Biological Adaptation: Aptitudes and Acclimatization

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Perhaps no term in the biological and social sciences has such varied, vague, and equivocal meanings as ADAPTATION. Part of this difficulty has been one of nomenclature and definition. Dubos (1965a: 56) indicated " acclimatization, acclimation, adaptation, and habituation are often used interchangeably because the processes these words are supposed to denote usually overlap and because the fundamental mechanisms involved are poorly understood." Prosser (1958, 1964) was among the most prominent in providing a conceptual framework for dealing with adaptation, and in particular "physiological adaptation." Eagan (1963) and Folk (1966) examined the problems of nomenclature, and both suggested that adaptation be kept as a generic (note not genetic) term. There has been a widespread tendency, especially in physical anthropology, to consider adaptation as genetic adaptation, with the implication that natural selection is involved. (Dobzhansky (1968) attempted to clarify the concept of "adaptedness." He recognized that adaptation could refer to both individuals and populations, and he delineated adaptedness, fitness, and persistence; all were applied at the population level. Most nongeneticists and nonanthropologists do not consider adaptation primarily as populational but rather as individual, although it is recognized that individual adaptation can contribute to population adaptation (McCutcheon 1964). I have recently proposed a conceptual framework in which adaptation is used in a generic sense to apply to all levels of the biological and social hierarchy (Mazess i.p.). This report will outline some aspects of that framework and will discuss two aspects of individual adaptation, aptitudes and acclimatization, which are often confused with population adaptation.

THE MEANING AND REFERENCES OF ADAPTATION

Adaptation is usually defined as the ability to survive, function, and reproduce (McCutcheon 1964; Prosser 1958, 1964; Dobzhansky 1968; Baker 1966), without really noting, as does Lasker (1969), that the term is relative. Survival, maintenance of functioning, and reproduction, however, are mere existence; adaptation, if it is not to be teleological, must mean more than this. The essence of environmental adjustments deemed adaptive seems to be that they are considered **RELATIVELY** advantageous, beneficial, or meritorious, or that they are to a degree necessary. Survival is somewhat equivalent to necessity, and maintenance of function and reproduction are examples of relatively beneficial properties; necessity and relative benefit are, however, more general categories than those of the conventional definition of adaptation, and they are particularly useful if one is to deal with adaptation at suborganismic levels, for example, molecular adaptation.

Adaptive significance, in terms of relative benefit or necessity, can be applied to all levels of biological and social hierarchies, but the notions of what is beneficial and what is necessary will vary with the referential level. A great deal of confusion in biological anthropology has resulted from trying to apply notions of population adaptation, such as selection, to individual adaptation or from extrapolating from individual adaptation to populations. The biological hierarchy to which adaptive evaluations might be applied can be conceived as increasing in organizational complexity:

1. Physicochemical
2. Cellular
3. Organ systems
4. Organisms (individual)
5. Population
6. Ecosystem

Each succeeding level of this hierarchy forms the dominant environmental focus of the preceding level; the environment of the cell is the organ, and that of the population is the ecosystem.

At each referential level different criteria, or "adaptive domains," are used in assessing, benefit and necessity. At the physicochemical, cellular, and organ system levels, the major emphasis is on homeostasis. For individual organisms several major aspects of living are considered adaptive domains:

1. Reproduction survival, reproductive advantage
2. Health — morbidity, mortality, disease resistance

3. Nutrition — nutrient requirements, utilization, and efficiency
4. Nervous system — sensory, motor, and neural function
5. Growth and development — physical and mental progression in rate and attainment
6. Resistance and crosstolerance — generalized stress resistance
7. Physical performance — exercise and motor abilities; skills
8. Affective function — happiness, tolerance, sexuality
9. Intellectual ability — learning, expression

Traits or responses that are beneficial to one or more of these domains are usually considered adaptive to the individual. These domains are also pertinent to the definition of a "stress." Stress is not merely a large deviation of an environmental factor but a deviation that has a significant actual or potential effect on one or more adaptive domains. Much of the study of human adaptability consists of extrapolation from individual to population adaptation, and hence these domains are of primary import to that study. At the population level the emphasis is upon assessing benefit and necessity in relation to size, density, distribution, composition, and organization of the population. Selective advantage, fitness, and persistence (Dobzhansky 1968) become important at this level, at least for the genetically oriented biologist. Unfortunately, population adaptedness is almost impossible to evaluate directly in human populations, and many of our inferences are based on individual adaptation.

