1

Efficiency, effectiveness, perfection, optimization: their use in understanding vertebrate evolution

C. GANS

1.1 HISTORY

Since before Aristotle, naturalists have noted that organisms are more or less matched to the environments they occupy. They also noted imperfections in that some organisms, individuals and species appeared obviously mismatched to the environment they then occupied.

Around the end of the eighteenth and start of the nineteenth centuries, these observations led to the wide array of hypotheses in Idealistic Morphology. Underlying many of these views was the idea that tissues and organisms were trying to express an innate pattern, in some schools referred to as the archetype. It was assumed by some students that the perceived world actually represented but a variable expression of this innate plan. Some species represented a closer fit to the underlying pattern and with this gave a better indication of the nature of this archetype. Hence, a major task of comparative biology was the deduction of the true archetype from the diversity of surviving species.

The theory of natural selection and its corollaries has provided a more appropriate explanation both for the kinds of environmental matching ... and for the seeming degrees of mismatching to the environment. Still, for various reasons, some biologists and philosophers even today keep searching for alternate explanations for this matching and mismatching. Alternative hypotheses (with which I do not agree) for the existence of mismatching are, for instance, the Spandrels of Saint Mark hypothesis, according to which adaptation (curiously defined) does not derive from natural selection. Another is the concept of evolution by punctuated events in which an array of individuals or species exemplifying different phenotypic states arises and only those lines that encounter an environmental site matching their particular condition will survive. Alternative hypotheses for the existence of matching included the concept (often ascribed to Cuvier) that one could reconstruct an entire fossil skeleton by informed analysis of a single bone. A more recent version is seen in the claim that study of its morphology might be sufficient to reconstruct the habits of a poorly known or fossil species. The underlying assumption is that matching should allow derivation of function from structure.

Both the terms matching and mismatching imply extremes of a standard for comparison and its characterization has been the task of this symposium. My viewpoint on this issue overlaps some of the following accounts and is based on (or biased by!) much watching of animals in laboratory and field. It is offered here as a set of standards for comparison applicable to general accounts of this topic, rather than as a set of new discoveries. The mention of vertebrate evolution is incidental to the general argument. Hopefully it will be found correct or at least stimulating for the reevaluation of such topics.

1.2 QUESTIONS AND DEFINITIONS

Terms, such as efficiency, compare at least two states; correctly used they should characterize a continuum. The need for such comparison leads to the fundamental consideration of what we should expect to see. Adherents of the theory of evolution by natural selection must then consider the question of what it is that natural selection may be likely to generate. The answer should lead to a state in which one can establish plausible predictions that may then be subjected to falsification.

However, this approach requires some standardization of the terminology used. To the extent that old terms are being used in a new framework, their existing definitions need to be considered. Such definitions are taken up here so that they may be reconsidered in terms of a biological framework.

1.2.1 Efficiency

Efficiency is a measure of performance relative to a physical or biophysical process or law. It always characterizes an actual performance, relative to an ideal or perfect level. It is independent of purpose and must be applied to a single process at a time. Examples might be the amount of thermodynamically determined heat now existing in body A that can be transferred to body B. Alternatively, the efficiency might characterize the fraction of the amount of heat in body A that can be transformed into mechanical work. In a different sense, it may refer to the number of molecules required to activate an olfactory organ.

1.2.2 Effectiveness

Effectiveness represents a performance directed toward a particular purpose and registers the degree to which this is achieved. It does not necessarily involve a chemical or physical limit (as does efficiency), but rather may involve a combination of physical and other traits. An example for its use would be in evaluating the design of lever system or a gear train intended to generate a particular force or velocity. Another example would be the evaluation of a linkage pattern incorporated in the limb or an animal, facilitating its ability to gallop or to manipulate its food.

1.2.3 Perfection

Perfection represents the best state that is conceivable. It would thus be equivalent to an efficiency of 100%. Obviously, perfection is only pertinent to a particular physical process, i.e. to heat transfer or force transmission. It is obviously the abstract Platonic ideal and, as will be seen below, is hardly pertinent in a biological situation unless one can exhaustively evaluate the mechanically or chemically dissected organism.

1.2.4 Optimum

The optimum represents the best state, but as qualified by a set of limiting (constraining) circumstances. Any claim for an optimum must specify what is being optimized as well as the limiting circumstances which are presumably operative. In the absence of such specification, a claim for optimization only expresses congruence of the observed with the presumed environmental demand without quantifying the closeness of the match or magnitude of selection.

