than imagined phylogeny) at what we now loosely call the species level. These studies may reveal clusters of populations, and, where convenient for communication, these clusters may be given formal names. Their genetic relationships, when known, can be employed as characters but will not be involved in category definition. We recognize that changes which affect interbreeding are phenetic, and thus they may be used along with other features of the organism as characters in a quantitative comparison.

Recently Ehrlich (18) compared 13 male individuals of checkerspot butterflies (*Euphydryas editha* and *E. chalcidona*) on the basis of 75 characters of their external morphology, genitalia, and color pattern. Both the relationships of the individuals with each other (the *Q*-matrix) and of the characters (the

*R*-matrix) were computed, with product-moment correlation coefficients as the measure of similarity. Two primary clusters were discovered in a search for structure in the *Q*-matrix—*E. editha* (ten specimens) and *E. chalcidona* (three specimens). *Euphydryas editha* and *E. chalcidona* occur together in many areas, but in these places intermediate individuals are unknown. Two of the individuals in the study came from a population which, on the basis of classical taxonomic procedure, could not be assigned positively to one "species" or the other.

The correlation study placed them as a distinct subgroup of the *E. editha* cluster. The remaining eight *E. editha* individuals clustered according to their overall similarities, not their populations of origin. As a test of the "reality" of the pattern of relationships observed in the original *Q*-matrix, additional *Q*-matrices were calculated on the basis of different subsets of the 75 characters. Examination of these *Q*-matrices based on different character combinations showed that in eight out of nine matrices the correlations among the *E. chalcidona* specimens were all higher than any *E. chalcidona*-*E. editha* correlation. Despite the inadequate number of characters (all but two *Q*-matrices were based on less than 60) and the rather crude methodology, the same gross pattern of relationships emerged repeatedly. We have here the essence of an operational definition: several operations (measurement of different sets of characters) ascribe the same value to the variable (in this case the *Q*-matrix). The clusters thus operationally defined could be placed at any desired level in a taxonomic hierarchy. It seems possible that studies such as this of relationships of individuals may lead eventually to the development of a genetics of populations oriented toward genotype, rather than gene, frequencies (23).

This general approach to the "species problem" would permit relaxation of the rigid hierarchic structure of taxonomic categories which requires that all entities be arbitrarily assigned to some level (deme, subspecies, species, and so on) by the complex system of guesswork outlined above. We may now modify our system to permit more accurate and thus more useful description of the intricate relationships of organisms. Just as physics has been divested of the burden of absolute time, so biologists can be freed from the

necessity of imposing a platonic structure on nature. That this imposition on nature has been long recognized is shown by the following quotation from a work published in 1872 (24).

"It is of interest to note that in Aristotle the difference between plants and animals is already touched upon. . . . Regarding the nature of some marine growths one may be in doubt whether they are plants or animals. . . . Even the ascidians, says Aristotle, may properly be called plants since they give off no excrement. . . . One sees that Aristotle fell into the same error as almost all moderns. The term 'plant,' which came to us as a part of our language, was interpreted as a term that must correspond to a class of naturally occurring entities. The same thing has happened to later workers with respect to the term 'species.' Instead of investigating whether there exists in nature anything that is unchangeable and circumscribed and that corresponds to this term, and then, in the absence of such, to allow nature her liberty and only artificially to assign a meaning to it that corresponds to the current state of knowledge, one simply assumed that one was compelled to consider the word as a symbol for one of nature's secrets, a secret that one might still hope to unveil."