Acclimatization Responses

Folk (1966) has presented an extensive discussion of the term ACCLIMATIZATION and has shown its varying and often disparate usages. There has been a tendency by some ecologists and others to use acclimatization to describe adjustments made by a species over the course of several generations, or in a way nearly synonymous with " genetic adaptation," with the assumption of evolution and adjustment through natural selection. However, Folk showed that this is a quite restricted and unusual use of the term, and that an earlier and more frequent use of acclimatization is in a general sense to denote the adjustment of an organism to its environment. It is this general sense of the term, common to physiology, that is supported here.

Eagan (1963), following Prosser (1958) and Hart (1957), proposed that acclimatization refer to adjustments to an environmental complex, presumably a multistress environment, and included seasonal and cli

matic changes. The term ACCLIMATIZATION was reserved to deal with adjustments to a single environmental factor, as might be the case in controlled experiments, or even presumably in a natural environment with a single dominant stress (that is, a natural experiment). As Folk (1966: 24) indicated, there is no real priority for this distinction — and more often than not, the terms ACCLIMATE and ACCLIMATIZE are used interchangeably. However, the distinction may be worth maintaining — if only to demonstrate some respect for attempts at systematizing nomenclature. In the following I will use the term ACCLIMATIZATION, but the content applies equally to ACCLIMATION.

It is fairly clear that the widest use of acclimatization is in reference to the adjustments of individual organisms to the environment. It is usually neither organ systems nor populations that are thought to acclimatize, but rather the individuals within a population. The acclimatization responses of a population are aggregates of the adjustments of individuals. Moreover, acclimatization refers to responses, and hence to phenotypically plastic adaptive traits — that is, to those characteristics of an individual that change in response to environment. It is rather unfamiliar to talk of phenotypically stable characteristics when dealing with acclimatization. For example, adult stature or eye color would not be considered acclimatizational, but adjustments of heart rate, skin color (tanning), or even attention span would.

Phenotypic characteristics can be usefully categorized as structural (morphological), functional (physiological), and psychobehavioral. Ac climatization can be described using these modifying terms where appropriate, or using some equivalent terms such as HABITUATION and ACCOMMODATION.

1. STRUCTURAL ACCLIMATIZATION: changes of histology, anatomical relationships, morphology, and body composition. An example would be muscle hypertrophy, or change of fiber type, in response to exercise.

2. FUNCTIONAL ACCLIMATIZATION: changes in organ system function, which may be further subdivided into:

a. PHYSIOLOGICAL ACCLIMATIZATION: this is the most common meaning of acclimatization. Examples are shivering in cold and sweating in heat.

b. NEUROLOGICAL ACCLIMATIZATION OR HABITUATION: changes of sensory function and neural control. Habituation has usually meant diminutions of normal neural responses, for example, decreases of sensation such as pain. Other pertinent subcategorizations of neurological acclimatization include peripheral versus central and specific versus generalized (Eagan 1963).

3. PSYCHOBEHAVIORAL ACCLIMATIZATION: changes of complex neural functioning involving control and alteration of activity, and of affective and cognitive states. Several subclasses are useful:

a. AFFECTIVE ACCLIMATIZATION, OR ACCOMMODATION: the latter term, while often used more generally to specify adjustments, frequently has the connotation of an affective shift. Examples might be sublimation or personality changes.

b. COGNITIVE ACCLIMATIZATION, OR LEARNING: changes in complex perception and cognition, with obvious direct influences on behavior.