Optima are often applied to circumstances in which there are several partially or completely conflicting factors so that modification of one affects the others. The optimum then represents a condition which is defined as the best overall for the prescribed task.

1.2.5 Adequacy (sufficiency)

Adequacy is a state that meets minimum conditions. These conditions obviously need to be specified in any actual application and the term hence is relative to these. Adequacy does not demand any level of efficiency or effectiveness; indeed it is independent of these. The relation of effectiveness and adequacy may be exemplified on the basis of the record of a college team. The effectiveness of the team may be seen in terms of the number of goals scored or blocked, runs earned or similar statistics. However, for any contest, there will be a victory, representing a terminal datum, based on the team that achieved the highest score. For purposes of the seasonal championship, adequacy only implies being better than was the opposition at that moment. In short, natural selection acts to produce adequate, not perfect, results.

1.2.6 Improvement

Improvement refers to two or more events separated in time. Improvement implies that a particular characteristic or process became modified during this interval and the modification increased its relative efficiency or effectiveness. Improvement also implies that the initial state was imperfectly matched to a purpose and that the modification increased or exceeded the initial level of performance. Improvement often reflects intrapopulational selection or response to changing competitors, prey or predators.

1.2.7 Patterns in evolutionary biology

It is next useful to ask again how these terms apply to the description of biological phenomena (Fig. 1.1). Do the processes of adaptation and speciation allow predictions about the level of effectiveness likely to be observed? Such considerations may be analyzed by a simple reconsideration of processes of evolutionary change.

We know that any presently surviving species must be sufficient for the environment or environments it now occupies. This very obvious statement has sometimes been claimed to result in an adaptationist tautology; however, it remains true. However, persistence of survival can be assessed independently by physiological or structural criteria, for instance, cold-hardiness, tenacity of adhesion vs. maximal wave force. If we wish to make this statement for a form occupying an environment

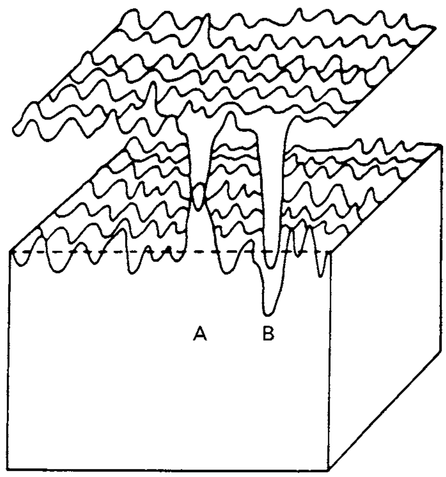

Fig. 1.1. Sketch to permit visualization of the relations between the multiple environmental demands imposed upon animals and the phenotypic state of individuals. The surface of the (lower) block is intended to indicate the multiplicity of components of the myriad related and independent aspects of the environment. The vertical dimension of each segment of the block represents the magnitude of that aspect. The (straight) horizontal line is adjusted to show the mean magnitude of that aspect and the complex surface shows the particular conditions encountered by a particular individual (at one moment in time). The complex top surface illustrates aspects of that individual's phenotype expressed in terms of its capacity to match the environmental demand during a particular interval of time (which may be its life span). [Note that it is impractical to map mean phenotypic response as its position will differ with the magnitude of what is sometimes called the 'factor of safety' for each aspect.] At point A, the momentary environmental demand is greater than the phenotypic capacity. Hence the element is likely to fail. The importance of the failure will depend on the significance of this and related phenotypic aspects to the life of the organism. At point B, the phenotypic aspect is insufficient to match the mean environmental demand. However, the actual demand that the individual encounters is less than this; hence the individual is adequate and the element does not fail. The general scheme indicates how most aspects of individuals are excessively constructed for much of their life history and that this 'excessive capacity' permits behavioral adjustments without failure.

that remains stable over one or more generations, the statement implies that individuals of all sexes and of all ontogenetic stages must be sufficient.

Obviously, the population of any species will show phenotypic variations. The concept of sufficiency does not imply that all phenotypic variants of a population will indeed be sufficient; it only implies that enough individuals will display sufficiency so that the species will be maintained. Whenever the species occupies variable or fluctuating environments, there will be complications, such as populational polymorphisms, but the same general considerations apply.