### Mendelian Populations and Gene Flow

In contrast to the "biological species," the concept of Mendelian population (in a restricted sense) may have some merit. Studies of local populations of newts (25) and butterflies (26) have shown a remarkable lack of interchange of individuals among various parts of the colonies. Similar situations have been noted in studies of other organisms. It seems likely that we will find in these organisms that entities which may conveniently be called Mendelian populations do exist, but that they are smaller than one would have expected on the basis of casual assumptions about gene flow. The whole problem of the movement of genetic information among evolving units has been given very spotty study. Here is an area where botany and zoology differ remarkably in a number of respects, but again the difference may be more apparent than real. Botanists have for a long time accepted the fact that plant "species" and even "genera" may hy-

bridize, and they have recognized the importance in evolution of even rare exchanges of genetic material. The concept of "introgressive hybridization" has become widely used as an explanation of taxonomic systems. It is only very recently that some zoologists have admitted that something more important than taxonomic problems is involved when individuals intermediate between accepted clusters are detected. Epling and Catlin (27), among others, have shown how our frozen concepts and terminology may have kept us from seeing important genetic relationships in natural populations. Perhaps some such neutral term as *evolutionary unit* might be used in evolutionary studies, the term *species* being reserved for pragmatic uses only, as mentioned earlier.

### Community Ecology

When we turn from the level of the single evolutionary unit to associations of species in nature, we find that no field of population biology has suffered as severely from hardening-of-the-concepts as community ecology. In spite of clear and well-reasoned arguments by a number of botanists (28), one still finds discussions, obviously taken very seriously, about succession, climax, biome, flora, and so on. Even if it be granted that these terms are clearly understood by specialists in the field and that they have a certain practical value, surely they are misunderstood by workers in other areas of population biology. The literature is still permeated with terms such as *chaparral*, *tundra*, *spruce-moose biome*, *dominant*, *Madro-Tertiary flora*, and *Holarctic fauna*, which are thought to be biologically meaningful. At best they are superficial descriptions of places and situations. At worst they obscure the intricate patterning of nature and lead to a mystical approach to problems of community structure, community migration, evolution of communities, and the like. *Tundra* is perfectly acceptable as a descriptive word meaning something like "treeless northern plain"; it is not acceptable as a general biological entity (once one tries to define *tundra* as more than "the absence of large trees in certain climatic regions," one encounters great difficulties) (29).

Consider also the so-called "redwood flora," which is commonly thought to be a clearly distinct grouping of forms which can be traced well back into the

Tertiary. Much effort has been spent in tracing its "migrations." Nevertheless, its floristic composition has changed drastically through time, and each entity (each interbreeding population of individuals) has had an evolutionary history dependent on, among other things, its own genetic processes. Concepts of floristic or faunistic sources or centers of origin can only obscure the genetic processes and confuse the evolutionary histories. As Mason has said: "Because of the differences in genetic constitution and in physiological capacity between the various species of the community, and because of the operation of different genetic mechanisms it is hardly to be expected that any two or more species of such a community will follow precisely the same historical pattern even for a relatively short time." That "species" occur in the same community implies to many biologists that they share the same general "adaptations" to the environment of that community. It should be obvious that the only unity such a community possesses is based upon the overlapping ranges of tolerance of the individual organisms for certain factors of the environment.

### Adaptation and Population Fitness

As everyone knows, one of the less fortunate results of the publication of the *Origin of Species* was the subsequent fanatical search for "adaptations." At one time it was asserted that flamingos were pink because this gave them cryptic coloration when they flew across the sunset! Few nonevolutionists realize that the term *adaptation* is one of the least understood and most misused in population biology. The entire "adaptation" approach to evolution needs re-examination. Natural selection has become widely recognized as an a posteriori description of events (differential reproductive contributions of different genotypes greater than or less than one would expect from sampling error). A few authors persist in considering selection to be some sort of weight or burden which can be lifted from the back of a poor struggling population. This latter view is most evident in works on human evolution (30), where we find that man has finally been freed from the dire load of natural selection. On the other hand, adaptation (31), the result of natural selection, has retained rather tenaciously its status as a "thing."