C. BEHAVIORAL ACCLIMATIZATION: shifts in sets of behavioral correlates, or activity patterns.

Within this framework, acclimatizational responses are systematically classified. Regardless of acclimatizational categorization, however, the adaptive significance of the response must be demonstrated if an assess ment of acclimatization is really to have purchase. It is not enough to demonstrate that a response occurs in relation to a single or multiple stress environment; it is mandatory to show that the response is of at least potential benefit. Because acclimatization deals essentially with responses of individual organisms, assessment of benefit is made in adaptive domains at the individual level.

APTITUDES

In the previous section it was pointed out that acclimatization and acclimation refer to responses of individuals, and hence to phenotypically plastic characteristics. The examination of adjustments to the environment must also deal with traits having stable phenotypic expression; there has been no scientific term in general use to describe these traits. APTITUDE, in the sense of suitability, ability, or capacity in relation to environment, is an appropriate term, and I believe that it would prove useful if accepted. One of the great misunderstandings and sources of equivocation in adaptability studies derives from the hiatus in terminology for relatively fixed individual characteristics. The terms ADAPTATION and PREADAPTATION are sometimes used to describe these aptitudes; as a consequence, there has been a tendency to mistake them for genetic adaptations. Aptitudes, like acclimatizational responses, are phenotypic characteristics, and the genetic basis and heritability of both must be determined prior to ascription of genetic adaptation.

Just as acclimatization may be categorized as structural, functional, and psychobehavioral, so may aptitudes.

1. STRUCTURAL APTITUDES: histological, anatomical, morphological, and body composition characteristics. An example would be large muscle mass in relation to exercise or dark skin color in relation to insolation.
2. FUNCTIONAL APTITUDES: organ system functions.
a. PHYSIOLOGICAL APTITUDES: an example would be a high cardiac output in exercise above the level associated with training (which is acclimatizational). Environmental physiologists who have compared different ethnic groups have tried to define the functional aptitudes of these populations.
b. NEUROLOGICAL APTITUDES: differences of sensory function and neural control, for example, visual acuity.
3. PSYCHOBEHAVIORAL APTITUDES: differences in behavioral patterns, activity levels, and affective and cognitive states. For example, a high intelligence quotient could be considered a cognitive aptitude, in contrast to the process of learning, which is cognitive acclimatization.

As is the case with acclimatization, the adaptive significance of aptitudes must be shown in terms of potential benefit or necessity at the individual level of adaptive domains.

Information and Misinformation

The study of adaptation, and in particular of human adaptation, often has been denigrated as errorprone and speculative, and unfortunately this opprobrium is frequently appropriate. Three striking problems are immediately evident.

First, there is confusion with regard to the concepts and nomenclature of adaptation. There has been lack of specificity as to the' level of organization referred to when examining adaptation, and in human studies there has been egregious equivocation between individual and populational adaptation. One consequence of this equivocation has been the tendency to view genetic and even aptitudinal differences among populations as being not only genetic adaptation but evidence of the operation of natural selection. Aptitudinal differences among populations may, of course, not have a firm genetic basis. As should be clear from preceding sections, aptitudinal or acclimatizational differences among populations which do have a firm genetic basis can be considered genetic adaptations regardless of the evolutionary mechanism by which they arose. Not all evolutionary changes are adaptive, and not all adaptive evolutionary changes arise through natural selection.

Second, the study of adaptation has been marred by the postulation

of erroneous relationships between characteristics or responses and environmental factors. For example, alterations of growth may be ascribed to a climatic stress, but they may actually be due to nutrition; metabolic alterations may be due to climatic factors rather than the nutritional stress to which they are ascribed. Many of these speculative relationships have been postulated on the basis of ecogeographical character gradients, or clines (Mayr 1956). In anthropology such relationships have been taken as evidence of man's climatic and nutritional adaptation (Newman 1953; Baker 1960; Schreider 1964). Ecogeographical gradients are useful for suggesting lines of investigation but should not be taken as evidence of an environmental relationship, and certainly not as evidence of adaptive import.