Every individual organism occupies a multidimensional volume within a parameter space representing aspects that have to be tolerated and those that may be exploited. Different parameter spaces will be occupied by individual members of a species at various times during their ontogeny. The axes of such a space are likely to specify an enormous number of phenotypic states. Examples might be: The maximum torsional strain in a midlevel humerus. The maximum deformation of a contour feather during loading (in the physiological range). The minimum turning radius while flying at a particular velocity. The minimum number of photons needed to activate a visual cell.

The limits of this parameter space are established by the conditions of the environment, both biological and physical. In the general case, each parameter changes continuously in time. Hence, individuals of a species that are marginal in one dimension may survive or not, depending on the time at which they live. This is another way of stating that sufficiency will be relative to the present environmental conditions testing the system.

The organism involved in such a system must grow, during which time their phenotype is transformed into a juvenile phenotype and this into that of the adult. As the transcription of any genotypic instructions is modified by the environment, which is in turn variable, the developmental process inevitably involves (environmentally induced) variations. These likely incur selection, the magnitude of which depends on the closeness of their fit to the particular limits of the volume of selective pressures. The closer the mean phenotype matches a particular limit, the greater the chance that some individuals of the population will be inadequate for that limit. However, an increased factor of safety will likely incur a greater cost in generation and maintenance of a phenotype matching or surpassing the particular limit.

More important is that there are other and often unpredictable factors limiting the matching of the phenotypic range to the environmental limits; all of these constrain the distribution of phenotypes. As the other factors may interact, they generate synergistic or interference effects, linear or otherwise. Examples of such sources of unpredictable noise in the process of phenotype specification are the pleiotropy of genes, the fact that characters generally have multiple roles, simultaneously or sequentially, and that genetic instructions must code for juveniles and adults, with the transitions involving further compromises. Such factors vitiate simple attempts to resolve the structure-function match, and to derive function from the structure of an individual.

1.2.8 The structure/role match

Hence, the phenotype of an individual does not permit simple extrapolation to its roles, those of its functions that are of significance to the organism. Not even the range or mean phenotypes of a species will allow accurate determination of most roles. However, we may assume that the importance of the role of a phenotypic aspect to the organism, and the cost of the aspect, will influence the tightness of the match to the limits of the parameter space.

All of this has been stated for a steady state. However, environments are never steady and individuals always test their limits, or conversely, environments always test the limits of organisms. Sometimes this testing lets the individual reach adjacent areas of the heritable character space. If their phenotype is incidentally at least sufficient for local maintenance, they may survive there as individuals. If enough such individuals do reach these zones, and if they are sufficient to achieve reproduction, this may lead to a shift of all or part of the original population into a modified character space. As the invaders need not be genetically typical of the original population, there is then the potential for a genetically different population, which in turn may change its phenotypic range further under the selective effect of the modified space. In essence, they will incur improvement toward a new set of limits potentially generating further transitional and intermediate states.

The phenotype, particularly of more complex organisms, also incorporates the capacity for degrees of behavioral adjustment in the use of its other aspects to match the conditions of a modified environment. This may complicate identification by the investigator of the roles shaping the organism. However, it may also permit closer matching of phenotype to particular limits.

1.2.9 Evaluation of performance

If these observations are correct, what level of performance should we expect to see in organisms? A significant fraction of the offspring of any mating should be adequate for the limits of their environment.

This fraction will reflect the reproductive rate, i.e., it will be smaller in a halibut or a sea turtle (with offspring counted in the thousands or hundreds) than in giraffe or humans (which produce one or two at a time). In each such case one may be able to identify one or more limiting conditions (i.e. axes of the parameter space) in which a subgroup of the population will be adequate under some but inadequate under other environmental circumstances.

The adequate fraction of offspring likely may be greater for physiological aspects than for the avoidance of predators. In short, many individuals taken by predators may be expected to have been otherwise adequate. However, in other species the presence of nutrients, or water, or heat, or settling sites might be as critical for (or associated with) the ability to avoid predation.