It is difficult to see much merit in

the term, as all known organisms are the result of more than a billion years of selection and are therefore "highly adapted." At best, "adaptation" is used in vague comparisons of the way of life of an organism with the extent of usable habitat (parasites are more "narrowly adapted" than omnivores). At worst, it is often a device for inciting wonder at the diversity of vertebrate forelimbs, bird beaks, or pollination mechanisms (one is reminded of Lincoln's remark that his legs were, miraculously, just long enough to reach the ground). In the former instance, once the relationships (preferably quantified) have been described, the comment on adaptation seems extraneous. Under present conditions elephants cannot survive in as many places as human beings; does it really help to add that "elephants are more narrowly adapted than people"? The continuing feeling that adaptation is some phlogiston-like, beneficial substance that a population may possess in varying quantities has been at least partially responsible for the difficulties (mentioned earlier) which theorists have had in coming to grips with the problems attendant on the question of population fitness.

In highly specified competition experiments, such as those with *Tribolium*, or in comparable population-cage experiments in which the standards of "success" are carefully stated (7), population fitness can be given meaning. In a provocative paper on possible game-theory approaches to evolutionary problems, Lewontin (3) suggests using the one-generation probability of survival as a measure of population fitness and briefly outlines experiments to test various strategies against this standard. At present it is difficult to visualize how such approaches can be applied to investigations of populations in the field. In most cases (if not all), expressions such as "populations with structure *X* are more fit than those with structure *Y*" or "species *A* is more fit than species *B*" are meaningless.

### Evolutionary Theory

Finally, consider the third question posed earlier: "What accounts for the observed patterns in nature?" It has become fashionable to regard modern evolutionary theory as the *only* possible explanation of these patterns rather than just the best explanation that has been developed so far. It is conceivable,



even likely, that what one might facetiously call a non-Euclidean theory of evolution lies over the horizon. Perpetuation of today's theory as dogma will not encourage progress toward more satisfactory explanations of observed phenomena. As Hardin puts it (9): "There is always a considerable lag in teaching. Many years ago it was remarked that the Military Academy of St. Cyr in France trained its students splendidly to fight the battles of the last war. So it is in science teaching; we too often train our students to fight battles already won, or equip them with weapons that no longer fire." We hope that population biologists will begin to break the bonds of tradition which have thus far strongly inhibited the development of a rigorous and unified approach to problems at the highest level of biological organization.

### Summary

In summary, then, we would like to suggest that in broad investigations of the patterns of interaction and relationship among organisms the artificial and stultifying fragmentation of population biology into divisions such as taxonomy, population genetics, and ecology should be ignored. Care also should be taken to scrutinize current concepts such as "species," "niche," and "community." If some emergent patterns seem to correspond to a great degree with these concepts, then the concepts may be given operational definitions and the labels should be retained. If there is no such correspondence, then the concepts will have outlived their usefulness and should be discarded.

The basic units of population biology are not communities, species, or even populations, but individual organisms (32). In populations, variation, growth, genetic equilibria, selection, behavior, and so on are not "things" but relationships. Therefore, what is of interest in population biology is the pattern in which organisms are related in space and time (33).