The third problem is in fact that of adaptive import. One of the fundamental errors is the ascription or denial of adaptive benefit without investigation or demonstration of a relationship with any adaptive domain. It is in this area that teleology appears to encroach on scientific caution. One could argue that mere survival, especially in a stressful environment, is evidence of adaptation (Baker 1966), and hence the variations among populations, especially the differences existing in stressed populations, might be taken as adaptive. For example, barrelchestedness at high altitude and a low ratio of surface area to weight in cold have been broadcast as adaptive for certain human populations without any real evaluation of their functional import. I have previously criticized the tendency to deal with highaltitude populations in this way (Mazess 1970), and the same criticisms apply to other stressed populations.

APTITUDES, ACCLIMATIZATION, AND HUMAN ADAPTABILITY

The description and categorization of characteristics and responses providing adjustment to environmental stress, with consequent benefit, are indeed formidable tasks. Comparisons among individuals, and among populations, are needed to delineate the nature and extent of environmental adjustments. Among the parameters of interest are:

1. TIME COURSE: period of exposure requisite to development of the adjustment, and also the effects of rate of exposure and of intermittent exposure.

2. REVERSIBILITY: many responses to stress, particularly those occurring during the developmental period, may be irreversible or only partially reversible (Brauer 1965). This also raises the possibility that a

beneficial characteristic developed during childhood may prove maladaptive yet irreversible in the adult.

3. CRITICAL AGES: are there critical times, for example, during growth, when certain characteristics or responses may develop in response to stress? Developmental physiological acclimatization seems to be very important in determining peripheral responses to cold and in exercise and ventilatory performance in hypoxia.

4. GENETIC BACKGROUND: the heritability of aptitudes and acclimatizational responses needs elucidation so that inferences with regard to genetic adaptation may be made. Are there genetic differences within populations and among populations?

Examination, in detail, of aptitudes and acclimatization will provide one basis for more general formulations with regard to adaptability. The type of individual adaptation to different stresses, as well as population differences, will then become much clearer. For example, with regard to human climatic adaptations, it seems that shortterm reversible physiological acclimatization is of paramount importance in the sense that such acclimatization provides the primary adjustment for individuals within *any* population or within the species. This is followed by longterm and developmental physiological acclimatization. Differences among individuals, and populations, of comparable age and sex may be in part attributable to the large variance in aptitudes. The genetic basis for differences in aptitudes and acclimatization appears minimal, and genetic adaptation does not appear to account for much of the adjustment of humans to climatic stresses. A somewhat different pattern appears evident with regard to human adaptation to other stresses, such as disease.

In addition to such generalization with regard to adaptive strategies, there is a need for examination of and generalization about the relationships among adaptive domains. Because adaptive significance is relative to operationally defined domains, it becomes important to achieve some precision in this area, specifically, in the formulation of a relatively coherent set of priorities among the domains. The construction and elaboration of a theory of human adaptability depends upon both the biological documentation and the socialpsychological documentation of valuational criteria.

Adaptation and the Optimal Environment

Adaptation is essentially valuational, despite all disclaimers to the contrary, and assessment of adaptation involves judgments and decisions

as to benefit, good, or necessity. The contemporary revival of interest in adaptation over the past decade is occurring, interestingly enough, after almost a century of eschewing valuation in science, and at a time when there is widespread acceptance of the notion of an "objective reality." There are implications of this apparent contrast for the study of human adaptability, and vice versa. If human adaptability is to remain viable, we must ask to what extent valuation of environmental adjustments may be dealt with objectively. Success in this area will depend upon the operational precision and accuracy in exploring adaptive domains and assessing adaptation. Dubos (1965b) has pointed out the importance of viewing models and scientific knowledge as describing regularities rather than realities, and there is every reason to presume that the regularities in valuation of environmental adjustments may be studied scientifically.

But is the study of human adaptability of any value? Dubos (1965b) suggests that the role of biology is to provide the essential information, describing biological potentials and limitations, within which man formulates goals and makes personal decisions. Adaptation provides analogous information on the valuation of biology in relation to environment; it is not mere description of the regularities of response, but of the regularities in how men value these responses. Human goals with relation to environment have been variously expressed, from a Garden of Eden to Utopia. The formulation and creation of an optimal environment requires more than a listing of environmental likes and dislikes; it is the knowledge of human adaptability that forms the basis for this task.

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