It is likely that the categories glibly defined are interactive. For instance, predation is likely to be successful against a subset of the physiologically less adequate or otherwise marginal, even though the 'inadequacy' is independent of the predator's success. This suggests that definition of the limiting condition must be handled carefully. For instance, simply affecting survivorship of a population by eliminating predation at one stage may have unexpected consequences. Identification of the limiting circumstances is sometimes possible for a particular condition (i.e. axis of the parameter space). Among other cases, this includes the situations in which 'adaptation' for a particular (presumably limiting) role seems obvious. One would expect these cases to have the following characteristics:

1. The role is very important to the organism and may differ from performance factors of related forms.
2. The role has persisted for a substantial time in the history of the clade (so that it is generally expressed and possibly associated negative factors are being buffered).

Tests will be needed to monitor the resulting congruence or the closeness of fit between environment and role. Sample tests might be the following:

1. What is the range of variability for the characteristic. How close is the mean, 80% of population or 95% of population to the putative environmental limit? What is the distribution - normal, skewed, etc.?
2. Are these values and distributions different for other aspects?
3. To what extent are these values heritable?

4. What kinds of environmental factors affect population phenotype and what is the direction of such effect? How variable are these factors, i.e. what is time constant of change relative to the life span of the organism?

1.2.10 Terminology revisited

We may now return to the question of how these terms fit into evolutionary biology. The term efficiency had best be set aside or confined to physiology. It is rarely usable, only pertinent to physical laws and by implication to a single aspect at a time, an aspect which is compared to perfect state.

The term effectiveness should be used for most biological systems to which efficiency is often misapplied. It represents a general measure of performance in a well-defined role. Optimality or optimization represents the best state (or process) from among a set of limiting circumstances. Optimality does not necessarily quantify closeness to an ideal; however, this may be specified. As the particular environmental framework establishes the relative needs, the available parameter space must be specified in any definition. Hence, optimality remains a relative term, often pertinent only to express what might be called the degree of adequacy. We have seen that optimum does not imply any independent level of efficiency or effectiveness. Even less should there be the implication that levels of optimality will be equivalent for the steps or stages of a physiological or behavioral process. However, it may be useful to introduce the term Congruence here, defined as the degree (closeness) of matching of phenotypic and environmental parameter spaces. A degree of congruence may reflect that selection upon heritable characters is indeed occurring.

Hence, congruence may document current adaptedness, particularly if experimental modification of the factor alters fitness. The concept of congruence makes it possible to measure improvement over time; however, the nature of the task or role must first be defined.

1.2.11 Vertebrate evolution

Courses in the Comparative Anatomy of Vertebrates often derive their justification from the possibility of a sequential arrangement of the vertebrate 'classes'. This is reflected in the occurrence of paraphyletic groups that raises such ire among some taxonomists.

One byproduct is the tendency to claim increases in efficiency or performance with changes from fishes to reptiles to mammals. However, only some characteristics, such as gas exchange, water balance and perhaps locomotor patterns do show general trends; even in these, there are exceptions and repeated attempts at special solutions, for instance, for return to the oceans or conquest of the air. Other characteristics lack continuing trends; for instance, the vertebrate feeding mechanisms are spectacularly opportunistic, as are internal fertilization and vivipary. If we look at energy metabolism, we see the reverse to a long-term trend in effectiveness. The shift from cephalochordates to vertebrates was marked by an enormous increase in metabolic scope without obvious increase in the capacity to generate more energy or the efficiency of that generation. Rather, the increased scope allowed the resulting vertebrates to expend five or more times as much energy because possession of the scope allowed them to increase the quantity and quality of ingested food. Similarly, the transition from ectothermy to endothermy generated a ten times more profligate life style that could be supported because previously unavailable nutrients could be harvested. Efficiency or effectiveness was not the determining factor; the animals used what was available to be harvested. Thus, horses and elephants high grade their food, extracting a limited fraction from a very large potential harvest, rather than extracting a greater fraction from a potentially smaller resource. Hence, increase in absolute values can be just as significant as increase in relative effectiveness.

1.3 CONCLUSIONS

The key question of this symposium has been at what level different aspects of the phenotype match the limits of the environment, and what are the concepts that such comparisons imply. Resolution requires understanding of the current role or roles. Also of the time base on which comparisons are made. The main problem to achieving resolution remains that environmental conditions vary unpredictably and that organisms are intrinsically variable and respond opportunistically. They use their existing phenotypes in varied, often novel ways. Species can tolerate varying phenotypic states because phenotypes only need to be adequate. Analysis of groups of organisms in a systematically comparative framework can often establish direction of past modifications. Most of all, we need comparisons of the extent of congruence of the phenotype-