### References and Notes

1. G. A. Radnitsky, *Behavioral Sci.* 6, 153 (1961). Until and unless the Whorfean hypothesis can be shown to be incorrect, it is very important to preserve the diversity of human languages.
2. G. E. Hutchinson and R. H. MacArthur, *Am. Naturalist* 93, 117 (1959).
3. R. C. Lewontin, *J. Theoret. Biol.* 1, 382 (1961).
4. G. E. Hutchinson, *Cold Spring Harbor Symp. Population Biol.* 22, 415 (1957).
5. H. L. Mason and J. H. Langenheim, *Ecology* 38, 325 (1957).
6. H. L. Mason, *ibid.* 42, 158 (1961).
7. J. A. Beardmore, T. Dobzhansky, O. H. Pavlovsky, *Heredity* 14, 19 (1960).
8. K. E. Boulding, *Conflict and Defense* (Harper, New York, 1962).
9. The gaucho example is taken from Garrett Hardin, *Am. J. Psychiat.* 114, 75 (1957). Hardin is a pioneer in applying Whorf's ideas to biological problems; see, for example, his remarkable paper "Meaninglessness of the word protoplasm," *Sci. Monthly* 82, 112 (1956).
10. References to the literature of numerical taxonomy can be found in P. H. A. Sneath and R. R. Sokal, *Nature* 193, 855 (1962).
11. E. Anderson, *Introgressive Hybridization* (Wiley, New York, 1949).
12. See C. H. Waddington, *The Strategy of the Genes* (Allen and Unwin, London, 1957), and I. M. Lerner, *Genetic Homeostasis* (Wiley, New York, 1954), for discussions of this general problem.
13. The word *character* is used here in the idiom of the numerical taxonomist to mean any feature which varies in the group under study.
14. F. J. Rohlf, personal communication.
15. C. D. Michener and R. R. Sokal, personal communication.
16. W. H. Camp, *Brittonia* 7, 113 (1951).
17. R. W. Holm, *Ann. Missouri Bot. Garden* 37, 377 (1950).
18. P. R. Ehrlich, *Systematic Zool.* 10, 167 (1961).
19. E. Mayr, *Science* 134, 1501 (1961).
20. G. S. Myers, *Systematic Zool.* 9, 338 (1960).
21. T. Park, *Physiol. Zool.* 27, 177 (1954).
22. I. M. Lerner and F. K. Ho [*Am. Naturalist* 95, 329 (1961)] have shown that genotypic differences in competitive ability exist in *Tribolium confusum* and *T. castaneum*, supporting this hypothesis. Further discussion may be found in I. M. Lerner and E. L. Dempster, *Proc. Natl. Acad. Sci. U.S.A.* 48, 821 (1962).
23. We do not mean genotype frequencies with reference to one or two loci only. Again, the loss of detail in translation from genotype must be accepted.
24. J. V. Carus, *Geschichte der Zoologie* (Munich, 1872), p. 31. We are indebted to R. G. Schmieder for translating this passage and bringing it to our attention.
25. V. C. Twitty, *Science* 130, 1735 (1959).
26. P. R. Ehrlich, *ibid.* 134, 108 (1961).
27. C. Epling and W. Catlin, *Heredity* 4, 313 (1950).
28. H. L. Gleason, *Torrey Bot. Club Bull.* 53, 7 (1926); H. L. Mason, *Ecol. Monographs* 17, 201 (1947); R. H. Whittaker, *Botan. Rev.* 28, 1 (1962).
29. P. R. Ehrlich, *Entomol. News* 69, 19 (1958).
30. The following statement of W. La Barre [*The Human Animal* (Univ. of Chicago Press, Chicago, 1953), p. 144] is an example: "man is no longer subject as an individual to the full effects of natural selection and to the other evolutionary mechanisms which operate on wild animals." La Barre's book is, in most respects, excellent.
31. We are not considering physiological adaptation in this discussion. Adaptation clearly is a panchreston in Hardin's sense [*Sci. Monthly* 82, 112 (1956)].
32. In this article we have chosen not to discuss in detail how "individual" may be defined. Here again taxonomic concepts have biased our thinking badly. The idea of an individual connotes uniqueness. If a plant reproduces vegetatively and the various parts become separated to form a clone, are we dealing with one individual or with several? The problem as phrased is insoluble. An individual is a machine (or set of operations) programmed in advance to do a particular thing. A group of genetically identical organisms is one individual reproductively. Ecologically these organisms represent a population of individuals with different epigenetics. In an instance such as this, if historically we had begun to think about biology in ecological rather than taxonomic terms we would now deal with biological "facts" very differently.
33. We have discussed the ideas presented in this article with numerous colleagues at Stanford and elsewhere and have presented them in a series of seminars at several institutions. We have been particularly stimulated by the views of H. V. Daly and H. L. Mason (University of California, Berkeley), N. H. Russell (Arizona State University), and R. R. Sokal (University of Kansas). Daly and Sokal, C. D. Michener (University of Kansas), and W. R. Briggs and D. Kennedy (Stanford) were kind enough to read and criticize the manuscript. A long discussion with K. W. Cooper (Dartmouth Medical School) on "What is population biology?" was our immediate incentive for writing the article.